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Small-scale spatial variation of benthic algal assemblages in a peat bog

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ABSTRACT

Spatial patterns on a very small scale (10 cm), and the effect of artificial barriers on the composition of phytobenthic algal assemblages along two transects within different microhabitat types were investigated. Samples were taken in a peat bog along linear transects on a scale of 10 cm, and water chemistry was examined. The distribution of algae along both transects was influenced by both spatial distance and environmental conditions in similar proportions. Differences in species composition in various parts of the transects were observed, but this pattern was primarily related to the abundance of species, rather than to their presence/absence in samples. Similarity in species composition correlated with spatial distance and environmental parameters in both microhabitat types. I concluded that, given a homogenous environment on a small scale, spatial distribution of algae is affected by both the environmental conditions of the microhabitats and their dispersal limitations. Moreover, an artificial barrier constituted an obstruction for water and nutrient flow, as well as algal migration, and had an impact on species composition.

Introduction

Variation in distribution, abundance and composition of species in relation to environmental conditions or spatial scale are important for our understanding of the ecology and diversity of organisms. We are able to identify general factors that are significant for individual spatial scales in marine and freshwater habitats. On a macroscale (kilometers or greater) differences in species composition of marine algal assemblages are principally influenced by hydrodynamics (Méléder et al., 2007), or by the texture and composition of rocky substratum (Rindi and Battelli (2005)); in freshwater habitats they largely correlate with basic chemical variables (e.g. hardness, Mg, Ca, conductivity, SO_4, total solids, conductivity, total P), geographic location and spatial-dispersal factors (Soininen et al., 2004). On a mesoscale (tens of meters or greater), spatial heterogeneity of algal assemblages seems to be determined by several factors, including: marine habitat abiotic conditions, granulometric composition of substrate (Saburova et al., 1995), phenological patterns and input of propagules (Santelices, 1990; Rindi and Guiry, 2004), variations in recruitment (Menge et al., 1993), and substratum heterogeneity (Archambault and Bourget, 1996). In rivers, factors related to water quality, such as BOD (biological oxygen demand), P, NH_4 and turbidity were the most important pressures driving heterogeneity of algal assemblages on an intermediate spatial scale (Charles et al., 2006). In addition, heterogeneity of diatom communities was shown to be induced by changes in light and current regimes, grazing, successional stages and variation in substratum (Ledger and Hildrew, 1998; Soininen, 2003). Small-scale biotic interactions, such as competition, grazing, colonization processes (input of propagules), variations in recruitment, or low movement ability affected composition of algae species both in marine and freshwater habitats on a scale of centimeters or greater (Saburova et al., 1995; Rindi and Cinelli, 2000; Hillebrand et al., 2001; Coleman, 2002). At the same time, physical and chemical parameters creating small-scale patchiness of microhabitat (Underwood and Chapman, 1996), substrate complexity and heterogeneity (Komárek, 2003), and water current effect (Passy, 2001) also play an important role.

Knowledge of the spatial distribution of species in phytobenthos is important prior to identification and description of their diversity. In order to describe the ecology, occurrence patterns, or abundance of species of any assemblage, it is necessary to determine the scale of its variation. If, for example, small-scale variation goes undetected, differences due to impacts may be confused with differences due to natural spatial variability (Underwood, 1993; Coleman, 2002). That is, if the spatial scale sampled is greater than the scales of natural spatial variation then effects may be assumed that do not really exist; the perceived impact simply being a result of small-scale spatial variation (Coleman, 2002). Spatial patterns of species diversity provide important clues about the underlying mechanisms that regulate biodiversity and are central in the development of biodiversity theory (Hubbell, 2001). Assumptions regarding the spatial scaling

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of biodiversity are a fundamental component of conservation biology, and are frequently used to identify local- and global-scale priority conservation areas (Desmet and Cowling, 2004).

