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Research Paper

Spatial Distribution of Algal Assemblages in a Temperate Lowland Peat Bog

key words: spatial autocorrelation, spatial scale, phytobenthos, Mantel test

Abstract

Samples of phytobenthos were collected during three different seasons in 2005 along a linear transect of a lowland peat bog at various spatial scales (10 cm, 1 m, 10 m) to investigate the seasonal dynamics, diversity, and factors influencing the spatial patterns of microalgal communities. Non-metric multidimensional scaling (NMDS), similarity percentage (SIMPER) analyses, ANOSIM, Mantel tests and diversity indices were used to analyze the data. Seasonal dynamics were exhibited by an increase in diversity, and a decrease in dominance from May to October, with significant differences in species composition. Mantel tests showed the significant influence of distance, microhabitat type, and conductivity on maintaining the similarity of species composition on scales of 1 m and 10 m. The small-scale processes (colonization and niche differentiation), microhabitat type, geographic distance and conductivity were found to be the main factors influencing the distribution of algal assemblages. We conclude that these factors are related to winter disturbance, and the consequent colonization and subsequent niche differentiation.

1. Introduction

Knowledge of the spatial structure of benthic assemblages underlies the understanding of ecological processes such as: succession, colonization, niche differentiation, and competition (RICKLEFS and SCHLUTER, 1993). Moreover, identifying the spatial pattern of species composition in water ecosystems is crucial for evaluation of their biodiversity and formulation of conservation strategies (COLEMAN, 2002). Thus, spatial analysis has recently become a rapidly growing field in benthology and aquatic ecology.

Small-scale differences in species composition and abundance were found to be significant for several organismal groups, primarily in marine environments. UNDERWOOD and CHAPMAN (1996) described the differences in abundance of intertidal snails and barnacles, on scales of centimeters to 1 to 2 meters by their ecological responses to small-scale patchiness of a microhabitat. Also in 1999, ARCHAMBAULT and BOURGET found increasing abundance of benthic marine algae from smooth, to rough and more heterogeneous, surfaces on small scales. It was demonstrated a few years later by DOWNES *et al.* (1998) that both niche differentiation and higher substratum complexity correlated with invertebrate species richness and abundance in a perennial, upland stream.

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COLEMAN (2002) examined the high variation in assemblages of marine turfing algae on a small spatial scale (10 cm). These findings, which were temporally consistent, appeared to be due to small-scale ecological processes. Others, RINDI and CINELLI (2000) and RINDI and BATELLI (2005) discussed the importance of small-scale differentiation in Mediterranean intertidal algal assemblages. They stressed the importance of substratum heterogeneity, as well as colonization processes (input of propagules), competition and variation in recruitment. It was revealed by BENEDETTI-CECCHI (2001) that a significant proportion of horizontal variation in marine littoral benthic algal and invertebrate communities could be explained on the scale of 10 s of centimeters, and related to physical processes of the environment. SABUROVA *et al.* (1995) defined the main factors influencing spatial distribution of sandflat microphytobenthic communities in relationship to scale: on a microscale (up to 2 m^2), biotic interspecies interactions are the most important; on the mesoscale (up to 18 m^2), distribution is mainly determined by the granulometric composition and a complex of abiotic conditions in the sediments; on the macroscale (up to 10,000 m^2), distribution depends upon the emersion period during low tide. Similar results were obtained by MÉLÉDER *et al.* (2007), who studied microphytobenthic assemblages of a macrotidal flat. They found that hydrodynamics related globally to the occurrence of spatio/temporal biotic or abiotic gradients, whereas oyster beds and ridge and runnel features appeared to be local spatial structuring factors.

Most of the studies conducted in marine ecosystems referred to small-scale variation as a result of substrate heterogeneity and biotic processes (colonization, competition). Increasing patchiness of benthic assemblages was positively correlated with diversity (UNDERWOOD and CHAPMAN, 1996; ARCHAMBAULT and BOURGET, 1999).

In freshwater benthic habitats, data on small-scale algal differentiation are less numerous. Recent studies concentrated on regional or large-scale processes of individual catchment areas (CHARLES *et al.*, 2006), water bodies (PALS *et al.*, 2006) or running waters (*e.g.*, PASSY, 2001; SOININEN, 2005). The spatial organization of benthic invertebrate communities in two oligotrophic lakes was characterized by STOFFELS *et al.* (2005). They found that the small-scale structure was typically driven by substrate heterogeneity. Many authors concentrated on spatial distribution of diatoms, especially in streams. PASSY (2001) revealed current velocity as the major factor controlling diatom distribution in streams, and only a minor influence for other, mostly biotic, factors in shaping diatom communities. Conversely, SOININEN (2005) reported that the current velocity did not strongly shape diatom communities in turbid rivers. SOININEN and KÖNÖNEN (2004), also studied diatom benthic communities in many boreal streams and found that environmental factors, principally conductivity, total phosphorus content, and water color were related to algal distribution. In addition, a clear spatial configuration of algal distribution, within distinctly different communities in different parts of the country, was revealed (SOININEN *et al.*, 2004).

However, data on the spatial distribution of algal assemblages in stagnant freshwater habitats are missing. Therefore, in this study we concentrated on a Central European lowland peat bog, where we investigated the spatial structure of phytobenthos and periphyton along a linear transect. The aims of this study were to: (1) describe the algal species composition of the locality, and its diversity and dynamics throughout the year, (2) identify the distribution and patterns of spatial autocorrelation of assemblages, and describe factors influencing this pattern.

2. Materials and Methods

The study area is located in the Břehyně-Pecopala National Natural Reserve and Ramsar locality, Czech Republic (50°34´N, 14°42´E). The central part of the reserve is occupied by Břehyňský fishpond (area 90 ha) created in the first half of the 13th century. The pond is surrounded by a huge area of sandstone-based lowland peat bogs that gradually turn into semi-artificial wetland pine forests (ČERMÁK

and MRKVA, 2003). Since the 1970s the time of the Soviet occupation of the former Czechoslovakia, the reserve was part of a large military area established around the Ralsko Soviet military airport and rocket base. At that time, a system of drainage ditches was dug in parts of the wetland. However, today these linear ditches are functionless, and partly overgrown with peat bog vegetation that impedes the current such that they become filled with stagnant water.

