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conservation importance based on phytobenthos

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## **Allgemeine Einleitung**

### **Quellen**

Quellen sind Orte, an welchen Grundwasser an die Erdoberfläche dringt. Sie bilden damit oftmals den Ursprung von Oberflächengewässern (Glazier, 2009). Als Schnittstelle zwischen terrestrischen Lebensräumen, Grund- und Oberflächenwasser stellen Quellen ein einzigartiges Beispiel eines dreiseitigen Ökoton bzw. Saumbiotops (Übergangsbereich zwischen mehreren Ökosystemen) dar (Barquín & Scarsbrook, 2008; Schaefer, 2012). Quellen sind sehr divers und können hinsichtlich Geologie, Hydrologie, Chemismus, Temperatur, Ökologie oder Art der menschlichen Nutzung klassifiziert werden. Aus Sicht der Biologie werden sie vor allem danach unterschieden, welche Form aquatischen Habitats sie erschaffen. Im Falle von Fließgewässern spricht man von Rheokrenen, bei stehenden Gewässern und Sümpfen ist von Limnokrenen und Helokrenen die Rede (Glazier, 2009). Die hier untersuchten Quellen sind allesamt Rheokrenen. Ausströmendes Quellwasser wird kontinuierlich aus thermisch gepufferten Grundwasservorkommen nachgeliefert, daher zeigen sich auch nur geringe Temperaturschwankungen im tageszeitlichen, saisonalen und jährlichen Verlauf (Glazier, 2009).

### **Thermalquellen**

Eine allgemeingültige und einheitliche Definition des Begriffes 'Thermalquelle' existiert nicht. Gemäß den Heilvorkommen- und Kurortegesetzen der österreichischen Bundesländer beispielsweise gelten Grundwässer ab 20°C (an der Entnahmestelle) als Thermalwässer (Philippitsch & Elster, 2016). Nach geologischer/hydrologischer Ansicht gelten jene Quellen als thermal, deren Wassertemperatur über der mittleren Jahresdurchschnittstemperatur der Luft liegt (Glazier, 2009). Diese relative Definition ist jedoch aus Sicht der quellbewohnenden Organismenwelt kaum geeignet. Eine sinnvollere Definition von Thermalquellen richtet sich nach deren Lebensgemeinschaften. Vouk (1950) unterscheidet lauwarmer Quellen oder Chliarithermen (18-28°C), warme Quellen oder Euthermen (28-44°C), heiße Quellen oder Akrothermen (44-65°C) und siedende Quellen oder Hyperthermen (>65°C). Er definiert hypothermale (oder nicht thermale) Quellen damit bis zu einem Grenzpunkt von 18°C und orientiert sich dabei an empirischen Beobachtungen, wonach sich spezifische thermale Lebensgemeinschaften bei Temperaturen zwischen 30 und 50°C ausbilden. Mit

höherer Temperatur steigt auch die Löslichkeit von Mineralstoffen, Thermalwasser ist daher auch oft stärker mineralisiert (White, 2010). Die Mineralstoffzusammensetzung ist hierbei von den jeweiligen durchströmten Gesteinsschichten geprägt.

### **Thermenlinie**

Die vorliegende Masterarbeit untersucht benthische Algen-Gemeinschaften in ausgesuchten Thermalquellen entlang der gemeinhin als 'Thermenlinie' bekannten Region in Ost-Österreich (Standortdetails siehe Fig.1, Table 1). Die Thermenlinie bezeichnet eine tektonische Bruchzone im südlichen Wiener Becken und fasst mehrere lokale Störungszonen (z.B. Badener Bruch, Leopoldsdorfer Bruch) zusammen. Thermalwasseraustritte (Thermen) finden sich entlang des Bereichs, in dem die alpinen Schichten in die Neogenen Sedimente des Beckens absinken. Durch die Brüche kann (thermales) Grundwasser an die Erdoberfläche gelangen. Die Störungszone setzt sich nach Norden hin bis Südmähren fort (Küpper et al., 1951; Wessely, 2016). Im Süden schließen die Thermalwässer des Steirischen Beckens an.

### **Algen**

An den Quellaustritten bilden sich sehr kleinräumige und besondere Lebensräume für eine Reihe aquatischer Organismen. Typische Lebensformen hier sind Biofilme an vom Wasser überströmten Oberflächen. Biofilme sind Schichten geringer Dicke, die sich aus unterschiedlichsten Organismen zusammensetzen. Algen sind eine wichtige Komponente in belichteten Systemen. Als von Sonnenlicht lebende (=photoautotrophe) Organismen nehmen Algen in diesen Lebensräumen die Klasse der Primärproduzenten ein. Unter Phytobenthos versteht man die am Gewässergrund festsitzende Pflanzenwelt bzw. die Mikroflora (Algen) (Schaefer, 2012). Der Begriff 'Alge' ist als biologischer Organisationstyp zu verstehen. Er umfasst eine Reihe einfach gebauter, oxygene Photosynthese (mit Sauerstoff als Nebenprodukt) betreibender Organismen, die nicht den Embryophyta (=Landpflanzen, also Gefäßpflanzen inklusive Moose) zugerechnet werden (Bresinsky et al., 2008). Dazu zählen verschiedenste miteinander nicht näher verwandte Gruppen innerhalb der Eukaryoten als auch die prokaryotischen Cyanobakterien. Neben ihrer weltweiten Bedeutung als Nahrungsgrundlage für die tierische Lebewelt sind sie außerdem für etwa 45% des atmosphärischen Sauerstoffeintrags verantwortlich (Graham & Wilcox, 2000).

## **Thermen als Schutzgut**

Quellen im Allgemeinen beherbergen aufgrund ihres Inselcharakters (also ihrer räumlichen Isoliertheit) und dem daraus resultierenden geringen genetischen Austausch oftmals endemische Organismen (Dudgeon et al, 2006). Endemiten sind Taxa die nur in einem bestimmten, räumlich klar abgegrenzten Gebiet vorkommen (Schaefer, 2012). Als konkretes Beispiel dafür ist hier die Organismengruppe der Gastropoda (Schnecken) zu nennen. In zwei der untersuchten Standorte finden sich endemische Schnecken. Quellen als Kleinstökosysteme gelten als Biodiversitätshotspots, unterliegen jedoch keinem ausreichenden rechtlichen Schutz (Cantonati et al., 2012a).

Thermen werden schon seit Urzeiten vom Menschen genutzt. Besonders die Hygieneanforderungen und Effizienzsteigerungen dieser Nutzung haben im letzten Jahrhundert zerstörerische Effekte auf die Vegetation der Thermen nach sich gezogen (Vouk, 1950). Das Konrad Lorenz zugeschriebene Zitat "Nur was der Mensch kennt, lernt er lieben. Nur was er liebt, verteidigt er" verdeutlicht, wie wichtig die Forschung an diesen noch zu wenig bekannten Lebensräumen ist.

## **Hypothesen**

Die Diversität von Algen, wie auch jene von Tieren und Pilzen, sinkt mit steigender Temperatur des Quellwassers (Angaben im Bereich von 35 bis 60°C) (Glazier, 2009). Es wurde geprüft, ob diese Beziehung auch an den von uns untersuchten Quellen unterhalb von 35°C zu beobachten ist. Wir nahmen an, dass sich Unterschiede in der Hydrochemie und Temperatur auch in der Artenzusammensetzung der Algen widerspiegeln. Außerdem vermuteten wir eine signifikant höhere Artenzahl an naturnäheren Standorten im Vergleich zu jenen mit starker anthropogener Beeinträchtigung (mit Einwirkungen auf Umweltparameter und Struktur des Lebensraumes).

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## Abstract

Spring biotopes are biodiversity hotspots, but inadequate protective legislation and high utilisation pressure pose high risk to these sensitive systems. The current study provides insight into these microhabitats along the East-Austrian 'Thermenlinie'. Characterised through increased water temperature and often paired with elevated mineral contents, thermal springs represent a special habitat type, which is also reflected in the community composition. We focused on phytobenthos as an essential component of photoautotrophic biofilms, as this group is commonly used for bioindication. Springs differed significantly in environmental conditions such as temperature and ion composition, which was also reflected in phytobenthos patterns. We found sites with temperature  $>25^{\circ}\text{C}$  rich in  $\text{SH}_2$ , others with increased  $\text{Na}^+$ ,  $\text{HCO}_3^-$  and  $\text{Cl}^-$ , and carstic springs with temperature between 18 and  $25^{\circ}\text{C}$  and comparatively lower ion contents. Environmental conditions were very stable, which was also reflected in similar algae composition throughout the year. Taxa adapted to high water temperature were predominantly cyanobacteria, springs with highest temperatures were dominated by them. Diatoms showed the highest share of total species number of all springs. Taxa number between sites was negatively related with temperature and hemeroby. We also found some Red List species in the springs, which points to very peculiar and worthy of protection habitats. The absence of the expected cosmopolitan thermophilic cyanobacterium *Mastigocladus laminosus* (COHN ex KIRCHNER) was surprising. It could be explained by the impact of  $\text{SH}_2$  at two of the high temperature sites. Based on phytobenthos composition, the sites could be assigned to thermo-mineral spring types. Furthermore, suitable conservation approaches could be identified: the utilisation of thermal water for spa purposes does not necessarily require interventions on spring habitats. In fact, the strict protection of (thermal) spring sites and the sustainable use of the water downstream can be a compatible.

**Keywords:** benthic, algae, mineral spring, temperate thermal spring, Thermenlinie

## Introduction

Springs are unique aquatic habitats; they are ecotones linking the groundwater aquifer with the origin of surface water (Cantonati et al., 2006a). They exist where hydro-, litho-, atmo- and biosphere are overlapping, extended by influences from anthroposphere. Mosaic structure, high individuality and azonal character are typical features of spring environments due to their physicochemical stability (Cantonati et al., 2006a). Compared with other aquatic habitats, springs often show increased species-richness and contain more Red List taxa (Cantonati et al., 2012a). Considering the large number of different spring types and the habitat complexity, they are a significant contribution on local and regional biodiversity (Cantonati et al., 2012a). Furthermore, insularity and disjunct distribution are characteristic attributes of spring biotopes. Therefore, low gene flow and local radiation (in the absence of human disturbance) can lead to interdrainage variation in biodiversity and to high levels of endemism (Dudgeon et al, 2006). Although springs are biodiversity hotspots, they are still much less studied than other aquatic ecosystems and insufficiently covered by protective legislation. More precisely, the European Union Water Framework Directive is not covering springs and small headwater catchments (< 10 km<sup>2</sup>) (Cantonati et al., 2012a). The Habitats Directive (1992 European Union Directive on the conservation of natural habitats and of wild fauna and flora) contains only three spring types in its Annex I, which are '31A0\* Transylvanian hot-spring lotus beds', '7160 Fennoscandian mineral-rich springs and springfens' and '7220\* Petrifying springs with tufa formation (Cratoneurion)' (European Commission, 2013).

The current study provides new insights into the very specific type of thermal springs. In accordance with the established practice of geology, springs with water temperature approximating mean annual air temperature (MAAT) are defined as ambient springs, whereas the water temperature of thermal springs (also called geothermal or superambient springs) is higher than MAAT; water temperature of hot springs exceeds human body temperature ( $\approx$  37–38°C) (Glazier, 2009). This anthropocentric definition is not applicable to many organisms also temperature relative to MAAT is not decisive, thus another classification is recommended. According to Vouk (1950), specific thermal coenoses develop generally between 30 and 50°C. He proposed hypothermal (< 18°C), chliarothermal or tepid (18-28°C), euthermal or warm (28-44°C), akrothermal or hot (44-65°C) and hyperthermal

springs ( $\geq 65^{\circ}\text{C}$ ) (Vouk, 1950). Considering spring biocoenoses, this classification seems much more suitable.

Increased water temperature of thermal springs is caused by heated seepage due to geothermal energy, which causes on average  $1^{\circ}\text{C}$  increase for every 33 m depth (Richter, 1992). Hydrochemistry of springs is related to its geological environment (Glazier, 2009). As solubility of minerals is temperature-dependent, thermal spring water often has increased mineral content (White, 2010). Mineral water contains at least  $1\text{ gL}^{-1}$  dissolved substances (Zötl, 1993). The wide range regarding mineral content results from different bedrocks. Spring chemistry differs considerably from surface waters of lakes or streams (Castenholz, 1969). Regarding the origin, juvenile, formation and meteoric water is distinguished. Juvenile waters originate from geochemical processes and are not yet part of the water cycle. They play an almost negligible role in Austria. Formation water shows a high concentration of salt, because it is seawater trapped during sedimentation processes. In contrast to that, meteoric waters are part of the global water cycle. Due to long and deep-reaching circulation, meteoric waters can be several thousands of years old (Elster, 2016d).

Archaeological findings suggest that numerous Austrian thermal springs were already used by Romans. From the 1960s onwards, a significant increase in balneological treatment is recognized (Elster, 2016c). Along with the intense use, constructional interventions were progressively introduced to improve hygienic conditions, although negative impacts on bathers never have been documented before. Such measures have serious consequences for organisms inhabiting springs. Already Vouk (1950) mentioned that the very common tapping of springs impedes growth of photoautotrophic biofilms and as consequence the development of zoobenthos. A prime example are highly threatened endemic snail species at the two spring sites Bad Vöslau and Bad Fischau. *Belgrandiella parreyssii* (L. PFEIFFER, 1841), classified as Critically Endangered (CR), only exists at the thermal spring of Bad Vöslau. The distribution of *Theodoxus prevostianus* (C. PFEIFFER, 1828) and *Esperiana daudebartii* (PREVOST, 1821), both CR, is limited to the thermal springs of Bad Vöslau and Bad Fischau (Reischütz & Reischütz, 2009). With this study, we provide basic information about their potential nutritional basis.

Glazier (2009) stated that algal diversity (besides animal and fungal diversity) decreases as spring temperature increases showing a diagram which reaches from 35 to 60°C. We checked, if this negative relation is also valid for lower water temperature. We studied the phytobenthos community of several thermal (most of them also mineral) springs located in Eastern Austria along the so-called Thermenlinie, where the Tertiary basins border on the Eastern Alps. We compared the springs over a one-year period and included both traditional algal taxonomy and hydrochemistry. We assumed that (1) differences in hydrochemistry and temperature are reflected in species composition and that (2) near-natural thermal springs have a significantly higher taxa richness than anthropogenic altered ones (impacts on environmental conditions and habitat structure).

To protect such special habitats within a legal framework, it is mandatory to study and characterise their ecology on a larger scale. Although this purpose is beyond the scope of this study, it shall serve as an inspiration for further research. So far, literature on thermal springs in Austria deals with balneology (the study of the therapeutic application of mineral water) and geology. The first approach to understand the complex ecology was undertaken by Vouk (1950). He provided insights into the distribution of organisms, ecological demands and categorised thermal springs based on biology. Zötl & Goldbrunner (1993) published a comprehensive review on geology and dissolved substances of almost all Austrian thermal springs. Recently, Elster et al. (2016) published a geological map with detailed explanations on thermal waters of Austria. Although phytobenthos is at the base of the food web, there is almost no information for temperate thermal springs available. The current study provides an algae species inventory for selected springs. Moreover, we list impacts of human use and provide advices to minimize negative effects in terms of conservation.

### **Description of sites**

There exist several thermal springs along the Thermenlinie, but due to the common tapping of springs for human utilisation, many of them are nowadays enclosed by steel basins or completely drained underground. After a preliminary investigation, we selected the most promising seven sites (Fig. 1, Table 1).

Marienquelle & Johannesquelle

Baden ranks among the oldest spa towns throughout Europe. Numerous thermal springs, located on the western edge of the southern part of the Vienna Basin (Badener Bruchzone), emerge with temperatures from around 23 to 35°C and a discharge of approx. 30 to 50 Ls<sup>-1</sup> (Elster, 2016b). According to Hacker (1992), around 50% of the water originates from thermal deep groundwater aquifer, the other half consists of shallow and deeper carst waters. The thermal springs are classified as Ca<sup>2+</sup>-Na<sup>+</sup>-Mg<sup>2+</sup>-SO<sub>4</sub><sup>2-</sup>-Cl<sup>-</sup>-S<sup>2-</sup> type with a total mineral content of about 1700 mgL<sup>-1</sup> (same for Marien-, Römer- and Josefsquelle). A high content of SH<sub>2</sub> (> 5.0 mgL<sup>-1</sup>) is characteristic (Elster, 2016b) and recognized as pungent smell in town. Possible origins of SH<sub>2</sub> are the impact of the thermal water on [SO<sub>4</sub>]<sup>2-</sup> deposits or bacterial metabolism (Hacker & Zötl, 1993a; Götzl et al., 2012). Eight of the 15 tapped springs are used by spas (Elster, 2016b), all of them drain into the river Schwechat that runs through the city centre. Marienquelle (BM) is located directly at the Schwechat river bank (Fig 2). The spring originally arose from the streambed or the shore and was tapped in 1924 and again in 1965 (Hacker & Zötl, 1993a). Despite a strong decrease of discharge as consequence of the formation of secondary outlets (Kaiser, 2000) BM still has the highest discharge of all Baden springs with around 18.6 Ls<sup>-1</sup> (Elster, 2016b). Most of the thermal water is captured underground and is then piped to the spas. The actual site for the investigation consists of a concrete basin that collects untreated water. The water temperature is 34.7°C on average (current data from this study).

Only about 200 m upstream, Johannesquelle (BJ) is located (Fig. 3). It has a discharge of about 2.7 Ls<sup>-1</sup> and is currently not used (Elster, 2016b). The water flows out of a downward angled pipe and gushes over a concrete rock.

#### Ursprungsquelle

Bad Vöslau is located about 4 km south of Baden. Similar as for Baden, Mesozoic carbonate rocks covered with dense Neogene sediments emerge on the edge of the Vienna Basin. Within the town Bad Vöslau, thermal and non-thermal springs emerge very close to each other. Six thermal springs around the thermal bath emerge from clefts in the conglomerate rock. The main spring (discharge: approx. 35 Ls<sup>-1</sup> on average) is called Ursprungsquelle (BV) and got trapped with a metal tube in 1927, through which the outflowing water gushes into the upper basin, known as Grünes Becken (Hacker, 1993a). Characteristic values from hydrochemistry and isotope analysis indicate that

the thermal water is mixed with young, cold carst water. The proportion of carst water is higher than at Baden. BV is classified as acratitic  $\text{Ca}^{2+}\text{-Mg}^{2+}\text{-HCO}_3^-$ - $[\text{SO}_4]^{2-}$  type (Hacker, 1993a). The main spring outflow from a metal tube is directly discharging into the basin; it is not suitable for visible biofilm development. We therefore sampled a lateral outflow of the same spring with visible algae cover, located a few meters away (Fig. 4).