This study follows our previous study (Machová-Černá and Neustupa, 2009) concerning spatial distribution of algae in a lowland peat bog. In that study, we found that the spatial heterogeneity of algal assemblages was mainly influenced by seasonal succession related to winter disturbance, microhabitat type, spatial distance between samples and conductivity. The pattern of spatial autocorrelation was observed on scales of 1 m and greater, but it could not be established on a scale of 10 cm; this concurs with the results of Coleman (2002) or Komárek (2003). Consequently, in the present study I focused on the spatial structure of algal assemblages in the homogenous environment of an acidic mountain peat bog, and only on a scale of 10 cm; my primary concern being the effect of artificial barriers in the natural environment on the species composition of algal assemblages. I attempted to determine if there is a difference in spatial structure of benthic algal assemblages on a small scale in a lowland and mountain peat bog. I utilized similar statistical methods in order to compare these results. Therefore, I asked the following questions: (1) Can I identify alterations in species composition of algal assemblages caused by artificial barriers two years after revitalization? and (2) Are there differences in the small-scale spatial structure of benthic algal assemblages in two distinct microhabitat types (epipelon and periphyton within Sphagnum moss)?

Materials and methods

The locality examined, "Mlynářská slať" peat bog, is situated in the Bohemian Forest National Park in the south of the Czech Republic (49°0′26″N, 13°28′26″E). This peat bog is surrounded by a pine grove and largely overgrown with spruce. In the past, the locality was intensively used in forestry and many channels were excavated to drain the water. In 2004, a revitalization process took place wherein the drainage channels were artificially blocked by sheet pile walls to retain the natural height of the water and to prevent water outflow.

Samples of cyanobacteria and algae were collected on 24th September 2006 from two drainage channels with different microhabitat types: phytobenthos from the fine-grain bottom of the first drainage channel, and periphyton within the *Sphagnum* biomass overgrown the second channel surface. Samples were taken along linear transects 3 m long in epipelon, and 5 m long in the moss biomass; these were divided in the middle by a sheet pile wall (Fig. 1). Sampling sites were 10 cm apart, and sampling was conducted either with a glass pipette (from the bottom), or by squeezing (for the moss). The pH and electrical conductivity were measured in the field using Hanna portable combined pH/conductometer. Concentrations of total nitrogen and total phosphorus were determined colorimetrically with a continuous flow analyzer (FIA-STAR, Tecator, Sweden). Total nitrogen (TN) was determined following the reduction of all nitrogen forms in the sample to nitrates with perchloric acid. Subsequent reduction of nitrates to nitrites was achieved in a Cd–Cu column and reaction with sulfanilamide and N-(1-naphthyl)-ethylenediamine producing a final pink color that was detected at 540 nm. Total phosphorus concentrations (TP) were estimated following the mineralization of the samples by persulphate (Grasshoff et al., 1983) that converted all phosphorus forms into dissolved reactive phosphorus, and its concentration was subsequently estimated using the standard phosphomolybdenum complex method (Parsons et al., 1984). The final intensive blue color was quantified at 690 nm. Humic acid concentrations were established spectrophotometrically, if acidic conditions, after their extraction to pentanol and then to NaOH, according to TNV 757536 (2003).

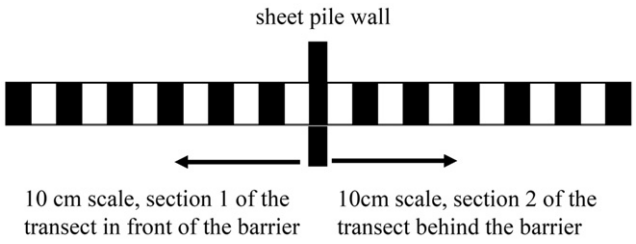

Fig. 1. The sampling design indicating positions of individual samples along the linear transect. Samples were collected on a 10 cm scale on both sides of an artificial barrier in drainage channels on "Mlynářská slať" peat bog (Czech Republic) in September 2006.