The ditch we examined is situated in the southern part of the reserve, and its length is approximately 400 m. It is partly overgrown with mosses (*Sphagnum* spp.), and the depth of the water column varies from 10 to 30 cm. The pH of the water ranged between 3.8 and 4.5, its conductivity ranged between 80 and 170 $\mu S\ cm^{-1}$.

Samples of phytobenthos were collected in three different seasons in 2005: spring: May 12th, summer: August 30th, and autumn: October 28th. They were collected along a transect of the entire 400 m lengthwise axis of the ditch. We collected 40 samples separated by a distance of 10 m from each other, 21 samples 1 m apart, and 20 samples taken 10 cm from each other (Fig. 1). The samples taken for analyses at each site consisted of 10 ml of phytobenthos and periphyton. Conductivity, temperature and pH at each sampling site were measured using a Hanna portable combined pH/conductometer. In addition, the microhabitat type of each site was recorded. We distinguished five physiognomically discernible microhabitat types: (1) epipelic phytobenthos on a fine detritus bottom, (2) benthos dominated by a submerged *Sphagnum* biomass, (3) periphyton within submerged *Sphagnum* tussocks filling-up the water column, (4) periphyton within half-emersed *Sphagnum* tussocks (up to 5 cm above water level), and (5) periphyton within emersed *Sphagnum* tussocks. At individual sampling sets, the microhabitats were differentially represented, as a result of seasonal fluctuation of the water level.

The samples were fixed with Lugol's solution in the field, and later, examined under an Olympus BX 51 light microscope and identified to the lowest possible taxonomic level. Diatoms were identified in mineralized samples mounted on Naphrax permanent slides (HOUK, 2003). The identification was based on standard taxonomic monographs (Süsswasserflora von Mitteleuropa, Binnengewässer, Diatoms of Europe, *etc.* – for references see *e.g.*, ŠEJNOHOVÁ *et al.*, 2003). Semiquantitative estimates of algal populations were deduced from slides, and individual species were classified into three categories: (1) up to 1% of individuals revealed, (2) up to 50% of individuals, and (3) more than 50% of individuals of a particular assemblage (KINROSS *et al.*, 1993; FAUCONNIER, 1995; GAISER and JOHANSEN, 2000; HUSA *et al.*, 2004; KOMÁREK and SUKAČOVÁ, 2004). Approximately 500 cells per sample were observed.

Non-metric multidimensional scaling (NMDS; KRUSKAL, 1964) was used in each set of samples to display the species' structural composition data using the PRIMER® (Plymouth Routines In Multivariate Ecology, PRIMER-E Ltd., Plymouth, UK) software package. To reduce the chance of local optima, 100 random starts were carried out in 2- and 3-dimensional analyses (CLARKE and WARWICK, 2001).

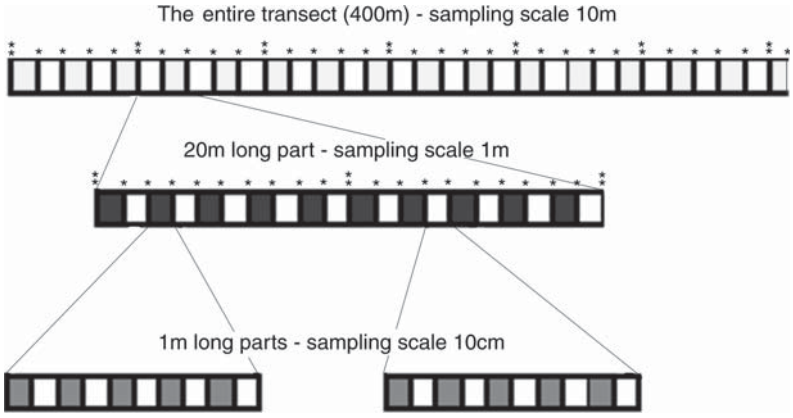

Figure 1. The sampling design indicating position of individual samples along the linear transect. Stars indicated sample set on 10 m scale compared to corresponding sample set on 50 m scale and sample set on 1 m scale compared to corresponding sample set on 10 m scale.

In all cases, the 3-dimensional solutions had slightly lower stress values than the 2-dimensional ones, but we utilized the 2-dimensional data because of the superior representation of sample position. In all analyses, we used Bray-Curtis similarity index (Bray and Curtis, 1957; Clarke, 1993; Méléder *et al.*, 2007). To retain the contribution of each species according to its semi-quantitative abundance, we made no data transformations (Clarke *et al.*, 2006).

The species composition of different microhabitats within and between individual seasonal sets of samples was compared using a non-parametric two-group ANOSIM test based on Bray-Curtis similarity index, which is a non-parametric distribution-free analogue of one-way ANOVA (Clarke and Green, 1988; Clarke, 1993). The procedure was carried out in PAST software (ver. 1.62; Hammer *et al.*, 2001) with 10,000 permutations used.

Subsequently, we identified species responsible for the individual microhabitat types using the SIMPER (similarity percentage) routine of PRIMER® (Clarke and Warwick, 2001; Méléder *et al.*, 2007). All species observed were included in the analysis. The SIMPER analysis compared the average contribution of each species to the average Bray-Curtis similarity within a group. The SIMPER procedure also examined community patterns defining inter-group dissimilarity.

Additionally, community structure was studied using diversity indices that were calculated for all microhabitat samples in individual season sets throughout the collection period. We used species number, Shannon index, H' (Shannon and Weaver, 1949) that takes into account the number of individuals as well as number of taxa (it varies from 0 for communities with only a single taxon to high values for communities with many taxa, each with few individuals), and Pielou's evenness (or equitability), J' (Pielou, 1969, 1975) that was calculated as Shannon diversity divided by the logarithm of number of taxa (this expresses how uniformly individuals are distributed among the different species, and its values are the opposite of dominance values). Differences between calculated diversity indices were evaluated using permutation *t*-test in PAST software (ver. 1.62; Hammer *et al.*, 2001) with 10,000 permutations used. Identical analyses as those described above were used to evaluate seasonal dynamics in species composition.