#### Damenquelle

The thermal springs of Bad Fischau are the southernmost ones of the Vienna Basin (Wessely, 1993). The water passes along fractures in the Neogene and leaks out through carst cavities (Küpper, 1977). Three larger springs emerge in the thermal bath; they are probably fed by a shared cave system. The considerable discharge and its seasonal fluctuation classify the springs as carstic ones. Only moderate temperature variations, the slightly increased total mineralisation and the long mean residence time indicate an admixture of deep groundwaters and deep carst waters (Hacker, 1993b). The spring has a total mineral content of about  $500 \text{ mgL}^{-1}$  (acratitic) and is classified as  $\text{Ca}^{2+}\text{-Mg}^{2+}\text{-HCO}_3^-$  type. The two larger springs with a discharge of around  $100 \text{ Ls}^{-1}$  on average supply the bathing pools. They also represent the origin of the stream Warne Fischa (Elster, 2016b). All three springs on the thermal bath area, along with the upper part of the streambed, are protected site (natural monument). The samples were taken from the confluence of the two branches of Damenquelle (BF) which feeds the Damenbecken of the thermal bath (Fig. 5). The discharge of BF is  $60 \text{ Ls}^{-1}$  (Götzl et al., 2012).

#### Badquelle

The thermal springs of Mannersdorf are located on the western ridge of the low mountain range Leithagebirge that borders on the eastern edge of the Vienna Basin. The thermal water aquifer consists mainly of carbonates from Middle Triassic. At the basin edge, water wells up through fractures, which extend from SW to NE (Elster, 2016b). The Badquelle (MA) with a discharge of  $4 \text{ Ls}^{-1}$  (Elster, 2016b) is used for filling the Thermalsportbad. It is captured in a deep pit and gushes into a steel basin, where it flows off underground. Therefore, the sampling had to be shifted to about 1 km northeast of the Thermalsportbad at the end of a pipe (Fig. 6). During rainfall, the thermal water is mixed with street runoff, thus heavily influencing abiotic conditions. Water temperature at the

sampling site is decoupled from the spring (22°C), however it still has a constantly higher temperature than nonthermal waters during the cold seasons. The spring water is characterised as  $\text{Ca}^{2+}\text{-Mg}^{2+}\text{-HCO}_3^-$ - $[\text{SO}_4]^{2-}$  with a mineral content of around 1600  $\text{mgL}^{-1}$  (Elster, 2016b). The  $[\text{SO}_4]^{2-}$  concentration suggests contact with gypsum or anhydrite. The water age of the main spring dates to the last glacial epoch with only marginal influence of near-surface waters (Elster, 2016b).

#### Leithaprodersdorf Thermal

The second notable thermal spring along the eastern Thermenlinie is located at Leithaprodersdorf. At the NW-margin of the Leithagebirge, thermal water rises through a N-S fissure of Mesozoic limestones (Hacker & Zötl, 1993b). The thermal spring (LP) without a toponym is privately owned and was never utilised economically (Fig. 7). The spring with a discharge of 4  $\text{Ls}^{-1}$  is a  $\text{Ca}^{2+}\text{-Mg}^{2+}\text{-HCO}_3^-$ - $[\text{SO}_4]^{2-}$  type with a total mineral content of 2900  $\text{mgL}^{-1}$  (Elster, 2016b). The hydrochemical composition resembles MA, but with ion concentrations partially about twice as high (Hobiger, 2011c; 2011b). Three components contribute to the unique hydrochemistry: highly mineralised thermal water from the basin aquifer is mixed with an alimentation of waters from SE, rich in  $\text{CO}_2$  (approx. 180  $\text{mgL}^{-1}$ ), and a near-surface component (Carlé, 1975). The  $[\text{SO}_4]^{2-}$  content indicates contact with gypsum or anhydrite layers. Like MA, LP water dates to the last glacial epoch (Elster, 2016b).

#### Vulkaniaquelle

Bad Blumau is situated in the Styrian Basin. The thermal springs in the spa complex 'Rogner Bad Blumau' are artesian wells. The first deep drilling was spudded for hydrocarbon exploration (Zetinigg, 1993), but thermal water was extracted instead. The deep drilling 'Bad Blumau 2' (depth: 2840 m), named as 'Vulkania<sup>®</sup> Heilquelle' (BB), crosses several geological layers, through which the thermal water rises through artesian pressure and by gas lift effect (discharge: 24.5  $\text{Ls}^{-1}$ ; Eisner & Goldbrunner, 2009; Goldbrunner & Eisner, 1997). The 107°C hot water is used for geothermal power generation. After cooling, part of the water is pumped to the spa, which is located about 2 km from the borehole. Except bathing water, water is reinjected into the ground (Eisner & Goldbrunner, 2009). BB has a very high mineral content, the water is characterised as  $\text{Na}^+\text{-HCO}_3^-$ - $\text{Cl}^-$  type with a total mineralisation of round 18000  $\text{mgL}^{-1}$  ( $\text{HCO}_3^-$  with round 8000  $\text{mgL}^{-1}$ ; Elster et al., 2016). The spring

water emerges at an artificial rock formation and discharges after a few m into the pool (Fig. 8). Along a small rivulet, photoautotrophic biofilm is growing.

## **Material & Methods**

### **Environmental parameters**

Table 1 shows coordinates and abbreviations of springs. Samplings took place in February, May, July, September and December 2017. Water temperature, specific conductivity (WTW LF197i), pH (WTW pH 330i with Metrohm glass electrode 6.0253.100), oxygen content (WTW Oxi 3310) were measured in the field. Also, total alkalinity was analysed on site by endpoint titration to pH 4.3. To record temperature over longer periods, data loggers were installed (Onset UA-002 HOBO, logging interval 15 min). The local light conditions were estimated by digital imaging as 'sky openness' (i.e., percentage of open sky) after taking photos with a digital camera (Nikon Coolpix 4500 equipped with fisheye converter Nikon FC-E8) and conversion/counting of black and white pixels with the image editing software GIMP (V 2.10.8).

For total organic carbon (TOC), total phosphorus (P<sub>tot</sub>), Si, SH<sub>2</sub> and major ions (Ca<sup>2+</sup>, Mg<sup>2+</sup>, Na<sup>+</sup>, K<sup>+</sup>, [SO<sub>4</sub>]<sup>2-</sup>, Cl<sup>-</sup>), samples were transported in an ice box at 4°C to the laboratory and subsequently analysed. TOC-analysis: before sampling, TOC glass vials (40 ml) were combusted in a muffle furnace to prevent contaminations. Raw samples were analysed with a Sievers 900 Portable Total Organic Carbon Analyzer. Ions were analysed by ion chromatography according to OENORM EN ISO 14911 for cations and OENORM EN ISO 10304 for anions (Metrohm Compact IC 761, cation column: Metrohm Metrosep C2, anion column: Metrohm Metrosep A Supp 5). P<sub>tot</sub> was measured spectrophotometrically as P-molybdenum blue (Hach-Lange DR 2800) at 890 nm after wet combustion according to OENORM EN ISO 6878. Si was measured at 400 nm without reduction of silicomolybdic acid (DIN 38405). SH<sub>2</sub> was measured spectrophotometrically (Hitachi U-2000) with a standard-based colour indicator test (MColortest™, Sulfid-Test) and Na<sub>2</sub>S·9H<sub>2</sub>O as a standard.

### **Phytobenthos**

Life material was sampled from all visible choriotopes and identified to the lowest taxonomical level possible and their abundance ranked on a semiquantitative scale from 1 (rare) to 5



(massive). Identification was done using a light microscope (Zeiss Axio Imager M1) at magnifications of 600x and 1000x. For diatom identification, cells were prepared by heat combustion on cover slips followed by rinsing in 5% HCl and MiliQ water. After drying, diatoms were embedded in the synthetic resin Naphrax™ with strong light-diffracting properties. For high-resolution images, a scanning electron microscope (SEM) was used with wet combustion of diatoms. For wet combustion, material was treated with concentrated HCl followed by mixture of H<sub>2</sub>SO<sub>4</sub> and HNO<sub>3</sub> (3:1) for 12 h each (MiliQ rinsing and centrifugation between and after steps). For SEM, acid-treated material was applied onto coverslips, dried and sputtered with a gold coat. Identification followed keys of Krammer & Lange-Bertalot (2004, 2007a, 2007b, 2008), Komárek & Anagnostidis (1998, 2005), Komarek (2013), Ettl & Gärtner (1988), Ettl & Rieth (1980), Eloranta et al. (2011), Krause (1997), Hofmann et al. (2011), Gutowski & Foerster (2009). Species name and author cross-checking followed AlgaeBase (Guiry & Guiry, 2009).

For quantifying algal groups, we used information of class-specific photosynthetic pigments, which we analysed by means of high-performance liquid chromatography (HPLC). Phytobenthos samples were stored on glass fibre filters (Ederol BM-C) until analysis at -80°C. After homogenizing the filters in 90% acetone with an ultrasonicator (Branson Sonifier 250) and extraction for 12 h in the dark at 4°C, the extract was centrifuged, and the supernatant injected into a Merck-Hitachi LaChrom Elite HPLC System (Hitachi FL Detector L-2485, column: Merck-Superspher RP-18, software: EZ Chrom Elite). Gradient programme according to Wright et al. (1991), peak detection at 440 nm (Schagerl & Donabaum 2003, Schagerl et al. 2003). To calculate group affiliations, the factor analysis routine CHEMTAX V1.95 was used (Mackey et al., 1996). The software uses a data matrix of pigment concentrations plus an initial estimation of the most appropriate pigment/Chlorophyll-a ratios for those algae classes that are expected in the samples (Mackey et al., 1996; Higgins et al., 2011). Based on microscopical observations, we limited the groups to relative contributions of Cyanobacteria, Bacillariophyceae, and Chlorophyta to total algal biomass based on Chlorophyll-a.

### **Statistics**

Non-metric multidimensional scaling (NMDS) was used to estimate distances between sites in ordination space based on environmental data. After data were normalised, a Euclidean distance was

calculated, which resulted a two-dimensional NMDS1 solution with 0.01 minimum stress (Kruskal stress value, 1000 iterations). As site BB was completely separated from all other springs (data not shown), NMDS2 was repeated without BB to get more detailed insight into differences of the remaining sites (minimum stress value of two-dimensional solution: 0.05). Significant groups were defined with SIMPROF (999 permutations,  $p < 0.05$ ). For interpretation of the pattern, environmental variables contributing significantly to the model were identified using the non-parametric routine BIOENV (1000 permutations,  $p < 0.001$ ; resemblance matrix based on Euclidean distances).

Species distribution patterns were studied by indirect gradient analysis. As gradient length was  $> 3$ , a unimodal model was performed. Results of the detrended correspondence analysis (DCA, detrending by 2<sup>nd</sup> order, polynomial and downweighting of rare species), were displayed in ordination diagrams with points representing cases (five samplings per site) or species; afterwards explanatory variables (vectors) were plotted for interpretation of species patterns. Before that, a principal component analysis (PCA) based on ions was done to reduce the number of input variables without losing information and to avoid the problem of multicollinearity.

NMDS, SIMPROF and BIOENV were calculated with the software package Primer V6.1.18 (Primer-E Ltd., 2015), DCA with Canoco V5.1 (Biometrics, 2017), and PCA with Statgraphics 18 (Statgraphics Technologies).

## **Results**

### **Environment**

To reduce number of variables, we performed a PCA (Principal Component Analysis) with ions, which resulted in two principal components explaining 97% of total variance in the data set (Table 3). PC1 showed high loadings with most of the ions except  $Mg^{2+}$  and  $Ca^{2+}$ ; we therefore interpreted it as 'salt' content. PC2 was highly related to  $Mg^{2+}$  and  $Ca^{2+}$  and named as 'carst' component. BB with high salt content and deep artesian water was clearly separated from all other springs located in the Vienna Basin (Fig. 9). A closer look revealed also some differences in the other springs. BV and BF were very similar in ion concentrations. BJ, BM and MA had slightly elevated mineral contents, followed by LP with even higher conductivity and  $Ca^{2+}/Mg^{2+}$  amounts.

BM had low oxygen (29%) and TOC concentrations (148 ppb, Table 2). Conductivity (2.19 mScm<sup>-1</sup>) indicated high mineral content, which is mainly caused by Ca<sup>2+</sup>, Na<sup>+</sup>, [SO<sub>4</sub>]<sup>2-</sup> and Cl<sup>-</sup> (Table 2). Noteworthy, SH<sub>2</sub> could be detected with 4 mgL<sup>-1</sup>. The water temperature was very stable between 34.5 and 35.0°C throughout the year (Fig. 10). The nearby spring BJ had slightly elevated oxygen (54.5%) and TOC (295 ppb) contents. Temperature was lower (26.4°C), same for conductivity (1.76 mScm<sup>-1</sup>) but ions had a comparable composition (Table 2). SH<sub>2</sub> was still detectable (1.8 mgL<sup>-1</sup>).

The acratia water of BV had comparably low temperature (19.8°C) and conductivity (0.7 mScm<sup>-1</sup>) characterised by Ca<sup>2+</sup>, Mg<sup>2+</sup> and [SO<sub>4</sub>]<sup>2-</sup> (Table 2). BF was very similar to BV (Table 2). The temperature profile of BF (Fig. 10) shows very stable conditions throughout the year.

Sky openness (74%), oxygen content (98.4%), pH (8.2), TOC (454 ppb), and P<sub>tot</sub> (26 µgL<sup>-1</sup>) of MA were higher than at BM, BJ and BV. Temperature and conductivity were 21.5°C and 1.82 mScm<sup>-1</sup>, respectively dominated by Ca<sup>2+</sup>, Mg<sup>2+</sup>, and especially [SO<sub>4</sub>]<sup>2-</sup> (Table 2). Water temperature of MA was fluctuating between 13.0 and 24.4°C. It strongly correlated with ambient air temperature and showed a strong decrease after cold rainwater drained into the system (Fig. 10). Water temperature during late winter was 18.8°C, which indicated thermal origin of the water.

In contrast to MA, LP showed low sky openness (27%), oxygen concentration (33%), and pH (7.1). Temperature (24.1°C) and conductivity (3.21 mScm<sup>-1</sup>) were higher, compared to the former sites. Like MA, the water was dominated by Ca<sup>2+</sup> and Mg<sup>2+</sup> as cations; also, K<sup>+</sup> was elevated compared to other springs. [SO<sub>4</sub>]<sup>2-</sup> showed very high amounts of about 1.4 gL<sup>-1</sup> (Table 2). Median water temperature of LP was 24.2°C (Fig. 10).

BB had very specific conditions: highest water temperature (36.1°C), conductivity (32.7 mScm<sup>-1</sup>), alkalinity (22.9 mmolL<sup>-1</sup>) and TOC (10.91 ppm). Sky openness is 80%, pH is 8.1. The dominating ions are Na<sup>+</sup>, HCO<sub>3</sub><sup>-</sup>, Cl<sup>-</sup> and [SO<sub>4</sub>]<sup>2-</sup> (Table 2).

NMDS1 (not shown) revealed a big dissimilarity between BB and all other springs, based on very high salt content (see Table 2). BM and BJ (except BJIV) clustered together; also, the acratia springs BV and BF. MA (except MAIII) and LP were separated from each other. BJIV was isolated due to extremely high TOC, MAIII had P<sub>tot</sub> content surpassing other samplings several times (Fig. 11). Grouping was best explained by oxygen content, P<sub>tot</sub>, Mg<sup>2+</sup>, K<sup>+</sup> and Na<sup>+</sup> (Fig. 12). BM and BJ

showed comparatively low levels of oxygen and P<sub>tot</sub>, high Na<sup>+</sup>, and moderate Mg<sup>2+</sup> and K<sup>+</sup> levels (Table 2). On contrary, BV and BF were rich in oxygen and low in P<sub>tot</sub>, Na<sup>+</sup>, Mg<sup>2+</sup> and K<sup>+</sup>. Despite both springs MA and LP are characterised as Ca<sup>2+</sup>-Mg<sup>2+</sup>-[SO<sub>4</sub>]<sup>2-</sup>-HCO<sub>3</sub><sup>-</sup>-type, they differ significantly from each other. Compared to LP, lower water temperature accompanied by lower conductivity was found at MA; sky openness, oxygen and pH were higher at MA.

### Species

We found 114 algal taxa in total (Fig. 13, Table 6). Bacillariophyceae comprised most taxa (74), followed by Cyanobacteria (21), green algae (10) and other groups, such as Rhodophyta (4), Euglenophyta (2), Xanthophyceae (2) and Phaeophyceae (1). Red List species, like *Hildenbrandia rivularis* (LIEBMANN) (endangered), are listed in Table 4. Fig. 13 presents a comparison of the algae group pattern for each spring, based on taxa number. For major algae groups composition, based on biomass, findings from HPLC analysis are presented in Fig. 14. Some sites show a distinct patchy vegetation pattern; therefore, the HPLC results relate to the respective dominant algal patches; macroalgae are mentioned separately.

#### BM (13 taxa)

Cyanobacteria were dominating the coenosis (Fig. 14). They also contributed most to taxa number (7), followed by diatoms (4) (Fig. 13). The artificial substrate provided an ideal habitat for biofilm development, which had coloration from greenish, brownish to whitish. Most of the biofilm, which was up to 20mm in thickness, consisted of filamentous sulphur bacteria covering the whole surface with dense, thick whitish tufts (Fig. 2). Also patches of purple-sulphur bacteria were recognized. The whitish slurry was overgrown with comparatively thin blue-greenish and brownish coloured photoautotrophs. They almost exclusively consisted of *Limnothrix lauterbornii* (SCHMIDLE) (brown), *Leptolyngbya laminosa* and *Spirulina subsalsa* (OERSTED ex GOMONT) (bluegreen). Aside from cyanobacteria, only *Tetraspora cf. lemmermannii* (FOTT) could be found in macroscopic quantities. *Nitzschia nana* (GRUNOW) was the most frequent diatom species, accompanied by *Pinnularia appendiculata* (C. AGARDH) and *Caloneis lancettula* (SCHULZ). Some taxa are shown in Fig. 15.

#### BJ (20 taxa)

Algae vegetation cover was comparable with BM. Although diatoms were not detected in high quantities, they showed high taxa richness (10). Most frequent diatoms were *Navicula cryptocephala* (KÜTZING), *Nitzschia denticula* (GRUNOW), *Pinnularia appendiculata* and *Brachysira neoexilis* (LANGE-BERTALOT). In addition to the ubiquitous sulphur bacteria mats, characteristic brownish patches were observed, consisting of *Limnothrix lauterbornii*. Beside *Tetraspora* cf. *lemmermannii* also *Spirogyra* sp. (LINK) formed macroscopic greenish layers. For examples see Fig. 16.