Algal species were identified to the lowest possible taxonomic level, within three days of collection without fixation, by Olympus BX51 light microscopy. Diatoms were identified in mineralized samples mounted on Naphrax permanent slides (Houk, 2003). For each sample, one microscope slide was prepared to observe living cells for algae identification, and one prepared to observe and identify diatoms. The identification of algal taxa was based on standard taxonomic monographs (Süsswasserflora von Mitteleuropa, Diatoms of Europe, etc. – for references see e.g. Veselá, 2009). Semiquantitative estimates of algal populations were deduced from microscopic examination, and species were classified into three categories: (1) up to 1% of cells revealed, (2) up to 50% of cells found, and (3) more than 50% of cells of a particular assemblage detected by light microscopy (Kinross et al., 1993; Komárek and Sukačová, 2004). Approximately 500 cells per sample were examined.

Non-metric multidimensional scaling (NMDS) was used to display the major patterns in the species' composition data using the PRIMER® (Plymouth Routines In Multivariate Ecology, PRIMER-E Ltd., Plymouth, UK) software package. One hundred random starts were carried out in 2- and 3-dimensional analyses to reduce the chance of local optima (Clarke and Warwick, 2001). In both cases, the 3-dimensional solutions had lower stress values than the 2-dimensional ones, but we utilized the 2-dimensional data because of its superior representation of sample position. Resemblance of species composition between sites was assessed by Bray–Curtis similarity index (Bray and Curtis, 1957; Méléder et al., 2007). To retain the contribution of each species, according to its semiquantitative abundance, we made no data transformations (Clarke et al., 2006). The possible role of the sheet pile walls on differences in species composition on either side of the barrier was evaluated using non-parametric two-group ANOSIM tests based on Bray–Curtis similarity index performed with PAST software (ver. 1.81; Hammer et al., 2001) using 10,000 permutations. Subsequent SIMPER (similarity percentage) analyses, carried out in PRIMER®, were used to identify species typical in specified sections along the transect, and species responsible for the differentiation between the two divisions of the transects (Clarke and Warwick, 2001; Méléder et al., 2007). The effect of spatial distance and abiotic parameters on the similarity of algal composition along the transect was evaluated using simple and partial Mantel tests (Mantel, 1967; Smouse et al., 1986). Mantel tests were calculated for the entire length of transects in benthic and moss substratum types, and independently for both sides of the transect separated by the sheet pile wall. The similarity matrix was calculated from paired comparisons of species composition between two samples using Bray–Curtis similarity index, and matrices of environmental distances were composed of unsigned differences among values of variables for all possible pairs of samples. The significance of correlations was tested with simulation of 10,000 randomizations. Mantel tests were performed using *zt* software (ver. 1.0; Bonnet and Van der Peer, 2002). The effects

of environmental (pH, conductivity, total nitrogen, total phosphorus, humic acids) and spatial parameters (geographical distance of samples from the beginning of transect and location on the transect) on species composition were evaluated using linear ordination techniques, including redundancy analysis (RDA) and partial RDA (Lepš and Šmilauer, 2000). Percentage of variation in species data explained by environmental and/or spatial factors was partitioned according to Borcard et al. (1992). Ordination methods were performed in CANOCO for Windows version 4.5 (ter Braak and Šmilauer, 1998, 2002).

Results

Measured abiotic parameters are presented in Table 1. Generally, pH was higher in the benthic microhabitat, but all other chemical parameters were higher in the submerged *Sphagnum* moss microhabitat. In both microhabitat types the abiotic parameters spanned a wider range of values in the second section of the transects.

Non-metric multidimensional scaling (NMDS) analyses illustrated a difference in the order between benthic and periphytic samples in the plots (Fig. 2). In the case of benthic samples, we observed clear separation of samples collected in front of vs. behind the barrier. In addition, the cloud of points in the ordination plot representing samples taken from the beginning portion of the transect was more condensed in contrast to those representing samples from the second part of the transect that were expanded. This pattern was also observed on the ordination plot of moss squeezing samples from periphyton. But, in contrast to benthic samples, in the case of periphytic samples, we did not observe a clear separation between the two parts of the transect.