The effect of spatial autocorrelation in species data along the studied transect in individual sample sets was evaluated using two-matrices and partial Mantel tests (Mantel, 1967; Smouse *et al.*, 1986). We tested the mutual relationships among five different matrices: (1) matrix of spatial distances between pairs of sites along a transect, (2) matrix of similarity in species composition (Bray-Curtis similarity index), (3) matrix of differences in pH values between sites; (4) matrix of differences in conductivity values between sites, (5) matrix of similarity in microhabitat type (1 designates the same microhabitat type for a compared pair of samples, *e.g.*, both samples collected from emersed moss tussocks, 0 designates a different microhabitat type; McCune and Grace, 2002). Mantel tests were conducted for individual spatial scales (10 cm, 1 m, 10 m, and 50 m – this last including every fifth sample taken on 10 m scale) in each sample set using *zt* software (ver. 1.0; Bonnet and Van der Peer, 2002).

Finally, we tested the species diversity of various pairs of sample sets to ascertain on which scale the highest species diversity was detected during the sampling period. Differences in species diversity were evaluated by permutation tests on Menhinick diversity index (Magurran, 2004) using R 2.3.1 routine (R Core Development Team, 2006). In total, 10,000 permutations were used in diversity testing. All the corresponding sets were tested on individual scales across the seasonal sampling sets. In addition, we tested within-season diversity differences in samples taken in the various microhabitat types on the 10 cm scale, and in all of the 40 samples taken 10 m apart *vs.* eight samples taken 50 m apart (every fifth sample taken on 10 m scale) from the corresponding transect, and in the 21 samples taken on the 1 m scale *vs.* three samples separated by 10 m (Fig. 1).

3. Results

3.1. The Structure in Species Composition

The structure in species composition, based on non-metric multidimensional scaling (NMDS), revealed that the differences in microhabitats clearly accounted for the greatest portion of the variation in species composition of individual sets of samples (Fig. 2). In May (Fig. 2a), the periphyton samples from submerged *Sphagnum* tussocks were separated from two epipelic microhabitats (epipelic phytobenthos on a fine detritus bottom, and benthos

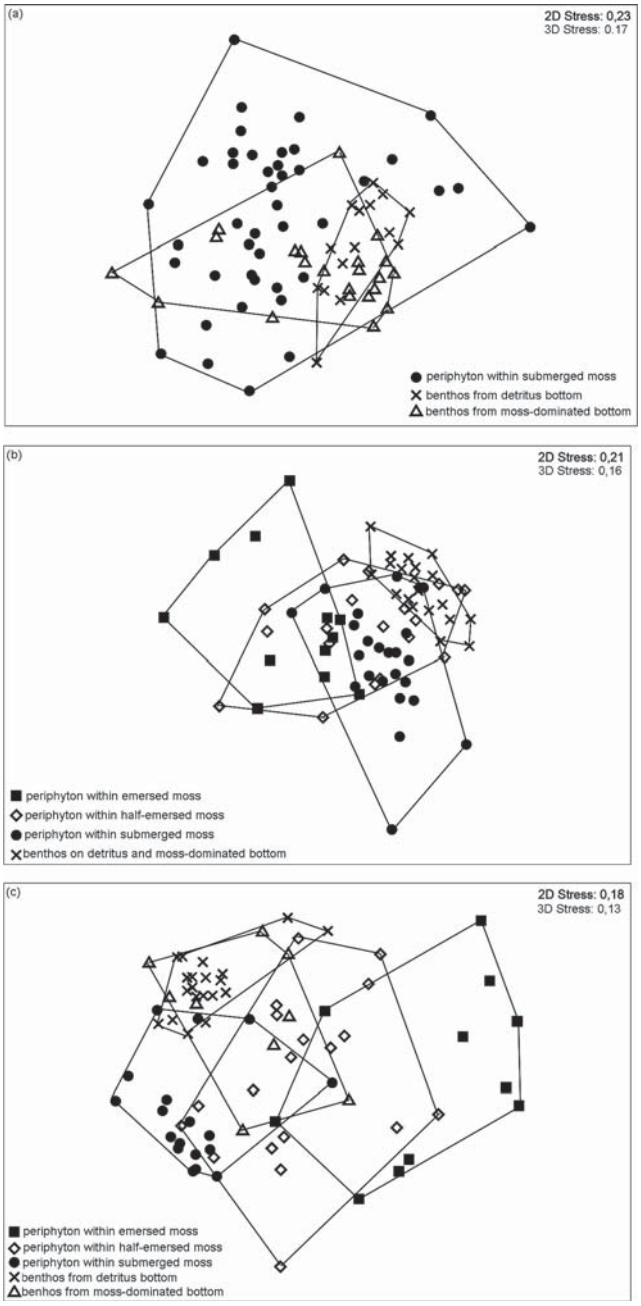

Figure 2. (a–c) Non-metric multidimensional scaling (NMDS) of samples collected in individual seasons of the year – (a) May, (b) August, (c) October. (emersed moss = periphyton within the emersed *Sphagnum* tussocks, half-emersed moss = periphyton within the half-emersed *Sphagnum* tussocks, submerged moss = periphyton within the submerged *Sphagnum* tussocks filling-up the water column, bottom with moss = benthos dominated by the submerged *Sphagnum* biomass, bottom with detritus = the epipelic phytobenthos on the fine detritus bottom).

dominated by a submerged *Sphagnum* biomass). In August and October, we observed a clear separation of the two sample sets; on one side samples that were collected from the emersed *Sphagnum* tussocks (that developed as a result of decreasing water level), and were distinct from the epipelic microhabitats on the opposite side of the sample position plot (Fig. 2b, c). The samples taken from half-emersed and submerged *Sphagnum* tussocks were located in between these two.

