Aquatic Sciences

Littoral periphyton dynamics in newly established post-mining lakes

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Abstract

Hydric recultivation—flooding of abandoned mining pits—creates a completely new, underexplored habitat for a wide range of aquatic organisms. Periphyton, dominated by algae and cyanobacteria, is frequently a key component of newly established aquatic ecosystems. Periphyton and its response to abiotic factors were studied in the littoral zone of three post-mining lakes with different ages of foundation situated in the Czech Republic. The microbial diversity of phototrophs as a major component of periphyton is largely unknown in such localities. The studied habitat proved to harbour a huge periphytic diversity—25% of diatom species found in the respective watershed (~ 5500 km^2) inhabited exlusively the studied lakes. Species composition of phototrophic microorganisms varied significantly (Permutational Multivariate Analysis of Variance) among the studied lakes, seasons, and sampling years. However, the sampling depths and sampling site of the studied lake have not shown a significant impact on the diversity, indicating the homogeneous composition of the littoral periphyton within a particular lake and growing season. The seasonal dynamics of periphyton were unique for each lake, documenting three distinct successional patterns. The proportion of diatoms in the periphytic community decreases with the higher trophic state and flooding age of the post-mining lakes. Cyanobacteria and mobile diatom forms prevailed later in the growing season, suggesting that they could utilise nutrients released from the accumulated periphyton biomass. Calcium ions were one of the best correlates of species data among other abiotic variables tested, offering the intriguing question of the role of calcium in the formation of periphytic mats for future research.

Keywords Periphyton diversity · Post-mining lake · Land restoration · Oligotrophic environment · Seasonality · Algal mats

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Introduction

General introduction

More than 50% of Earth's ice-free land area has been directly modified by human actions. Up to 0.4% of this area is occupied by open mines (Hooke et al. 2012). After the exhaustion of mining goods, hydric recultivation—flooding of abandoned mining pits—is one way of landscape recovery. Post-mining lakes established during reclamations are artificial surface water bodies resembling reservoirs, whose monitoring and management are mandatory according to the Water Framework Directive (WFD; EC 2000) to achieve and maintain a state of so-called good ecological status. In terms of nutrient concentrations, post-mining lakes are often oligotrophic (i.e., nutrient-poor) due to their young age and high volume to surface area ratio (Gammons et al. 2009). Although post-mining lakes' physical, chemical and limnological characteristics are relatively well-understood,

their biological characteristics are understudied. Most of the post-mining lakes colonisation and succession research has focused on phytoplankton, zooplankton, invertebrates, and fish (e.g., Nixdorf et al. 1998a, 1998b; Steinberg et al. 1998; Bylak et al. 2019). Although microbial communities forming periphyton mats have a high level of diversity and physiological versatility allowing them to quickly colonise and dominate disturbed and barren environments (Fierer et al. 2010), information on the establishment, diversity and a succession of periphyton mats in such systems is scarce. Well-developed periphyton mat can be formed within a few weeks (Johnson et al. 1997), so it can easily dominate the littoral zone of the newly established lake and assist the primary production of macroscopic algae and plants limited by low nutrient concentrations.

Periphyton represents an assemblage of aquatic organisms attached to the substrate, composed of multi-layered consortia of photoautotrophs—(algae and cyanobacteria) and heterotrophs (bacteria, fungi, and protozoa) with the photoautotrophic microorganisms usually forming the dominant component (Cantonati and Lowe 2014). Periphyton carries out important ecological functions, such as nutrient uptake and retention (Battin et al. 2016; Wyatt et al. 2019; Vymazal and Richardsons 1995; Sabater et al.2002; Doods 2003), energy fluxes associated with primary production and respiration (Brothers et al. 2016) and conforms to the energetic base of the food web (Vander Zanden et al. 2006). Many of these functions are accomplished through microscale interactions within the biofilm matrix, where microorganisms of various trophic levels exchange energy and matter (Battin et al. 2007; Wyatt et al. 2019).

Traditionally, periphyton has been investigated in streams and lacustrine systems (for review, see Stevenson et al. 1996; DeNicola and Kelly 2014). Due to these studies, we have obtained a fair amount of knowledge on periphyton substrate preferences, community structure, and its sensitivity to environmental drivers in natural water bodies (Lowe 1996; Li et al. 2020). Numerous studies also deal with periphyton of artificial wetlands (most recently, e.g., Oberholster et al. 2022) or investigate the periphytic community on artificial substrates (for critical discussion, see, e.g., Cattaneo and Amireault 1992). A large knowledge gap, however, still exists concerning periphyton communities in newly established artificial lakes and reservoirs at the early successional stages. The post-mining lakes represent a specific type of man-made ecosystem whose number is increasing due to the popular hydric recultivation and the general trend of coal mining suppression all over the world (Søndergaard et al. 2017; Larondele and Haase 2012; Říhová-Ambrožová and Ivanovová 2013). Because the post-mining lakes, similar to other recultivated areas, are going to be used as recreation districts with high socioeconomic potential, the knowledge

of their ecosystem structure and functioning is gaining importance.

It has been shown that the ecology of newly established post-mining lakes is distinctly different from the natural lakes of the same area (Lessmann and Nixdorf 2000, 2002; Wollmann et al. 2000; Deneke 2000). In opposite, the post-mining lakes of different geographical locations are closely similar in many biotic and abiotic aspects depending on the mining type and substrate (Gammons et al. 2009). Thus, a description of a particular lake succession stage can reasonably predict the general successional development in a particular type of post-mining lake. Our study aimed to offer comprehensive information about the periphyton community at the early stages of post-mining lakes succession. We investigated the diversity of the periphyton community of three post-mining lakes with different ages of full capacity flooding (2010, 2014 and 2016 for Milada, Most, and Medard, respectively). The sampling of periphyton covered temporal (three seasons in each of two subsequent years) and spatial gradients (two depths per two opposite shores per three lakes) to address the following research questions: (1) what are the spatial and temporal dynamics in the periphytic autotrophic community in terms of species composition and growth forms? (2) How does periphyton composition respond to measured environmental variables?

Study sites

The three studied post-mining lakes (Medard, Most and Milada) (Fig. 1) situated in the Ohře River watershed (Czech Republic) represent endorheic artificial systems with a special aquatic regime. The stable water level of lake Medard and lake Most is maintained by artificial inflows from the Ohře River, while lake Milada is largely supplied from the borehole and sporadically from the nearby Zalužanský stream. Besides, groundwater rich in dissolved salts and precipitation contribute to the water balance. Medard lake, the largest lacustrine water body in the Czech Republic, is a meromictic lake with common dimictic stratification in the upper 30–40 m. Lake Most and lake Milada are typical dimictic lakes. All lakes were established during recultivation projects in NW Bohemia (Ústí nad Labem and Karlovy Vary regions, the Czech Republic). Lake Medard and Lake Most can be regarded as oligotrophic, and lake Milada reaches the mesotrophic level according to the most critical parameters. However, DN (dissolved nitrogen) concentrations correspond to the eutrophic level. Average pH and conductivity values place the lakes among alkalic, fresh-brackish water bodies. The main limnological and physicochemical characteristics of the lakes are summarised in Tables 1 and 2.