The ANOSIM tests confirmed statistically significant differences in species composition based on Bray–Curtis similarity index in both studied transects (benthos $r=0.392$, $p<0.0001$, periphyton $r=0.233$, $p<0.0001$). The SIMPER analyses detected species identifying individual parts of the transects (Table 2). The algal assemblages from specific sections of the transects in benthos and periphyton did not essentially differ in species composition, but rather, in the relative abundance of the species. The benthic algal assemblages (Table 2a) were composed of a higher number and diversity of species (species richness=54, Shannon diversity index=6.07), and were characterized by the occurrence of ciliates (e.g. *Euglena sp.*, *Trachelomonas abrupta*, *T. hispida*), desmids (e.g. *Closterium intermedium*, *Hyalotheca dissiliens*, *Stuarodesmus triangularis*) and diatoms (e.g. *Caloneis alpestris*, *E. bilunaris var. mucophila*, *E. exigua*, *Frustulia saxonica*). Average dissimilarity between the two portions of this transect was 31.3%. The periphyton algal assemblages (Table 2b) were principally characterized by lower species diversity (species richness=30, Shannon diversity index=3.95), and the occurrence of diatoms (*Eunotia glacialis*, *E. bilunaris var. mucophila*, *Pinnularia rupestris*) and filamentous green algae (*Microspora tumidula*, *Microthamnion kuetzingianum*, *Mougeotia sp.*). Average dissimilarity between the two divisions of the transect was 49%. Similarity in species composition of benthic assemblages was statistically significantly spatially correlated in both parts of the transect and along the entire length of the transect, even when using covariates (Table 3). I found only total phosphorus and humic acids as having an effect on the similarity in species composition. I also found correlations between pH and other abiotic parameters (conductivity, total nitrogen, total phosphorus and humic acids), as well as between total phosphorus and humic acid concentrations. The pH, total nitrogen, total phosphorus, and humic acids were spatially correlated and indicated a gradient of these factors. Similarity in species composition of periphytic assemblages was also spatially correlated in the second section of the transect behind the barrier, and along the entire length of the transect, even when using covariates (Table 3). It was determined that pH, conductivity, total nitrogen and humic acids exerted an effect on the similarity in species composition, but only on individual parts of the transect or only over its entire length. I found correlations between all pairs of abiotic parameters, and all abiotic parameters were spatially correlated on at least one part of the transect (Table 3).

In the redundancy and partial redundancy analyses performed for benthic species composition data 17.7% of the variation was explained by environmental data (including: pH, conductivity, total phosphorus, nitrogen, and humic acids), 13.5% of the variation was accounted for by spatial data (spatial distance of samples

Table 1
The environmental characteristics of the transects investigated in drainage channels on "Mlynářská slať" peat bog in the Czech Republic in September 2006.

	Benthos part 1	Benthos part 2	Periphyton part 1	Periphyton part 2
pH	5.13–5.37	5.06–5.42	3.78–3.93	3.61–3.87
Conductivity [$\mu S\ cm^{-1}$]	13–24	8–18	12–15	15–21
Total nitrogen [$\mu g\ l^{-1}$]	430.3–584.9	466.2–762.9	523.2–807.3	544.2–1325.9
Total phosphorus [$\mu g\ l^{-1}$]	81.9–91.4	77.9–98.1	79.03–110.1	82.4–140.8
Humic acids [$mg\ l^{-1}$]	15.2–19.8	14.9–21.9	22.6–29.8	24.9–50.7