#### BV (31 taxa)

The three groups diatoms, green algae and cyanobacteria occurred in similar quantities. Diatoms was the group with highest diversity (20). The biofilm on horizontal surfaces consisted mainly of cyanobacteria such as *Phormidium corium* (GOMONT ex GOMONT) and *Phormidium autumnale* (GOMONT), the green alga *Klebsormidium flaccidum* (KÜTZING) and diatoms such as *Achnanthydium minutissimum* (KÜTZING) and *Caloneis fontinalis* (GRUNOW). The crustose rhodophyte *Hildenbrandia rivularis* (Rhodophyta) was covering vertical areas. Taxa are shown in Fig. 17.

#### BF (38 taxa)

Diatoms, cyanobacteria and green algae had similar contributions to overall algal biomass. Again, taxa composition was also dominated by diatoms (27). *Epithemia goeppertiana* (HILSE), *Diploneis krammeri* (LANGE-BERTALOT & E. REICHARDT), and *Platessa hustedtii* (KRASSKE) could be identified down to species level. Interestingly, we found a healthy and large population of the stonewort *Chara globularis* (THUILLER) (Fig. 5). Additionally, mosses and filamentous algae mats comprising *Spirogyra* sp. and *Vaucheria debaryana* (WORONIN) were identified. The gravel bed is covered with crusts of *Hildenbrandia rivularis*, *Heribaudiella fluviatilis* (ARESCHOUG) (Ochromphyta, Phaeophyceae) and *Gongrosira incrustans* (REINSCH) (Chlorophyta). Gravel and concreted sidewalls were covered by various cyanobacteria, e.g. *Calothrix parietina* (THURET ex BORNET & FLAHAULT). Algae are shown in Fig. 18.

#### MA (59 taxa)

Regarding both biomass and taxa number (44), diatoms were dominating, with *Rhoicosphenia abbreviata* (C. AGARDH), *Tabularia fasciculata* (C. AGARDH) and *Cocconeis pediculus* (EHRENBERG)

as most abundant ones. In between, other algae, e.g. *Audouinella chalybea* (ROTH) (Rhodophyta) and *Lyngbya martensiana* (MENEHINI ex GOMONT) (Cyanobacteria) were found. Besides, crusts of *Gongrosira incrustans* were recognized on gravel and green filamentous tufts consisting of a mixture of *Rhizoclonium hieroglyphicum* (C. AGARDH), *Vaucheria* sp. (A.P.DE CANDOLLE) and *Cladophora glomerata* (LINNAEUS) were dominating. Epiphytes on filamentous macroalgae were diatoms, but also the rhodophyte *Chroodactylon ornatum* (C. AGARDH). For examples see Fig. 19.

#### LP (15 taxa)

The coenosis was dominated by cyanobacteria and diatoms, the latter showing highest taxa number (12). Vegetation cover was limited to walls dampened with splashing water. Besides mosses, only thin bluegreen biofilms were visible, mainly consisting of cyanobacteria *Phormidium molle* (GOMONT) and *Lyngbya martensiana*, accompanied by the green alga *Gongrosira incrustans*. Most frequent diatoms were *Halamphora normanii* (RABENHORST), *Nitzschia amphibia* (GRUNOW) and *Caloneis fontinalis*. Some diatom taxa are shown in Fig. 20.

#### BB (4 taxa)

Cyanobacteria were dominant regarding both biomass and taxa (3). Biofilms developed on the submerged artificial rocks and the surrounding splash zone. The spray- and steam- influenced flanks are partially covered with aerophilic brownish to blackish patches of *Nitzschia pusilla* (GRUNOW) and *Chroococcus varius* (A. BRAUN). Submerged dark-green thalli were predominated by *Leptolyngbya laminosa* and *Phormidium laetevirens* (P. CROUAN & H. CROUAN ex GOMONT). Taxa are shown in Fig. 21.

### **Linking species and environment**

For results obtained from DCA see Tables 4 and 5. High taxa numbers were coinciding with moderate water temperature and low mineral content (Fig. 22). According to the species pattern, four clusters of springs could be distinguished (Fig. 23). Both groups BB and BM/BJ had high temperature, P<sub>tot</sub> and salt contents, the latter with lower values. SH<sub>2</sub> was decisive between these groups. The remaining groups MA/LP and BV/BF were similar concerning water temperature and conductivity, but they had big differences in pH, sky openness and carst water.

Some of the species are characteristic for certain conditions, others such as *Halamphora normanii* or *Caloneis fontinalis* appear ubiquitous at most sites. The thermophilic prokaryote *Leptolyngbya laminosa* (GOMONT ex GOMONT), was exclusively found in the warm springs BM, BJ and BB (Fig. 24). Also, *Spirulina subsalsa* was identified only at some sites offering high temperature and dissolved substances (BM, BJ). BB hosts a single diatom species *Nitzschia pusilla*, which was also found exclusively at this site. The cyanobacteria *Chroococcus varius* and *Phormidium laetevirens* were also detected exclusively at BB.

Although clusters BV/BF and MA/LP experience several differences in environmental parameters, species composition was overlapping (see Fig. 24). Species like *Rhizoclonium hieroglyphicum* (MA) and *Chara globularis* (BF) were found exclusively at a single site. Others such as *Hildenbrandia rivularis* and *Achnantheidium pyrenaicum* (HUSTEDT) were characteristic for a whole cluster (BV/BF).

When comparing the environment results from NMDS (Fig. 11) and species-based results from DCA (Fig. 23), it emerges that both patterns show some similarities. BV/BF and BM/BJ are clustering together in both cases, which shows the unique features of these sites regarding both environmental characteristics and species composition.

## **Discussion**

### **Environment**

Data of the current study are comparable to published values (Elster et al., 2016). Seasonal differences were almost absent (Fig. 10), which underlines the stable abiotic conditions of springs. Already Vouk (1950) mentioned the importance of temperature stability as one key feature of thermal springs.

#### **BM & BJ**

With exception of BJIV, BM and BJ samplings are forming one single unit mainly defined by SH<sub>2</sub>. For BJIV, a contamination with organic matter (probably sulphur bacteria) during sampling is likely, resulting in an extremely high TOC value. The lower water temperature of BJ, compared to BM, results also in a slightly reduced conductivity and ion contents (though the proportional

composition of ions is similar) (Table 2). Due to the presence of  $\text{SH}_2$ , oxygen levels are low at both sites. The higher  $\text{SH}_2$  content at BM, compared to BJ, consequentially results in lower oxygen.

#### BV & BF

BV and BF had comparatively low mineral content with only marginal differences of some ions, such as  $[\text{SO}_4]^{2-}$ . There also are no larger differences in sky openness, oxygen content, temperature, conductivity or pH. Water temperature of BV decreased slightly over the last decades: Hacker (1993a) mentioned 22.8 °C, whereas Elster (2016b) listed 21.5 °C. Our measurements resulted in 19.8 °C (median). An answer to this decrease might be the exploitation of the thermal water body for bottled water by the Vöslauer Mineralwasser GmbH, which possibly influences the complex groundwater system.

#### MA & LP

Although it was below detection limit,  $\text{SH}_2$  was obviously present in trace amounts, as water had the characteristic pungent smell. Despite comparable mineral compositions, the sites are quite separated because of differences in certain environmental parameters (Fig. 11). The higher temperature at LP results in increased ion contents. Further differences are sky openness and oxygen concentration, which probably results from higher photosynthetic activity at MA. At LP, any surface in contact with spring water was covered with iron precipitates, which is caused by dissolved  $\text{Fe}^{2+}$  of more than 450  $\mu\text{gL}^{-1}$  (Hobiger 2011b). Also, the very low oxygen concentration at LP suggests oxygen consumption through iron oxidation. Elevated  $\text{P}_{\text{tot}}$  of MAIII, deviating from the other samplings (Fig. 11), was probably caused from street runoff. Generally, MA rather resembles a spring creek than a typical thermal spring habitat.

#### BB

Compared to all other sites, BB had a completely different hydrochemistry due to formation water. Besides very high ion content, also TOC was increased, which could have been caused by chemical treatment. Hydrochemical composition changed from 1997 to 2007 due to a decrease of the formation water component (Eisner & Goldbrunner 2009), which can be deduced from particularly  $\text{Na}^+$  (decline of 1000  $\text{mgL}^{-1}$ ) and  $\text{Cl}^-$  (decline of 600  $\text{mgL}^{-1}$ ). Also, the total mineral content dropped from 27 to 18  $\text{gL}^{-1}$  (Elster, 2016a). In the last years, a clear countertendency was observed especially in terms of



conductivity (32 vs. 20 mScm<sup>-1</sup>), Na<sup>+</sup> (8690 vs. 5570 mgL<sup>-1</sup>) and Cl<sup>-</sup> (6000 vs. 3620 mgL<sup>-1</sup>) (Table 2). Moreover, we found an unexpected increase of HCO<sub>3</sub><sup>-</sup> (13606.7 vs. 8090 mgL<sup>-1</sup>), K<sup>+</sup> (927 vs. 139 mgL<sup>-1</sup>) and [SO<sub>4</sub>]<sup>2-</sup> (2466 vs. 506 mgL<sup>-1</sup>).

### Species

Among major algae groups, cyanobacteria are the most abundant ones growing at water temperatures from around 30°C upward (Vouk, 1950). Their preference for warm conditions makes them suitable for thermal spring type characterisation (Vouk, 1950). Regarding the species number, diatoms are the second important group; although they are not forming a main component of the biofilm but grow only occasionally in larger quantities (Vouk, 1950). Green algae prefer moderate temperature ranges, where they can form blooms (Vouk, 1950). A more recent study by Stoyneva (2003) revealed quite wide temperature ranges of several green algae, studied on several Bulgarian thermal springs. These observations could also be verified for our sites.

The cyanobacterium *Leptolyngbya laminosa* is a common species of thermal habitats. Between the filaments, other coccal cyanobacteria such as *Aphanothece stagnina* (SPRENGEL) are found (Vouk, 1950). The sites BM, BJ and BB, characterised by elevated temperature, were dominated by *Leptolyngbya laminosa*. Although no thermophilic diatoms are known, some euryoecious species like *Pinnularia appendiculata* - also abundant in thermal waters (Vouk, 1950) – were observed at BM, BJ, LP with water temperature above 24°C. Interestingly, *P. appendiculata* was not detected at BB, although it is known also from soda lakes (Hofmann et al., 2011). According to Vouk (1950) common green algae in thermal springs are *Spirogyra* sp., *Cosmarium* sp., *Cladophora* sp. and *Rhizoclonium hieroglyphicum*; also, the rhodophyte *Audouinella chalybea* is quite abundant. *Spirogyra* sp. occurred at BF, *Cosmarium* sp. was found at BV and BF. At MA all five taxa were present. Stoyneva (2003) mentioned the genus *Spirogyra* in several Bulgarian thermal springs.

Temperature is not only directly affecting the composition of phytobenthos, but it is also decisive for dissolution processes thus indirectly influencing community composition. Temperature and salt in DCA diagrams are therefore pointing in the same direction (Fig. 22-24). The carst vector is however differently orientated, as the highest values were measured at sites with lower temperature

(MA, LP). BB on the contrary is high in temperature and low in carst, which illustrates the importance of the particular catchment geology.

The species inventory of the two thermal sulphur springs BM and BJ matches almost congruently, which perfectly fits to the hydrochemistry and geographical proximity. Besides sulphur bacteria, the benthic community was dominated mostly by three cyanobacteria species: the SH<sub>2</sub>-tolerant *Limnothrix lauterbornii*, accompanied by the cosmopolitan thermobionts *Leptolyngbya laminosa* and *Spirulina subsalsa*. Thermal springs worldwide are often dominated by *Mastigocladus laminosus* (COHN ex KIRCHNER) (Vouk, 1950). However, this cyanobacterium was not observed in this study. A possible explanation for the absence was provided by Castenholz (1976). SH<sub>2</sub> represents the strongest species-determining effect besides pH; *Mastigocladus laminosus* seems to react very sensitive to this toxic substance. In contrast, *Spirulina* seems to be highly competitive in the presence of SH<sub>2</sub>, even using it as reductant in photosynthesis (Castenholz, 1977). Perhaps an analogue situation applies to BB, where *Mastigocladus laminosus* is also replaced by *Leptolyngbya laminosa* and other cyanobacteria. Here the alkaline-saline water may have a repressing effect.

The acrotic springs of BV and BF are overlapping in respect of their species composition (Fig. 23), sharing some taxa which occur only at these sites, like *Hildenbrandia rivularis* and *Achnantheidium pyrenaicum*. *Hildenbrandia rivularis* reflects the environmental conditions of these sites, favouring shaded, calcareous waters (Eloranta et al., 2011). Different species richness of BV and BF results very likely from their different habitat structure, more specifically additional choriotoxes of BF. BV provides only concrete surface. BF has a rather diverse habitat structure including gravel and mosses.

MA and LP are forming a cluster of Ca<sup>2+</sup>-Mg<sup>2+</sup>-[SO<sub>4</sub>]<sup>2-</sup>-HCO<sub>3</sub><sup>-</sup> springs (Fig. 23). Characteristic taxa are *Lyngbya martensiana*, *Nitzschia amphibia* or *Halamphora normanii*. According to Komárek & Anagnostidis (2005), *Lyngbya martensiana* was already recorded from various thermal springs, although these data are described as problematic. *Nitzschia amphibia* favours alkaline waters with medium to high trophic levels (Hofmann et al., 2011). Main occurrence of *Halamphora normanii* were MA and LP, though it was also found at BM, BF and BV. The taxon is known from aerophilic habitats like wet rocks, but also from springs, where it sometimes can be found

at higher abundance (Krammer & Lange-Bertalot, 2007b). Species richness of spring coenoses not only depends on hydrochemistry but also on substrate type (e.g. Weber, 2006). MA rather resembles a spring creek offering several choriotopes, such as macro-algae with epiphytic algal cover. Contrarily, only vertical homogenous surface is offered at LP. Also, light supply, estimated in the current study as sky openness, is quite different between sites. For diatom species composition and diversity, the availability of sunlight seems to be a highly relevant factor (Cantonati et al., 2006), which may be decisive considering that diatoms have the species number at MA. High light supply at MA also favours *Cladophora glomerata*, occurring mainly at high light intensity (Gutowski & Foerster, 2009). Iron precipitates at LP probably also trigger differences in community composition of MA and LP.

Some similarities in species pattern were also obvious for BF, BV, MA and LP. It is noticeable that several species (especially diatoms) occur predominantly or exclusively in calcareous or alkaline waters. For instance, *Rhizoclonium hieroglyphicum*, *Gongrosira incrustans*, *Vaucheria debaryana*, *Cosmarium laeve* (RABENHORST) or diatoms like *Epithemia goeppertiana*, *Achnantheidium pyrenaicum* and *Rhoicosphenia abbreviata* (Gutowski & Foerster, 2009; Hofmann et al., 2011). Especially *Caloneis fontinalis*, identified at all four sites (BF, BV, MA, LP), frequently occurs in calcareous springs and their run-offs (Hofmann et al., 2011). Limestone is known to hosts many cosmopolitan diatom species (Cantonati, 1998; Sabater & Roca, 1992). At these four sites, *Navicula tripunctata* (O. F. MÜLLER), *Cocconeis pediculus* and *Ellerbeckia arenaria* (D. MOORE ex RALFS) indicate calcareous bedrock (Hofmann et al., 2011; Krammer & Lange-Bertalot, 2007b, 2008). Carst is the main explanatory parameter for the distance between the two clusters BV/BF and MA/LP (Figs. 22 to 24). *Rhizoclonium hieroglyphicum*, preferring calcareous waters, only occurs at MA. Besides already mentioned differences in habitat structure, high  $[\text{SO}_4]^{2-}$  content distinguishes those sites at the eastern thermal line (MA, LP) from those in the west (BF, BV). Additionally, geographical distance between the two clusters might play a key role for differences in species pattern, as springs can be seen as island in the landscape.

At BB, splashing water and steam favour growth of colony-forming coccal cyanobacteria *Chroococcus varius*. It typically grows aerophytic on wet rocks and is also known from indoor spa areas (Komárek & Anagnostidis, 1998; Vouk, 1950). The submerged surfaces are dominated by

assemblages of filamentous cyanobacteria such as thermobiotic *Leptolyngbya laminosa* and *Phormidium laetevirens*, the latter known from marine environments but also from outflows of salty (and sulphur) thermal springs (Komárek & Anagnostidis, 2005). *Nitzschia pusilla*, as the only diatom species at BB, is commonly known from electrolyte-rich or salty waters (Hofmann et al., 2011).

Information on categories of threat of benthic algae (Table 6) was based on German Red Lists (Knappe et al., 1996; Lange-Bertalot, 1996), though the use of such lists outside Germany needs to be questioned. For an Austrian Red List, it would be a prerequisite to have extensive records on the algae flora. To make reliable statements about the endangerment of species, detailed historical information of taxa occurrences is also essential. Unfortunately, both raised preconditions are not met for most areas in Austria (Kusel-Fetzmann, 1999). German Red Lists may however be used for approximate assessments. Except for a few diatom taxa and red algae, no classification is at hand. Concerning diatoms, no assessment can be done. The few red algae species listed for Austria are adapted to cool, flowing, shady and unpolluted waters so all of them might be treated as endangered (Kusel-Fetzmann, 1999).

Although physico-chemistry of spring water turned out to be stable, light supply might change significantly depending on the season. Samplings (I-V) however did not reveal seasonal shifts in species composition, which can be interpreted that irradiance intensity does not play a key role for community composition. This attribute favours perennial stayers, an ecological life strategy of long-term persistence (During, 1979). The vegetation of springs is therefore defined as an azonal, perennial association (Siebum & Schaminée, 1991), whereby the azonal character is even more pronounced for thermal springs. Cox (1990) and Cantonati (1998) also found only marginal seasonal changes in diatom species composition of investigated spring sites. Several species of cyanobacteria and some diatoms are described as (probably) cosmopolitan; amongst them also taxa from thermal waters (Komárek & Anagnostidis, 2005; Krammer & Lange-Bertalot, 2007a). Highest abundances of cosmopolitan algae were detected at sites with water temperatures above 23°C, like LP, BM, BJ and BB (*Leptolyngbya laminosa*, *Spirulina subsalsa*, *Phormidium tergestinum*, *Phormidium molle*, *Nitzschia pusilla*). Apparently, there is a trend in higher proportions of cosmopolitans in springs with higher temperature.