3.2. Microhabitat Differentiation

The statistical significance of within-season differences in species composition between all tested microhabitat pairs was confirmed by the non-parametric ANOSIM tests for all three seasonal sets (Table 1). If we used the values of R-statistic from the ANOSIM analysis as the scale factor, the difference between identical pairs of microhabitats generally increased throughout the sampling period. At the same time, statistically significant differences in between-season species composition of individual microhabitat types were detected in most cases, with only two exceptions in the emersed and submerged *Sphagnum* tussocks species composition that showed no statistically significant difference between August and October (Table 1).

The SIMPER analyses detected species identifying individual microhabitat types (Table 2). The algal assemblages from individual microhabitats did not essentially differ in species composition, but rather, in the relative abundance of these species. The algal periphyton growing within the emersed *Sphagnum* tussocks was characterized by the dominance of

Table 1. Comparison of species composition of microhabitats within and between seasons calculated through the use of two-group ANOSIM tests. Values of R statistic are represented. *: $P < 0.05$. **: $P < 0.01$, ***: $P < 0.001$. (Comparison between species composition of benthos on fine detritus bottom and benthos on moss-dominated bottom in August was omitted because of low number of samples collected at the second microhabitat mentioned. Non-significant values are in bold.)

Pairs of microhabitats compared within seasons	May	August	October
Periphyton of emersed moss × Periphyton of half-emersed moss		0,22**	0,18**
Periphyton of emersed moss × Periphyton of submerged moss		0,44***	0,83***
Periphyton of emersed moss × Benthos on moss-dominated bottom		0,81***	0,74***
Periphyton of emersed moss × Benthos on fine detritus bottom		0,81***	0,93***
Periphyton of half-emersed moss × Periphyton of submerged moss		0,15***	0,4***
Periphyton of half-emersed moss × Benthos on fine detritus bottom		0,39***	0,65***
Periphyton of half-emersed moss × Benthos on moss-dominated bottom		0,32***	0,36***
Periphyton of submerged moss × Benthos on moss-dominated bottom	0,16**	0,37***	0,54***
Periphyton of submerged moss × Benthos on fine detritus bottom	0,22***	0,37***	0,62***
Benthos on fine detritus bottom × Benthos on moss-dominated bottom	0,104*	–	0,48***

Microhabitats compared among seasons	May × August	May × October	August × October
Periphyton within emersed moss			**0.026**
Periphyton within half-emersed moss			0.1*
Periphyton within submerged moss	0.18***	0.15**	**0.065**
Benthos on fine detritus bottom	0.28***	0.4***	0.23***
Benthos on moss-dominated bottom	0.42***	0.32**	0.21*

Table 2. SIMPER analyses – tables represented species typical for individual microhabitat types and seasons. S_i(%) – percentage contribution of individual species to intra-group similarity, $S_i : SD(S_i)$ – contribution of individual species to intra-group similarity to standard deviation of the contribution ratio.

Periphyton within emersed moss			**Periphyton within half-emersed moss**			**Periphyton of submerged moss**		
	S_i(%)	$S_i : SD(S_i)$		S_i(%)	$S_i : SD(S_i)$		S_i(%)	$S_i : SD(S_i)$
Eunotia exigua	21.99	5.81	*Cryptomonas* sp.	13.64	2.78	*Eunotia exigua*	12.39	1.91
Cryptomonas sp.	15.9	2.48	*Eunotia exigua*	13.54	2.53	*Eunotia bilunaris*	11.01	2.50
E. paludosa	15.45	2.30	*Eunotia bilunaris*	10.68	4.10	*Cryptomonas* sp.	9.84	1.95
E. bilunaris	13.83	2.53	*Eunotia paludosa*	7.72	1.34	*Mougeotia* sp.	9.6	1.82
Brachysira serians	5.89	1.49	*Mougeotia* sp.	5.5	1.18	*Merismopedia glauca*	5.79	1.25
Eunotia glacialis	3.89	0.68	*Brachysira serians*	4.62	1.59	*Chroococcus obliteratus*	5.69	1.26
Euglena sp.	3.32	0.92	*Merismopedia glauca*	3.9	1.02	*Cylindrocystis brebissonii*	4.15	0.94
Mougeotia sp.	2.8	0.68	*Frustulia saxonica*	3.48	1.07	*Brachysira serians*	3.82	0.98
Pinnularia rupestris	1.68	0.50	*Cylindrocystis brebissonii*	3.36	1.03	*Staurastrum punctulatum*	3.78	1.18
Others	15.25		*Euglena* sp.	3.26	1.18	*Frustulia saxonica*	3.62	1.02
			Chroococcus obliteratus	3.25	0.83	*Euastrum binale*	3.44	0.68
			Staurastrum punctulatum	3.2	1.05	*Eunotia paludosa*	2.91	0.56
			Eunotia glacialis	2.09	0.64	*Chroococcus minor*	2.81	0.64
			Merismopedia angularis	1.99	0.77	*Binuclearia tectorum*	2.42	0.69
			Others	19.77		Others	18.73	

Benthos on fine detritus bottom			**Benthos on moss-dominated bottom**		
	S_i(%)	$S_i : SD(S_i)$		S_i(%)	$S_i : SD(S_i)$
Eunotia bilunaris	7.91	4.19	*Eunotia exigua*	8.79	2.12
Merismopedia glauca	7.72	3.31	*Eunotia bilunaris*	8.68	2.87
Frustulia saxonica	7.19	3.68	*Mougeotia* sp.	7.78	2.25
Eunotia exigua	6.67	2.45	*Merismopedia glauca*	7.02	2.21
Mougeotia sp.	6.45	2.35	*Brachysira serians*	6.41	1.68
Merismopedia angularis	6.37	2.19	*Frustulia saxonica*	6.15	1.78
Brachysira serians	6.32	1.69	*Merismopedia angularis*	5.94	1.74
Cylindrocystis brebissonii	5.03	1.27	*Cryptomonas* sp.	5.78	1.66
Croococcus obliteratus	4.81	1.39	*Cylindrocystis brebissonii*	4.18	1.05
Cryptomonas sp.	4.63	1.84	*Chroococcus obliteratus*	4.09	1.02
Staurastrum punctulatum	3.46	1.76	*Euglena* sp.	2.94	1.24
Pinnularia biceps	3.2	1.29	*Pinnularia rupestris*	2.91	0.83
Pinnularia viridis	3.18	1.74	*Synura* sp.	2.8	1.46
Euglena sp.	2.84	1.50	*Pinnularia viridis*	1.85	0.89
Staurastrum simonyi	1.96	0.83	*Pinnularia biceps*	1.8	0.79
Euastrum binale	1.74	1.01	*Tabellaria flocculosa*	1.78	0.91
Others	20.52		Others	21.1	