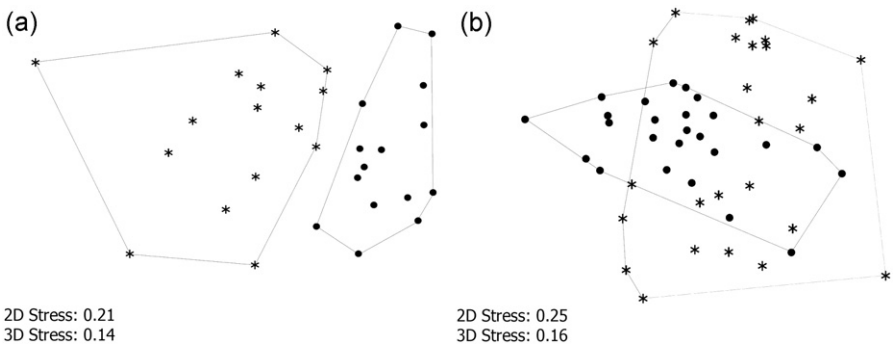

Fig. 2. Non-metric multidimensional scaling (NMDS) of data collected from two transects on the study site "Mlynářská slať" peat bog (Czech Republic) in September 2006. (a) A transect in the benthic microhabitat, (b) A transect in the periphitic microhabitat (● and ∗ indicate samples taken in front of, and behind the barrier, respectively).

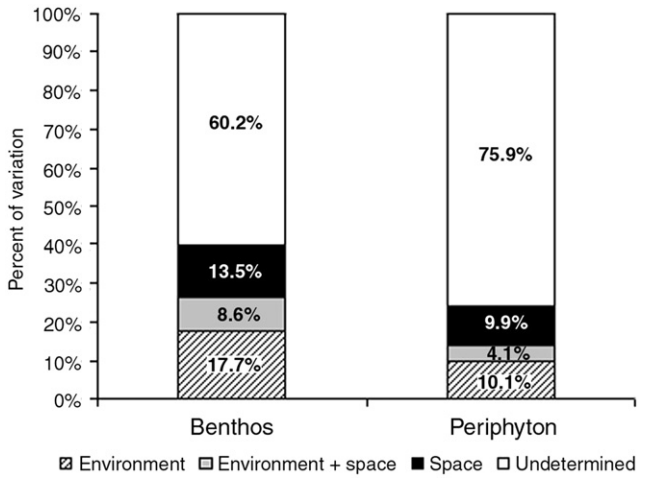

Fig. 3. Variation partitioning of the transects' data matrices.

from the beginning of the transect and location along the transect), 8.6% of the variation was explained by both environmental and spatial data, and the cause of 60.2% of the variation remained undetermined (Fig. 3). In the periphytic species composition data 10.1% of the variation was explained by environmental data, 9.9% of the variation was described by spatial data, 4.1% of the variation was accounted for by both environmental and spatial data, and the reasons for 75.9% of the variation remained undetermined (Fig. 3).

