Temporal and Spatial Dynamics of Diatom (Bacillariophyceae) Communities in a Peatland Area

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Source: Cryptogamie, Algologie, 38(3):253-266.
Published By: Association des Amis des Cryptogames
https://doi.org/10.7872/crya/v38.iss3.2017.253
URL: http://www.bioone.org/doi/full/10.7872/crya/v38.iss3.2017.253

Cryptogamie, Algologie, 2017, 38 (3): 253-266

Temporal and spatial dynamics of diatom (Bacillariophyceae) communities in a peatland area

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Abstract – This study was conducted to simultaneously investigate the spatial and temporal dynamics of diatom communities inhabiting two microhabitat types (Sphagnum periphyton and epipelon) in a peatland area of the Czech Republic. The changes in diatom community structure and corresponding diversity indices at both large (*i.e.*, variation between sites) and small (*i.e.*, variation between two microhabitats) scales were assessed through time. The results indicated clear spatial patterns at large, but not at small scale, and only limited seasonal dynamics in the diatom community. At the large scale, significant differences in diatom communities among sites were associated with both geographic position and environmental conditions (pH and conductivity). A significant effect of microhabitat type was detectable within sampling sites; the relationship between other factors and species data was not important on a small scale. The results of this study showed that both diatom diversity and community structure are good indicators of ecological heterogeneity associated with relatively high spatial and/or environmental variability. However, subtle differences in environmental conditions are hardly detectable or hidden using traditional diatom species.

Diatoms / microhabitat / peatland / spatial dynamics / temporal dynamics

INTRODUCTION

The temporal and spatial dynamics of communities are important components of biodiversity. The focus on these aspects of communities has increased in recent years, because knowledge of biodiversity aids understanding of ecosystem functions and improves monitoring and restoration programs (Legendre *et al.*, 2005). Peatlands are inhabited by specific protist communities, which play key roles in the nutrient and energy cycles of the habitat (Gilbert *et al.*, 1998a, 1998b; Mitchell *et al.*, 2003). The majority of existing research on this topic has considered testate amoebae (Arcellinida and Euglyphida; e.g. Lamentowicz & Mitchell, 2005; Mieczan, 2007, 2009) and desmids (Desmidiales; e.g. Štěpánková *et al.*, 2008; Šťastný, 2010; Neustupa *et al.*, 2012; Svoboda *et al.*, 2014). These two characteristic protist groups are dominant in peatlands, and they are frequently used in paleoecological studies

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doi/10.7872/crya/v38.iss3.2017.253

and peatland monitoring programs (Coesel, 2001, 2003; Mitchell *et al.*, 2008). Diatoms (Bacillariophyceae) are also potential model organisms for biomonitoring (Dixit *et al.*, 1992; Poulíčková *et al.*, 2004; Charles *et al.*, 2006; Kelly *et al.*, 2012), and they are equally as important as testate amoebae and desmids in the peatland microbenthos. However, studies focusing on the community structure of diatoms in peatlands are relatively scarce and rather covered by those considering the entire microphytobenthos (Mataloni, 1999; Borics *et al.*, 2003; Nováková, 2007; Tropea *et al.*, 2007; Machová-Černá & Neustupa, 2009).

Generally, freshwater microalgae are affected in space and time by prevailing environmental conditions, particularly pH, conductivity, and nutrients (e.g. Mataloni, 1999; Potapova & Charles, 2002; Poulíčková *et al.*, 2004; Soininen, 2004; Soininen *et al.*, 2004; Nováková, 2007; Štěpánková *et al.*, 2008; Fránková *et al.*, 2009; Machová-Černá & Neustupa, 2009; Neustupa *et al.*, 2013). The effects of random processes and biotic interactions, which are typically indirectly estimated, may also be important for community structure (Leibold *et al.*, 2004; Svoboda *et al.*, 2014). Seasonal dynamics have significant effects on the structure of planktonic communities, and this is commonly described by the PEG-model (Phytoplankton Ecology Group; Sommer *et al.*, 1986, 2012). However, the microphytobenthos is more likely to be spatially structured, and geographic distance significantly affects microphytobenthos species composition at a large scale (e.g. Potapova & Charles, 2002; Soininen, 2004; Soininen *et al.*, 2004; Pals *et al.*, 2006; Machová-Černá & Neustupa, 2009; Veselá, 2009; Heino *et al.*, 2010; Neustupa *et al.*, 2012, 2013; Svoboda *et al.*, 2014; Mutinová *et al.*, 2016). Noticeable within site differences have been detected at a small scale, and these differences might be enhanced if two distinct microhabitat types (e.g., soft versus hard substrates or biologically active versus biologically inert substrates) are considered (Lim *et al.*, 2001; Borics *et al.*, 2003; Poulíčková *et al.*, 2004; Soininen & Eloranta, 2004; Potapova & Charles, 2005; Townsend & Gell, 2005; Veselá, 2009). Nevertheless, in most cases, the differences in the microphytobenthos at a large scale (i.e., between ecologically distinct sites) are usually more striking as compared to spatial variation within a single site (Soininen, 2004; Pals *et al.*, 2006; Mutinová *et al.*, 2016), and this could lead to the false assumption that the microhabitats have minor effects on the structure of their associated communities.

This study aimed to investigate the diversity of diatoms and to quantify the importance of temporal and spatial factors on the diatom community structure in a peatland area. Variation in the following response variables was statistically partitioned: *time* (seasonal and inter-annual environmental changes), *space* (distance between sampling sites and different types of microhabitats), and *environment* (pH, conductivity, and temperature). In previous studies (Nováková, 2007; Neustupa *et al.*, 2011), temporal dynamics have primarily been examined as seasonal changes in the community. We sampled for two successive years to study inter-annual or aperiodic fluctuations in diatom diversity and community structure that may be attributed to seasonal changes during a short-term investigation. The spatial dynamics of diatom communities were studied at two scales: among sampling sites (hereafter referred to as "large scale") and within sites (*i.e.*, among microhabitats; hereafter referred to as "small scale"). We expected to find profound spatial dynamics and at least some detectable temporal changes in the diatom communities in peatland microhabitats. We hypothesized that dark shallow peatland pools undergo numerous, rapid changes in environmental factors, which would result in detectable temporal dynamics of microphytobenthic communities (as reported by Machová-Černá & Neustupa (2009) and Neustupa *et al.* (2012) in relation to winter disturbances).

MATERIAL AND METHODS

Sampling and sample processing

Samples were collected at six sites from two microhabitats in the peatland pools surrounding Mácha Lake (altitude 266 m a.s.l.) in the Czech Republic (Table 1). The samples were collected from May 2010 to March 2012, and collections were made during all four seasons (Supplementary Table 1, see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.). During the winter months, an ice cover was carefully removed and replaced after sampling. This study design resulted in eight successive sampling events (Supplementary Table 1), so it was possible to detect both intra-annual (*i.e.*, seasonal) and inter-annual variability of the diatom communities.

Sites 1 and 2 were located in the lowland minerotrophic fen "U Klůčku". The other four sites were set in the adjacent peatland pools of the Swamp Nature Reserve and in the northern part of Mácha Lake. All sites were classified as lowland minerotrophic transitional bogs characterized by acidic and oligo-mesotrophic conditions (Neustupa *et al.*, 2013). Environmental factors (pH and conductivity) were measured in the field using a combined pH/conductometer WTW 340i (WTW GmbH, Weilheim, Germany) in the immediate vicinity of sampled microhabitats. Mean temperatures for a period of 30 days prior to sampling were obtained from publicly available websites for the Prague Ruzyně Station that is located 63 km from the sampling area (http://www.vurv.cz/meteo/default.asp). A summary of the sampling sites and environmental conditions are shown in Table 1 and Supplementary Table 1 (see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.). The difference among sampling sites based on pH and conductivity values are illustrated in a scatter plot (Fig. 1).