May			**August**			**October**		
	S_i(%)	$S_i : SD(S_i)$		S_i(%)	$S_i : SD(S_i)$		S_i(%)	$S_i : SD(S_i)$
Eunotia exigua	13.35	2.32	*Eunotia exigua*	11.12	1.98	*Eunotia exigua*	11.94	1.91
Eunotia bilunaris	11.41	2.52	*Eunotia bilunaris*	9.48	2.79	*Eunotia bilunaris*	10.76	3.15
Mougeotia sp.	9	1.70	*Cryptomonas* sp.	9.11	1.70	*Cryptomonas* sp.	10.58	1.77
Cryptomonas sp.	8.64	1.83	*Mougeotia* sp.	6.61	1.52	*Mougeotia* sp.	6.98	1.42
Cylindrocystis brebissonii	6.04	1.08	*Chroococcus obliteratus*	5.82	1.37	*Brachysira serians*	6.52	1.86
Merismopedia glauca	5.53	1.31	*Merismopedia glauca*	5.75	1.31	*Merismopedia glauca*	5.5	1.07
Frustulia saxonica	4.13	0.98	*Brachysira serians*	5.15	1.41	*Frustulia saxonica*	4.7	1.40
Brachysira serians	3.67	0.88	*Frustulia saxonica*	4.08	1.05	*Chroococcus obliteratus*	4.55	1.02
Pinnularia rupestris	3.33	0.88	*Eunotia paludosa*	3.79	0.70	*Cylindrocystis brebissonii*	3.89	1.01
Euglena sp.	3.31	1.14	*Euglena* sp.	3.7	1.40	*Staurastrum punctulatum*	3.68	1.21
Chroococcus obliteratus	3.13	0.78	*Cylindrocystis brebissonii*	3.11	0.99	*Eunotia paludosa*	3.52	0.57
Eunotia paludosa	3.08	0.54	*Chroococcus minor*	3.08	0.66	*Eunotia glacialis*	2.66	0.73
Staurastrum punctulatum	2.55	0.82	*Merismopedia angularis*	2.85	0.80	*Synura* sp.	2.4	0.90
Dinobryon sociale	2.4	0.84	*Staurastrum punctulatum*	2.71	0.98	*Merismopedia angularis*	2.22	0.67
Synura sp.	2.28	0.82	*Synura* sp.	2.2	0.93	*Euglena* sp.	1.85	0.75
Others	18.15		Others	21.44		Others	18.25	

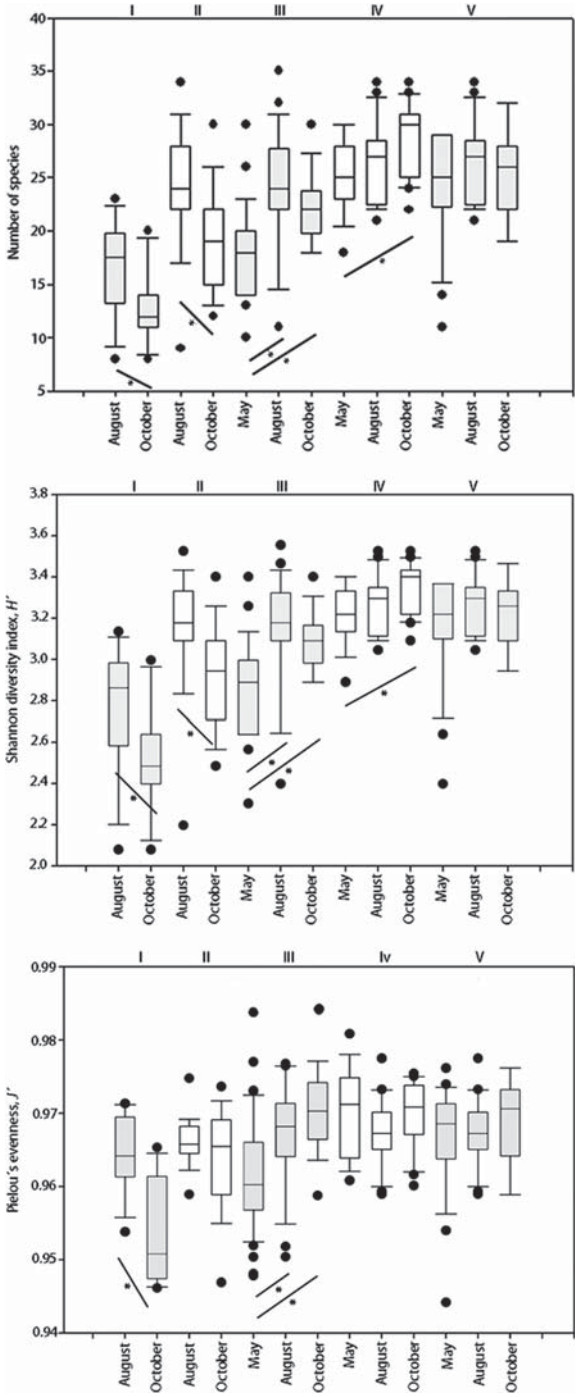

Figure 3. Different diversity indices calculated for individual microhabitat types in different seasons: number of species, Shannon diversity index, *H´*, Pielou´s evenness, *J´*. Significant differences between different diversity indices are indicated with stars and pairs are joined with lines. (I – periphyton within the emersed *Sphagnum* tussocks, II – periphyton within the half-emersed *Sphagnum* tussocks, III – periphyton within the submerged *Sphagnum* tussocks filling-up the water column, IV – the epipelic phytobenthos on the fine detritus bottom, V – benthos dominated by the submerged *Sphagnum* biomass).

the single species *Eunotia exigua* (BRÉBISSON) RABENHORST which, along with a few other diatom species, formed the assemblage. In other microhabitat types, diatoms also made up a significant part of the assemblage, but cyanobacteria, desmids, flagellates and filamentous green algae were also found in abundance. The highest average within-group similarities were detected in benthos of a fine-detritus bottom, and in periphyton growing within emersed *Sphagnum* tussocks (Table 3). These two microhabitat types also exhibited the highest inter-microhabitat dissimilarity (60.7%); they were distinguished from each other by the dominance of a few diatom species in the periphyton microhabitat, and the presence of desmids in the fine-detritus benthos. Nevertheless, the two benthic microhabitats were the most similar in their species composition.