Fig. 1 Maps of the investigated post-mining lakes. The locations of the sampling sites are marked with asterisks. Lake positions within the Czech Republic are marked with blue dots
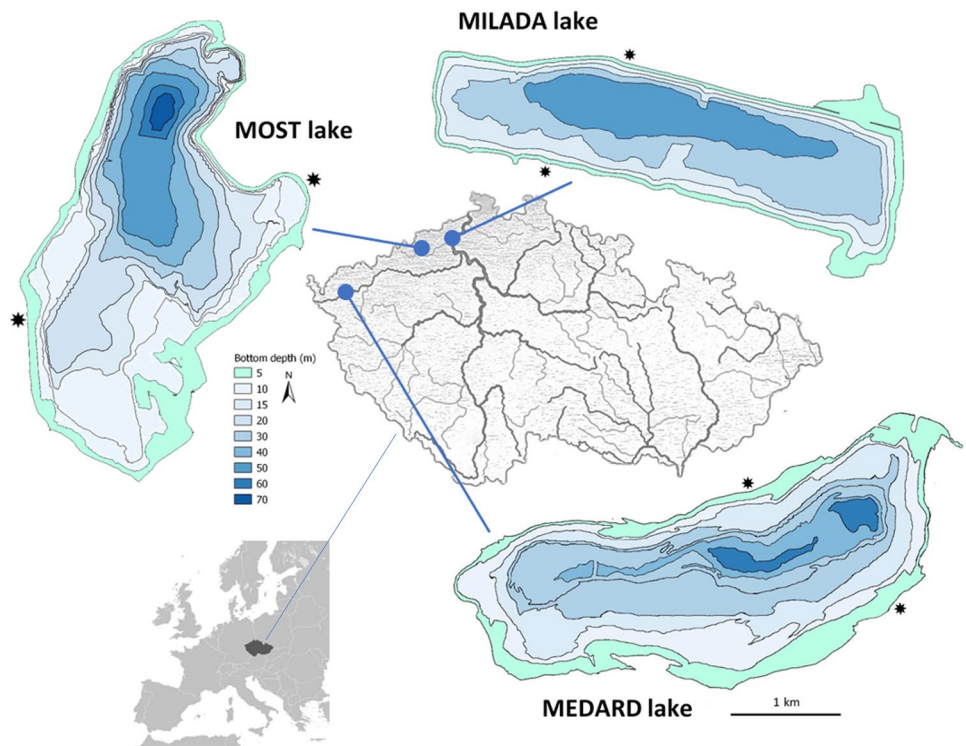
Table 1 Basic characteristics and GPS position of the studied lakes

	Established years	Flooded years	Area ha	Max depth m	Avg depth m	Euphotic zone m	Chl a μg L^{-1}	Coordinates
Medard	2008	2016	493	59	28	10	2	50°11′08.8″N 12°36′05.0″E
Most	2008	2014	311	75	22	10	2,7	50°32′06.5″N 13°38′06.9″E
Milada	2001	2010	252	25	16	10	12	50°39′29.9″N 13°56′46.5″E

Flooded—the year when the lake was fully flooded to its maximal capacity

Table 2 Averages and ranges (first and second row, respectively) of open water physical parameters, nutrient concentrations and amount of organic matter in the periphyton from the littoral zone of investigated post-mining lakes in the years 2019–20

	Tw °C	Conductivity μS m^{-1}	pH	Ca^{2+} mg L^{-1}	DN mg L^{-1}	DOC mg L^{-1}	Si mg L^{-1}	Fe mg L^{-1}	N–NO$_3$ mg L^{-1}
Medard	13.7 ± 5.6	1108.1 ± 17.9	7.9 ± 0.1	104 ± 10	1.4 ± 0.2	3.2 ± 0.21	2.5 ± 042	0.069 ± 0.028	1.1 ± 0.4
	6.5–22	1080–1130	7.7–8.1	87–116	1.2–1.6	3–3.6	1.9–2.9	0.05–0.122	1–1.3
Most	17.4 ± 5.0	542.3 ± 15.9	8.5 ± 0.3	45 ± 2	0.9 ± 0.2	4.7 ± 0.3	0.8 ± 0.4	0.012 ± 0.003	0.6 ± 0.2
	10.4–24.1	515–566	8.2–8.9	43–48	0.6–1.1	436–5.3	0.4–1.3	0.008–0.016	0.3–0.9
Milada	16.1 ± 6.3	1027.7 ± 13.2	8.9 ± 0.2	38 ± 2	0.7 ± 0.1	7.9 ± 0.9	0.8 ± 0.4	0.023 ± 0.004	0.3 ± 0.9
	7.7–24.9	1000–1037	8.7–9.1	35–40	0.6–0.8	6.8–8.9	0.7–0.9	0.015–0.025	0–0.1

Tw Temperature, *DN* dissolved nitrogen, *DOC* dissolved organic carbon

Materials and methods

Chemical analysis

Three open water samples were gathered each sampling season at each locality from 0.5 m depth using a Friedinger sampler for water chemical analyses. Chlorophyll-a concentration was quantified spectrophotometrically after ethanol extraction (ISO 10260 1992). Dissolved organic carbon (DOC) and dissolved nitrogen (DN) concentrations were determined using the Shimadzu TOC/TN analyser (Shimadzu Corp., Kyoto, Japan). Total phosphorus (TP) was measured by colourimetry after nitric–perchloric acid digestion (Kopáček et al. 2001). Si and soluble reactive phosphorus (SRP) were determined spectrophotometrically according to Mackereth et al. (1989) and Murphy and Riley (1962), respectively. The concentration of $N–NO_3$ was determined following the procedure of Procházková (1959). Determination of chloride concentration was done by flow analysis with spectrophotometric detection according to the norm for surface water of the Czech Republic (ISO 15682 2000). The concentration of Ca^{2+}, Mg^{2+} and Fe were measured with inductively coupled plasma atomic emission spectrometry (ICP AES) (ISO 11885 2007). Turbidimetric analysis of SO_4^{2-} followed US EPA Method 375.4 1983 and $ANC_{4.5}$ (Acid neutralising capacity) determination was based on the norm for surface water of the Czech Republic (ISO 9963-1 1994). Conductivity was measured in situ with Combo pH/EC HI 98129 (Hanna Instruments, Woonsocket, RI, USA).

Sampling of periphyton and measurement of the organic matter

Periphyton was sampled three times during the growing season (April, July, and October) in 2019 and 2020 at two different depths (0.5 and 1.5 m) at two opposite shores in all studied lakes (72 samples in total). At least five stones from the studied depths were randomly selected and all biomass of periphyton was collected into a plastic dish using a toothbrush or a knife. The composite samples were stored at 4 °C and transported to the laboratory, where the microscopic analyses were immediately conducted.

For the content of organic matter, biomass from 5 additional stones was collected as described above. Stone surface covered by periphyton was estimated by the wrapping of stones in the aluminium foil with the consequent weight to area conversion (Dudley et al. 2001). The collected biomass was dried at 110 °C to the constant weight, and the dry weight (DW) was determined. Drying was followed by loss on the ignition step (4 h 450 °C) to determine the ash mass (AM). Organic matter was calculated as DW-AM and related to the unit area.

Diatom data acquired within Water Framework Directive monitoring (34 localities sampled twice in the years 2019–2020 including both riverine and reservoir sites) situated in the Ohře River watershed were provided by Povodí Ohře, state enterprise. There are no natural lakes in the region. Diatoms were treated, and diatom analysis was performed similarly to our samples (hydrogen peroxide digestion, LM at 1000 × magnification). These data were used for the assessment of post-mining lakes' contribution to regional algal diversity.