Discussion

The algal assemblages of transects investigated were characterized by species typical for acidic and oligotrophic peat bog localities (Coesel, 1982; Mataloni, 1999; Neustupa et al., 2009). The occurrence of species was principally influenced by the severe conditions of their microhabitats, especially in periphyton within moss (low pH and conductivity) that are typically characterized by low species diversity (Coesel, 1982; Mataloni, 1999). The measured values for total phosphorus, especially in the *Sphagnum*-dominated microhabitat, are comparable to those observed in Finnish boreal peatland surface waters having a similar pH (Tolonen and Hosiaisluoma, 1978). Higher amounts of total nitrogen and total phosphorus in *Sphagnum*-dominated microhabitats could be related to a lower pH that consequently affected the slower decomposition rate and reduced biomass of nutrient consumers – microbes and algae (Walbridge and Navaratnam, 2006). The pattern of differences in species composition was principally related to the division of this transect into two sections by artificial barriers, as illustrated by the NMDS plots. The differences were clearly evident in benthic samples. This pattern could be related to changes in small-scale environmental conditions of microhabitats characterized by the variations in abiotic parameters between the two portions of the investigated transect, or by a unique colonization history in each part, with a consequent dissimilarity in species composition of algal assemblages. The condensed ordination plots of samples from the initial sections of both transects, compared to the more expanded ordination plots of samples taken further along the transects, could be related to a narrower vs. wider range of abiotic parameters. Differences in species composition were associated more with the abundance of individual species than with the presence/absence of different species in specific parts of the transects. This pattern was also described previously for algal assemblages in an acidic lowland peat bog (Machová-Černá and Neustupa, 2009), and I concluded that these differences were related to the environmental conditions of the microhabitats studied (low pH and conductivity); conditions that generally support a smaller number of species (Coesel, 1982; Mataloni, 1999). I observed a strong spatial correlation of species composition in both microhabitat types even when using covariates. But I also observed that environmental parameters influenced species distribution – in benthos, total phosphorus and humic acids affected similarity in species composition; in periphyton, pH, conductivity, total nitrogen and humic acids impacted the similarity of algal assemblages. These correlations were related to gradients of environmental parameters that were revealed along the transects. My data describing spatial correlation on a scale of 10 cm are generally incongruent with results from spatial structure studies of algal assemblages in streams (Komárek, 2003), lowland peat bogs (Machová-Černá and Neustupa, 2009), or of marine algae (Coleman, 2002); in these cases, either no, or a very rare pattern of spatial autocorrelation has been revealed on this scale. On the other hand, I observed a pattern of spatial autocorrelation on a scale of 10 cm in both microhabitat types. The pattern of spatial autocorrelation in a homogenous environment without the presence of a water current could be explained either by the limited ability for motion of propagules (Underwood and Chapman, 1996), or of whole organisms (Hillebrand et al., 2001), related to their small size or the absence of flagella. Another explanation is the effect of the environment itself that influences the fitness, and thus, the occurrence of individual organisms under specific environmental conditions (niche-based approach; Soininen, 2007). I suppose that both explanations are partially accurate, as both spatial correlation and influence of environmental parameters on spatial distribution, as well as a similarity among algal assemblages were found in our study. Results of RDA and partial RDA analyses appeared to correspond well with the results of Mantel tests that established a significant effect of geographic distance and environmental parameters on species composition. Similarly, with my data, these analyses showed that a high proportion of the observed variation could be explained either by environmental descriptors or by the spatial matrix. The spatially accounted for variation could also be considered a synthetic descriptor of unmeasured underlying processes such as external causes or biotic factors (e.g. social aggregation; Borcard et al., 1992). The variation explained by environmental and spatial parameters combined made up about one fifth of the observed variation. I speculate that this accounted for variation that is related to spatial correlation of environmental parameters along observed transects in both microhabitats, and corresponds to a somewhat similar spatial structuring of both the species and the environmental data. The large amount of unexplained variation, especially in the case of the periphytic analyses, could be related to either indeterminate overlooked, or insufficiently and/or inaccurately measured factors (especially biotic factors which are difficult to measure); alternatively, it might be due to a large amount of stochastic processes. However, the exact reasons remain unclear, and the ultimate causal factors cannot be ascertained from ecological studies of natural assemblages alone, without experimental research as well.

It is doubtless that the sheet pile walls established a barrier to water and nutrient flow, and to algal migration or movement with water current. This consequently leads to variations in environmental conditions and differences in algal species composition. Conversely, I believe that these barriers did not affect processes such as colonization, migration via other means, or niche differentiation. Thus, I conclude that species composition is more influenced by environmental conditions and small-scale processes (e.g. niche differentiation, competition, grazing) than by the barrier. In benthos the impact of the barrier and the

Table 2
SIMPER analyses: species typical in specific portions of transects on ''Mlynářská slat'' peat bog (Czech Republic), and species responsible for the differentiation of these sections. S_i (%) – percentage contribution of individual species to the intra-group similarity, S_i:SD (S_i) – contribution of individual species to intra-group similarity to standard deviation of the contribution ratio, contrib% – contribution in % of each species to the total similarity or dissimilarity, av.abundance 1, 2 – average abundance of species in the first or the second section of the transect.