The box-plots of the diversity indices illustrated different seasonal trends in individual microhabitats (Fig. 3). In emersed (I), and half-emersed (II), *Sphagnum* tussock microhabitats the numbers and diversity of species significantly decreased between August and October, and the decrease of evenness was statistically significant only for emersed *Sphagnum* tussocks. In submerged *Sphagnum* tussocks (III) a similar pattern was identified for species numbers and species diversity: an increase in August compared to May, with a subsequent decrease in October (the values were significantly different between May and August and May and October). In the microhabitat with a fine detritus bottom (IV), the number and diversity of species increased throughout the year, as indicated by statistically significant differences between indices values from May to October. In the microhabitat type (V), dominated by *Sphagnum* biomass on the bottom, no statistically significant changes in diversity indices were detected (Fig. 3).

3.3. Seasonal Dynamics

Seasonal changes in species composition were evaluated by two-group ANOSIM tests of samples taken in May, August and October. We found statistically significant differences in species composition between May and August ($R = 0.17$, $P < 0.0001$), May and October ($R = 0.145$, $P < 0.001$), and August and October ($R = 0.038$, $P < 0.01$). The SIMPER analyses of between-season samples resulted in a pattern similar to that of microhabitats – the individual species typifying the seasons were largely the same, but there were differences

Table 3. SIMPER analyses – tables represent average similarity within a group (microhabitat type/season; numbers in bold) and between groups (microhabitat types/season). I – periphyton within emersed *Sphagnum* tussocks, II – periphyton within half-emersed *Sphagnum* tussocks, III – periphyton within submerged *Sphagnum* tussocks, IV – benthos of fine-detritus bottom, V – benthos of moss-dominated bottom.

	May	August	October		
May	**52.9**				
August	50.97	**52.35**			
October	50.26	48.23	**53.14**		
	I	II	III	IV	V
I	**58.06**				
II	47.68	**55.4**			
III	54.25	48.17	**53.39**		
IV	58.48	50.39	50.41	**55.8**	
V	60.7	50.73	50.35	42.07	**62.33**

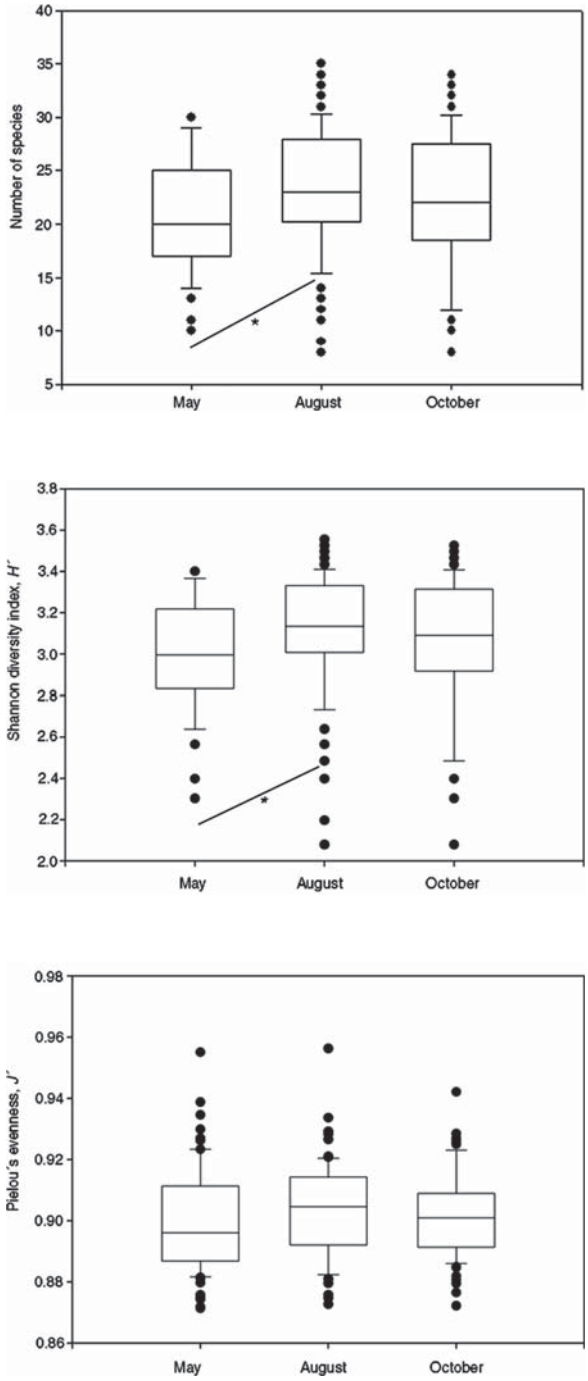

Figure 4. Different diversity indices calculated for individual seasons in the year: number of species, Shannon diversity index, *H´*, Pielou's evenness, *J´*. Significant differences between different diversity indices are indicated with stars and pairs are joined with lines.

Table 4. Results of simple and partial Mantel tests calculated through the use of different types of matrices at different scales. *: $P < 0.05$. **: $P < 0.01$, ***: $P < 0.001$. (Three numbers at each scale indicated results from individual seasons: May/August/October. Where results are not presented – these pairs of matrices were viewed as unreasonable to calculate because of same type of microhabitat of compared samples. Covariables are indicated in italics.)