Microscopic analyses

Periphytic assemblages were divided into two subsamples that required different processing and whose species composition was, therefore, analysed separately: (1) fresh periphytic samples, hereinafter referred to as non-diatom algae—all algal and cyanobacterial taxa, including diatoms as a further unresolved group and (2) permanent diatom slides providing detailed information about the diatom species composition. Species composition was assessed using an Olympus BX 50 light microscope equipped with DIC optics and a DP-72 digital camera, and available determination literature (Ettl and Gärtner 1988; Hindák 1996; Komárek and Fott 1983; Komárek and Anagnostidis 1998, 2005; Komárek 2013; Kaštovský et al. 2018a, b). The diatom permanent slides were prepared from material processed in hot hydrogen peroxide (Houk 2003) using the Pleurax resin (Fott 1954). The species determination followed Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Krammer (2000, 2002, 2003) and Lange-Bertalot (2001). Nomenclature was updated according to AlgaeBase (Guiry and Guiry 2021). The relative abundance of algal and cyanobacterial species was estimated within LM observation using a modified Braun-Blanquet (1932) semi-quantitative scale of 7-degree reflecting the individual species biomass/total biomass proportion (1— < 0.1%, 2—0.1–1%, 3—1–5%, 4—5–20%, 5—20–50%, 6—50–90%, 7— > 90%) as proposed by Komárková in Hindák (1978). Diatom data gathered from the relevant watershed within WFD monitoring by Povodí Ohře, state enterprise was provided on the same 7-degree estimation scale and taxonomically harmonised with the lake species list.

Growth forms

Assignment of algae and cyanobacterial species to functional guilds, also called growth forms, has been widely used to allow the assessment of their response to environmental factors, often exceeding the explanatory power of raw species data (DeNicola and Kelly 2014). Studied non-diatom algae and diatom growth forms matrix partially followed the classification by DeNicola et al. (2006), but the growth

forms of the non-diatom algae and the diatoms were treated separately. The data set of non-diatom algae contained algae and cyanobacteria divided into seven groups: eukaryotic coccal (e.g., *Chlamydocapsa* spp.), eukaryotic filamentous (e.g., *Spirogyra* spp.), cyanobacterial coccal (e.g., *Chroococcus* spp.), cyanobacterial filamentous (e.g., *Phormidium* spp.), motile (e.g., *Trachelomonas* spp.), planktic (e.g., *Scenedesmus* spp.) and undifferentiated diatoms. The data set of diatoms was based on detailed diatom analysis with the following diatom growth forms distinguished: prostrate (e.g., *Cocconeis* spp.), erect (e.g., *Fragilaria* spp.), stalked (e.g., *Gomphonema* spp.), mobile (e.g., *Navicula* spp.) and planktic (e.g., *Cyclotella* spp.).

Numerical analyses

All statistical analyses and visualisation of their outputs were performed in R (R Core Team 2019) using packages vegan (Oksanen et al. 2019), EcolUtils (Salazar 2020) and Goeveg (Goral and Schellenberg 2017). Non-diatom algae and diatoms were tested separately, as well as the non-diatom and diatom growth forms. The sampling hierarchy and hydrochemical and physical variables were tested separately. PERMANOVA (Permutational Multivariate Analysis of Variance) based on Bray–Curtis dissimilarities was applied to non-transformed species and environmental data. Significance was proved through Monte-Carlo permutation tests with 999 permutations restricted to the tested level when testing the sampling hierarchy. *P* values in pairwise comparisons were adjusted according to Benjamini and Hochberg (1995). While PERMANOVA of sampling hierarchy was performed on a complete set of samples (72), analysis of physico-chemical variables had to be reduced to include species data averaged for the six studied seasons on individual lakes (18 samples) having physical and chemical data measured. Separate models were calculated for each physical and chemical variable to show the portion of explained variability for a single parameter. Variables with significant models after the Holm–Bonferroni correction (Holm 1979) were then used to construct stepwise selection models chosen based on Akaike Information Criterion (AIC, Akaike 1973) to avoid multicollinearity. Species occurring only once during the investigated period were removed from PERMANOVA calculation to prevent issues resulting from a large number of zeros in the matrix (Peres-Neto et al. 2006). Shannon diversity indices (Shannon and Weaver 1964), diatom trophic (TI, Rott et al. 1999) and saprobic indices (SI, Rott et al. 1997) calculated in Omnidia 6.0.8 software (Lecointe et al. 1993) were tested using ANOVA (analysis of variance). The correlation matrix of growth forms and organic matter content was based on Spearman correlation coefficients. Graphical expression of Bray–Curtis dissimilarities of studied lakes periphytic samples and the comparative samples from the catchment area was based on non-metric multidimensional scaling (NMDS).

Results

Species composition and diversity

During our survey, 437 taxa in total were identified in the lakes under study. Soft algae (referred to as non-diatom algae later in the text) (Cyanobacteria, Chlorophyta, Rhodophyta, Conjugatophyceae, Cryptophyceae, Dinophyceae, Euglenophyta and Xanthophyceae) represented 43% (187 taxa), whereas diatoms 57% (250 taxa). The Shannon diatom values (3.1–4.1) were higher than those calculated for non-diatom algae (0.7–3.3), being significant on the level of lake and season for both non-diatom algae and diatoms (Fig. 2, Table S1). Diatoms were relatively more diversified in lake Medard, while the diversity of non-diatom algae was higher in lakes Most and Milada (Fig. 2). Maxima in diatom diversity were observed in fall (lake Medard) and spring (lakes Most and Milada), while the diversity of non-diatom algae reached its minimum in spring at all three lakes.

The sampling year, the identity of the lake and the sampling season proved to be significant explanatory variables for both non-diatom and diatom species data (Table 3), with by far the most explained marginal variability on the level
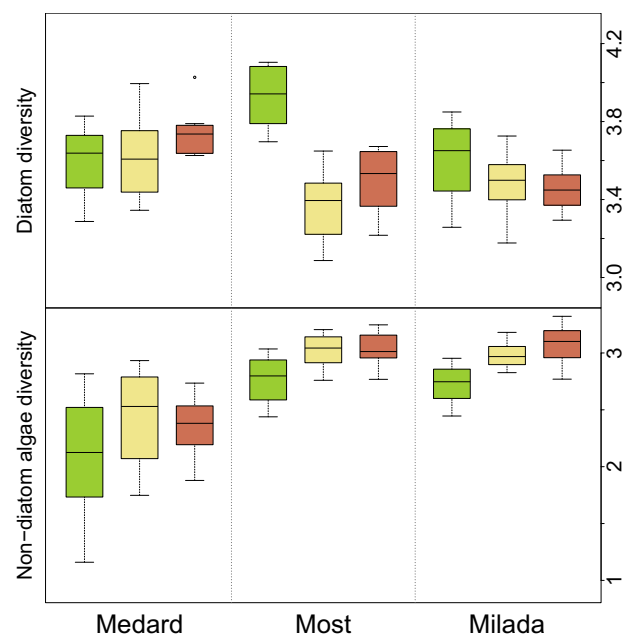
Fig. 2 Shannon diversity of algae and diatom assemblages. Spring—green, Summer—yellow, Fall—red

Table 3 PERMANOVA (Permutational Multivariate Analysis of Variance) of sampling hierarchy applied on the Bray–Curtis dissimilarities matrix of species data and growth forms