(*A*). *The transect in the benthic microhabitat*

Species typifying the section in front of the barrier (Average similarity 74.9%)

	S_i (%)	S_i:SD(S_i)	Contrib%
Eunotia bilunaris var. mucophila	6.3	8.21	8.4
Trachelomonas hispida var. hispida	6.3	8.47	8.4
Eunotia exigua	6.01	6.77	8.02
T. hispida var. crenulatocollis	4.83	5.68	6.45
Pinnularia subcapitata var. subcapitata	4.54	6.94	6.05
Hyalotheca dissiliens	4.47	9.58	5.96
Frustulia saxonica	4.41	14.52	5.88
Caloneis alpestris	4.41	14.52	5.88
Placoneis paraelginensis	4.18	2.77	5.57
Eunotia glacialis	2.77	2.98	3.7
Pinnularia anglica	2.26	1.34	3.02

Species typifying the section behind the barrier (Average similarity 71.4%)

	S_i (%)	S_i:SD(S_i)	Contrib%
Eunotia bilunaris var. mucophila	7.78	9.37	10.89
Trachelomonas hispida var. hispida	7.47	5.48	10.46
Eunotia exigua	7.07	6.19	9.89
Pinnularia subcapitata var. subcapitata	4.79	5.68	6.7
Frustulia saxonica	4.5	2.43	6.29
Synura sp.	4.4	2.0	6.15
Caloneis alpestris	3.26	2.9	4.56
Placoneis paraelginensis	3.26	2.95	4.56
Hyalotheca dissiliens	2.69	1.43	3.76
Pseudanabaena sp.	2.46	2.03	3.44
Eunotia glacialis	2.36	2.08	3.3
T. hispida var. crenulatocollis	2.19	0.85	3.06

Species discriminating between the two parts of the transect (Average dissimilarity 31.3%)

	Av. abund 1	Av. abund 2	Av. dissimilarity	Contrib%
T. hispida var. crenulatocollis	2.47	1.47	1.37	4.37
Stauroneis anceps	1.27	0.2	1.31	4.18
Synura sp.	1.27	2.07	1.26	4.01
T.abrupta var. minor	1.07	0.07	1.21	3.86
Cryptomonas sp.	1.0	0.93	1.17	3.72
Pseudanabaena sp.	0.87	1.27	1.09	3.49
Placoneis paraelginensis	2.27	1.53	1.07	3.4
Microspora tumidula	1.2	0.73	1.0	3.19

(*B*). *The transect in the periphytic microhabitat*

Species typifying the section in front of the barrier (Average similarity 61.3%)

	S_i (%)	S_i:SD(S_i)	Contrib%
Eunotia bilunaris var. mucophila	17.36	4.18	28.33
Mougeotia sp.	15.3	1.56	24.97
Pinnularia rupestris	7.47	1.16	12.18
Eunotia glacialis	7.19	1.28	11.72
Microspora tumidula	6.29	1.31	10.27
Cryptomonas sp.	3.06	0.59	4.99

Species typifying the section behind the barrier (Average similarity 51.5%)

	S_i (%)	S_i:SD(S_i)	Contrib%
Eunotia bilunaris var. mucophila	15.23	2.82	29.56
Pinnularia rupestris	11.83	1.62	22.96
Mougeotia sp.	7.11	1.15	13.8
Microspora tumidula	4.29	0.61	8.33
Microthamnion kuetzingianum	3.28	0.67	6.36
Eunotia exigua	3.09	0.68	5.99
Eunotia glacialis	2.33	0.63	4.53

Species discriminating between the two parts of the transect (Average dissimilarity 49%)

	Av. abund. 1	Av. abund. 2	Av. dissimilarity	Contrib%
Mougeotia sp.	2.36	1.48	5.46	11.15
Pinnularia rupestris	1.44	2.08	4.41	8.99
Eunotia glacialis	1.44	0.88	4.38	8.94
Microspora tumidula	1.28	1.12	4.35	8.88
Microthamnion kuetzingianum	0.76	1.16	4.1	8.36
Eunotia exigua	0.08	1.16	3.87	7.89
Cryptomonas sp.	0.92	0.24	3.72	7.6
Eunotia bilunaris var. mucophila	2.48	2.4	2.68	5.48
Placoneis paraelginensis	0.44	0.48	2.38	4.86