## Linking species and environment

Obtained data were used to characterise the sites according to the thermal spring habitat types according to Vouk (1950). This differentiation of thermal spring main types is primarily based on similarities in algae vegetation and was meant to serve as a rather provisional suggestion. Nonetheless, there have been no comprehensive attempts to classify thermal springs based on biology since that time, because it became increasingly hard to study natural thermal spring habitats, especially in Central Europe. Also, for (nonthermal) springs in low altitudes this problem was already noted by other authors such as Cantonati et al. (2012b), and Gieserich & Kofler (2010). For low temperate thermal springs, we applied nonthermal phytobenthos-based classification systems, whereby the applicability here is only proved for mountainous areas so far (Cantonati et al., 2012b; 2012c). To compare chemical-physical parameters with diatom assemblages, Werum & Lange-Bertalot (2004) suggested considering the morphology of springs. Limnocrenes and helocrenes are springs with stagnant water, rheocrenes are characterised by the constant drain of water (Glazier, 2009). Basically, all sites can be treated as rheocrenes.

### BM

With dominance of cyanobacteria and sulphur bacteria in eothermal water, this spring type can be classified as 'sulphur-blue thermal spring' (in the original: 'Schwefel-Blau-Therme'). Sulphur bacteria are not thermophilic organisms but only thermotolerant. Nevertheless, they are forming the main vegetation cover of sulphur springs. These chemoautotrophic bacteria are taking their energy from the oxidation of  $\text{SH}_2$ , regardless from the availability of sunlight. Purple sulphur bacteria carry out anoxygenic photosynthesis by using  $\text{SH}_2$  and light. *Leptolyngbya laminosa* is furthermore listed as a typical blue alga for the *Phormidium*-subtype of 'blue thermal springs' ('Blauthermen'), which are most common in akro- and hyperthermal springs from 44°C upwards (Vouk, 1950).

### BJ

Also, BJ can be classified as sulphur-blue-thermal spring, though the chliarothermal water temperature (26.3°C) indicate the 'sulphur springs' type ('Schwefel-Thermen'). This type usually occurs at temperatures below 28°C. Compared to sulphur-blue-thermal springs, cyanobacteria play a smaller role for the expense of by sulphur bacteria (Vouk, 1950). Obviously, this differentiation

cannot be confirmed in this case, as cyanobacteria are very dominant, especially *Limnothrix lauterbornii* - a species known for its high tolerance against SH<sub>2</sub> (Komárek & Anagnostidis, 2005).

#### BV

Following the classification by Vouk (1950), the algae composition (see Fig. 14) in chliarothermal (18-28°C) water of BV indicates 'blue-green thermal spring' (in the original: 'Blau-grün-Therme'). Since the tepid temperature at BV is not fostering cyanobacteria dominated vegetation, applying nonthermal classification systems is justified. Several taxa (*Hildenbrandia rivularis*, *Phormidium retzii* (KÜTZING ex GOMONT), *Amphora pediculus* (KÜTZING), *Caloneis fontinalis*, *Cocconeis pseudolineata* (GEITLER)) indicate 'spring type 2' for both diatom and non-diatom classification according to Cantonati et al. (2012b, 2012c). 'Spring type 2' includes low-altitude rheocrenes on carbonate substrate and shaded conditions. It however needs to be mentioned that only low frequencies of the listed taxa were recognized, and strong indicator species were missing. Apart from that, the classification matches quite well.

#### BF

Algae group composition (Fig. 14) is comparable to BV, which is characterised as 'blue-green thermal spring', with typical taxa like *Spirogyra* sp. and *Chara globularis*. Following the nonthermal spring types, *Pleurocapsa minor* (HANSGIRG), *Hildenbrandia rivularis*, *Amphora pediculus*, *Caloneis fontinalis*, *Cocconeis pseudolineata* and *Cocconeis placentula* var. *lineata* (EHRENBERG) are also indicating 'spring type 2'. Like for BV, frequency of indicator species does not perfectly match with our findings (Cantonati et al., 2012b, 2012c), but the classification seems to be reasonable.

#### MA

Considering the algae group composition (Fig. 14), and occurrence of *Rhizoclonium hieroglyphicum*, this site can be characterised as 'blue-green thermal spring' type as well (Vouk, 1950). There are at least partly notable frequencies of several indicator species for 'spring type 2' (Cantonati et al., 2012b, 2012c): *Audouinella* spp. (BORY), *Amphora pediculus*, *Caloneis fontinalis*, *Cocconeis placentula* var. *lineata*. Despite highly exposed to anthropogenic impact, and not directly a spring habitat, the site does not seem to be strongly affected. *Audouinella chalybaea* and *Gongrosira*

*incrustans* are quite sensitive to elevated phosphorous contents; their occurrence indicates high ecological quality (Gutowski & Foerster, 2009).

#### LP

Both low species number and low algal abundance are striking. Iron precipitates obviously act as stressor to algal biofilms, which is in accordance to Cantonati et al. (2012c), who observed poorly developed filamentous green algae and yellow-green algae in (nonthermal) iron springs. We therefore classified the site as 'spring type 7' or iron spring referring to Cantonati et al. (2012b). Vouk (1950) described an 'iron-blue thermal spring' type ('Eisen-Blau-Thermen') as eothermal (28-44 °C) springs dominated by cyanobacteria and iron bacteria. Although the water temperature at LP is about four degrees below the mentioned type, the dominance of cyanobacteria and iron bacteria is a clear indicator for this thermal spring type.

#### BB

Following Vouk (1950), pure cyanobacteria and diatom assemblages can be observed mainly in eothermal (28-44 °C) water paired with high salinity, which matches perfectly with BB. The species-poor, extremotolerant algae vegetation clearly indicates a 'blue-diatom thermal spring' ('Blau-Kiesel-Therme').

#### Conclusions

We found a negative correlation of water temperature and species number (Fig. 22), which was found already by Glazier (2009) at temperature above 35°C. Since sites with highest temperatures (BM, BJ, BB) are also very specific mineral springs, the temperature influence always must be linked to indirect effects, which influence hydrochemistry. In addition, choriotope diversity and other environmental parameters may also blur the aforementioned pattern. The question arises if a certain temperature threshold value does exist for characteristic thermal springs in a proper sense, however the environment is a multifactorial space. Within the same spring, exemplified by BM, some species ecological preferences are described in terms of specific dissolved substances, like SH<sub>2</sub> tolerant *Limnothrix lauterbornii*, while others, such as *Leptolyngbya laminosa* are described as thermophilic (Komárek & Anagnostidis, 2005). It seems there is a rather wide range of thermo-mineral springs with species sets determined by at least both temperature and mineral content. Nevertheless, minimum

temperature limits for growth of thermophilic cyanobacteria are still poorly studied (Castenholz, 1969). A comparative study on temperate thermal and nonthermal springs would provide more insight into this topic. Following the abovementioned statements, temperature and mineral contents are obviously affecting the species composition.

Derived from this, the question rises how far it is possible to characterise springs based on these parameters. The proportion of cyanobacteria in phytobenthos tends to rise along with temperature. The algae group composition may be a rough but nonetheless practical indicator for assessment (Vouk, 1950). In freshwater ecology, diatoms are well-proven bioindicators. It is also known that different spring types exhibit a characteristic diatom flora (Cantonati et al., 2012b, 2012c; Werum, 2001). Villeneuve & Pienitz (1998) could not find a diatom flora specific to thermal springs on a global scale, since physico-chemical characteristics and geographical distance lead to differences in diatom assemblages. Available classifications developed by Cantonati et al. (2012b, 2012c) were already applied successfully in this study for the lower temperature sites (BV, BF, MA). At higher temperatures, the overall tendency towards euryoecious taxa might impede precise separation.

Besides classification attempts, it is important to recognise the unique nature of each spring (Vouk, 1950), which can be concluded from both environmental characteristics and the phytobenthos community. Characteristic diatoms in a case study on thermal sulphur waters performed by Mannino (2007), were not matching with those identified at the thermal sulphur springs BM and BJ. For nonthermal springs, Cantonati et al. (2012b) were also stressing, that most diatom taxa were found only at single sites. Following Castenholz (1969, 1976), there are significant differences in species pattern between thermal springs with similar temperature and chemistry, which seems to be the result of specific ions excluding certain taxa. Not only ion contents are decisive, but also their proportion (Prát, 1956). On the other hand, there are also cases of high species similarity between chemically different sites (Castenholz, 1976).

We applied the concept of hemeroby to compare our sites based on their ecological integrity. Hemeroby describes overall human impact to an ecosystem with classes from ahemerob (unaffected), oligohemerob (minor influence), mesohemerob (medium influence), euhemerob (strong influence), polyhemerob (very strong influence) to metahemerob (destroyed) (Schaefer, 2012). The original



concept developed by Jalas (1955) and its elaboration by Sukopp (1972) was adapted to stream water landscapes by Grabherr et al. (1993), however no adequate hemeroby system for (thermal) springs does exist so far. We therefore tried a first classification attempt and compared the studied sites based on their habitat structure. Considering the artificial substrates at BM, BJ, LP, BV and BB, we classify these springs as euhemerob. BF and MA are also concreted streambeds, but the bed consists of gravel with some macrophyte cover. These sites are classified as mesohemerob. Additional choriotypes (like macrophytes) contribute to species richness. Yet species numbers also depend on other attributes like water temperature, the comparison of sites within a joint cluster (Fig. 23) like BV (31 taxa) / BF (38 taxa) reveals the effect of hemeroby on species number. Though this effect may not be very evident, it can still be assumed that the other sites would have a potentially higher species number under more natural conditions. It has to be pointed out that species-poor sites are not per se less worthy of protection, as this is also a general feature of extreme habitats; known as one of the biocoenotic basic rules of Thienemann (Lampert & Sommer, 1993). Moreover, it is also worth to look at microdiversity. As an example, populations of the well-known cosmopolitan, thermophilic cyanobacterium *Mastigocladus laminosus* turned out to be genetically isolated both on a global scale, and regional scale (Miller et al., 2006, 2007).

### **Conservation approaches**

Inadequate protective legislation and high utilisation pressure pose serious threats to thermal spring ecosystems. Springs generally cover only very small areas hence adequate conservation approaches are highly needed. In the case of BF, the designation as natural monument is based on three highly endangered freshwater snail species. These umbrella species are also protecting the whole habitat. Nevertheless, the scattered selection of conservation sites does not sufficiently acknowledge thermal spring habitats in general. As mentioned earlier, more research is needed to define specific thermo-mineral springs types, to be included on the Appendix I list of FFH habitat types. A more comprehensive approach would certainly be an extension of the scope of the Water Framework Directive towards headwaters. Besides legislative protection, information of the public about the high value of thermal vegetation is highly recommended. Due to widespread unawareness, algae are generally regarded as bad or unpleasant. To change this public opinion, educated persons in spas could

function as multipliers to arouse interest among visitors. This could be achieved, through information panels or ideally based on well-preserved spring habitats in themselves, functioning as sights. Vouk (1950) also mentioned the use of so-called 'barépine' for therapeutic purposes. At some places, this medicinal mud, consisting of diverse thermal algae or also purple bacteria, is used to treat physical ailments (Vouk, 1950). A sustainable harvesting of local thermal vegetation may also protect organisms and diversity. The classical approach is based on the effort to keep the bathing water 'clean', which means the destruction of thermal spring vegetation. Spring water for drinking must be free from pathogens, but for bathing these hygienic precautions do not make sense, as biofilms belong to the natural environment, just as in any other natural habitat. Benthic algae mainly cause problems because of slippery grounds (Vouk, 1950). Therefore, it is often necessary to clean overgrown bathing areas. In the case of structural changes, it usually would have been easy to split the bathing area from the spring habitat or to keep at least part of the outflow untouched (Vouk, 1950). Looking at the sites of this study, BF represents a good practice example of how to use thermal water without destroying the spring habitat. Here, the natural monument preserves the spring environment with simultaneous use of the water directly downstream. This strategy is however not considering conservation of spring creek habitats below thermal baths. Unfortunately, (near) natural thermal spring habitats represent an exception case. Therefore, the question arises whether damaged or destroyed sites can be restored. If a suitable habitat structure is available, algae tend to regain their territory in a short time, although the restoration of previously destroyed habitats will most likely not directly return the initial biocoenosis (possible endemic species are most likely irretrievably lost). Nevertheless, such habitats could also serve as stepping stones for stenoeccious organisms. Even though they do not correspond to all the environmental parameters of the original thermal spring, spa water outlets usually contain at least remnants of the initial thermal vegetation. Such areas can be found in many spa establishments (Vouk, 1950) as in the case of MA. Of course, the quality of such substitute habitats depends very much on how external factors affect the development of a typical biocoenosis. Regarding the situation at MA, temperature decline and fluctuations, and impacts on water chemistry are obvious. It is therefore recommended to maintain (near) natural sites or even to restore them towards the initial conditions.

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## Tables and Figures

**Table 1.** Site details. ID: abbreviation used in this study; coordinates: dd°mm'ss.s".

location	spring-name	ID	coordinates	m a.s.l.
Baden bei Wien	Marienquelle	BM	N 48°00'19.5" E 16°13'58.2"	226
	Johannesquelle	BJ	N 48°00'22.8" E 16°13'45.9"	226
Bad Vöslau	Ursprungsquelle	BV	N 47°58'00.8" E 16°12'38.1"	259
Bad Fischau-Brunn	Damenquelle	BF	N 47°49'57.8" E 16°09'53.5"	285
Mannersdorf am Leithagebirge	Badquelle (substitute site)	MA	N 47°58'38.1" E 16°35'40.7"	185
Leithaprodersdorf	Thermalquelle Leithaprodersdorf	LP	N 47°55'33.4" E 16°28'19.5"	202
Bad Blumau	Vulkaniquelle	BB	N 47°07'31.4" E 16°02'51.0"	268

**Table 2.** Environmental parameters for the respective sites; values given as minimum-median-maximum. For BM, BF, MA and LP temperature data are extracted from temperature profiles (Fig. 2).

<b>Environmental parameter / Site</b>	<b>BM</b>	<b>BJ</b>	<b>BV</b>	<b>BF</b>	<b>MA</b>	<b>LP</b>	<b>BB</b>
<b>Sky openness [%]</b>	38-40-42	33-36-38	35-46-57	35-38-38	66-74-76	18-27-48	79-80-82
<b>Oxygen content [%]</b>	22.3-29.0-44.5	50.4-54.5-61.0	60.8-64.3-71.1	79.8-83.4-87.8	96.0-98.4-99.2	28.5-33-35.9	72.1-78.3-100.1
<b>Temperature [°C]</b>	34.5-34.7-35.0	25.8-26.4-27.0	19.5-19.8-20.2	18.8-19.1-19.9	13.0-21.5-24.4	23.0-24.2-24.5	34.9-36.1-36.1
<b>Conductivity [mScm<sup>-1</sup>]</b>	2.18-2.19-2.21	1.72-1.76-1.80	0.70-0.70-0.72	0.59-0.59-0.60	1.67-1.82-1.83	3.10-3.21-3.25	29.2-32.70-36.20
<b>pH</b>	7.40-7.60-7.60	7.60-7.70-7.70	7.30-7.70-7.70	7.70-7.90-7.95	8.10-8.20-8.31	7.10-7.10-7.15	7.90-8.10-8.25
<b>mean TOC [ppb]</b>	101-148-533	244-295-(12533)	322-3434-1090	174-192-6727	292-454-697	215-268-434	1721-39200-864000
<b>Na<sup>+</sup> [mgL<sup>-1</sup>]</b>	148.7-157.6-159.9	111.8-114.2-117.3	9.1-9.4-9.6	12.1-12.4-20.8	17.3-18.6-22.4	153.9-162.3-167.8	7761.6-8096.3-10344
<b>K<sup>+</sup> [mgL<sup>-1</sup>]</b>	0.0-0.0-8	0.0-6.9-9.1	0.0-1.7-1.8	0.0-1.5-2.0	6.1-8.6-9.3	17.5-23.5-24.9	719.3-927.0-1020.2
<b>Ca<sup>2+</sup> [mgL<sup>-1</sup>]</b>	248.3-248.5-254.7	195.0-201.0-210.0	91.8-93.8-97.4	81.6-83.2-85.5	276.2-307.9-310.3	435.0-462.1-483.5	0.0-0.0-27.1
<b>Mg<sup>2+</sup> [mgL<sup>-1</sup>]</b>	68.1-68.8-69.3	60.0-62.7-64.5	36.8-37.5-38.6	24.4-24.8-25.1	82.5-91.5-96.3	149.8-150.6-157.1	0.0-0.0-14.8
<b>Cl<sup>-</sup> [mgL<sup>-1</sup>]</b>	251.7-254.1-270.8	173.6-179.2-189.1	14.6-14.9-16.2	18.0-18.3-22.0	11.1-21.0-33.8	183.4-191.3-208.6	5291.7-6062.6-6578.6
<b>HCO<sub>3</sub><sup>-</sup> [mgL<sup>-1</sup>]</b>	272.1-299.0-305.1	272.1-286.8-311.2	292.9-323.4-329.5	292.9-299.0-329.5	244.1-262.4-272.1	543.0-549.2-555.3	12508.4-13606.7-15803.4
<b>[SO<sub>4</sub>]<sup>2-</sup> [mgL<sup>-1</sup>]</b>	635.6-643.8-684.5	462.7-484.4-496.5	112.8-115.3-125.9	47.8-49.1-57.2	881.8-943.1-974.8	1305.0-1366.8-1495.6	2025.0-2466.0-2821.7
<b>Ptot [µgL<sup>-1</sup>]</b>	6-8-13	4-5-22	3-5-8	4-4-8	18-26-271	8-16-33	965-1162-1219
<b>Si [µgL<sup>-1</sup>]</b>	10-10-16	8-8-10	4-4-4	3-3-4	9-10-10	11-12-12	11-54-62
<b>SH<sub>2</sub> [mgL<sup>-1</sup>]</b>	2.38-4-7.84	0.1-1.8-5	BOD	BOD	BOD	BOD	BOD

**Table 3.** PCA of ions. Reduction from nine highly correlated variables to two.

	<b>salt</b>	<b>carst</b>
Explained variance [% total]	78%	97%
Conductivity [mScm <sup>-1</sup> ]	<b>0,949088</b>	-0,294844
Na <sup>+</sup> [mgL <sup>-1</sup> ]	<b>0,934832</b>	-0,349377
K <sup>+</sup> [mgL <sup>-1</sup> ]	<b>0,933819</b>	-0,340795
Ca <sup>2+</sup> [mgL <sup>-1</sup> ]	-0,206386	<b>0,97651</b>
Mg <sup>2+</sup> [mgL <sup>-1</sup> ]	-0,188732	<b>0,977415</b>
Cl <sup>-</sup> [mgL <sup>-1</sup> ]	<b>0,928589</b>	-0,343945
HCO <sub>3</sub> <sup>-</sup> [mgL <sup>-1</sup> ]	<b>0,924788</b>	-0,352147
[SO <sub>4</sub> ] <sup>2-</sup> [mgL <sup>-1</sup> ]	<b>0,971656</b>	0,203413
Si [μgL <sup>-1</sup> ]	<b>0,915649</b>	-0,152444