Table 1. Overview of the sampling sites, corresponding environmental factors (mean ± standard deviation), and species richness based on 300 cell counts. Species richness is also given separately for epipelon (EPI) and *Sphagnum* spp. periphyton (PERI) microhabitats

Site	*GPS*	*pH*	*Conductivity [µS/cm]*	*Species richness*		
				EPI	*PERI*	*Total*
1	50°34'39.4"N, 14°39'46.0"E	6.7 ± 0.3	281 ± 113	27	30	35
2	50°34'36.7"N, 14°39'46.7"E	6.3 ± 0.2	383 ± 113	23	25	30
3	50°34'33.0"N, 14°40'15.5"E	5.0 ± 0.4	95 ± 43	32	26	40
4	50°35'40.7"N, 14°38'44.9"E	5.0. ± 0.6	70 ± 32	21	17	24
5	50°34'30.7"N, 14°40'06.1"E	4.5 ± 0.5	104 ± 37	24	12	26
6	50°35'43.1"N, 14°38'36.8"E	4.0 ± 0.2	92 ± 38	8	9	10

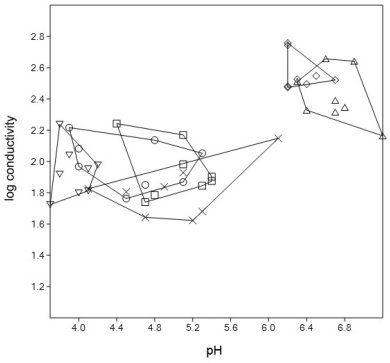

Fig. 1. Scatter plot illustrating the differences in environmental parameters among individual sites. Triangle = site 1, diamond = site 2, square = site 3, cross = site 4, circle = site 5, inverted triangle = site 6.

Two types of microhabitats, epipelon (EPI) and *Sphagnum* spp. periphyton (PERI) were chosen. Epipelon microhabitat samples were carefully collected from an area of approximately 0.25 m², but only the top surface layer of sediment was sampled to prevent mixing with the underlying sediment layer. Samples from the periphyton microhabitat were obtained by squeezing the tops of *Sphagnum* clumps (approximately 25 g) until no water could be expressed from them by manual pressure. At each sampling event, samples were taken at almost exactly the same spots within each site to avoid small-scale differences in the diatom communities (as reported in e.g. Machová-Černá & Neustupa, 2009). Samples were immediately preserved in Lugol's solution in the field to prevent changes to the species ratio in each community, which could have been caused by sudden changes to the ambient conditions. In total, 84 samples were collected. Epipelon samples were collected during all eight sampling events (48 samples; eight sampling events at six sites). Periphyton samples were not collected during the first two samplings, so only 36 samples (six sampling events at six sites) were obtained (see also Supplementary Table 1, see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.).

Community structure was based on the relative abundances of diatom species in the samples. Diatoms were counted using permanent slides, which were made according to the standard method of annealing over a gas burner flame (Battarbee *et al.*, 2001) and subsequent mounting into Naphrax medium (Brunel Microscopes Ltd. Wiltshire, UK). From each sample, 300 randomly encountered diatom cells were identified to the species level using an Olympus CX 31 light microscope at 1000× magnification and standard taxonomic monographs: Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b), Krammer (2000, 2002, 2003), Lange-Bertalot & Metzeltin (1996), Lange-Bertalot (2001), Lange-Bertalot *et al.* (2011). Up to 10 cells were counted for diatom colonies that occasionally occurred in the samples.

Statistical analyses

The original species data were initially tested for the influence of rare and less common species. The first dataset included a complete set of all 300 identified cells from each sample (hereafter referred to as the complete dataset). In the second dataset, all rare diatom species, that did not reach greater than 1% abundance in any of the samples, were excluded. The third dataset was comprised of the top 25% of the most common species in the complete dataset. As suggested by Heino & Soininen (2010) and subsequently supported by Neustupa *et al.* (2012), this approach should be sufficient to reveal ecological patterns in aquatic communities. The degree of dataset concordance was estimated with the Procrustes statistics (PROTEST; Peres-Neto & Jackson (2001), for an explanation see also Neustupa *et al.* (2012) and Mutinova *et al.* (2016)) using 9999 permutations. The compared distance matrices were based on the two-dimensional non-metric multidimensional scaling (NMDS; Kruskal, 1964) using the Bray-Curtis index (Bray & Curtis, 1957). Pair-wise comparisons revealed that there were no significant differences between datasets, so the first complete dataset was used for subsequent statistical analyses. Statistical analyses were conducted using PAST version 3 software (Hammer *et al.*, 2001) and the *vegan* package (Oksanen *et al.*, 2012) in R version 2.15.1 software (R Development Core Team, 2012).

Regarding large-scale processes, factors were separated into three groups. Time-series and seasons were merged into the *time* factor group. Geographical

distances (hereafter referred to as GPS; included sampling site information) and microhabitat type were merged into the *space* factor group. The geographic distances were obtained from GPS coordinates by creating a similarity matrix that was used for principle coordinates analyses (PCoA) using PAST. The scores from the first 12 PCoA axes were used as a space variable. The pH, conductivity, and mean temperature factors were standardized and then merged into the *environment* factor group.

The complete species dataset was Hellinger-transformed (Legendre & Gallagher, 2001). The quantification of joint and pure effects of factor groups on the diatom community structure was performed in R (R Development Core Team, 2012) with a permutational multivariate analysis of variance using the Bray-Curtis similarity index and 9999 permutations (permutational MANOVA; Anderson, 2001). Factor effects were sequentially estimated in the model. For example, when *environment, space,* and *time* were on the first, second, and third rows, respectively, the first row quantified the pure effect of *environment* plus the joint effects of *environment* with other two factors. The second row included the pure effect of *space* plus the joint effects of *space* and *time*, minus the effect of *environment*. The last row estimated the pure effect of *time* after the effects of the other two factors were subtracted.

To investigate variation in the diatom community in detail at a large scale, similar models of permutational MANOVA analyses were conducted using individual variables (only those variables that were found to have significant effects in the preceding analysis were considered, Table 2). The same approach was used to investigate small-scale processes within single sites. The complete dataset was divided into six sub-datasets corresponding to the individual sampling sites, and only the microhabitat type was included in the analysis as a spatial factor. It is important to note that the resulting R^2 values are highly dependent on the number of samples in the dataset and the degrees of freedom associated with each factor. Therefore, R^2 values are not comparable between different permutational MANOVA models. Thus, we also provided adjusted R^2 values, which are comparable with each other in all cases, and we refer always to adjusted R^2 values below.

Table 2. Partitioning of variation in the diatom community structure at the large scale (*i.e.*, within sites) by permutational MANOVA tests using the Bray-Curtis similarity index and 9999 permutations. The analysis considered (A) *time*, *space*, and *environment* factor groups and (B) individual GPS, microhabitat, pH, conductivity, and temperature factors. In each case, only the pure effect is shown. Complete results of individual permutational MANOVA tests are listed in Supplementary Tables 4 and 5. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. $P > 0.05$

		df	*Sums of squares*	*F ratio*	R^2	*Adjusted* R^2	*P value*
A	time	6	1.083	1.237	0.040	0	n.s.
	space	13	10.019	5.284	0.371	0.254	***
	environment	2	0.825	2.829	0.031	0.007	**
	residuals	61	8.897	–	0.330	–	–
B	GPS	12	9.813	5.490	0.363	0.256	***
	microhabitat	1	0.321	2.156	0.012	0.000	n.s.
	temperature	1	0.065	0.436	0.002	0	n.s.
	conductivity	1	0.585	3.924	0.022	0.010	**
	pH	1	0.147	0.985	0.005	0	n.s.
	residuals	67	9.979	–	0.370	–	–

Two-dimensional NMDS diagrams (Kruskal, 1964; Clarke, 1993), allowed for visualization of the effects of season, site, or microhabitat on diatom communities, were constructed in PAST using the Bray-Curtis similarity index. We also examined diversity indices, particularly species richness, and the Shannon diversity index. These indices were calculated for every sample using the complete dataset (Supplementary Table 2, see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.), and were subsequently divided into the following groups of variables: time-series, season, site, and microhabitat. The Mann-Whitney test (Mann & Whitney, 1947) was used to compare the two microhabitat types. In all other cases, the Kruskal-Wallis test (Kruskal, 1964), with post-hoc Mann-Whitney pair-wise comparisons using the Bonferroni correction, was performed. Boxplots were created to illustrate differences in the diversity indices of individual groups. Lastly, the relationships between diversity indices and particular environmental factors (pH and conductivity) were tested using ordinary least square regression and were illustrated with biplots.