Scale	50 m	10 m	1 m	10 cm benthos	10 cm submerged moss
Similarity index × distance	$-0.6^{**}/-0.77^{***}/-0.84^{***}$	$-0.68^{***}/-0.61^{***}/-0.61^{***}$	$-0.44^{***}/-0.09/-0.15^{*}$	$-0.5^{***}/-0.28^{*}/0.2$	$-0.13/-0.39^{*}/-0.26$
Similarity index × pH	0.14/–0.29/0.12	$-0.14^{*}/-0.09/-0.12$	$-0.002/0.05/-0.21^{*}$	–0.17/0.1/–0.09	0.18/–0.14/–0.1
Similarity index × conductivity	$-0.37^{*}/-0.38^{*}/-0.17$	$-0.43^{***}/-0.41^{***}/-0.4^{***}$	–0.07/0.14/0.1	–0.003/0.06/–0.16	0.02/0.004/0.21
Similarity index × microhabitat	0.06/0.15/0.33	$0.18^{**}/0.27^{***}/0.34^{***}$	$0.23^{*}/0.22^{**}/0.32^{***}$	–	–
pH × distance	$-0.08/0.46^{*}/0.09$	$0.06/0.17^{**}/0.2^{**}$	$0.25^{**}/0.06/0.25^{**}$	$0.25/0.5^{*}/-0.22^{*}$	0.08/0.1/0.07
pH × conductivity	$-0.09/0.66^{**}/0.52^{*}$	$0.11/0.49^{***}/0.51^{***}$	$0.04/0.36^{*}/-0.02$	0.1/0.24/–0.19	$0.22/0.86^{***}/0.22$
pH × microhabitat	–0.44/–0.79/–0.25	$-0.12^{**}/-0.15^{**}/-0.1^{**}$	–0.14/–0.02/0.07	–	–
Conductivity × distance	$0.44^{*}/0.55^{*}/0.3$	$0.45^{***}/0.6^{***}/0.52^{***}$	0.16/0.007/–0.04	$0.43^{*}/-0.06/-0.14$	0.2/0.21/0.05
Conductivity × microhabitat	–0.17/–0.22/–0.27	$-0.2^{**}/-0.16^{**}/-0.17^{***}$	–0.01/0.008/0.04	–	–
Microhabitat × distance	–0.17/–0.05/–0.27	$-0.09^{*}/-0.13^{**}/-0.26^{***}$	$-0.25^{**}/-0.04/-0.067$	–	–
S. index × distance × pH	$-0.59^{**}/-0.75^{***}/-0.86^{***}$	$-0.68^{***}/-0.61^{***}/-0.61^{***}$	$-0.45^{***}/-0.1/-0.1$	$-0.5^{***}/-0.29/0.19$	$-0.18/-0.37^{*}/-0.25$
S. index × distance × conductivity	$-0.52^{*}/-0.73^{**}/-0.83^{***}$	$-0.6^{***}/-0.5^{***}/-0.52^{***}$	$-0.43^{***}/-0.09/-0.15^{*}$	$-0.51^{***}/-0.3^{*}/0.19$	$-0.16/-0.39^{*}/-0.27$
S. index × distance × microhabitat	$-0.59^{**}/-0.77^{***}/-0.82^{***}$	$-0.67^{***}/-0.6^{***}/-0.58^{***}$	$-0.4^{***}/-0.09/-0.18^{*}$	–	–
S. index × microhabitat × distance	–0.05/0.17/0.2	$0.16^{**}/0.25^{***}/0.24^{***}$	$0.14/0.22^{**}/0.34$	–	–

in their abundance (Table 2). However, there were distinct seasonal trends in the occurrence of various algal groups. Cyanobacteria, autotrophic flagellates (*Euglena mutabilis* SCHMITZ, *Dinobryon sociale* EHRENBERG) and filamentous green algae (*Mougeotia* sp., *Ulothrix* spp., *Microthamnion kuetzingianum* NÄGELI) species decreased in numbers and abundance. On the other hand, the abundance and number of species of desmids and diatoms increased. The average within-group similarities remained consistent in all seasons (52.9–53.14%), while the inter-season dissimilarities varied between 48.23 and 50.97% (Table 3).

The seasonal course of the algal assemblages as a whole, as indicated by diversity indices, showed a similar pattern of diversity that increased during the year (Fig. 4). Furthermore, a statistically significant increase in the number and diversity of species was detected between May and August. Changes in evenness were insignificant.

3.4. Spatial Autocorrelation

Correlation between spatial distance and similarity in species composition among samples was detected on 50 m, 10 m and 1 m scales (Table 4). However, this correlation on a 1 m scale was non-significant in August. Significance of spatial distance on these scales was generally confirmed by partial Mantel tests with effects of pH, conductivity, and microhabitats controlled for (Table 4). Correlation of external factors (pH, conductivity, microhabitat type) with spatial distance was mostly insignificant on 50 m and 1 m scales; however, the correlation between conductivity and microhabitat type were typically significant on the 10 m scale. Correlations between similarity in species composition and distance for samples taken on a 10 cm scale were insignificant, with exceptions in May (benthic samples) and August (samples in submerged moss microhabitat; Table 4).

3.5. Spatial Structure of Diversity

Using diversity comparisons, we evaluated the variation in species diversity with increasing spatial distance. Diversity did not differ significantly between seasonal samplings on different scales from 10 cm to 50 m, nor indeed, along the entire transect. Correspondingly, diversity did not differ among the 10 cm samplings collected in different microhabitats. Diversity of samples taken along transects of various scales was found to be significantly higher on the smaller scale only in the single case of May collections from 10 m *vs.* 50 m sets (permutation $P = 0.0019$). In all other cases (10 m *vs.* 50 m in August and October, and all the 1 m *vs.* 10 m seasonal sets) no statistically significant difference in diversity was found.