**Table 4.** DCA results.

Axes	1	2	3	4
Eigenvalues	0,913	0,662	0,423	0,192
Cum % variance of response data	17,5	30,1	38,2	41,9
Sum of all eigenvalues: 5,2246				

**Table 3.** Results from DCA. Correlation of taxa with environmental variables.

	season	sky	O <sub>2</sub>	temp	pH	TOC	Ptot	SH <sub>2</sub>	salt	carst
<i>Achnanthydium exile</i>	-0,7308	-0,6792	0,6508	-0,7159	0,2548	-0,1207	-0,279	-0,3715	-0,3599	-0,5515
<i>Achnanthydium minutissimum</i>	-0,1153	-0,0119	0,1571	-0,4918	-0,0384	-0,1223	-0,2292	-0,3715	-0,2946	-0,1564
<i>Achnanthydium pyrenaicum</i>	-0,0019	-0,3051	-0,2295	-0,4623	-0,5113	-0,1254	-0,2884	-0,3715	-0,3439	-0,4258
<i>Amphora ovalis</i>	0,4653	0,6131	0,8766	-0,6955	0,6791	-0,1247	-0,2393	-0,3715	-0,2071	0,2868
<i>Amphora pediculus</i>	-0,0152	0,1718	0,2039	-0,4713	0,0931	-0,1211	-0,2223	-0,3715	-0,2183	0,2768
<i>Aphanothece stagnina</i>	0,5849	-0,7325	-1,3211	1,3215	-0,6477	-0,1275	-0,2672	2,0204	-0,1496	0,2586
<i>Audouinella chalybaea</i>	-0,7841	1,1797	1,1023	-0,4904	1,4056	-0,1214	0,0892	-0,3715	-0,1137	0,8669
<i>Aulacoseira granulata</i>	0,9312	1,4886	1,1324	-0,4993	1,0584	-0,1254	-0,2023	-0,3715	-0,1162	0,7656
<i>Brachysira neoexilis</i>	1,0005	-0,8865	-0,5777	0,7594	-0,5178	-0,0256	-0,2912	0,0869	-0,1898	0,1441
<i>Caloneis alpestris</i>	0,6542	-0,5903	0,3738	-0,6225	-0,0542	-0,1278	-0,2953	-0,3715	-0,3611	-0,5671
<i>Caloneis budensis</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Caloneis cf. tenuis</i>	1,3467	-0,7976	-0,609	0,7034	-0,6724	-0,127	-0,2912	0,4784	-0,1934	0,1683
<i>Caloneis fontinalis</i>	-0,1349	-0,2756	-0,3906	-0,3554	-0,6113	-0,1224	-0,2439	-0,3715	-0,2427	0,1949
<i>Caloneis lancettula</i>	0,3574	0,2939	-0,6479	0,9515	0,0562	-0,126	-0,244	0,7356	-0,1082	0,5149
<i>Calothrix parietina</i>	-0,0117	-0,661	0,4446	-0,6513	0,0349	-0,1055	-0,2922	-0,3715	-0,3568	-0,557
<i>Chantransia-Stadien</i>	0,7927	-0,075	-0,4124	-0,4545	-0,796	-0,1285	-0,2823	-0,3715	-0,3402	-0,4058
<i>Chara globularis</i>	-0,0383	-0,6555	0,4757	-0,6599	0,1003	-0,1047	-0,292	-0,3715	-0,3574	-0,5631
<i>Chroococcus varius</i>	-0,0383	1,8322	0,4131	2,5746	0,9039	1,9299	4,2531	-0,3715	4,3287	-3,0825
<i>Chroodactylon ornatum</i>	-0,4538	1,1096	1,127	-0,6898	1,3861	-0,1227	-0,2081	-0,3715	-0,1276	0,8052
<i>Cladophora glomerata</i>	-0,2114	1,2902	1,1344	-0,3611	1,3521	-0,1237	0,0421	-0,3715	-0,121	0,8398

<i>Cocconeis pediculus</i>	-0,2692	1,2557	1,1094	-0,5541	1,2903	-0,1224	-0,048	-0,3715	-0,1139	0,8309
<i>Cocconeis placentula</i> var. <i>lineata</i>	-0,1076	-0,081	0,6472	-0,6543	0,4496	-0,1088	-0,2172	-0,3715	-0,285	-0,1541
<i>Cocconeis pseudolineata</i>	-0,0383	-0,2448	0,0641	-0,579	-0,1263	-0,1248	-0,2939	-0,3715	-0,3549	-0,5056
<i>Cosmarium laeve</i>	0,5003	-0,2251	0,0564	-0,4648	-0,3976	-0,1263	-0,2255	-0,3715	-0,3201	-0,3103
<i>Craticula buderi</i>	-0,3846	1,2813	1,1181	-0,391	1,3459	-0,1227	0,0859	-0,3715	-0,1144	0,856
<i>Cyclotella meneghiniana</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Cymbella compacta</i>	-0,5577	0,2241	-0,4884	-0,4685	-0,3942	-0,1234	-0,2851	-0,3715	-0,3413	-0,3903
<i>Cymbella cymbiformis</i>	0,6542	-0,9753	-0,5464	0,8154	-0,3633	0,0758	-0,2912	-0,3046	-0,1863	0,1199
<i>Diadsmis confervacea</i>	1,0499	1,4785	1,1033	-0,5825	1,0055	-0,1252	-0,1975	-0,3715	-0,119	0,7338
<i>Diadsmis contenta</i>	-0,7308	1,0385	1,1601	-0,6039	1,5221	-0,1232	-0,2056	-0,3715	-0,1358	0,8245
<i>Diploneis krammeri</i>	-0,2547	0,2463	0,5441	-0,5618	0,4693	-0,1043	-0,1396	-0,3715	-0,2608	-0,0165
<i>Diploneis oculata</i>	-0,0383	1,2162	1,0774	-0,8186	1,1821	-0,1219	-0,2117	-0,3715	-0,1154	0,7763
<i>Ellerbeckia arenaria</i> f. <i>arenaria</i>	0,1348	-0,7532	0,615	-0,6225	0,1003	-0,1259	-0,2912	-0,3715	-0,3609	-0,5606
<i>Encynopsis microcephala</i>	0,2387	-0,614	-0,1073	-0,0567	-0,2397	-0,0856	-0,2949	0,1076	-0,2832	-0,2646
<i>Epithemia goeppertiana</i>	0,005	-0,6607	0,4883	-0,6575	0,0907	-0,1062	-0,2922	-0,3715	-0,3576	-0,5631
<i>Euglena</i> cf. <i>adhaerens</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Fallacia lenzii</i>	0,2214	1,0903	1,0506	-0,5548	1,0275	-0,1237	-0,0971	-0,3715	-0,1431	0,6364
<i>Fallacia monoculata</i>	-0,1537	-1,3307	-1,8308	0,2676	-2,192	-0,1262	-0,2511	-0,3715	0,0184	1,8781
<i>Fallacia pygmaea</i> ssp. <i>subpygmaea</i>	0,6542	1,3642	1,1053	-0,6225	1,1125	-0,1246	-0,1975	-0,3715	-0,1244	0,7433
<i>Fragilaria</i>	0,6542	-0,5903	0,3738	-0,6225	-0,0542	-0,1278	-0,2953	-0,3715	-0,3611	-0,5671



<i>construens f. venter</i>										
<i>Fragilaria elliptica</i>	0,6542	-0,6397	0,4751	-0,6225	-0,0542	-0,1277	-0,2953	-0,3715	-0,3612	-0,566
<i>Fragilaria gracilis</i>	0,1804	-0,4828	-0,4987	-0,3532	-0,9343	-0,1255	-0,2895	-0,3715	-0,3029	-0,1655
<i>Fragilaria ulna</i>	0,2387	-0,1994	0,3912	-0,6524	0,0385	-0,1254	-0,2806	-0,3715	-0,3056	-0,2413
<i>Frustulia vulgaris</i>	1,0697	1,4768	1,0984	-0,5964	0,9966	-0,1252	-0,1966	-0,3715	-0,1195	0,7285
<i>Gloeocapsa atrata</i>	0,6542	-0,7384	0,6776	-0,6225	-0,0542	-0,1275	-0,2953	-0,3715	-0,3613	-0,5637
<i>Gomphonema clavatum</i>	-0,2692	1,2359	1,0916	-0,5499	1,2954	-0,1224	0,0137	-0,3715	-0,1194	0,8133
<i>Gomphonema italicum</i>	0,3079	1,3939	1,102	-0,4078	1,1898	-0,124	0,0472	-0,3715	-0,1186	0,7973
<i>Gomphonema olivaceum</i> var. <i>olivaceum</i>	-0,1768	1,3465	1,1109	-0,2752	1,3181	-0,1234	0,1923	-0,3715	-0,1173	0,8459
<i>Gomphonema parvulum</i> var. <i>parvulum</i> f. <i>parvulum</i>	-0,3269	-0,773	-0,7798	-0,1992	-0,9943	-0,1174	-0,2647	-0,3715	-0,1977	0,5235
<i>Gomphonema pumilum</i>	-0,1477	-0,4391	0,3273	-0,5704	0,0678	-0,1091	-0,232	-0,3715	-0,3402	-0,4508
<i>Gomphonema subclavatum</i>	0,3079	-0,1498	0,0525	-0,5292	-0,3247	-0,1258	-0,277	-0,3715	-0,3001	-0,197
<i>Gomphosphenia lingulatiformis</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Gongrosira incrustans</i>	-0,0148	0,1029	0,4718	-0,4848	0,2863	-0,1158	-0,1699	-0,3715	-0,2156	0,2763
<i>Halamphora normanii</i>	-0,2272	-0,1336	-0,3124	-0,1336	-0,4373	-0,1244	-0,1508	-0,2912	-0,1098	0,9516
<i>Heribaudiella fluviatilis</i>	-0,0383	-0,6555	0,4757	-0,6599	0,1003	-0,1047	-0,292	-0,3715	-0,3574	-0,5631
<i>Hildenbrandia rivularis</i>	-0,0383	-0,4482	0,0553	-0,5478	-0,2768	-0,1149	-0,2904	-0,3715	-0,3491	-0,4815
<i>Hydrococcus rivularis</i>	-0,3846	0,6831	0,309	-0,1743	0,4094	-0,1238	0,2571	-0,3715	-0,2217	0,2443

<i>Karayevia ploenensis</i>	-0,7308	1,0385	1,1601	-0,6039	1,5221	-0,1232	-0,2056	-0,3715	-0,1358	0,8245
<i>Klebsormidium flaccidum</i>	-0,0383	-0,2409	-0,3651	-0,4358	-0,6538	-0,125	-0,2888	-0,3715	-0,3408	-0,3999
<i>Leptolyngbya aeruginea</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Leptolyngbya laminosa</i>	-0,0383	0,0654	-0,8946	1,7852	-0,1757	0,6101	1,0362	1,2696	1,1523	-0,695
<i>Leptolyngbya valderiana</i>	-0,1277	-0,6219	0,2363	-0,3984	-0,0094	-0,1084	-0,2924	-0,0162	-0,3209	-0,4194
<i>Limnothrix lauterbornii</i>	-0,0383	-0,6496	-1,3389	1,4877	-0,6106	-0,1059	-0,277	1,926	-0,1321	0,2658
<i>Lyngbya martensiana</i>	0,3208	-0,201	-0,5552	-0,0685	-0,7399	-0,1255	-0,1194	-0,3715	-0,0771	1,2222
<i>Melosira varians</i>	0,7801	1,1892	0,9513	-0,4884	0,9348	-0,125	-0,2063	-0,2943	-0,1295	0,6917
<i>Microcystis cf. flos-aquae</i>	-1,4234	-0,5607	-2,0966	2,1413	-0,8578	-0,1219	-0,2708	2,2787	-0,016	0,3763
<i>Navicula antonii</i>	-0,6443	-0,2127	-0,7419	-0,0319	-0,8424	-0,1245	-0,2357	-0,3715	-0,0265	1,5233
<i>Navicula cincta</i>	-0,0383	-0,9753	-1,7973	0,2054	-2,2178	-0,1257	-0,2572	-0,3715	0,0269	1,8415
<i>Navicula cryptocephala</i>	1,0499	-0,8738	-0,5822	0,7514	-0,5399	-0,0401	-0,2912	0,1428	-0,1903	0,1476
<i>Navicula cryptotenelloides</i>	-0,0383	-0,5607	0,3807	-0,6412	0,048	-0,1094	-0,2925	-0,3715	-0,3568	-0,5498
<i>Navicula tripunctata</i>	-0,0383	1,231	1,1031	-0,7276	1,2246	-0,1226	-0,2112	-0,3715	-0,1172	0,7902
<i>Navicula trivialis</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Naviculadicta absoluta</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Nitzschia abbreviata</i>	-1,4234	0,9792	1,1243	-0,8466	1,4912	-0,1192	-0,2382	-0,3715	-0,1047	0,8981
<i>Nitzschia amphibia</i>	-0,1768	0,079	-0,2769	-0,2167	-0,3283	-0,1245	-0,2178	-0,3715	-0,0586	1,3245
<i>Nitzschia communis</i>	0,5157	1,2872	1,0823	-0,7159	1,1326	-0,1241	-0,1934	-0,3715	-0,13	0,7225
<i>Nitzschia constricta</i>	0,4234	1,5321	1,0216	-0,2179	1,0791	-0,1231	0,4671	-0,3715	-0,1105	0,7984

<i>Nitzschia denticula</i>	0,814	-0,7612	0,0048	0,0153	-0,2682	-0,0806	-0,2934	-0,1599	-0,2821	-0,2381
<i>Nitzschia fonticola</i>	0,3079	1,3998	1,0975	-0,4843	1,1512	-0,1235	-0,0087	-0,3715	-0,1122	0,8019
<i>Nitzschia linearis</i>	0,5619	0,3672	0,3041	-0,5329	-0,0254	-0,1257	-0,2529	-0,3715	-0,2561	0,0352
<i>Nitzschia nana</i>	-0,0916	-0,4787	-1,8124	1,821	-0,8341	-0,1257	-0,2828	2,4053	-0,0856	0,323
<i>Nitzschia palea</i> var. <i>debilis</i>	-0,3076	0,387	0,285	-0,0281	0,4643	-0,1013	-0,1435	0,1535	-0,1686	0,4131
<i>Nitzschia pusilla</i>	-0,1153	1,8085	0,3694	2,5563	1,0447	4,0783	4,5551	-0,3715	4,6778	-3,2294
<i>Nitzschia recta</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Nitzschia solgensis</i>	-1,4234	0,9792	1,1243	-0,8466	1,4912	-0,1192	-0,2382	-0,3715	-0,1047	0,8981
<i>Nitzschia vermicularoides</i>	-0,5	1,1767	1,1027	-0,6039	1,3469	-0,122	-0,0466	-0,3715	-0,1183	0,8284
<i>Oscillatoria limosa</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Oscillatoria</i> sp.	-1,4234	-0,3238	-0,8368	0,6847	-0,3633	-0,1216	-0,2953	1,9574	-0,1567	0,185
<i>Phacus</i> sp.	1,3467	-0,5607	-2,2753	2,1226	-1,2905	-0,1289	-0,279	3,6439	-0,0602	0,3551
<i>Phormidium autumnale</i>	-0,5	-0,1856	-0,4288	-0,4482	-0,7445	-0,1231	-0,2885	-0,3715	-0,3414	-0,3893
<i>Phormidium corium</i>	-0,4112	-0,342	-0,3269	-0,4286	-0,6129	-0,1227	-0,2953	-0,3715	-0,3413	-0,4006
<i>Phormidium laetevirens</i>	0,1348	1,8418	0,33	2,5673	0,8247	1,7916	4,309	-0,3715	4,3631	-3,0986
<i>Phormidium molle</i>	-0,4279	-1,1197	-1,8523	0,2668	-2,1791	-0,1256	-0,2413	-0,3715	0,0214	1,9196
<i>Phormidium puteale</i>	1,3467	-0,5607	-2,2753	2,1226	-1,2905	-0,1289	-0,279	3,6439	-0,0602	0,3551
<i>Phormidium tergestinum</i>	0,4811	-0,8519	-0,9894	1,0177	-0,523	-0,0594	-0,2719	1,3908	-0,1661	0,1908
<i>Phormidium retzii</i>	0,1464	-0,0987	-0,4115	-0,4507	-0,695	-0,1258	-0,2861	-0,3715	-0,3408	-0,3996
<i>Pinnularia appendiculata</i>	0,7119	-0,6792	-1,3167	0,9539	-1,136	-0,0762	-0,277	0,8616	-0,1004	0,6275
<i>Planothidium frequentissimum</i>	-0,2692	1,2227	1,1079	-0,6184	1,292	-0,1224	-0,1019	-0,3715	-0,1167	0,818
<i>Planothidium rostratum</i>	1,3467	-0,3238	0,2934	-0,7159	-0,3633	-0,1278	-0,2953	-0,3715	-0,3611	-0,5707
<i>Platessa hustedtii</i>	1,0005	-0,4817	0,2927	-0,6412	-0,3118	-0,1273	-0,296	-0,3715	-0,3576	-0,5439

<i>Pleurocapsa</i> sp.	-0,0383	-0,6681	0,4743	-0,6517	0,11	-0,1062	-0,2922	-0,3715	-0,3576	-0,5631
<i>Rhizoclonium hieroglyphicum</i>	-0,0383	1,3109	1,1064	-0,4955	1,2501	-0,1231	-0,0099	-0,3715	-0,1158	0,8174
<i>Rhoicosphenia abbreviata</i>	-0,0985	0,732	0,8703	-0,5218	0,9106	-0,1104	-0,0618	-0,3715	-0,1876	0,3985
<i>Sellaphora saugerresii</i> sensu WETZEL et al. (2015)	-0,3846	0,1796	-0,475	-0,4638	-0,4189	-0,1244	-0,2839	-0,3715	-0,341	-0,3919
<i>Spirogyra</i> sp.	-0,0561	-0,5288	0,2419	-0,2763	0,1257	-0,0861	-0,2846	-0,2077	-0,2885	-0,2416
<i>Spirulina subsalsa</i>	-0,0383	-0,6496	-1,3389	1,4877	-0,6106	-0,1059	-0,277	1,926	-0,1321	0,2658
<i>Stigeoclonium</i> sp.	0,6542	1,5123	1,2003	-0,3051	1,1821	-0,1259	-0,2138	-0,3715	-0,1096	0,8397
<i>Surirella ovalis</i>	1,3467	1,4531	1,0305	-0,7906	0,873	-0,1247	-0,1852	-0,3715	-0,1261	0,6544
<i>Tabularia fasciculata</i>	-0,3531	1,3077	1,1089	-0,3492	1,331	-0,1226	0,1502	-0,3715	-0,1134	0,8574
<i>Tetraspora</i> cf. <i>lemmermannii</i>	-0,5923	-0,5489	-1,3666	1,4578	-0,5735	-0,0837	-0,2855	1,4756	-0,1127	0,2653
<i>Thalassiosira pseudonana</i> / <i>Cyclotella pseudostelligera</i>	1,3467	0,2093	-0,4437	-0,4731	-0,6724	-0,1307	-0,279	-0,3715	-0,3397	-0,4145
<i>Ulothrix aequalis</i>	-0,1768	1,2991	1,1699	-0,5217	1,3057	-0,1232	-0,2235	-0,3715	-0,1076	0,863
<i>Vaucheria debaryana</i>	-0,0383	-0,6555	0,4757	-0,6599	0,1003	-0,1047	-0,292	-0,3715	-0,3574	-0,5631
<i>Vaucheria</i> sp.	-0,4538	1,1569	1,1444	-0,6356	1,3799	-0,1227	-0,215	-0,3715	-0,1202	0,8326

**Table 4.** List of all taxa found at the respective sites with low (+), medium (++) and high (+++) abundance. Red list classification according to Knappe et al. (1996) and Lange-Bertalot (1996); strongly endangered (2), endangered (3), endangerment of unknown magnitude (G), rare (R), early warning list (V).