RESULTS

In total, 73 diatom species, belonging to 31 genera, were identified in 84 samples (Supplementary Table 3, see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.). The species richness per sample ranged from 2 to 26, and mean species richness was 11.3 with a standard deviation of 5.0. Species richness values that were recorded during individual seasons and at individual sites are given in Table 1 and Supplementary Table 1 (see doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.). The top 25% of the most abundant species are as follows in descending order: *Frustulia saxonica* Rabenhorst, *Eunotia bilunaris* (Ehrenberg) Schaarschmidt, *Brachysira serians* (Brébisson) Round & D.G. Mann, *Eunotia paludosa* Grunow, *Encyonopsis* cf. *delicatissima* (Hustedt) Krammer, *Eunotia* cf. *arcubus* Nörpel & Lange-Bertalot, *Achnanthidium minutissimum* (Kützing) Czarnecki, *Brachysira neoexilis* Lange-Bertalot, *Brachysira* cf. *neoexilis* Lange-Bertalot, *Eunotia exigua* (Brébisson *ex* Kützing) Rabenhorst, *Pinnularia rhombarea* Krammer, *Pinnularia pseudogibba* Krammer, *Cymbella falaisensis* (Grunow) Krammer & Lange-Bertalot, *Kobayasiella* sp., *Eunotia glacialis* Meister, *Pinnularia macilenta* Ehrenberg, *Tabellaria flocculosa* (Roth) Kützing, *Fragilaria construens* (Ehrenberg) Grunow, *Nitzschia* sp. 1.

Variation partitioning of pure and joint factor effectsrs by permutational MANOVA, showed strong spatial structuring of diatom communities at both scales (Tables 2, 3). At the large scale (i.e., differences among all six sites), the pure effect of *space* accounted for 25% ($P < 0.001$) of the total variation in the diatom community structure (Table 2). The fraction of variance explained by the *environment* decreased from 22.7% ($P < 0.001$) to 0.7% ($P < 0.01$) after *space* and *time* were included in the model (Supplementary Table 4). Both the NMDS ordination plot (similarity among diatom communities, Fig. 2) and scatter plot (pH versus conductivity values, Fig. 1) revealed clear differences among localities. Temporal changes within sites were not significant at the large scale (Table 2 and Supplementary Table 4 (doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.)). Moreover, high covariation of geographic position with environmental factors was observed at the large scale (Supplementary Tables 4, 5), and covariation of temporal changes with environmental factors was seen at the small scale (Table 3). For example, sites 1 and 2 were characterized by relatively high pH and conductivity, whereas site 6 had the lowest

Table 3. Partitioning of variation in the diatom community structure at the small scale (*i.e.*, within sites) by permutational MANOVA tests using the Bray-Curtis similarity index and 9999 permutations. In each case, only the pure effect is shown. The analyses accounting for microhabitat, *time*, and *environment* factors were conducted for all six sites. The pure effect of the *environment* was imperceptible, so it was excluded from the table. For site 1, tests considering the individual variables microhabitat, time-series, and season were conducted. *** P < 0.001, ** P < 0.01, * P < 0.05, n.s. P > 0.05

		df	*Sums of squares*	*F ratio*	R^2	*Adjusted* R^2	*P value*
site 1	time	4	0.195	2.261	0.361	0.077	**
	microhabitat	1	0.124	5.740	0.049	0	***
	residuals	5	0.108	–	0.200	–	–
site 2	time	4	0.181	1.022	0.126	0	n.s.
	microhabitat	1	0.780	17.577	0.541	0.503	***
	residuals	5	0.222	–	0.154	–	–
site 3	time	4	0.154	1.140	0.164	0	n.s.
	microhabitat	1	0.491	14.551	0.522	0.483	***
	residuals	5	0.169	–	0.179	–	–
site 4	time	4	0.117	1.080	0.182	0	n.s.
	microhabitat	1	0.145	5.364	0.225	0.161	**
	residuals	5	0.135	–	0.210	–	–
site 5	time	4	0.225	1.242	0.285	0	n.s.
	microhabitat	1	0.105	2.324	0.133	0.061	n.s.
	residuals	5	0.227	–	0.286	–	–
site 6	time	4	0.050	1.201	0.278	0	n.s.
	microhabitat	1	0.049	4.726	0.273	0.213	*
	residuals	5	0.052	–	0.289	–	–

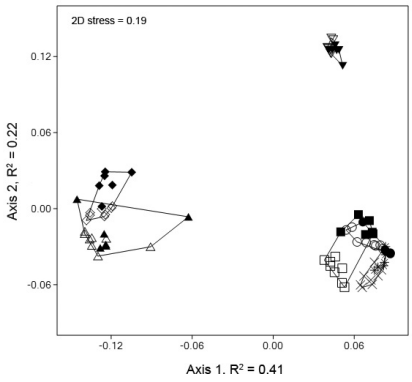

Fig. 2. NMDS ordination plot based on the diatom composition of samples collected at individual sites and individual microhabitats. Triangle = site 1, diamond = site 2, square = site 3, cross = site 4, circle = site 5, inverted triangle = site 6. Empty symbol = epipelon, filled symbol and star = *Sphagnum* spp. periphyton.

pH of all sites (Table 1, Fig. 1). A similar separation of sites based on the diatom community is clear in the NMDS graph as well (Fig. 2), even though in this case the separation of site 6 seems more profound than in the illustration based on environmental factors (Fig.1).

We also focused on the effects of individual spatial and environmental variables between sites (Table 2 part B, complete models are given in Supplementary

Table 5 (doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.)) in subsequent analyses. The detailed inspection of pure and joint effects of individual variables at the large scale indicated that the spatial variability of diatom communities was affected by the geographic positions of sites (represented by GPS coordinates) but not differences between microhabitats (Supplementary Table 5, see doi/10.7872/crya/v38.iss3.2017. Suppl.Mat.; also shown in Fig. 2). Regarding environmental factors, only conductivity was found to have a significant effect on diatom community structure after the effects of other variables were removed from the model.

A significant effect of the pure effect of microhabitat was revealed in the analysis of variation at a small scale (*i.e.*, within sites; Table 3). Microhabitat type played a significant role in shaping diatom communities at five of the six sites, whereas the effect of time was mostly insignificant (Table 3). As expected, the pure effects of both *environment* and *time* were imperceptible at the small scale. Temporal changes were not important at the large scale, and environmental variability mainly represented temperature values. In the case of site 1 only, there was as much as 7.7% of variation in the diatom community structure that was significantly explained by *time* ($P < 0.01$). Regarding all models that considered both the small and large scale, the fraction of unexplained variability, ranged from 15.4% to 37% (R^2 values of residuals; Tables 2 and 3).

Comparisons of diversity indices (species richness and Shannon diversity index) revealed that there were no detectable differences associated with temporal changes (including both time-series and season), but the effect of space on species diversity was clear at both the large (Fig. 3) and small scales (Kruskal-Wallis tests, $P < 0.001$ at both scales). Post-hoc Mann-Whitney pair-wise comparisons using Bonferroni corrections indicated that sites could be generally divided into three groups with more or less similar species richness and Shannon diversity index values (also shown in Fig. 3):

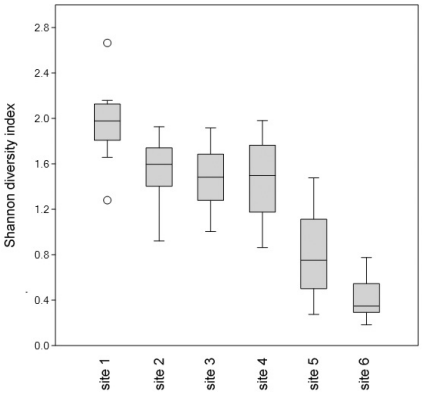

Fig. 3. Box plots illustrating differences in Shannon diversity indices of diatom communities among individual sites.