	Species data						Growth forms					
	Non-diatom algae			Diatoms			Non-diatom algae			Diatoms		
	F	R^2	p	F	R^2	p	F	R^2	p	F	R^2	p
lake	11.85	0.26	**0.001**	28.29	0.45	**0.001**	46.72	0.58	**0.001**	6.09	0.15	**0.001**
season	3.48	0.09	**0.001**	2.75	0.07	**0.001**	5.01	0.13	**0.001**	8.13	0.19	**0.001**
year	5.76	0.08	**0.001**	3.31	0.05	**0.003**	0.19	0.00	0.810	2.74	0.04	**0.048**
sampling site	0.88	0.01	0.49	0.88	0.01	0.43	0.55	0.01	0.447	0.82	0.01	0.400
depth	0.47	0.01	0.96	0.65	0.01	0.74	0.10	0.00	0.908	0.52	0.01	0.672
Residuals		0.56			0.41			0.29			0.60	
Medard <—> Milada	15.89	0.26	**0.001**	41.28	0.47	**0.001**	37.16	0.45	**0.001**	8.59	0.16	**0.001**
Medard <—> Most	14.32	0.24	**0.001**	22.64	0.33	**0.001**	38.78	0.46	**0.001**	8.54	0.16	**0.001**
Milada <—> Most	5.43	0.11	**0.001**	21.03	0.31	**0.001**	4.73	0.09	**0.005**	2.20	0.05	0.107
Spring <—> Summer	3.83	0.08	**0.004**	2.60	0.05	**0.040**	5.18	0.10	**0.003**	9.25	0.17	**0.001**
Spring <—> Fall	4.89	0.10	**0.003**	3.73	0.08	**0.006**	6.76	0.13	**0.003**	12.34	0.21	**0.001**
Summer <—> Fall	1.81	0.04	0.055	1.94	0.04	0.065	2.12	0.04	0.109	1.97	0.04	0.126

R^2 was based on marginal effects. P values < 0.05 are in bold. P values for pairwise comparisons were corrected using Benjamini and Hochberg (1995)

of the lake (non-diatom algae 26%, diatoms 45%). The complete sampling hierarchy (year, lake, season, sampling site, depth) explained 44% of the non-diatom and 59% of the diatom species variability. Pairwise comparison of the species data significantly distinguished all the studied lakes based on both the non-diatom algae and the diatoms. The difference between fall and summer proved to be insignificant for both algal groups (Table 3). Lake Medard was separated above all by numerous diatoms, a coccal green alga *Chlamydocapsa ampla*, and *Euglena* sp. (Figure S1), whereas the remaining lakes were typical by the occurrence of filamentous green algae (Figure S1). The separation of lake Milada from lake Most was not reflected in the composition of dominant non-diatom algae. Similarly, differences between the seasons were based rather on subdominant or rare species.

The insignificant differences in the levels of sampling site and depth point to a homogenous periphyton composition within a particular lake in a particular season of the year.

Non-diatom algae

In total, 77 genera comprising 187 taxa from 8 distinct taxonomic groups (Cyanobacteria, Chlorophyta, Rhodophyceae, Conjugatophyceae, Cryptophyceae, Dinophyceae, Euglenophyta and Xanthophyceae) were identified (Table S2). 27% of taxa were identified just once in all samples analysed. Milada lake contained 119 taxa from 59 genera, 175 taxa from 58 genera were found in Most lake, while Medard lake hosted 141 taxa from 47 genera. Numerous species were again present only in a particular lake (Figure S1): lake Milada hosted 27 (e.g., *Chroodactylon ornatum, Cylindrospermum* sp., *Phormidium* cf. *interrupted)*, lake Medard 20 (e.g., *Chroococcus dispersus, Rhabdoderma* sp.) and lake

Most 29 (*Chaetophora* sp., *Geitleribactron periphyticum*, *Cyanobacterium* cf. *stanieri*) unique taxa. The unique species constituted 17% of the community in the case of lakes Milada and Most and 5% for lake Medard. Nine taxa were found in all the studied lakes (e.g., *Aphanocapsa rivularis*, *Chroococcus minor*, *Chroococcus obliteratus*, *Phormidium lividum, Chlamydocapsa ampla*).

The highest taxonomic richness was observed in Cyanobacteria, with 96 taxa (Medard 51, Most 56, Milada 61) represented by 37 genera in total. Out of these 10 taxa were common and were observed in all three lakes, e.g., *Aphanocapsa parasitica*, *Aphanothece nidulans*, *Phormidium lividum*. More than 40% of cyanobacterial taxa occurred only once during the investigation. Chlorophyta exhibited the second highest taxonomic richness, represented by 64 taxa from 32 genera (Medard 26, Most 51, and Milada 39). Only three of those taxa were common to all lakes (*Aphanochaete* cf. *repens*, *Chlamydocapsa ampla*, *Oedogonium* sp. 3). Class Conjugatophyceae was represented by 13 taxa from 6 genera (Medard 4, Most 8, Milada 10), with only two taxa found in all investigated lakes. In total, three taxa from the class Rhodophyceae were found, and each lake had its specific taxon. Among these, *Chroodactylon ornatum* was an interesting finding repeatedly observed at the lake Milada during both sampling years. Two taxa were detected in the phylum Euglenophyta. Genus *Euglena* was determined in all lakes during both years. Class Xanthophyceae was represented only by *Vaucheria* sp. and only in 2020. However, *Vaucheria* sp. was often recorded as the dominant species below the depth of 3 m during the study. Planktic species were often found in the periphytic samples, likely due to sedimentation from the water column. Two classes (Dinophyceae and Cryptophyceae) were represented only by planktic taxa.

Diatoms

A total of 250 taxa from 68 genera were identified in investigated post-mining lakes (Table S3). Within this set of taxa, 24% were rare species observed only once during the studied period. The Milada lake contained 134 taxa from 47 genera, 175 taxa from 58 genera were found in the Most lake, while the Medard lake hosted 141 taxa from 47 genera.

A significant proportion of taxa (71) was common in the studied lakes. Besides widespread, ubiquitous species (e.g., *Achnanthidium minutissimum, Gomphonema pumilum*, and *Navicula cryptotenella*), also brackish (*Mastogloia smithii* v. *smithii*) and oligotrophic (*Encyonopsis microcephala, Encyonopsis subminuta, Gomphonema lateripunctatum, Cymbella lange-bertalotii*) diatoms occurred. However, the larger part of the species list comprised species unique to a particular lake or common only to a pair of lakes (Figure S2). Thus, Milada, with 35 unique taxa, was typical by the presence of brackish *Navicymbula pusilla, Mastogloia elliptica* and *Epithemia turgida,* Medard harbored 34 unique taxa, such as *Cymbella affinis* v. *affinis, Stauroneis gracilis* and *Navicula libonensis*, and the most unmatched species, as its name suggests, were found in lake Most: 50 unique species among which *Navicula gottlandica, Cymbella excisa* and *Dorofeyukea kotschyi* dominated (Figure S2). The unique species represented 14–18% of taxa. Planktic species were recorded in periphyton diatom assemblages due to sedimentation, e.g., *Stephanodiscus hantzschii, Diatoma tenuis* or *Pantocsekiella ocellata* (the planktic taxa are marked by asterisks in Table S3).

The uniqueness of the diatom community in post-mining lakes was demonstrated through comparison with data sampled in the Ohře River watershed from 34 reservoirs and riverine sites. A total of 407 diatom taxa were identified. 115 taxa were shared by post-mining lakes and watershed samples, while 134 species were found only in the post-mining lakes. These unique post-mining lakes taxa represent 25% of diatom species found in the respective watershed (~ 5500 km^2, Figure S3).

Growth forms

Non-diatom growth forms significantly explained 57% of variability on the level of the lake and 13% on the season level. In contrast, a major portion of the significantly explained variability in diatom growth forms fell to the level of the season (19%), while the level of the lake explained 15% of the variability and the level of year 4% (Table 3). In all three lakes, fall differed significantly from spring and spring from summer in general accordance with the outputs of the raw species data analysis (Table 3), but the difference in diatom forms between lake Milada and lake Most was insignificant. The difference between lake Most and

lake Milada was much lower (although significant) than between these lakes and lake Medard according to species data (Table 3) and non-diatom growth forms.