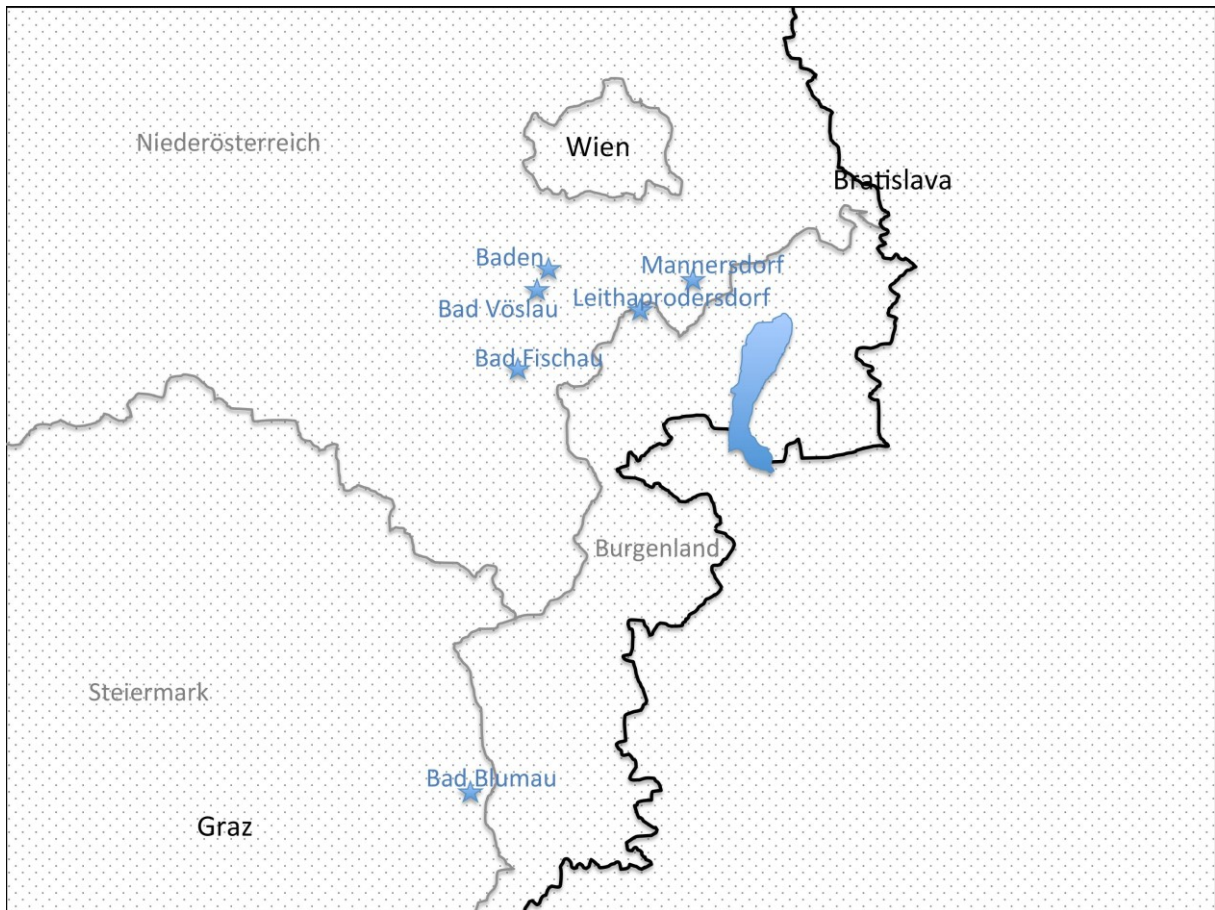
Species / Sites and RL	BM	BJ	BV	BF	MA	LP	BB	Red List
<i>Achnantheidium exile</i>				+				V
<i>Achnantheidium minutissimum</i>			+++	++	++			
<i>Achnantheidium pyrenaicum</i>			++	+				
<i>Amphora ovalis</i>				+	++			
<i>Amphora pediculus</i>			++	+	++	+		
<i>Aphanothece stagnina</i>	+	+						
<i>Audouinella chalybea</i>					+++			
<i>Aulacoseira granulata</i>					+			
<i>Brachysira neoexilis</i>		+						
<i>Caloneis alpestris</i>				+				G
<i>Caloneis budensis</i>					+			R
<i>Caloneis fontinalis</i>			+++	++	+	++		
<i>Caloneis lancettula</i>	+				+			
<i>Caloneis cf. tenuis</i>		+						G
<i>Calothrix parietina</i>			+	+++				
<i>Chantransia-Stadien</i>			+					
<i>Chara globularis</i>				+++				
<i>Chroococcus varius</i>							+++	
<i>Chroodactylon ornatum</i>					+			G
<i>Cladophora glomerata</i>					++			
<i>Cocconeis pediculus</i>					++			
<i>Cocconeis placentula var. lineata</i>				++	+			
<i>Cocconeis pseudolineata</i>			+	+				
<i>Cosmarium laeve</i>			++	+	+			
<i>Craticula buderi</i>					++			

<i>Cyclotella meneghiniana</i>					+	
<i>Cymbella compacta</i>		+				
<i>Cymbella cymbiformis</i>	+					V
<i>Diadесmis confervacea</i>					++	
<i>Diadесmis contenta</i>					+	
<i>Diploneis krammeri</i>			+	++	+	
<i>Diploneis oculata</i>					+	
<i>Ellerbeckia arenaria</i>				+		
<i>Encynopsis microcephala</i>	+	+		+		
<i>Epithemia goeppertiana</i>				++		R
<i>Euglena cf. adhaerens</i>					+	
<i>Fallacia lenzii</i>				+	+	3
<i>Fallacia monoculata</i>						+
<i>Fallacia pygmaea</i> ssp. <i>subpygmaea</i>					+	
<i>Fragilaria construens</i> f. <i>venter</i>				+		
<i>Fragilaria elliptica</i>				+		
<i>Fragilaria gracilis</i>			+++			+
<i>Fragilaria ulna</i>		+	+		+	
<i>Frustulia vulgaris</i>					+	
<i>Gloeocapsa atrata</i>				+		
<i>Gomphonema clavatum</i>					++	
<i>Gomphonema italicum</i>					+	
<i>Gomphonema olivaceum</i> var. <i>olivaceum</i>					+	
<i>Gomphonema parvulum</i> var. <i>parvulum</i> f. <i>parvulum</i>		+	+			+
<i>Gomphonema pumilum</i>		+	++		+	
<i>Gomphonema subclavatum</i>		++	+		+	
<i>Gomphosphenia lingulatiformis</i>					+	
<i>Gongrosira incrustans</i>		+	+++		+++	+
<i>Halamphora normanii</i>	+	+	+		++	++
<i>Heribaudiella fluviatilis</i>			+++			

<i>Hildenbrandia rivularis</i>			+++	+++					3
<i>Hydrococcus rivularis</i>			+			+			
<i>Karayevia ploenensis</i>						+			
<i>Klebsormidium flaccidum</i>			+++						
<i>Leptolyngbya aeruginea</i>						++			
<i>Leptolyngbya laminosa</i>	+++	+++						+++	
<i>Leptolyngbya valderiana</i>		++		+++					
<i>Limnothrix lauterbornii</i>	+++	+++							
<i>Lyngbya martensiana</i>			+			++	++		
<i>Melosira varians</i>		+				++			
<i>Microcystis cf. flos-aquae</i>	+								
<i>Navicula antonii</i>						+	+		
<i>Navicula cincta</i>							+		
<i>Navicula cryptocephala</i>		++							
<i>Navicula cryptotenelloides</i>			+	++					
<i>Navicula tripunctata</i>						++			
<i>Navicula trivialis</i>						+			
<i>Naviculadicta absoluta</i>						+			
<i>Nitzschia abbreviata</i>						+			
<i>Nitzschia amphibia</i>						+	+		
<i>Nitzschia communis</i>						+			
<i>Nitzschia constricta</i>						+			
<i>Nitzschia denticula</i>		+		+					
<i>Nitzschia fonticola</i>						+			
<i>Nitzschia linearis</i>			+	+		+			
<i>Nitzschia nana</i>	++	+							
<i>Nitzschia palea var. debilis</i>		++	+			+			
<i>Nitzschia pusilla</i>								++	
<i>Nitzschia recta</i>						+			
<i>Nitzschia solgensis</i>						+			V

<i>Nitzschia vermicularoides</i>						+
<i>Oscillatoria limosa</i>						+
<i>Oscillatoria</i> sp.		+				
<i>Phacus</i> sp.	+					
<i>Phormidium autumnale</i>			+++			
<i>Phormidium corium</i>			++			
<i>Phormidium laetevirens</i>						+++
<i>Phormidium molle</i>					+++	
<i>Phormidium puteale</i>	+					
<i>Phormidium tergestinum</i>	+	++				
<i>Phormidium retzii</i>			++			
<i>Pinnularia appendiculata</i>	+	+				+
<i>Planothidium frequentissimum</i>					++	
<i>Planothidium rostratum</i>				+		
<i>Platessa hustedtii</i>			+	+		
<i>Pleurocapsa</i> sp.				++		
<i>Rhizoclonium hieroglyphicum</i>					+++	
<i>Rhoicosphenia abbreviata</i>				+	+++	
<i>Sellaphora saugerresii</i> sensu WETZEL et al. (2015)			++			
<i>Spirogyra</i> sp.		++		+++		+
<i>Spirulina subsalsa</i>	+++	+++				
<i>Stigeoclonium</i> sp.						+
<i>Surirella ovalis</i>						+
<i>Tabularia fasciculata</i>						++
<i>Tetraspora</i> cf. <i>lemmermannii</i>	+	+				
<i>Thalassiosira pseudonana</i> / <i>Cyclotella pseudostelligera</i>			+			
<i>Ulothrix aequalis</i>						+
<i>Vaucheria debaryana</i>				+++		
<i>Vaucheria</i> sp.						++





**Fig. 1.** Location of sites in Eastern Austria.



Fig. 2. BM: thermal spring site (1) and phytoplankton (2, 3).



Fig. 3. BJ: thermal spring site (1) and phytobenthos (2, 3).



**Fig. 4.** BV: sampling site (1, 2) and Ursprungsquelle (3).



Fig. 5. BF: sampling (1, 3) at natural monument (2).



Fig. 6. MA: substitute site (1, 2) and phytobenthos (3).



**Fig. 7.** LP: sampling site (1); ambient spring (to the left) and thermal spring (in the back) in winter (2) and summer (3).



**Fig. 8.** BB: Vulkania Heilquelle<sup>®</sup>, Vulkania Heilsee<sup>®</sup> (1, 2) and phytobenthos (3).



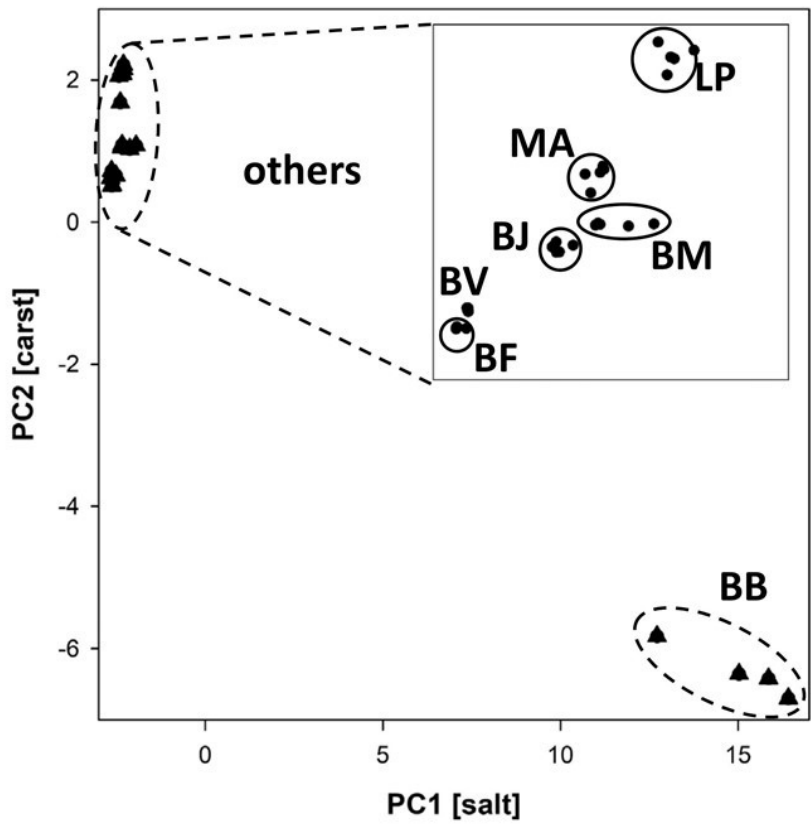
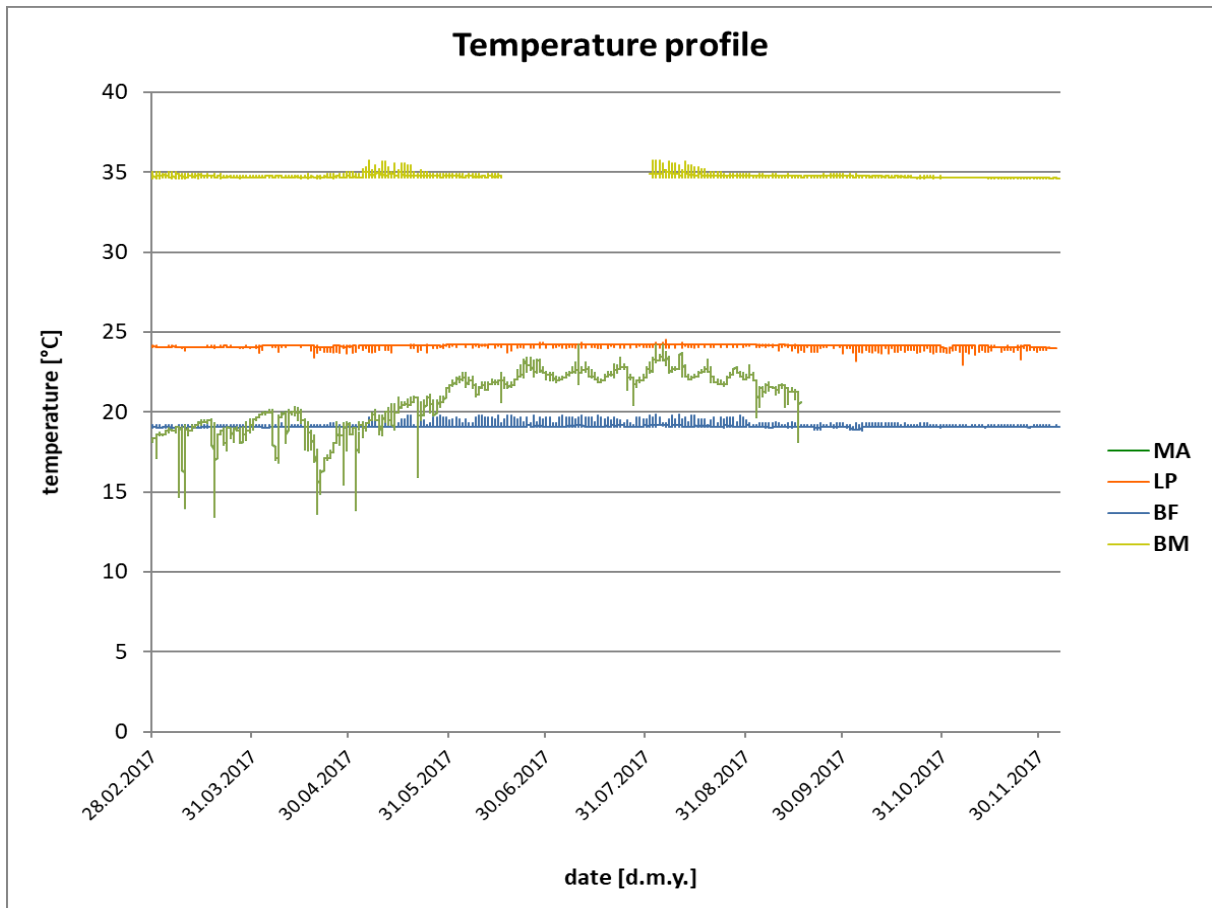
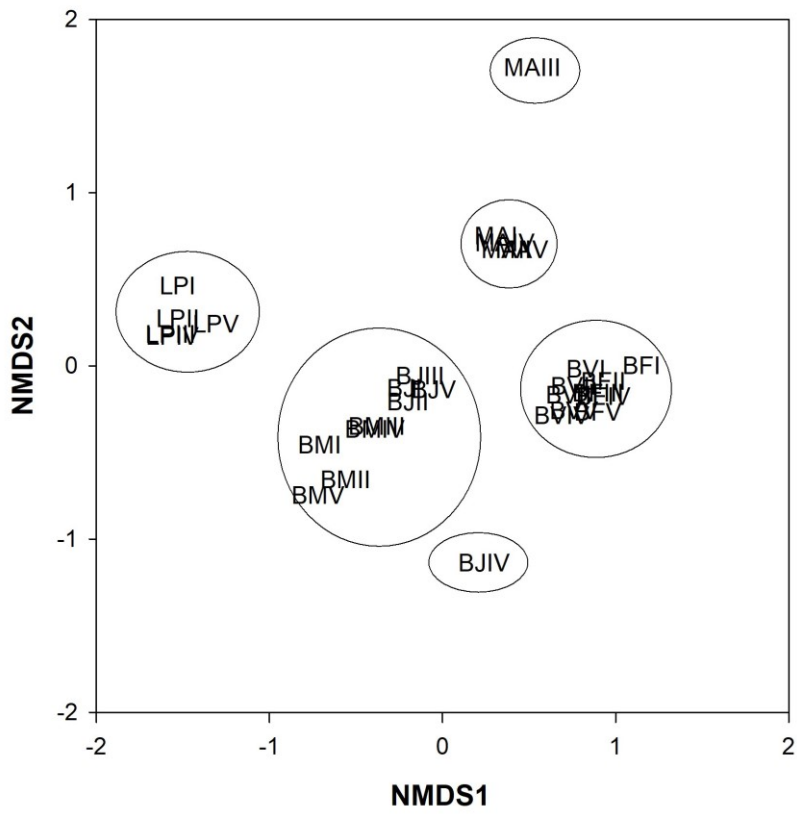