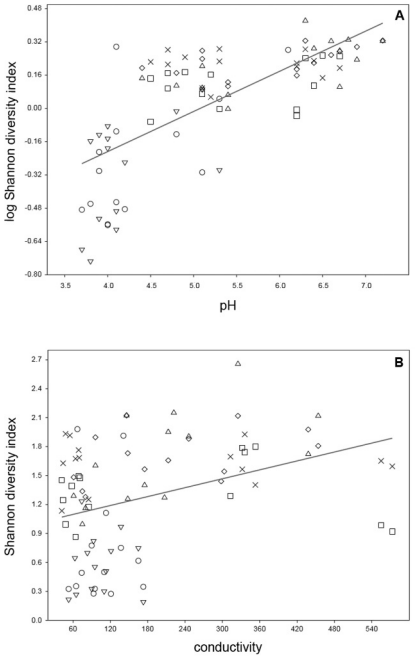

Fig. 4. Illustration of ordinary least square regression of Shannon diversity index depending on (A) pH and (B) conductivity. The individual sites are shown using the same symbols as in the ordinations. Triangle = site 1, diamond = site 2, square = site 3, cross = site 4, circle = site 5, inverted triangle = site 6.

(1) site 1 which was characterized by high diversity index values; (2) sites 2, 3, and 4 with intermediate values; and (3) sites 5 and 6 with low values. Differences in diversity between sites were associated with variability of the measured environmental factors. Species richness and the Shannon diversity index (Fig. 4) were positively correlated with both pH ($r = 0.7/0.7$, $R^2 = 0.49/0.5$, $P < 0.001$) and conductivity ($r = 0.38/0.4$, $R^2 = 0.15/0.1$, $P < 0.001$). Microhabitat type seemed to be an unimportant factor for diatom diversity at the large scale, but significant differences were revealed within the three sampling sites. In particular, species richness differed remarkably between sites 4 and 5, and the Shannon diversity indices differed at sites 3 and 4 (Mann-Whitney tests, $P < 0.05$ at all sites).

DISCUSSION

Distinct temporal dynamics of diatoms in peatland microhabitats were not found in this study. While this result is in agreement with the studies of Nováková (2007) and Svoboda *et al.* (2014), it does not support the findings of Machová-Černá & Neustupa (2009) and Neustupa *et al.* (2012), which detected noticeable changes in peatland microphytobenthos that were likely caused by freezing during the winter. The *time* factor group (both time-series and season) was essentially reflected in the temporal changes of environmental factors (as has been documented by Tahvanainen *et al.*, 2003). In our study, seasonal changes were detectable by the temperature. Two other investigated environmental factors, pH and conductivity, were not radically altered at a single site over time. We assumed that the lack of significant temporal dynamics in diatom communities detected at site 1 were due to the location of the site, which was very close to Mácha Lake. The temporal changes in the diatom communities and environmental conditions of Mácha Lake (Neustupa *et al.,* 2011) might affect both the species pool and environmental conditions at adjacent sites.

Consistent with our results, recent studies have demonstrated a significant effect of spatial distance on the structure of freshwater microphytobenthic communities (Potapova & Charles, 2002; Poulíčková *et al.*, 2004; Soininen, 2004; Pals *et al.*, 2006; Machová-Černá & Neustupa, 2009; Veselá, 2009; Heino *et al.*, 2010; Neustupa *et al.*, 2012, 2013; Svoboda *et al.*, 2014; Mutinová *et al.*, 2016). In our study, spatial variation was associated with the variability of measured environmental factors (pH and conductivity), microhabitat type (periphyton or epipelon), and undetermined site-specific factors. The unknown spatial factors might incorporate the history of the site as well as any unmeasured abiotic factors (e.g., nitrogen, phosphorus and silicate, as well as light intensity) and biotic interactions (e.g., predation, competition and mutualism) with a spatial distribution (Borcard *et al.*, 1992; Anderson & Gribble, 1998). The spatial heterogeneity of diatoms is evident at the large scale, and it may conceal the effects of factors with small-scale distributions (as shown in Soininen, 2004; Pals *et al.*, 2006; Mutinová *et al.*, 2016). Therefore, the significance of the effect of individual environmental and spatial factors might depend on the spatial scale that is being investigated. Our study showed that the community structure of diatoms within localities differed between *Sphagnum* periphyton and epipelon microhabitats but were not significantly different at the large scale. Total species richness and Shannon diversity indices were similar between the two microhabitats. We suggest that although the characteristics of those microhabitats differ (e.g., living vs. inert substrates), both *Sphagnum* periphyton and

epipelon have similar potential to support rich diatom communities. Lim *et al.* (2001) and Soininen & Eloranta (2004) claimed that diatom communities in sediments should exhibit high species diversity because the sediment usually contains sets of diatoms from adjacent microhabitats and empty frustules. *Sphagnum* periphyton is a complex and biologically active habitat, so it supports a highly diverse community of microorganisms (Soininen & Eloranta, 2004; Taniguchi & Tokeshi, 2004; Townsend & Gell, 2005). However, our study did not focus on specific microhabitat details, so it is not possible to assess whether small-scale differences between diatom communities represent the effect of specific substrates or the spatial heterogeneity of ecologically neutral substrates.

Future diatom ecology research could be improved by progressively increasing the sensitivity of measurements of environmental variability in space and time (as in Tahvanainen *et al.*, 2003). We propose that studies based on traditional diatom morphospecies are relevant to our understanding of the ecology and community dynamics of freshwater microphytobenthos within a particular geographic area (e.g. Dixit *et al.*, 1992; Coesel, 2001, 2003; Poulíčková *et al.*, 2004; Charles *et al.*, 2006) because the large factor gradients (e.g., differences among sites) are detectable using traditionally defined species (Mitchell *et al.*, 2014). However, small-scale and temporal community dynamics should be addressed using manipulated in situ experiments (Shurin, 2000) and/or by advanced morphological or molecular approaches (e.g., Lara *et al.*, 2011, Lew *et al.*, 2015) that provide higher taxonomic resolution to achieve more accurate diversity assessments (Heger *et al.*, 2009, Mitchell *et al.*, 2014). It was recently shown that some traditional diatom morphospecies represent different genetic and morphological entities that differ in their ecological preferences (Creach *et al.* 2006; Potapova & Hamilton 2007; Vanelslander *et al.* 2009; Veselá *et al.* 2012; Kulichová & Fialová 2016). In our study, several species complexes, which have been examined using a polyphasic approach, often occurred in high abundances: *Achnanthidium minutissimum* (Kützing) Czarnecki (Potapova & Hamilton, 2007; Pinseel *et al.*, 2017), *Eunotia bilunaris* (Ehrenberg) Schaarschmidt (Vanormelingen *et al.*, 2007), *Frustulia crassinervia-saxonica* (Veselá *et al.*, 2012; Kulichová & Fialová, 2016), *Gomphonema parvulum* (Kützing) Kützing (Kermarrec *et al.*, 2013), *Nitzschia palea* (Kützing) W.Smith (Trobajo *et al.*, 2009), and *Sellaphora* spp. (Mann *et al.*, 2004; Poulíčková *et al.*, 2008). It is probable that if hidden diversity within traditional diatom species had been taken into account, the differences between microhabitats and/or seasons would have become clearer. Diatom species complexes have the potential to be used as reliable indicators for small-scale and temporal patterns. However, it is questionable whether variability in species complexes will exhibit a general trend or whether particular species complexes will respond specifically to environmental conditions.

Acknowledgements. We would like to thank Jiří Neustupa for his initial help with our research and statistical analysis. This study was supported by the project partnership in the framework of Programme CZ07 – EEA Scholarship Programme; Bilateral Scholarship Programme number NF-CZ07-ICP-3-193-2015.

REFERENCES

ANDERSON M. & GRIBBLE N., 1998 — Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. *Australian journal of ecology* 23: 158-167.

ANDERSON M., 2001 — A new method for non-parametric multivariate analysis of variance. *Austral ecology* 26: 32-46.

BATTARBEE R.W., JONES V.J., FLOWER R.J., CAMERON N.G., BENNION H., CARVALHO L. & JUGGINS S., 2001 — Diatoms. *In*: Smol J.P., Birks H.J.B. & Last W.M. (eds), *Tracking environmental change using lake sediments, vol. 3: Terrestrial, algal, and siliceous indicators*. Dordrecht, The Netherlands, Kluwer Academic Publishers, pp. 155-202.