4. Discussion

Most of the 82 taxa of cyanobacteria and algae identified in this study were common lowland peat bog taxa (COESEL, 1986; BORICS *et al.*, 2003; NOVÁKOVÁ, 2007). The relatively low number of species encountered is likely related to extremely low pH-levels (3.5–4.5), or to seasonal water level fluctuations. There certainly were several coccoid green algal species that were left unidentified because of their tremendously complicated and confusing species concepts and cryptic diversity (JOHN and MAGGS, 1997; FAWLEY *et al.*, 2004). The high proportion of desmids and conjugates observed correlates with their reported preference for lower pH (COESEL, 1982; MATALONI, 1999), even though a pH level of less than 4.5 is reported to limit occurrence of most these species (COESEL, 1983, 1998).

The NMDS plots illustrate that the pattern of species was principally related to the differences in microhabitat types. The differences in species composition among microhabitats

were demonstrated by ANOSIM and Mantel tests. Abiotic factors were considered important in determining the different algal species components in freshwater benthic microhabitats (*e.g.*, SABUROVA *et al.*, 1995; DOWNES *et al.*, 1998; ARCHAMBAULT and BOURGET, 1999; RINDI and CINELLI, 2000; STOFFELS *et al.*, 2005). The emersed *Sphagnum* tussocks (occurring in summer and autumn, as a result of a decrease in water level) are typical due to acidity stress and desiccation, and consequently because of decreased competition (COESEL, 1982; MATALONI, 1999). We also detected low diversity in this microhabitat, with a decrease in diversity and dominance of species throughout the sampling period, not observed in other microhabitats. The assemblages were mainly composed of diatoms (especially a single dominant species: *Eunotia exigua*). In higher water levels, the submerged *Sphagnum* tussocks, the moss-biomass bottom and the fine-detritus benthos contained a greater number of species (including desmids) and greater evenness than the emersed *Sphagnum* microhabitat, thus indicating a more consistent abundance of species. In general, our report of different algal species composition in different freshwater benthic microhabitats corresponds with those of previous studies (COESEL, 1982, 1986; MATALONI, 1999).

We found seasonal variations in species composition accompanied by an increase in species diversity and a decrease in dominance over the course of the sampling period. Seasonal dynamics of microphytobenthic species was found significant in lakes (HAWES and SMITH, 1994; ABERLE and WILTSHIRE, 2006; O´REILLY, 2006), streams and rivers (POWER, 1992; PETERSON and STEVENSON, 1992; WERNER and KÖHLER, 2005), as well as in peat bogs (HAYWARD, 1957; DUTHIE, 1965; ŁAŹNIEWSKA, 2001). However, the higher difference of spring algal species composition from the rest of the season was not detected in studies investigating phytobenthos of large water bodies or rivers (ABERLE and WILTSHIRE, 2006; GIORGI *et al.*, 2005). We believe that this may be due to disturbance related to winter temperatures below freezing; these would have a greater impact on shallow wetland localities than on considerably larger or faster moving bodies of water (IYOBE and HARAGUCHI, 2005). Thus, the spring algal assemblages reflect the early succession stage with many r-strategists shifting the species composition to a relatively stable summer/autumn stage. Furthermore, the results of diversity measures validated the role of winter disturbance and assemblage succession. Increasing levels of environmental stress have historically been considered to decrease diversity, species richness and evenness, and increase dominance (CLARKE and WARWICK, 2001). However, CONNELL (1978) and HUSTON (1979) suggested that a greater amount of disturbance lead to species elimination by stress and, consequently, less diversity. Conversely, in situations with low disturbance, species diversity may be limited by competitive exclusion of species. Then, a slight increase in disturbance levels leads to an increase in competition, resulting in increasing diversity. In our samples, species diversity was lowest, and the dominance was highest in May, possibly as a result of winter disturbance. In August, the species diversity had increased, perhaps due to niche differentiation and the level of medium disturbance (PADISÁK, 1993). Although, by October, diversity slightly decreased, most likely as a result of increased competition in low disturbance conditions, according to HUSTON (1979).

Similarly to RINDI and BATTELLI (2005) and SOININEN (2003), we determined that on a scale from 1 m upwards there was significant spatial autocorrelation in all the seasonal data sets. In addition, the correlation on large spatial scales was stronger in October. We conclude that the spatial structure in autumn was more developed, durable and resilient due to maturity and stability of communities that also harbored species other than pioneers. Conversely, the 10 cm scale did not show spatial autocorrelation in most samples, thus agreeing with results of KOMÁREK (2003) and COLEMAN (2002), who found the small-scale differences along transects of benthic algae non-significant up to a limit of tens of centimeters. The 10 cm distance between samples might, therefore, be considered as the minimal spatial limit for species composition differences in benthic microalgal assemblages, especially in studies based on morphological species concepts. However, in our study, the 10 cm data in

spring benthic microhabitat and summer submerged moss microhabitat were spatially autocorrelated. Similarly to species composition data, we propose the effect of spring succession following winter disturbance of the benthic community as a possible explanation. The low ability of propagules to disperse (UNDERWOOD and CHAPMAN, 1996), or the lower dispersal capacity of whole organisms (HILLEBRAND *et al.*, 2001) was suggested as the cause of spatial autocorrelation. Alternatively, the niche-based approach assumes that individuals have different fitness according to different environmental conditions (SOININEN, 2007). In this situation, spatial autocorrelation of species composition correlates primarily with similarities in their local environmental characteristics (abiotic factors – as *e.g.*, in RINDI and BATELLI, 2005; CHARLES *et al.*, 2006 – or biotic factors *e.g.*, COLEMAN, 2002; UNDERWOOD and CHAPMAN, 1996). This model presumes that dispersal limitations do not matter (at least within an investigated region), and so the species pools of individual localities are more or less identical. However, in our data the spatial distance significantly affected species composition at different scales, especially in spring, even after the effects of important environmental factors (pH, microhabitat type and conductivity) were removed. This clearly indicates that the dispersal limitation effect could play a significant role, at least in early succession stages of phytobenthic communities, even on small spatial scales.

In conclusion, the small-scale processes, microhabitat type, geographic distance and conductivity were found to influence species composition of benthic assemblages in the shallow peat bog habitat. Spatial distance was the prime factor, especially in spring, when the patchiness of a benthic community was at its greatest, possibly as a consequence of niche colonization following winter disturbance. The significant spatial effect found on larger scales corresponds well to data reported by others.

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