Table 3
Results of simple and partial Mantel tests calculated through the use of different types of matrices over the entire transect in individual microhabitat type, and for the two divisions of each transect on "Mlynářská slať" peat bog (Czech Republic), *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$. (Results for the entire transect are indicated in bold; results for the section in front of the barrier are indicated in italics, and results for the portion behind the barrier are indicated in standard).

	Transect in benthos	Transect in periphyton
Similarity × distance	−0.502***/−0.468***/−**0.227****	*−0.1*/−0.166*/−**0.203****
Similarity × distance × pH	*−0.489****/−0.492***/−**0.226****	*−0.109*/−0.166*/−**0.164****
Similarity × distance × conductivity	*−0.502****/−0.467***/−**0.235*****	*0.015*/−0.167*/−**0.196*****
Similarity × distance × TN	*−0.519****/−0.465***/−**0.213****	*−0.068*/−0.167*/−**0.17****
Similarity × distance × TP	*−0.527****/−0.123/−**0.216****	*−0.116*/−0.17*/−**0.203*****
Similarity × distance × humic acids	*−0.507****/−0.409**/−**0.213****	*−0.1*/−0.244**/−**0.194*****
Similarity × pH	*−0.137*/−0.089/−**0.16**	*0.038*/0.022/−**0.147***
Similarity × conductivity	*−0.01*/−0.03/**0.139**	*−0.217**/0.046/−**0.64**
Similarity × total nitrogen	*−0.039*/0.068/−**0.163**	*−0.235*/0.017/−**0.143***
Similarity × total phosporus	*0.071*/0.55***/−**0.366****	*0.082*/0.139/−**0.21**
Similarity × humic acids	*0.128*/−0.267*/−**0.08**	*−0.018*/0.162*/−**0.072**
pH × distance	*0.34***/0.505**/**0.097**	*0.173**/0.001/**0.349*****
pH × conductivity	*0.003*/0.348**/**0.186**	*0.126*/0.316**/**0.164***
pH × TN	*0.006*/0.252*/**0.064**	*−0.056*/0.489**/**0.486*****
pH × TP	*0.41**/0.414**/**0.415*****	*0.224**/0.557***/**0.483*****
pH × humic acids	*−0.136*/0.563***/**0.294****	*0.118*/0.448**/**0.5*****
Conductivity × distance	*0.02*/0.063/**0.048**	*0.52****/0.027/**0.457*****
Conductivity × TN	*−0.094*/0.17/−**0.133**	*−0.075*/0.387**/**0.517*****
Conductivity × TP	*0.181*/0.242/**0.065**	*−0.043*/0.134/**0.252***
Conductivity × humic acids	*0.4*/0.148/**0.115**	*0.154**/0.292*/**0.42*****
TN × distance	*−0.187**/−0.08/−**0.01**	*0.148*/0.048/**0.3*****
TN × TP	*−0.18*/−0.004/**0.047**	*−0.148**/0.57**/**0.529*****
TN × humic acids	*0.089*/0.105/−**0.007**	*0.2**/0.471**/**0.505*****
TP × distance	*0.192*/0.721***/**0.07**	*0.167**/0.02/**0.201*****
TP × humic acids	*−0.005*/0.453**/**0.297****	*0.084*/0.654***/**0.647*****
Humic acids × distance	*0.009*/0.705***/**0.285*****	*0.336****/0.361***/**0.499*****

resulting small-scale alterations in environmental conditions seemed to be of greater significance and have more influence on the variation in species composition throughout the transect. Furthermore, I concluded that the two years separation of the microhabitat by the sheet pile walls represents a relatively brief time period for the formation of diverse algal assemblages.

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