BORCARD D., LEGENDRE P. & DRAPEAU P., 1992 — Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.

BORICS G., TÓTHMÉRÉSZ B., GRIGORSZKY I., PADISÁK J., VÁRBÍRÓ G. & SZABÓ S., 2003 — Algal assemblage types of bog-lakes in Hungary and their relation to water chemistry, hydrological conditions and habitat diversity. *Hydrobiologia* 502: 145-155.

BRAY J.R. & CURTIS J., 1957 — An ordination of the upland forest communities of southern Wisconsin. *Ecological monographs* 27: 325-249.

CABIN R.J. & MITCHELL R.J., 2000 — To Bonferroni or not to Bonferroni: When and how are the questions. *Bulletin of the ecological society of America* 81: 246-248.

CHARLES D.F., ACKER F.W., HART D.D., REIMER C.W. & COTTER P.B., 2006 — Large-scale regional variation in diatom-water chemistry relationships: rivers of the eastern United States. *Hydrobiologia* 561: 27-57.

CLARKE K. R., 1993 — Non-parametric multivariate analyses of changes in community structure. *Australian journal of ecology* 18: 117-143.

COESEL P. F., 2001 — A method for quantifying conservation value in lentic freshwater habitats using desmids as indicator organisms. *Biodiversity and conservation* 10: 177-187.

COESEL P. F., 2003 — Desmid flora data as a tool in conservation management of Dutch freshwater wetlands. *Biologia* 58: 717-722.

DIXIT S., SMOL J., KINGSTON J. & CHARLES D., 1992 — Diatoms: Powerful indicators of environmental change. *Environmental science & technology* 26: 23-33.

FRÁNKOVÁ M., BOJKOVÁ J., POULÍČKOVÁ A. & HÁJEK M., 2009 — The structure and species richness of the diatom assemblages of the Western Carpathian spring fens along the gradient of mineral richness. *Fottea* 9: 355-368.

GILBERT D., AMBLARD C., BOURDIER G. & FRANCEZ A.-J., 1998a — Short-term effect of nitrogen enrichment on the microbial communities of a peatland. *Hydrobiologia* 373/374: 111-119.

GILBERT D., AMBLARD C., BOURDIER G. & FRANCEZ A.-J., 1998b — The microbial loop at the surface of a peatland: Structure, function, and impact of nutrient input. *Microbial ecology* 35: 83-93.

HAMMER Ø., HARPER D.A.T. & RYAN P.D., 2001 — PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia electronica* 4: 9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm. Accessed 14 October 2016.

HEGER T.J., MITCHELL E.A.D., LEDEGANCK P., VINCKE S., VAN DE VIJVER B. & BEYENS I., 2009 — The curse of taxonomic uncertainty in biogeograhical studies of free-living terrestrial prostist: A case study of testate amoebae from Amsterdam Island. *Journal of biogeography* 39: 1551-1560.

HEINO J., BINI L.M., KARJALAINEN S.M., MYKRÄ H., SOININEN J., VIEIRA L.C.G. & DINIZ-FILHO J.A.F., 2010 — Geographical patterns of micro-organismal community structure: Are diatoms ubiquitously distributed across boreal streams? *Oikos* 119: 129-137.

HEINO J. & SOININEN J., 2010 — Are common species sufficient in describing turnover in aquatic metacommunities along environmental and spatial gradients? *Limnology and oceanography* 55: 2397-2402.

KELLY M.G., GÓMEZ-RODRÍGUEZ C., KAHLERT M., ALMEIDA S.F.P., BENNETT C., BOTTIN M., DELMAS F., DESCY J.P., DÖRFLINGER G., KENNEDY B., MARVAN P., OPATRILOVA L., PARDO I., PFISTER P., ROSEBERY J., SCHNEIDER S. & VILBASTE S., 2012 — Establishing expectations for pan-European diatom based ecological status assessments. *Ecological indicators* 20: 177-186

KRAMMER K. & LANGE-BERTALOT H., 1986 — Bacillariophyceae, 1. Teil. *In*: Ettl H., Gerloff J., Heynig H. & Mollenhauer D. (eds), *Süsswasserflora von Mitteleuropa 2/1*. Jena, G. Fischer Verlag.

KRAMMER K. & LANGE-BERTALOT H., 1988 — Bacillariophyceae, 2. Teil. *In*: Ettl H., Gerloff J., Heynig H. & Mollenhauer D. (eds), *Süsswasserflora von Mitteleuropa 2/1*. Jena, G. Fischer Verlag.

KRAMMER K. & LANGE-BERTALOT H., 1991a — Bacillariophyceae, 3. Teil. *In*: Ettl H., Gerloff J., Heynig H. & Mollenhauer D. (eds), *Süsswasserflora von Mitteleuropa 2/1*. Jena, G. Fischer Verlag.

KRAMMER K. & LANGE-BERTALOT H., 1991b — Bacillariophyceae, 4. Teil. *In:* Ettl H., Gerloff J., Heynig H. & Mollenhauer D. (ed.), *Süsswasserflora von Mitteleuropa 2/1*. Jena, G. Fischer Verlag.

KRAMMER K., 2000 — Diatoms of Europe, vol. 1: The genus *Pinnularia*. *In*: Lange-Bertalot H. (ed.), *Diatoms of the European inland water and comparable habitats*. Ruggell, A.R.G. Gantner Verlag K.G.

KRAMMER K., 2002 — Diatoms of Europe, vol. 3: *Cymbella*. *In*: Lange-Bertalot H. (ed.), *Diatoms of the European inland water and comparable habitats*. A.R.G. Gantner Verlag K.G.

KRAMMER K., 2003 — Diatoms of Europe, vol. 4: *Cymbopleura*, *Delicata*, *Navicymbula*, *Gomphocymbellopsis*, *Afrocymbella*. *In*: Lange-Bertalot H. (ed.), *Diatoms of the European inland water and comparable habitats*. A.R.G. Gantner Verlag K.G.

KERMARREC L., BOUCHEZ A., RIMET F. & HUMBERT J.-F., 2013 — First evidence of the existence of semi-cryptic species and of a phylogeographic structure in the *Gomphonema parvulum* (Kützing) Kützing complex (Bacillariophyta). *Protist* 164: 686-705.

KRUSKAL J.B., 1964 — Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1-27.

KULICHOVÁ J. & FIALOVÁ M., 2016 — Correspondence between morphology and ecology: Morphological variation of the *Frustulia crassinervia-saxonica* species complex (Bacillariophyta) reflects the ombro-minerotrophic gradient. *Cryptogamie, Algologie* 37: 15-28.

LAMENTOWICZ M. & MITCHELL E.A.D., 2005 — The ecology of testate amoebae (protists) in *Sphagnum* in north-western Poland in relation to peatland ecology. *Microbial ecology* 50: 48-63.

LANGE-BERTALOT H. & METZELTIN D., 1996 — Iconographia Diatomologica, vol. 2: Indicators of oligotrophy. 800 taxa representative of three ecologically distinct lake types: Carbonate buffered, oligodystrophic, weakly buffered soft water. Königstein, Koeltz Scientific Books,.

LANGE-BERTALOT H., 2001 — Diatoms of Europe, vol. 2: *Navicula* sensu stricto, 10 genera separated from *Navicula* sensu lato, *Frustulia*. *In*: Lange-Bertalot H. (ed.), *Diatoms of the European inland water and comparable habitats.* Ruggell, A.R.G. Gantner Verlag K.G.

LANGE-BERTALOT H., BĄK M., WITKOWSKI A. & TAGLIAVENTI N., 2011 — Diatoms of Europe, vol. 6: *Eunotia* and some related taxa. *In*: Lange-Bertalot H. (ed.), *Diatoms of the European inland water and comparable habitats*. A.R.G. Gantner Verlag K.G.

LARA E., MITCHELL E.A.D., MOREIRA D. & LÓPEZ GARCÍA P., 2011 — Highly diverse and seasonally dynamic protist community in a pristine peat bog. *Protist* 162: 14-32.

LEGENDRE P. & GALLAGHER E.D., 2001 — Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271-280.