The distribution of growth forms in Medard exhibited some typical features. All seasons were typical of the dominance of diatoms with spring maxima and the practical absence of eukaryotic filamentous algae (Fig. 3). Cyanobacterial coccal and filamentous forms formed up to 5% biomass on average, featuring a pattern of occurrence inverse to the diatoms (spring minima, summer, or fall maxima). Mobile forms were dominant among the diatoms during all seasons. Subdominants of diatoms were either erect or prostrate in dependence on the season. Planktic and stalked forms were rare (Fig. 3).

Lakes Most and Milada were predominantly occupied by eukaryotic filamentous algae except Lake Most spring samples, in which diatoms prevailed. The decrease in eukaryotic filamentous algae observed in the fall at lake Milada was compensated by an increase in cyanobacteria. The relative abundance and seasonal dynamics of coccal and filamentous cyanobacteria resembled those of the Medard assemblages, showing summer and fall maxima (Fig. 3). The remaining non-diatom forms were rather rare in both lakes. Diatoms were dominated by erect and mobile forms. Erect forms prevailed in spring, whereas mobile forms reached summer and fall maxima. Diatom subdominants were represented by stalked or prostrate taxa; lake Most also reached a high proportion of planktic diatoms (Fig. 3).

Relationship between physico-chemical characteristics and species data and growth forms

Most physicochemical variables are significantly influential on both species and growth forms data if tested as a single variable (Table 4, Fig.4, 5). However, there is an evidently high rate of inter-correlation between the factors (Table S4). The stepwise selection models favor DOC and Ca^{2+} for diatom species data ($F = 3.6$, $R^2 = 0.33$, $p = 0.001$), DOC and Si for diatom growth forms ($F = 8.2$, $R^2 = 0.52$, $p = 0.001$) and DN, Si, pH and N–NO$_3$ ($F = 8.9$, $R^2 = 0.73$, $p = 0.001$) for non-diatom algae growth forms. Stepwise selection models for non-diatom algae species data did not favour any of the tested variables based on the AIC criterion. The dynamics of factors chosen within the stepwise selection is briefly described because of their potential role in the determination of the periphytic community. Ca^{2+} concentrations were distinctly the highest at lake Medard (104 ± 10 mg L^{-1}) (Table 2), with maxima in fall (~ 115 mg L^{-1}). Although unambiguously separated, the Ca^{2+} values of lake Most (45 ± 2 mg L^{-1}) and lake Milada (38 ± 2 mg L^{-1}) were much closer to each other, with no regular seasonal changes observed. DOC values showed a trend opposite to calcium: lake Medard (3.1 ± 0.2 mg L^{-1}), lake
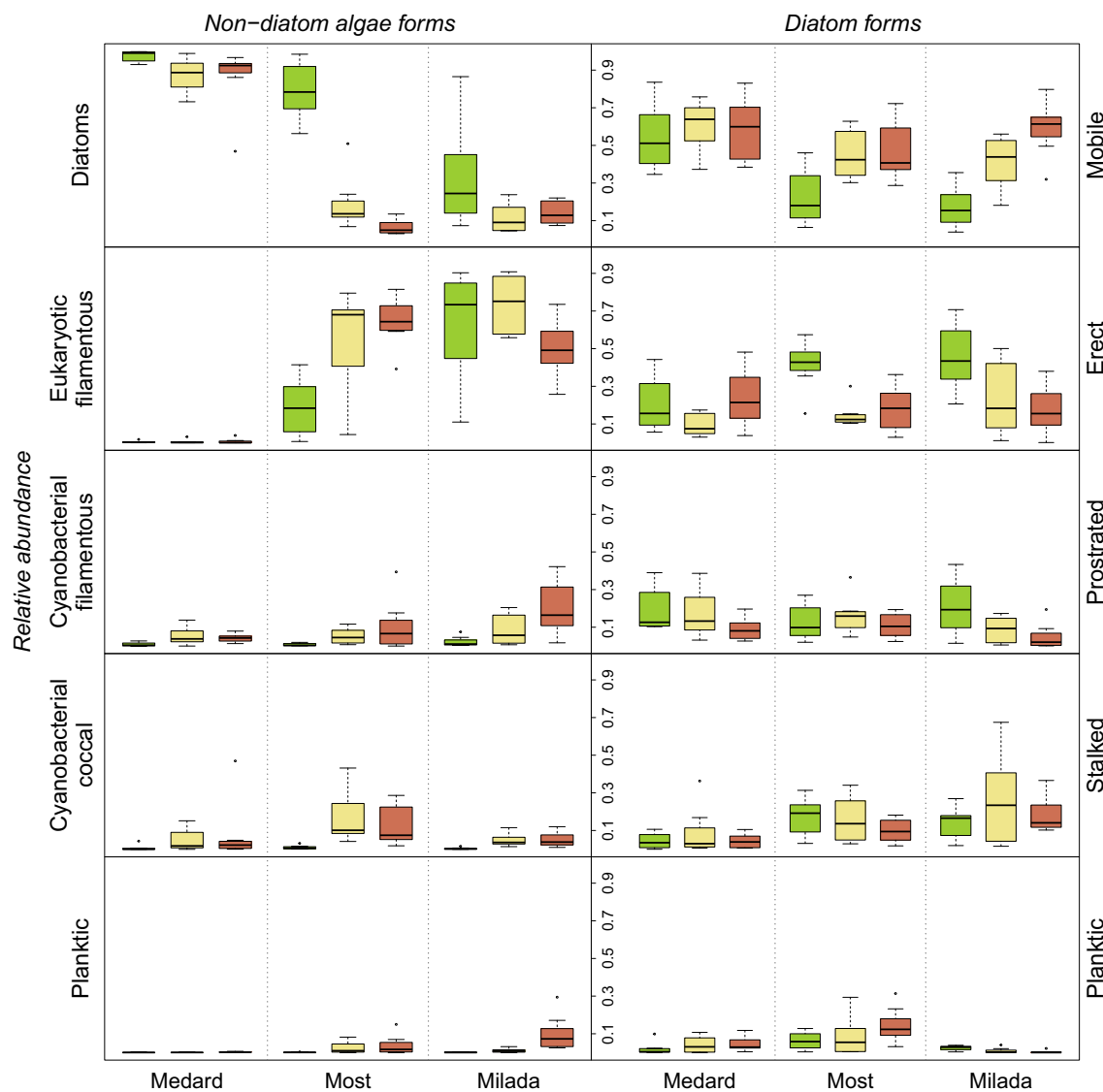
Fig. 3 Relative abundance of individual growth forms within studied seasons. The first column is devoted to forms comprising complete algal assemblages with no diatoms differentiated. The second column contains diatom growth forms. Spring—green, Summer—yellow, Fall—red

Most $(4.6 \pm 0.3 \text{ mg L}^{-1})$, and lake Milada $(8.1 \pm 0.7 \text{ mg L}^{-1})$. The DOC concentrations measured at lake Milada were substantially higher when compared to the remaining lakes, and distinct spring minima were recorded at all three lakes. DN, as well as N–NO$_3$ were gradually decreasing through the vegetation season in the water of all lakes, reaching the average values of $1.4 \pm 0.14 \text{ mg L}^{-1}$ at lake Medard, $0.9 \pm 0.19 \text{ mg L}^{-1}$ at lake Most, and $0.6 \pm 0.06 \text{ mg L}^{-1}$ at lake Milada. Si concentrations copied dynamics of nitrogen species with the exception of the lowest values at lake Most during summer and fall. Similarly, pH values followed the dynamics of the DOC curve, Figs. 4 and 5.