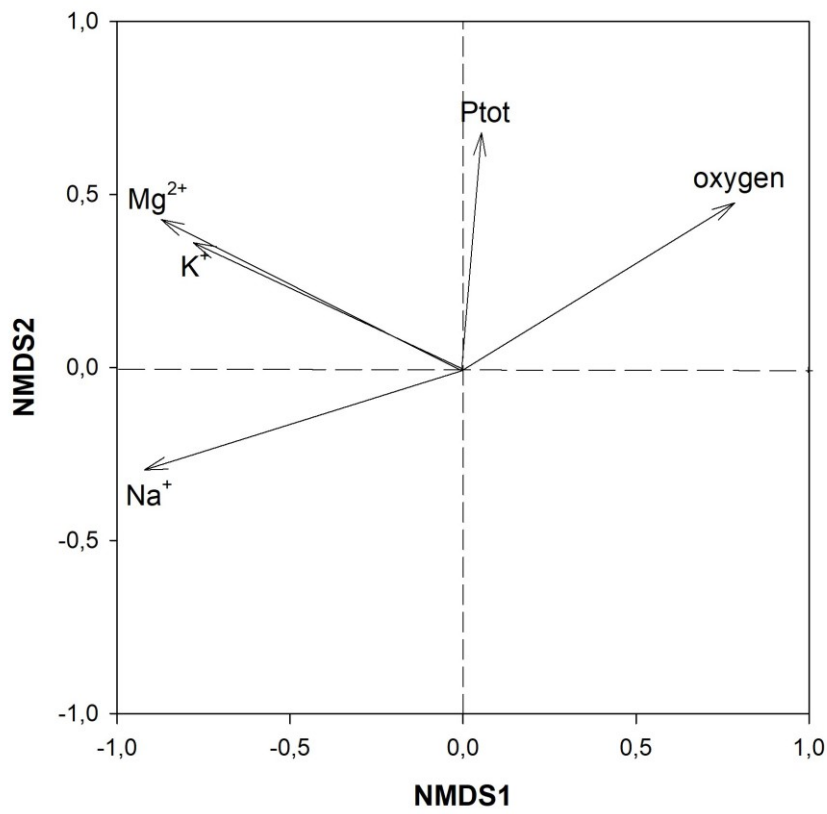
Fig. 9. Results from PCA. BB deviates widely from the other sites in both salt and carst.



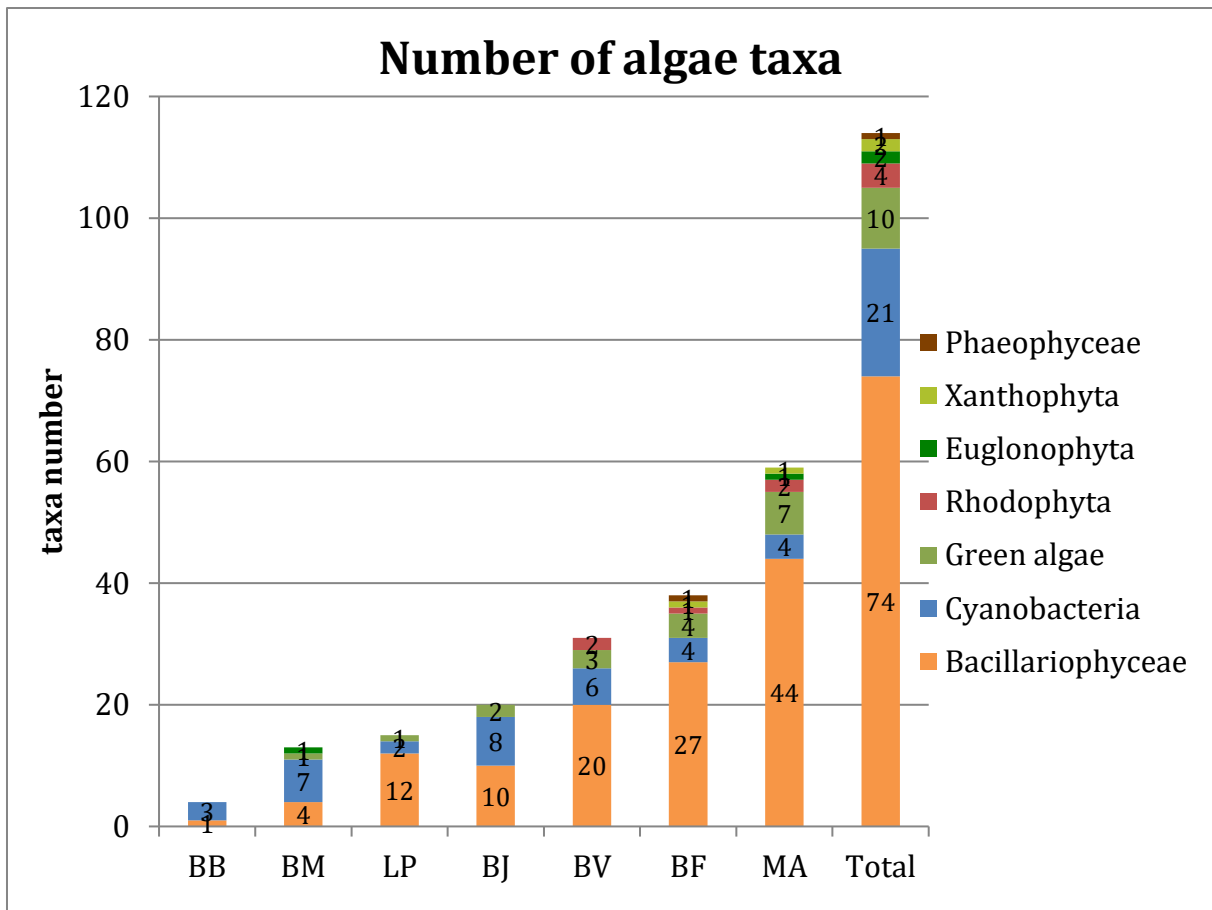
**Fig. 10.** Annual temperature profiles of thermal spring sites. BM: data from mid of June to beginning of August are missing due to air contact of the temperature logger; MA: data from September to December are missing due to logger malfunction.



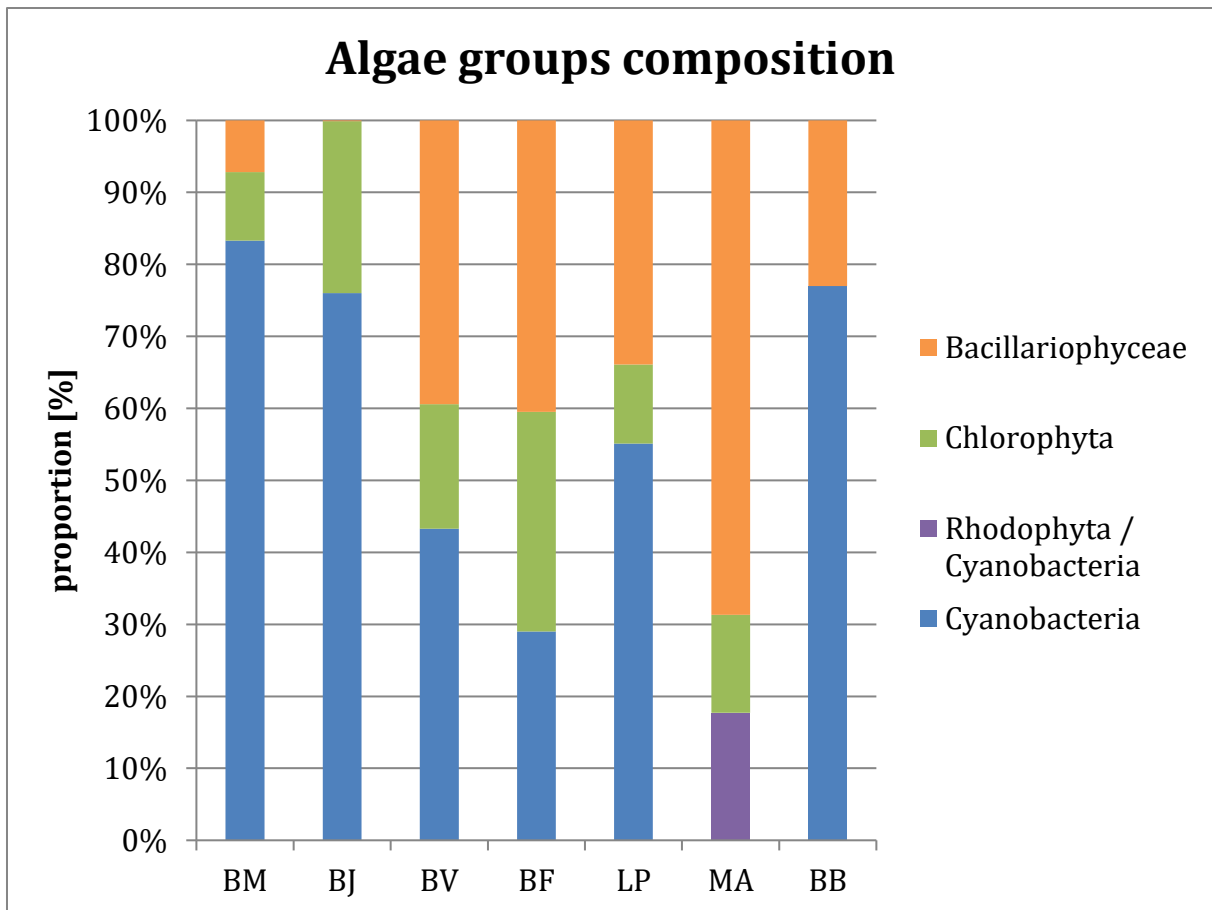
**Fig. 11.** Ordination diagram for NMDS findings. NMDS2 revealed six significant groups.



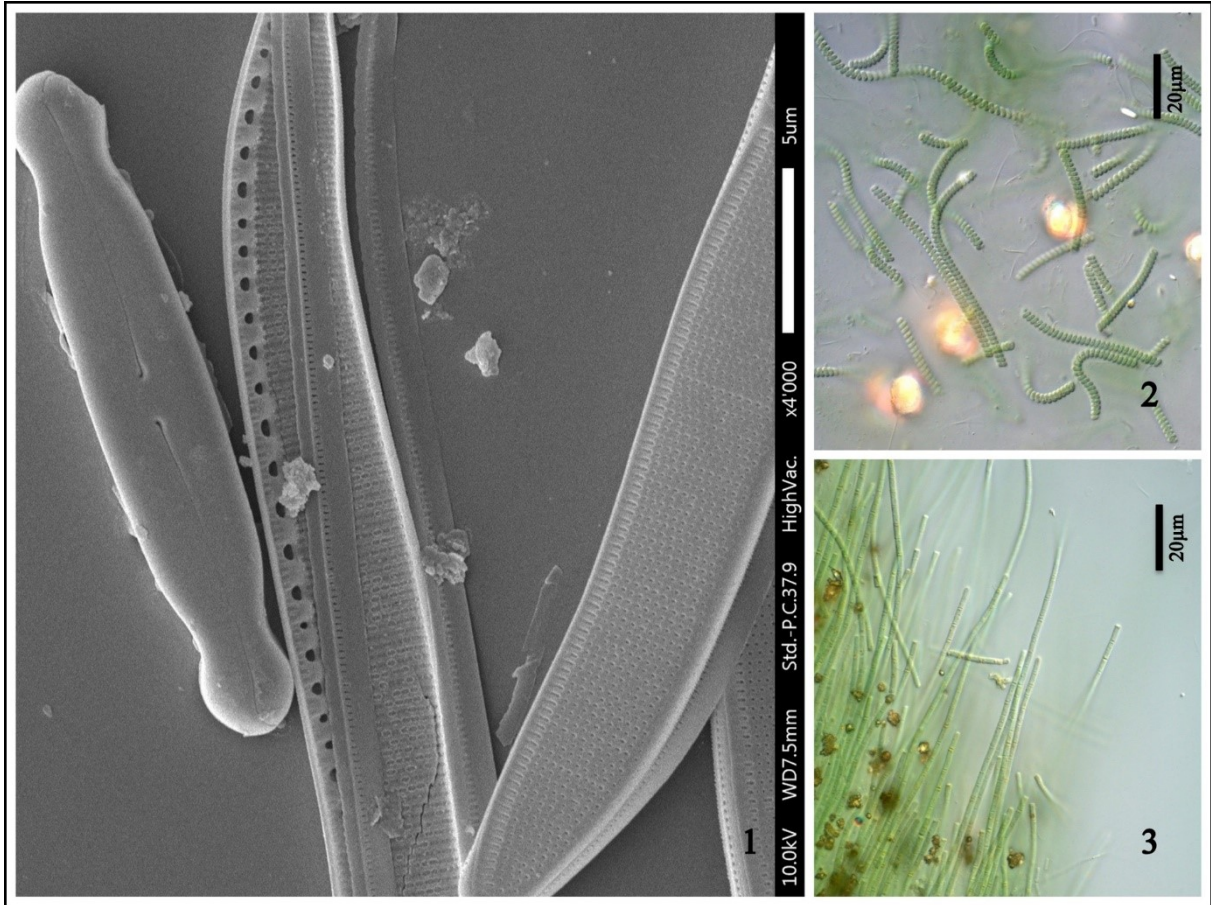
**Fig. 12.** Five explanatory variables (vectors) for pattern in Fig. 10.



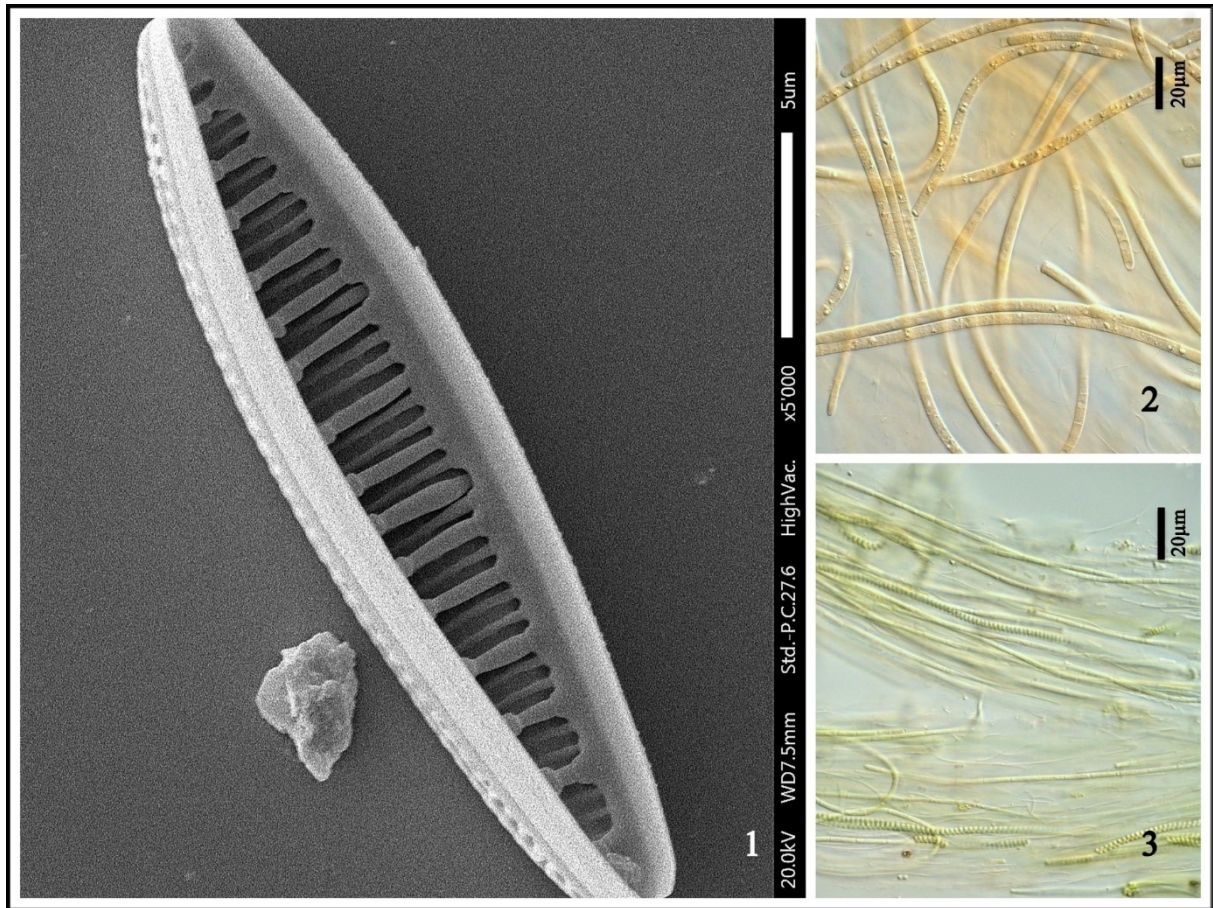
**Fig. 13.** Number of algae taxa determined at each site and in total; green algae column contains Chloropyhta and Streptophyta.