LEGENDRE P., BORCARD D. & PERES-NETO P.R., 2005 — Analyzing beta diversity: Partitioning the spatial variation of community composition data. *Ecological monographs* 75: 435-450.

LEIBOLD M.A., HOLYOAK M., MOUQUET N., AMARASEKARE P., CHASE J.M., HOOPES M.F., HOLT R.D., SHURIN J.B., LAW R., TILMAN D., LOREAU M. & GONZALEZ A., 2004 — The metacommunity concept: A framework for multi-scale community ecology. *Ecology letters* 7: 601-613.

LEW S., KOBLÍŽEK M., LEW M., MEDOVÁ H., GLIŃSKA-LEWCZUK K. & OWSIANNY M.P., 2015 — Seasonal changes of microbial communities in two shallow peat bog lakes. *Folia microbiologica* 60: 165-175.

LIM D., KWAN C. & DOUGLAS M., 2001 — Periphytic diatom assemblages from Bathurst Island, Nunavut, Canadian High Arctic: An examination of community relationships and habitat preferences. *Journal of phycology* 37: 379-392.

MACHOVÁ-ČERNÁ K. & NEUSTUPA J., 2009 — Spatial distribution of algal assemblages in a temperate lowland peat bog. *International review of hydrobiology* 94: 40-56.

MANN D.G., MCDONALD S.M., BAYER M.M., DROOP S.J.M., CHEPURNOV V.A., LOKE R.E., CIOVANU A. & DU BUF J.M.H., 2004 — The *Sellaphora pupula* species complex (Bacillariophyceae): Morphometric analysis, ultrastructure and mating data provide evodence for five new species. *Phycologia* 43: 459-482.

MANN H.B. & WHITNEY D.R., 1947 — On a test of whether one of two random variables is stochastically larger than the other. *The Annals of mathematical statistics* 8: 50-60.

MATALONI G., 1999 — Ecological studies on algal communities from Tierra del Fuego peat bogs. *Hydrobiologia* 391: 157-171.

MIECZAN T., 2007 — Seasonal patterns of testate amoebae and ciliates in three peatbogs: Relationship to bacteria and flagellates (Poleski National Park, Eastern Poland). *Ecohydrology and hydrobiology* 7: 295-305.

MIECZAN T., 2009 — Ecology of testate amoebae (Prostists) in *Sphragnum* peatlands of eastern Poland: Vertical micro-distribution and species assemblages in relation to environmental parameters. *Annales de limnologie - International journal of limnology* 45: 41-49.

MITCHELL E.A.D., GILBERT D., BUTTLER A., AMBLARD C., GROSVERNIER P. & GOBAT J.-M., 2003 — Structure of microbial communities in *Sphagnum* peatlands and effect of atmospheric carbon dioxide enrichment. *Microbial ecology* 46: 187-199.

MITCHELL E.A.D., CHARMAN D.J. & WARNER B.G., 2008 — Testate amoebae analysis in ecological and paleoecological studies of wetlands: Past, present and future. *Biodiversity and conservation* 17: 2115-2137.

MITCHELL E.A.D., LAMENTOWICZ M., PAYNE R.J. & MAZEI Y., 2014 — Effect of taxonomic resolution on ecological and palaeoecological inference: A test using testate amoeba water table depth transfer functions. Quarternary science reviews 91: 62-69.

MUTINOVÁ P.T., NEUSTUPA J., BEVILACQUA S. & TERLIZZI A., 2016 — Host specificity of epiphytic diatom (Bacillariophyceae) and desmid (Desmidiales) communities. *Aquatic ecology* 50: 697-709.

NEUSTUPA J., ČERNÁ K. & ŠŤASTNÝ J., 2011 — The effects of aperiodic desiccation on the diversity of benthic desmid assemblages in a lowland peat bog. *Biodiversity and conservation* 20: 1695-1711.

NEUSTUPA J., ČERNÁ K. & ŠŤASTNÝ J., 2012 — Spatio-temporal community structure of peat bog benthic desmids on a microscale. *Aquatic ecology* 46: 229-239.

NEUSTUPA J., VESELÁ J. & ŠŤASTNÝ J., 2013 — Differential cell size structure of desmids and diatoms in the phytobenthos of peatlands. *Hydrobiologia* 709: 159-171.

NOVÁKOVÁ S., 2007 — Structure and dynamics of the algal flora in subalpine mires in the Krkonoše Mountains (Giant Mountains; Czech Republic). *Nova Hedwigia* 84: 441-458.

OKSANEN J., BLANCHET F.G., KINDT R., LEGENDRE P., MINCHIN P.R., O'HARA R.B., SIMPSON G.L., SOLYMOS P., STEVENS M.H.H. & WAGNER H., 2013 — vegan: community ecology package. R package version 2.4-0. http://CRAN.R-project.org/package=vegan. Accessed 14 October 2016.

PALS A., ELST D., MUYLAERT K. & VAN ASSCHE J., 2006 — Substrate specificity of periphytic desmids in shallow softwater lakes in Belgium. *Hydrobiologia* 568: 159-168.

PERES-NETO P.R. & JACKSON D.A., 2001 — How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia* 129: 169-178.

PINSEEL E., VANORMELINGEN P., HAMILTON P.B., VYVERMAN W., VAN DE VIJVER B. & KOPALOVA K., 2017 — Molecular and morphological characterization of the *Achnanthidium minutissimum* complex (Bacillariophyta) in Petuniabukta (Spitsbergen, High Arctic) including the description of *A. digitatum* sp. nov. *European journal of phycology*: DOI: 10.1080/09670262.2017.1283540

POTAPOVA M. & CHARLES D.F., 2002 — Benthic diatoms in USA rivers: Distributions along spatial and environmental gradients. *Journal of biogeography* 29: 167-187.

POTAPOVA M. & CHARLES D.F., 2005 — Choice of substrate in algae-based water-quality assessment. *Journal of the North American benthological society* 24: 415-427.

POTAPOVA M. & HAMILTON P.B., 2007 — Morphological and ecological variation within the *Achnanthidium minutissimum* (Bacillariophyceae) species complex. *Journal of phycology* 43: 561-575.

POULÍČKOVÁ A., DUCHOSLAV M. & DOKULIL M., 2004 — Littoral diatom assemblages as bioindicators of lake trophic status: A case study from perialpine lakes in Austria. *European journal of phycology* 39: 143-152.

POULÍČKOVÁ A., ŠPAČKOVÁ J., KELLY M.G., DUCHOSLAV M. & MANN D.G., 2008 — Ecological variation within Sellaphora species complexes (Bacillariophyceae): Specialists or generalists? *Hydrobiologia* 614: 373-386.

R DEVELOPMENT CORE TEAM, 2012 — R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Accessed 14 October 2016.

RICE W. R., 1989 — Alalyzing tables of statistical tests. *Evolution* 43: 223-225.

SHURIN J. B., 2000 — Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81: 3074-3086.

SOININEN J., 2004 — Determinants of benthic diatom community structure in boreal streams: The role of environmental and spatial factors at different scales. *International Review of hydrobiology* 89: 139-150.