Indices of trophic state

Four indices of trophic state were selected to determine the differences in nutrient load between lakes (Fig. 6). The largest portion of significantly explained variability in diatom trophic and saprobic indices was explained at the level of the lake (SI = 76%, TI = 56%). However, for SI, also the level of the season (3%), and for TI, the levels of the season (4%) and sampling site (9%) were significant. The diatom trophic and saprobic indices, along with TP concentrations and values of OM, increased in the order lake Medard, lake Most, and lake Milada, following the increasing age of flooding (Fig. 6).

Table 4 PERMANOVA (Permutational Multivariate Analysis of Variance) of hydrochemical variables applied on the matrix of species data and growth forms averaged on the level of lake seasons in both studied years

| | Species data | | | | | | Growth forms | | | | | |
| | Non-diatom algae | | | Diatoms | | | Non-diatom algae | | | Diatoms | | |
	F	R^2	p	F	R^2	p	F	R^2	p	F	R^2	p
$ANC_{4.5}$ (mmol L^{-1})	2.04	0.11	0.225	8.84	0.36	**0.015**	6.26	0.28	0.345	3.90	0.20	0.345
Ca^{2+} (mg L^{-1})	4.21	0.21	**0.015**	8.62	0.35	**0.015**	28.33	0.64	**0.015**	11.54	0.42	**0.015**
Cond (µS cm^{-1})	2.52	0.14	**0.03**	1.34	0.08	3.18	0.32	0.02	9.945	0.96	0.06	5.535
DN (mg L^{-1})	3.93	0.20	**0.015**	8.91	0.36	**0.015**	40.75	0.72	**0.015**	9.58	0.37	0.06
DOC (mg L^{-1})	3.06	0.16	**0.015**	10.65	0.40	**0.015**	18.01	0.53	0.06	5.73	0.26	0.06
Fe (mg L^{-1})	3.31	0.17	**0.015**	4.64	0.22	**0.015**	11.95	0.43	**0.015**	7.36	0.31	**0.03**
Mg (mg L^{-1})	2.16	0.12	0.135	2.66	0.14	0.42	1.96	0.11	2.775	3.70	0.19	0.435
N–NO3 (mg L^{-1})	3.46	0.18	**0.015**	8.57	0.35	**0.015**	26.31	0.62	**0.015**	10.42	0.39	**0.015**
pH	3.52	0.18	**0.015**	7.96	0.33	**0.015**	30.93	0.66	**0.015**	9.30	0.37	0.03
Si (mg L^{-1})	3.99	0.20	**0.015**	5.74	0.26	**0.015**	40.18	0.72	**0.015**	13.40	0.46	**0.015**
SO_4^{2-} (mg L^{-1})	3.28	0.17	**0.015**	4.83	0.23	**0.03**	9.75	0.38	**0.045**	6.24	0.28	**0.045**
SRP (µg L^{-1})	1.26	0.07	3.255	1.11	0.07	4.77	0.43	0.03	8.775	2.91	0.15	0.81
TP (µg L^{-1})	2.69	0.14	**0.015**	5.69	0.26	**0.015**	16.44	0.51	**0.03**	9.44	0.37	**0.03**

Single model for each variable was constructed and p values were adjusted according to the Holm–Bonferroni method (Holm 1979)

Fig. 4 Non-metric multidimensional scaling (NMDS) of non-diatom algae assemblages. The calculation was based on Bray–Curtis dissimilarities between samples. Diatoms were treated as an undifferentiated group. Significant ($p < 0.05$) hydrochemical and physical variables are passively projected on the plot. Medard—rectangle, Most—triangle, Milada—circle, Spring—green, Summer—red, Fall—black, 2019—brown, 2020—blue
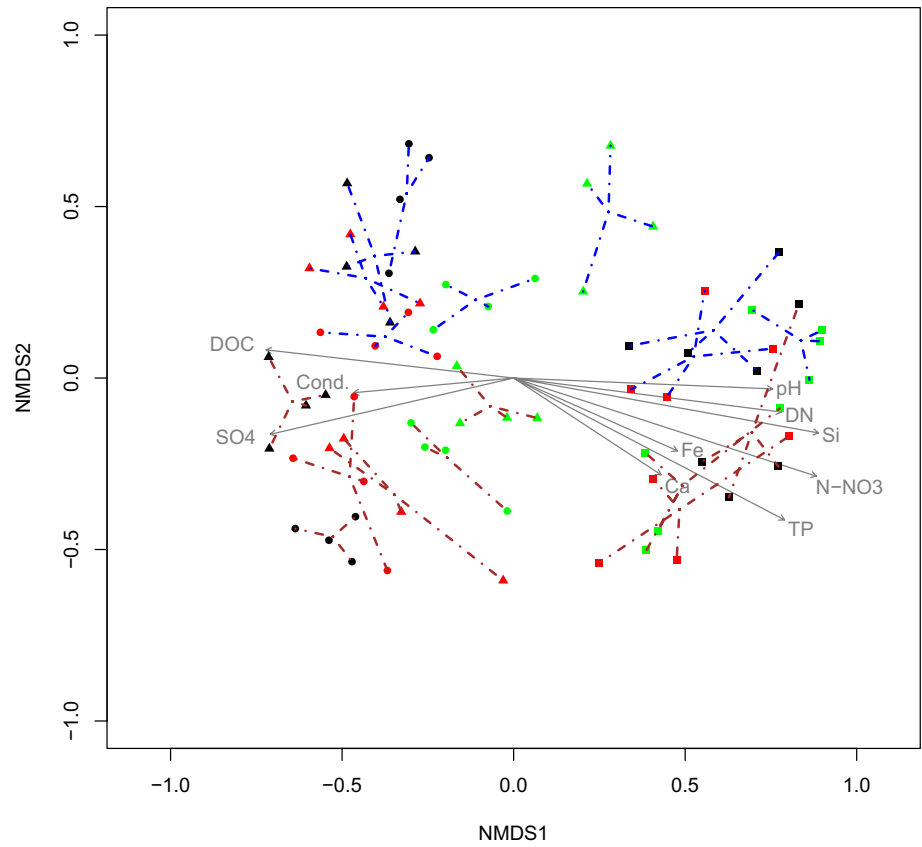
Fig. 5 Non-metric multidimensional scaling (NMDS) of diatoms. The calculation was based on Bray–Curtis dissimilarities between samples. Significant ($p < 0.05$) hydrochemical and physical variables are passively projected on the plot. Medard—rectangle, Most—triangle, Milada—circle, Spring—green, Summer—red, Fall—black, 2019—brown, 2020—blue
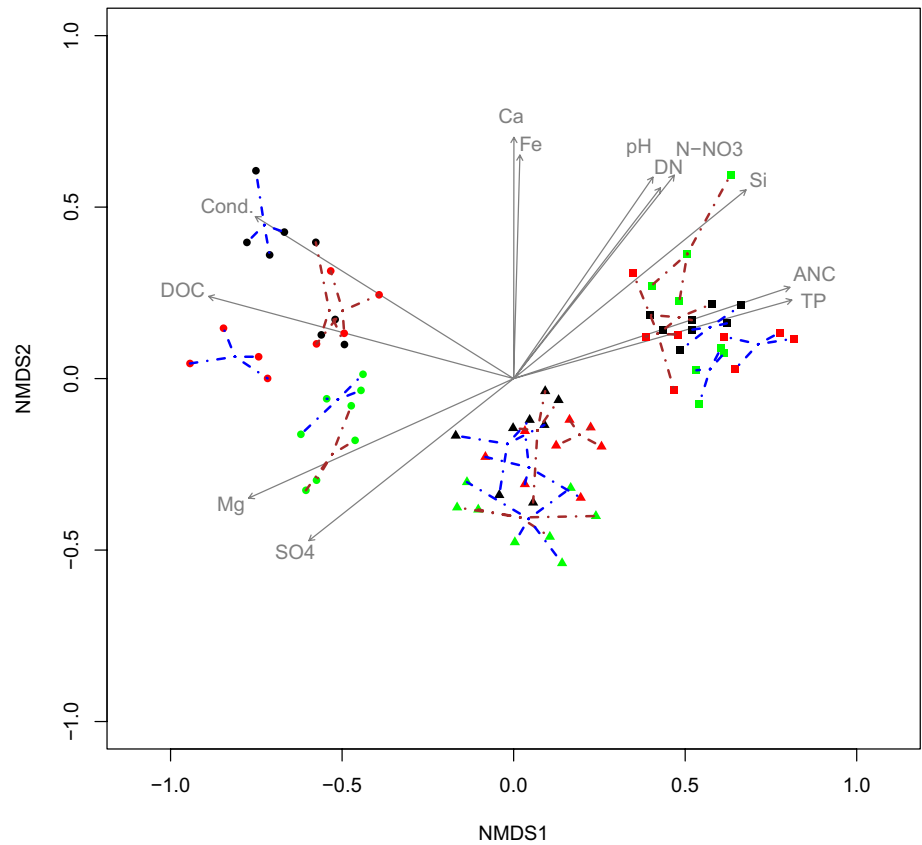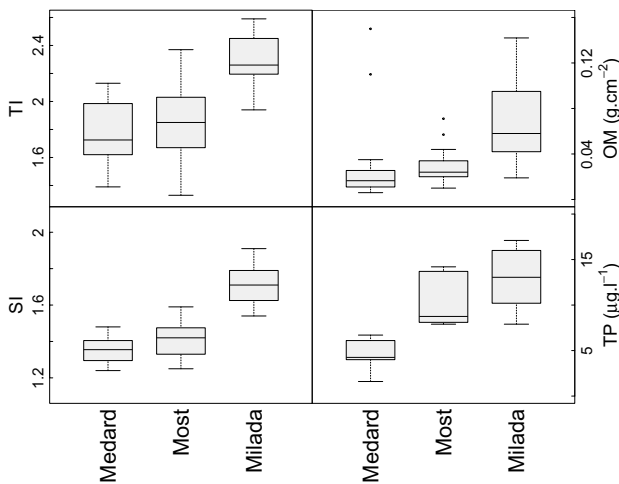
Fig. 6 Indices of lake trophic state. Lake diatom trophic (TI, Rott et al. 1999) and saprobic (SI, Rott et al. 1997) indices are based on diatom assemblages. *TP* total phosphorus, *OM* organic matter