SOININEN J. & ELORANTA P., 2004 — Seasonal persistence and stability of diatom communities in rivers: are there habitat specific differences? *European journal of phycology* 39: 153-160.
SOININEN J., PAAVOLA R. & MUOTKA T., 2004 — Benthic diatom community structure in boreal streams: Distribution patterns along environmental and spatial gradients. *Ecography* 27: 330-342.
SOMMER U., ADRIAN R., DE SENERPONT DOMIS L., ELSER J.J., GAEDKE U., IBELINGS B., JEPPESEN E., LÜRLING M., MOLINERO J.C., MOOIJ W.M., VAN DONK E. & WINDER M., 2012 — Beyond the Plankton Ecology Group (PEG) model: Mechanisms driving plankton succession. *Annual review of ecology, evolution, and systematics* 43: 429-448.
SOMMER U., GLIWICZ Z., LAMPERT W. & DUNCAN A., 1986 — The PEG-model of seasonal succession of planktonic events in fresh waters. *Archiv für Hydrobiologie* 106: 433-471.
SVOBODA P., KULICHOVÁ J. & ŠŤASTNÝ J., 2014 — Spatial and temporal community structure of desmids on a small spatial scale. *Hydrobiologia* 722: 291-303.
ŠŤASTNÝ J., 2010 — Desmids (Conjugatophyceae, Viridiplantae) from the Czech Republic; New and rare taxa, distribution, ecology. *Fottea* 10: 1-74.
ŠTĚPÁNKOVÁ J., VAVRUŠKOVÁ J., HAŠLER P., MAZALOVÁ P. & POULÍČKOVÁ A., 2008 — Diversity and ecology of desmids of peat bogs in the Jizerské hory Mts. *Biologia* 63: 895-900.
TAHVANAINEN T., SALLANTAUS T. & HEIKKILÄ R., 2003 — Seasonal variation of water chemical gradients in three boreal fens. *Annales botanici Fennici* 40: 345-355.
TANIGUCHI H. & TOKESHI M., 2004 — Effects of habitat complexity on benthic assemblages in a variable environment. *Freshwater biology* 49: 1164-1178.
TOWNSEND S.A. & GELL P.A., 2005 — The role of substrate type on benthic diatom assemblages in the Daly and Roper Rivers of the Australian wet/dry tropics. *Hydrobiologia* 548: 101-115.
TROBAJO R., CLAVERO E., CHEPURNOV V.A., SABBE K., MANN D.G., ISHIHARA S. & COX E.J., 2009 — Morphological, genetic and mating diversity within the widespread bioindicator *Nitzschia palea* (Bacillariophyceae). *Phycologia* 48: 443-459.
TROPEA A.E., GINN B.K., CUMMING B.F. & SMOL J.P., 2007 — Tracking long-term acidification trends in Pockwock Lake (Halifax, Nova Scotia), the water supply for a major eastern Canadian city. *Lake and reservoir management* 23: 279-286.
VANORMELINGEN P., CHEPURNOV V.A., MANN D.G., COUSIN S. & VYVERMAN W., 2007 — Congruence of morphological, reproductive and ITS rDNA sequence data in some Australasian *Eunotia bilunaris* (Bacillariophyta). *European journal of phycology* 42: 61-79.
VESELÁ J., 2009 — Spatial heterogeneity and ecology of algal communities in an ephemeral sandstone stream in the Bohemian Switzerland National Park, Czech Republic. *Nova Hedwigia* 88: 531-547.
VESELÁ J., URBÁNKOVÁ P., ČERNÁ K. & NEUSTUPA J., 2012 — Ecological variation within traditional diatom morphospecies: Diversity of *Frustulia rhomboides sensu lato* (Bacillariophyceae) in European freshwater habitats. *Phycologia* 51: 552-561.

Supplementary Table 1. Overview of sampling events with the number (no.) of collected samples and species richness based on 300 cell counts. Temperature (mean ± standard deviation) was counted for the 30 days preceding a sampling event. The number of samples and species richness values are given separately for epipelon (EPI) and *Sphagnum* spp. periphyton (PERI) microhabitats

Sampling event	*Date*	*Temperature [°C]*	*No. of samples*		*Species richness*		
			EPI	*PERI*	*EPI*	*PERI*	*Total*
spring 1	18.5.2010	11.6 ± 2.9	6	0	44	0	44
summer 1	31.8.2010	18.2 ± 3.1	6	0	43	0	43
autumn 1	4.11.2010	7.1 ± 2.7	6	6	41	34	47
winter 1	3.2.2011	– 0.3 ± 4.8	6	6	44	47	52
spring 2	4.5.2011	11.2 ± 3.7	6	6	41	33	46
summer 2	30.8.2011	19.4 ± 3.2	6	6	41	35	45
autumn 2	5.11.2011	7.3 ± 2.7	6	6	43	31	47
winter 2	18.3.2012	4.9 ± 3.3	6	6	43	38	49

doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.

Supplementary Table 2. Species richness and Shannon diversity index for individual samples. EPI = epipelon, PERI = *Sphagnum* spp. periphyton

Nr. sample	*Sampling event*	*Site*	*Microhabitat*	*Species richness*	*Shannon diversity index*
1	spring 1	1	EPI	13	1.280
2	spring 1	2	EPI	11	1.543
3	spring 1	5	EPI	17	1.477
4	spring 1	3	EPI	16	1.685
5	spring 1	4	EPI	14	1.981
6	spring 1	6	EPI	5	0.637
7	summer 1	1	EPI	20	2.159
8	summer 1	2	EPI	11	1.441
9	summer 1	5	EPI	12	1.393
10	summer 1	3	EPI	17	1.916
11	summer 1	4	EPI	12	1.913
12	summer 1	6	EPI	5	0.690
13	autumn 1	1	PERI	14	1.731
14	autumn 1	1	EPI	18	1.978
15	autumn 1	2	PERI	13	0.921
16	autumn 1	2	EPI	14	1.596
17	autumn 1	5	PERI	6	0.275
18	autumn 1	5	EPI	9	0.710
19	autumn 1	3	PERI	9	1.267
20	autumn 1	3	EPI	15	1.732
21	autumn 1	4	PERI	12	1.175
22	autumn 1	4	EPI	10	1.252
23	autumn 1	6	PERI	4	0.348
24	autumn 1	6	EPI	3	0.183
25	winter 1	1	PERI	26	2.665
26	winter 1	1	EPI	19	2.119
27	winter 1	2	PERI	16	1.800
28	winter 1	2	EPI	12	1.403
29	winter 1	5	PERI	10	1.113
30	winter 1	5	EPI	5	0.501
31	winter 1	3	PERI	16	1.612
32	winter 1	3	EPI	22	1.897
33	winter 1	4	PERI	7	1.247
34	winter 1	4	EPI	11	1.628
35	winter 1	6	PERI	4	0.328
36	winter 1	6	EPI	5	0.546
37	spring 2	1	PERI	15	2.127
38	spring 2	1	EPI	15	1.808
39	spring 2	2	PERI	12	0.987
40	spring 2	2	EPI	15	1.652
41	spring 2	5	PERI	5	0.618
42	spring 2	5	EPI	11	0.740

doi/10.7872/crya/v38.iss3.2017.Suppl.Mat.

Supplementary Table 2. Species richness and Shannon diversity index for individual samples. EPI = epipelon, PERI = *Sphagnum* spp. periphyton *(continued)*

Nr. sample	*Sampling event*	*Site*	*Microhabitat*	*Species richness*	*Shannon diversity index*
43	spring 2	3	PERI	10	1.409
44	spring 2	3	EPI	16	1.566
45	spring 2	4	PERI	8	1.497
46	spring 2	4	EPI	13	1.764
47	spring 2	6	PERI	2	0.500
48	spring 2	6	EPI	4	0.292
49	summer 2	1	PERI	15	1.960
50	summer 2	1	EPI	15	1.658
51	summer 2	2	PERI	11	1.288
52	summer 2	2	EPI	13	1.696
53	summer 2	5	PERI	5	0.277
54	summer 2	5	EPI	10	0.815
55	summer 2	3	PERI	10	1.298
56	summer 2	3	EPI	14	1.483
57	summer 2	4	PERI	14	1.454
58	summer 2	4	EPI	13	1.135
59	summer 2	6	PERI	3	0.326
60	summer 2	6	EPI	3	0.208
61	autumn 2	1	PERI	17	1.913
62	autumn 2	1	EPI	15	1.882
63	autumn 2	2	PERI	15	1.741
64	autumn 2	2	EPI	14	1.927
65	autumn 2	5	PERI	3	0.493
66	autumn 2	5	EPI	10	1.225
67	autumn 2	3	PERI	10	1.171
68	autumn 2	3	EPI	14	1.279
69	autumn 2	4	PERI	9	0.994
70	autumn 2	4	EPI	13	1.933
71	autumn 2	6	PERI	3	0.354
72	autumn 2	6	EPI	5	0.259
73	winter 2	1	PERI	18	2.131
74	winter 2	1	EPI	20	2.123
75	winter 2	2	PERI	15	1.786
76	winter 2	2	EPI	14	1.565
77	winter 2	5	PERI	6	0.752
78	winter 2	5	EPI	9	0.962
79	winter 2	3	PERI	12	1.004
80	winter 2	3	EPI	15	1.338
81	winter 2	4	PERI	7	0.863
82	winter 2	4	EPI	12	1.675
83	winter 2	6	PERI	8	0.776
84	winter 2	6	EPI	4	0.318

Supplementary Table 3. Complete list of 73 diatom species identified in 84 samples based on 300 cell counts per sample. The most abundant species (top 25%) are highlighted in bold

Adlafia minuscula (Grunow) Lange-Bertalot
Achnanthes sp.
***Achnanthidium minutissimum* (Kützing) Czarnecki**
Amphora ovalis (Kützing) Kützing
Brachysira brebissonii R.Ross
***Brachysira neoexilis* Lange-Bertalot**
***Brachysira* cf. *neoexilis* Lange-Bertalot**
Brachysira procera Lange-Bertalot & Gerd Moser
***Brachysira serians* (Brébisson) Round & D.G. Mann**
Caloneis tenuis (W.Gregory) Krammer
***Cymbella falaisensis* (Grunow) Krammer & Lange-Bertalot**
Cymbopleura inaequalis (Ehrenberg) Krammer
Denticula kuetzingii Grunow
Encyonema gracile Rabenhorst
Encyonema silesiacum (Bleisch) D.G.Mann
***Encyonopsis* cf. *delicatissima* (Hustedt) Krammer**
Epithemia adnata (Kützing) Brébisson
Eucocconeis flexella (Kützing) Meister
***Eunotia* cf. *arcubus* Nörpel & Lange-Bertalot**
Eunotia arculus Lange-Bertalot & Nörpel
***Eunotia bilunaris* (Ehrenberg) Schaarschmidt**
***Eunotia exigua* (Brébisson ex Kützing) Rabenhorst**
***Eunotia glacialis* Meister**
Eunotia implicata Nörpel, Lange-Bertalot & Alles
Eunotia incisa W.Smith ex W.Gregory
Eunotia intermedia (Krasske ex Hustedt) Nörpel & Lange-Bertalot
Eunotia minuta F.W.Hilse
Eunotia naegelii Migula
***Eunotia paludosa* Grunow**
Eunotia pectinalis var. *ventralis* (Ehrenberg) Hustedt
Eunotia praerupta Ehrenberg
Eunotia rhomboidea Hustedt
Eunotia tenella (Grunow) Hustedt
Fallacia vitrea (Østrup) D.G.Mann
Fragilaria brevistriata Grunow
Fragilaria capucina Desmazières
***Fragilaria construens* (Ehrenberg) Grunow**
Fragilaria tenera var. *nanana* (Lange-Bertalot) Lange-Bertalot & S.Ulrich
Fragilariforma exigua (Grunow) M.G.Kelly
***Frustulia saxonica* Rabenhorst**
Gomphonema acuminatum Ehrenberg
Gomphonema gracile Ehrenberg

Supplementary Table 3. Complete list of 73 diatom species identified in 84 samples based on 300 cell counts per sample. The most abundant species (top 25%) are highlighted in bold *(continued)*

Gomphonema parvulum(Kützing) Kützing
Hantzschia sp.
Chamaepinnularia mediocris (Krasske) Lange-Bertalot & Krammer
Chamaepinnularia soehrensis (Krasske) Lange-Bertalot & Krammer
***Kobayasiella* sp.**
Kobayasiella subtilissima (Cleve) Lange-Bertalot
Meridion circulare (Greville) C.Agardh
Neidium bisulcatum (Lagerstedt) Cleve
Nitzschia dissipata (Kützing) Rabenhorst
***Nitzschia* sp. 1**
Nitzschia sp. 2
Nitzschia sp. 3
Nitzschia sp. 4
Pinnularia cf. *frequentis* Krammer
Pinnularia gibbiformis Krammer
Pinnularia interrupta W.Smith
***Pinnularia macilenta* Ehrenberg**
***Pinnularia pseudogibba* Krammer**
***Pinnularia rhombarea* Krammer**
Pinnularia rupestris Hantzsch
Pinnularia sp.
Pinnularia subcapitata var. *elongata* Krammer
Pinnularia viridiformis Krammer
Placoneis cf. *explanata* (Hustedt) Lange-Bertalot
Rhopalodia gibba (Ehrenberg) Otto Müller
Staurosirella leptostauron (Ehrenberg) D.M.Williams & Round
Staurosirella pinnata (Ehrenberg) D.M.Williams & Round
Stenopterobia curvula (W.Smith) Krammer
Stenopterobia delicatissima (F.W.Lewis) Brébisson ex Van Heurck
Tabellaria fenestrata (Lyngbye) Kützing
***Tabellaria flocculosa* (Roth) Kützing**

Supplementary Table 4. Complete results of individual permutational MANOVA tests, partitioning variation in the diatom community structure on a large scale (*i.e.*, among six sampling sites), using the Bray-Curtis similarity index and 9999 permutations. The analysis considered the effect of the *time*, *space*, and *environment* factor groups. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. $P > 0.05$

		df	*Sums of squares*	*F ratio*	R^2	*Adjusted* R^2	*P value*
model A-1	environment	3	6.876	15.715	0.255	0.227	***
	space	13	10.147	5.351	0.376	0.260	***
	time	6	1.083	1.237	0.040	0	n.s.
	residuals	61	8.897	–	0.330	–	–
model A-2	time	7	1.096	1.073	0.041	0	n.s.
	environment	2	6.990	23.963	0.259	0.241	***
	space	13	10.019	5.284	0.371	0.254	***
	residuals	61	8.897	–	0.330	–	–
model A-3	space	13	16.199	8.544	0.600	0.526	***
	time	7	1.081	1.059	0.040	0	n.s.
	environment	2	0.825	2.829	0.031	0.007	**
	residuals	61	8.897	–	0.330	–	–

Supplementary Table 5. Complete results of individual permutational MANOVA tests, partitioning variation in the diatom community structure on a large scale (*i.e.*, among six sampling sites) using the Bray-Curtis similarity index and 9999 permutations. The analysis considered the effects of individual factors GPS, microhabitat, pH, conductivity, and temperature. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. $P > 0.05$

		df	*Sums of squares*	*F ratio*	R^2	*Adjusted* R^2	*P value*
model B-1	pH	1	6.054	40.646	0.224	0.215	***
	conductivity	1	0.499	3.349	0.019	0.007	*
	temperature	1	0.323	2.169	0.012	0	n.s.
	microhabitat	1	0.334	2.243	0.012	0	n.s.
	GPS	12	9.813	5.490	0.363	0.256	***
	residuals	67	9.980	–	0.370	–	–
model B-2	GPS	12	15.877	8.883	0.588	0.518	***
	pH	1	0.116	0.781	0.004	0	n.s.
	conductivity	1	0.647	4.340	0.024	0.012	**
	temperature	1	0.062	0.417	0.002	0	n.s.
	microhabitat	1	0.321	2.156	0.012	0	n.s.
	residuals	67	9.979	–	0.370	–	–
model B-3	microhabitat	1	0.367	2.462	0.014	0.002	n.s.
	GPS	12	15.832	8.858	0.586	0.516	***
	pH	1	0.116	0.782	0.004	0	n.s.
	conductivity	1	0.642	4.311	0.024	0.012	**
	temperature	1	0.065	0.436	0.002	0	n.s.
	residuals	67	9.979	–	0.370	–	–
model B-4	temperature	1	0.137	0.921	0.005	0	n.s.
	microhabitat	1	0.356	2.391	0.013	0.001	n.s.
	GPS	12	15.825	8.854	0.586	0.516	***
	pH	1	0.119	0.802	0.004	0	n.s.
	conductivity	1	0.585	3.924	0.022	0.010	**
	residuals	67	9.979	–	0.370	–	–
model B-5	conductivity	1	3.286	22.064	0.122	0.110	***
	temperature	1	0.234	1.569	0.009	0	n.s.
	microhabitat	1	0.387	2.596	0.014	0.002	*
	GPS	12	12.969	7.256	0.480	0.392	***
	pH	1	0.147	0.985	0.005	0	n.s.
	residuals	67	9.979	–	0.370	–	–