Discussion

Post-mining lakes—unique biotopes

We focused our study on the temporal and spatial variability of the algal and cyanobacterial periphyton community living in the littoral zone of newly established post-mining lakes. The importance of similar hydric recultivation is going to increase in the future due to the ongoing termination of the current mining activities in many developed countries and the still rising coal production in other regions, particularly in India, China, Australia, and South Africa (Costanza et al. 1997; 2011; Říhová-Ambrožová and Ivanovová 2013). The post-mining lakes in the Czech Republic represent unique, underexplored ecosystems deserving detailed research, since many environmental factors (e.g., mine water supply and artificial management) separate them from a natural water bodies. Their character allows the development of "natural" biotic communities and also distinguishes them from the situation in Eastern and Central Germany, where the revitalisation of more than 50% of recultivated lakes and pits was suppressed by the high salinity and sub-optimal pH in their initial stadium (Schultze et al. 2009; Schroeter and Gläßer 2011).

Diversity of post-mining lakes

Much of the periphyton diversity has been usually recorded below the maximal lacustrine thermocline, where stable communities can persist protected from physical and chemical disturbances (Lowe 1996). In contrast, the species richness in littoral and sublittoral zones was considered lower in earlier research (Blum 1982; Lowe 1996). In our study, the

assemblages gathered from the littoral zone at 0.5 and 1.5 m showed no significant difference. However, the Shannon index is not lower than 2.4 and altogether 437 (diatoms 250/non-diatom algae 187) identified taxa suggest that the littoral zone, generally disturbed by wave action and water level fluctuations, can harbour a huge periphytic species diversity. The fact that a large portion of species (~ 16% for diatoms, ~ 13% for non-diatom algae) was unique to a particular lake does not correspond to the findings of Lowe (1996) describing the littoral zone of lakes generally as a habitat for cosmopolitan taxa. The comparison with WFD diatom data shows that 25% of all diatom species in the River Ohře watershed (reservoir and river samples, ~ 5500 km^2) were found exclusively in the three studied post-mining lakes. It implies that the newly established post-mining lakes contribute significantly (even most significantly if taken proportionally) to the regional diatom diversity. The diatom species composition is also completely different from the subfossil sediment samples of the former lake Komořany situated in the close vicinity of the lake Most (Tichá et al. 2019). Thus, the recently established post-mining lakes seem to offer an entirely new environment with no historical parallel in the region. A relatively high diversity of diatoms is caused by the coexistence of halotolerant, oligotrophic, and common species in the periphytic community. The regional source of halotolerant taxa should be sought in the alkaline streamlets, and small shallow reservoirs on spoil heaps of the Sokolov coal basin situated close to the studied lakes (Pšererová 2004; Skácelová 2006, 2008).

Growth forms and the trophic state

The general hypothesis on growth forms says that more eutrophic localities are inhabited by non-diatom filaments accompanied by stalked and mobile diatoms (DeNicola and Kelly 2014), especially in epilithic samples (DeNicola et al. 2006; Fischer et al. 2006). The prosperity of mobile and stalked diatom forms in more eutrophic habitats is thought to be associated with their ability to avoid nutrient limitations inside the dense periphytic mat (Pringle 1987). Our results are in line with this hypothesis in the case of the eukaryotic filamentous algae and stalked diatoms, both occurring mostly at lake Milada and lake Most. Considering the mobile diatoms, our results partly contradict the hypothesis—the most oligotrophic lake Medard contains the highest proportion of mobile diatoms, a substantial proportion of mobile diatoms also occurred in lake Most, while they were more scarcely found in Milada (higher trophic status). The specific seasonal dynamics in the most abundant growth forms among the studied lakes indicate that other (unknown) factors may predominantly drive their distribution, as it was suggested by Soininen et al. (2021). Furthermore, great seasonal dynamics in the abundance of the diatom forms

were recorded, even though the proportion of their important growth substrate—microalgal filaments—had remained relatively stable. Such independent seasonal dynamics of non-diatom and diatom functional growth forms in the periphytic mat are surprising if competition for resources inside the mat is considered (Azim et al. 2005). Finally, the group of filamentous cyanobacteria tends to succeed rather in the Medard lake, which is the least productive of the three studied ecosystems. Filamentous cyanobacteria form an ubiquitous while the ecologically extremely heterogeneous assemblage of organisms; therefore, it is no surprise that some of them can thrive and even dominate in almost any habitat. Frequent occurrence of *Leptolyngbya*-like benthic cyanobacterial taxa, which prevailed in the investigated lakes, was previously reported from various oligotrophic fresh and brackish stagnant waters (Johnson and Castenholz 2000; Pessi et al. 2018).

Periphytic seasonal dynamics—three distinct successional patterns

Each of the studied lakes exhibits specific seasonal dynamics of periphyton on the gross scale during both studied years: Medard is characterised by the dominance of diatoms with no seasonal variability, lake Most has a spring diatom maximum followed by the dominance of eukaryotic filamentous algae in summer and fall, and lake Milada is dominated by eukaryotic filamentous algae during the whole studied period of the year. These three seasonal successional patterns correspond with the previously described shift from a diatom-dominated community toward a greater abundance of filamentous algae with the rising trophic state (Lowe 1996; Gaiser et al. 2011; de Nicola and Lellock 2015). However, the trophic gradient in our study was relatively short (oligotrophy–mesotrophy), thus additional factors should also be considered. Among them, the age of flooding (inverse to the trophic gradient) corresponding to the total time available for periphytic succession is the most obvious. Traditionally, succession in a periphytic community has been assigned to the influence of especially abiotic but also biotic factors (Lowe 1996). This set of factors determines the periphyton succession during the growing season, starting each spring de facto de novo. The changes in the periphytic community longer than one growing season have been studied sporadically (e.g., Admiraal et al. 1984) if the paleolimnological studies dealing with subfossil diatoms are not taken into account. Our results suggest that the age of flooding, and therefore, the absolute duration of the succession of the periphytic community, plays a significant role in the establishment of the periphytic community structure. Thus, the diatom-dominated community corresponds with the last flooded lake Medard. The community with prevailing filaments was established on the first fully flooded lake

Milada and lake Most, of the medium complete flooding age hosted diatoms in spring and filaments in summer and fall. This is in accordance with the trophic state of the individual lakes (Fig. 6).

Seasonal dynamics of cyanobacteria and mobile diatoms

The seasonal changes in mobile diatom forms are similar for all studied lakes but most evident at lakes Most and Milada. A spring minimum is followed by a remarkably higher proportion of mobile forms during summer and fall throughout both studied years (Fig. 3, Figure S4). This seasonal trend is significantly positively correlated with the abundance of cyanobacteria. Mobile diatoms and cyanobacteria are known for their ability to manage nutrient depletion. The mobile diatoms can achieve this through the active search for nutrient sources (DeNicola and Kelly 2014). Cyanobacteria are also partly capable of active movement and employ an array of specialised metabolic capabilities (N_2 fixation—diazocytes, heterocytes; P uptake—extracellular phosphatases, etc.) (Whitton and Potts 2000; Rychtecký et al. 2015). Such nutrient depletion can occur within the periphytic mat as the biomass (live or dead) accumulates throughout the growing season and prevents the diffusion of nutrients into the inner mat layers. However, there was no significant correlation between the absolute organic matter values and the proportion of mobile diatoms and cyanobacteria (Table S5). Results in Konopáčová et al. (2021) describing phosphorus uptake in analogous periphytic samples support the existence of a distinct spring nutrient uptake maximum followed by stagnation in summer and fall. It implies this scenario with a certain amount of rationalistic naivety: nutrients (phosphorus) are consumed by the periphyton mostly in spring. Thus, the development of biomass and the success of mobile diatoms and cyanobacteria later during the growing season would be linked with nutrient recycling from the already dead periphytic algae and/or the ability of mobile forms to reach the nutrient-rich spots. A more phenomenological explanation is a topic for future less in-detail holistic studies.

Environmental parameters affecting the periphyton community

The variable species composition of phototrophs in aquatic ecosystems can partially be explained by biotic factors, such as competition, facilitation, and niche differentiation between various taxa (Vanelslander et al. 2009; Koedooder et al. 2019). Other parts of variability in the composition are influenced by the species-specific tolerances to environmental factors, such as nutrient concentrations, conductivity, or light availability (Thornton et al. 2002; Cantonati et al. 2009; Ribeiro et al. 2013). The assumption beyond our reasoning

is that changes in a limiting factor should alter the species structure of a periphytic algal community. Thus, the strength of limitation rises with the percentage of explained variability in species data of the particular physico-chemical factor. Among chemical variables, nitrogen and phosphorus are usually found to be limiting nutrients in lakes (see review in Borchardt 1996), and numerous models (e.g., diatom transfer functions) deal with a species-specific affinity to these nutrient levels (e.g., Bennion 1994; Reavie et al. 2006) as well as with the affinity to TOC (Rosén et al. 2000) and pH (Sienkiewicz et al 2021). However, our data suggest that calcium concentration explained a great portion of species variability by the measured chemical and physical variables in both non-diatom and diatom data and growth forms. Calcium belongs to essential nutrients necessary for algal growth (Darley 1982 cited from Lowe 1996), but so strong correlation between the periphytic community and calcium concentration has not been, to the best of our knowledge, recorded yet. Calcium plays an important role in the phosphorus cycle through co-precipitation of phosphates with calcium carbonate at higher pH, which subsequently makes phosphorus less biologically available (Corman et al. 2016). This phenomenon has been widely studied in calcareous periphyton, in which the pH is locally elevated by photosynthesis, inducing $CaCO_3$ precipitation (Dodds 2003; Scinto and Reddy 2003). Nevertheless, prominent calcification was not observed in our samples macroscopically nor microscopically. It was proved that cations, including Ca^{2+}, influence a broad range of physiological processes in prokaryotes and eukaryotes (Torrecilla et al. 2004). Calcium is required for the germination of bacterial spores (Warth 1978), influences the biomass development of cyanobacteria in soil (Řeháková et al. 2017), leads to biofilm formation (Lopez et al. 2009, 2010), participates in quorum sensing (Wherten and Lundgren 2001), is involved in differentiation of heterocytes by cyanobacteria (Torrecilla et al. 2004) and promote the algal–bacterial symbiosis (Amin et al. 2009; Kazamia et al. 2012). Some prokaryotes, such as cyanobacteria, contain a Ca^{2+}/H^+ antiporter in their plasma membranes, which plays an important role in salt sensitivity and tolerance (Waditee et al. 2004) and thus can influence their vitality in an alkaline environment, typical for the studied lakes. However, because cyanobacteria did not form the dominant part of the studied periphytic community, calcium concentration is expected to have relevance also for the eukaryotic taxa.

Despite the increasing evidence about the importance of calcium for prokaryotic as well as for eukaryotic metabolisms, the role of calcium in periphytic mats is unknown, and the mechanistic explanation exceeds the scope of the current study. The role of micronutrients in aquatic ecosystems, where algae are important primary producers, needs more attention and provides an opportunity to increase our understanding of periphyton ecology. Contribution of dissolved nitrogen (DN) and dissolved organic carbon (DOC) was lower, and total phosphorus (TP) turned out to be an even insignificant environmental factor in our study. This is not that surprising, since the water column nutrients are often uncoupled with the benthic algal community (Cattaneo 1987) and periphyton biomass (Mahdy et al. 2015), and phosphorus can be actively recycled by the community from the substratum or sediment (Carlton and Wetzel 1988).

Conclusions

The following findings can be summarised as the most important ones resulting from our research:

(1) 25% of diatom species found in the studied watershed (~ 5500 km^2) were restricted to the studied post-mining lakes. The individual lakes contain $\sim 14\%$ and $\sim 16\%$ of unique non-diatom and diatom taxa, respectively, that do not occur in the other studied lakes. This illustrates the importance of these newly established biotopes as the hot spots of broader regional algal biodiversity.

(2) The seasonal dynamics in species composition are distinctly lake-specific. The proportion of diatoms in the periphyton decreases with the higher trophic state and flooding age of the post-mining lakes.

(3) Cyanobacteria and mobile diatom forms thrive later in the growing season, suggesting possible uptake and recycling of nutrients from the accumulated dead periphyton biomass.

(4) One of the best correlates, and therefore, an important driver of changes in the algal community, was water column calcium concentration. The role of phosphorus in the form of TP and SRP was markedly lower.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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