**Fig. 14.** Relative parts of algae groups in phytobenthos of thermal spring sites (data from HPLC analysis). At MA the cyanobacteria column contains also red algae which were detected in microscope but could not be differentiated in HPLC, due to high similarity of pigments.

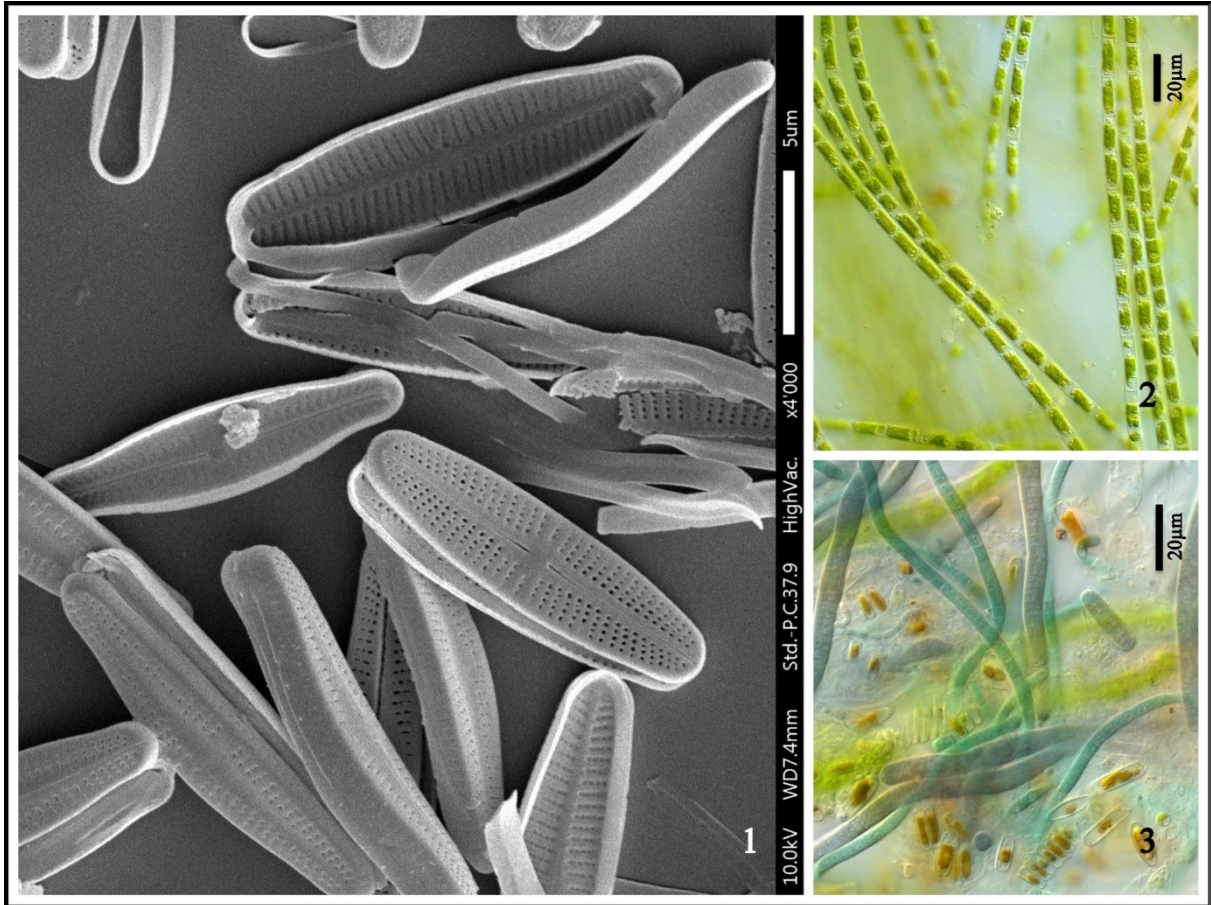


**Fig. 15.** Algae species at BM: *Pinnularia appendiculata* (1, left), *Nitzschia nana* (1, mid and right), *Spirulina subsalsa* (2) and *Leptolyngbya laminosa* (3).

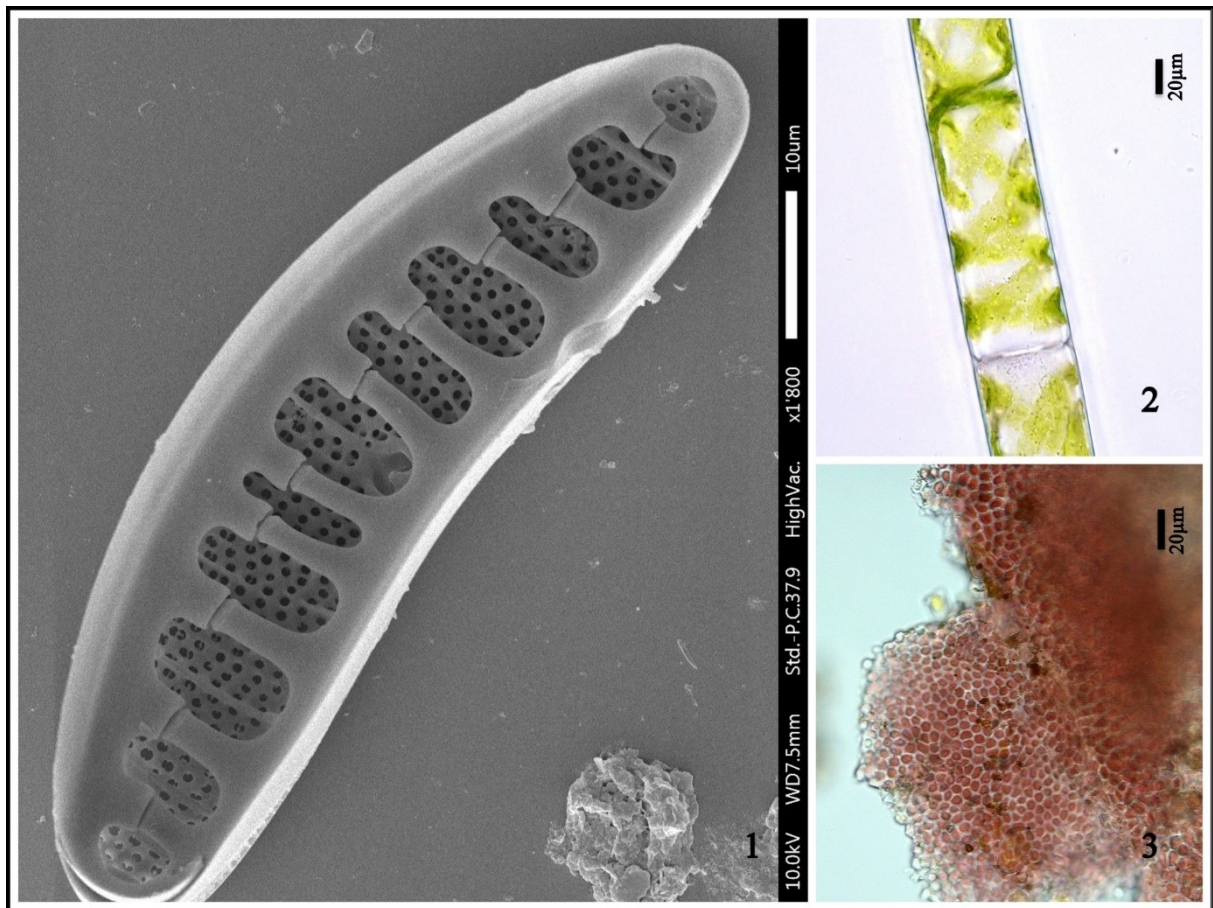


**Fig. 16.** Algae species at BJ: *Nitzschia denticula* (1), *Limnothrix lauterbornii* (2), *Spirulina subsalsa* (3) and *Leptolyngbya laminosa* (3).

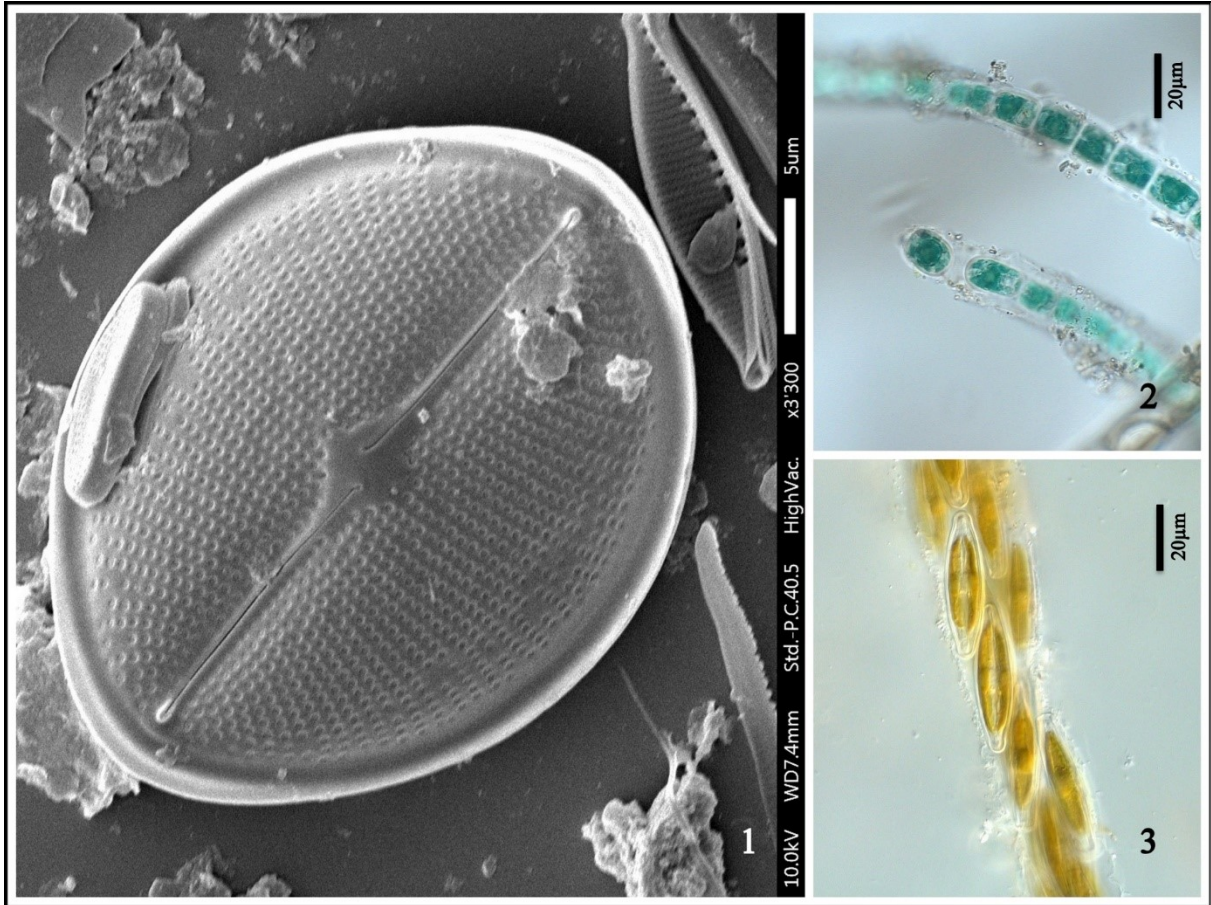




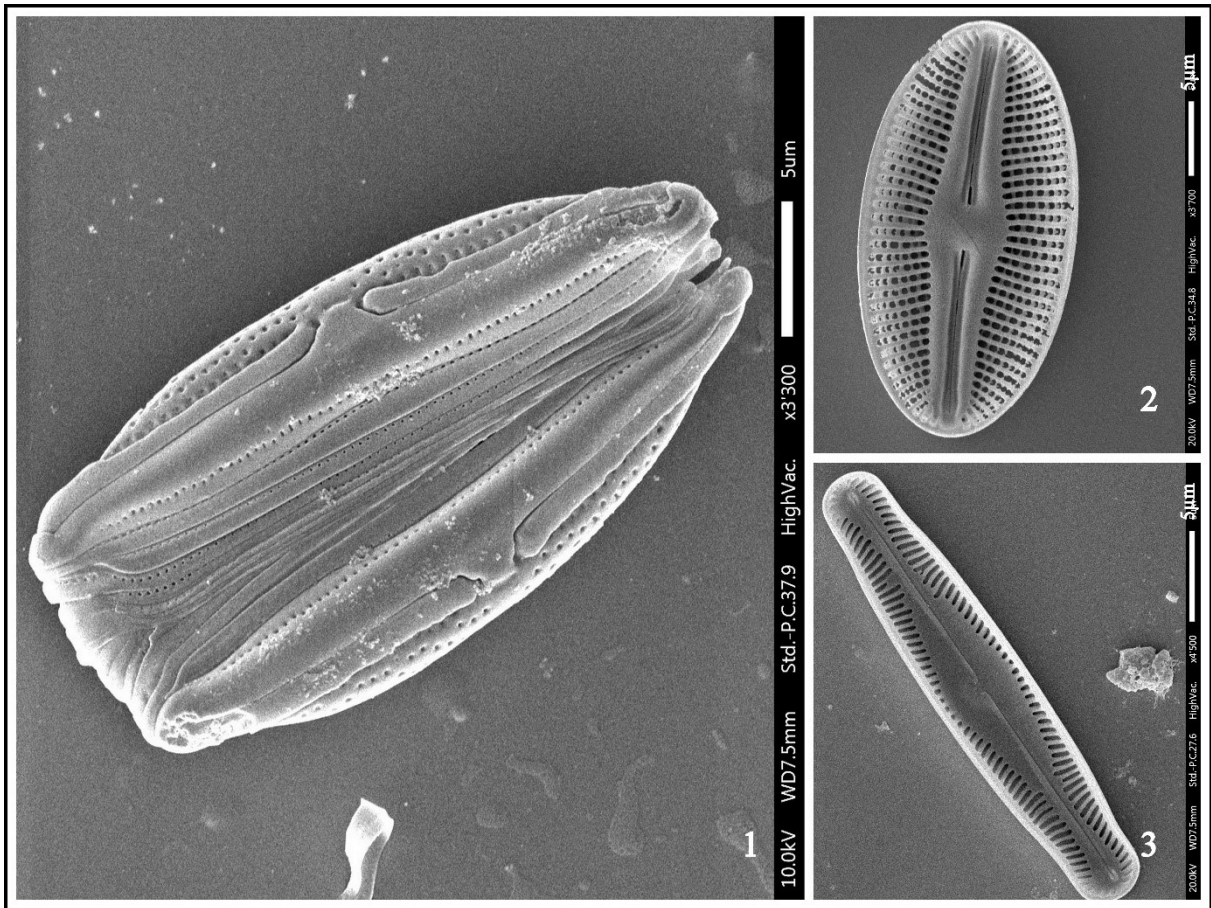
**Fig. 17.** Algae species at BV: *Achnantheidium minutissimum* (1), *Klebsormidium flaccidum* (2) and mixed thallus with *Phromidium corium* and *P. autumnale* (3).



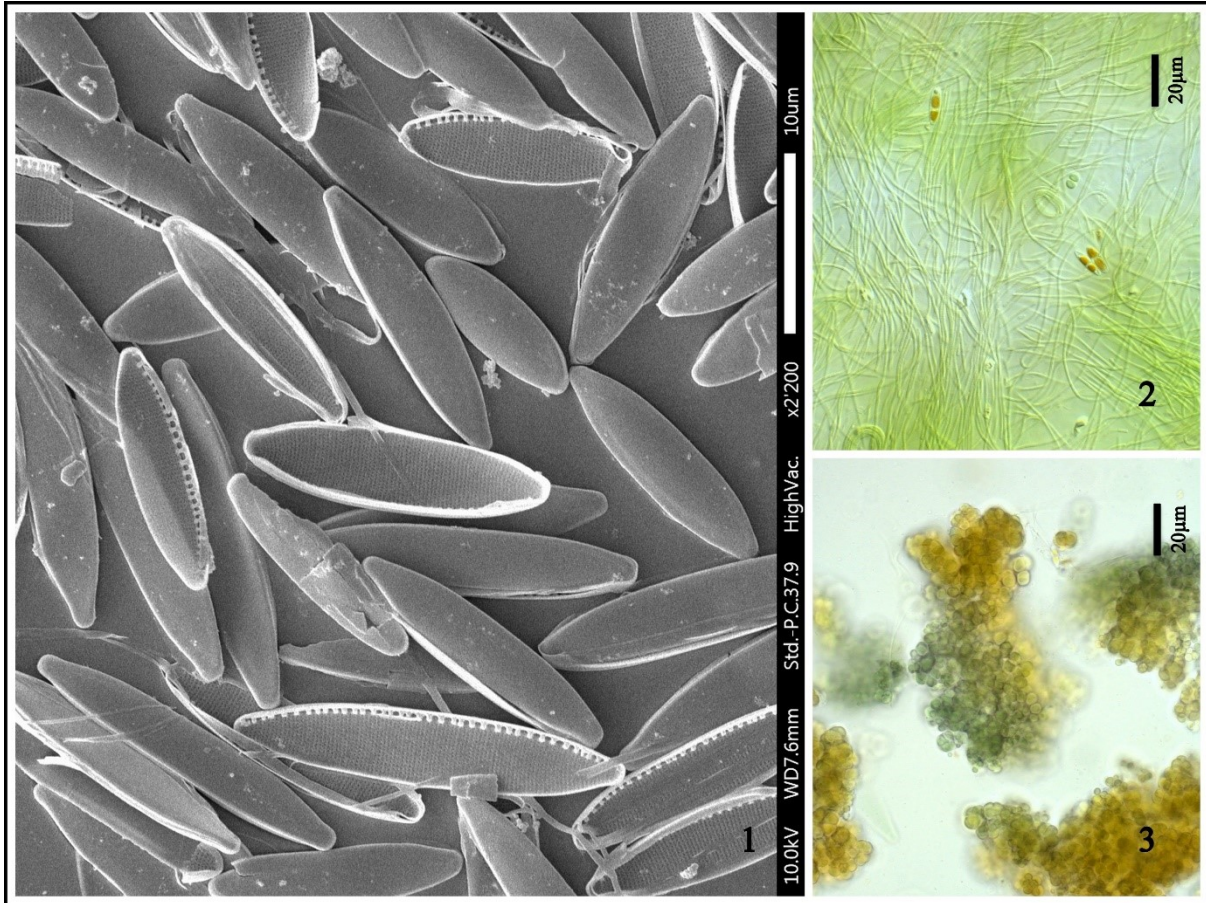
**Fig. 18.** Algae species at BF: *Epithemia goeppertiana* (1), *Spirogyra* sp. (2) and *Hildenbrandia rivularis* (3).



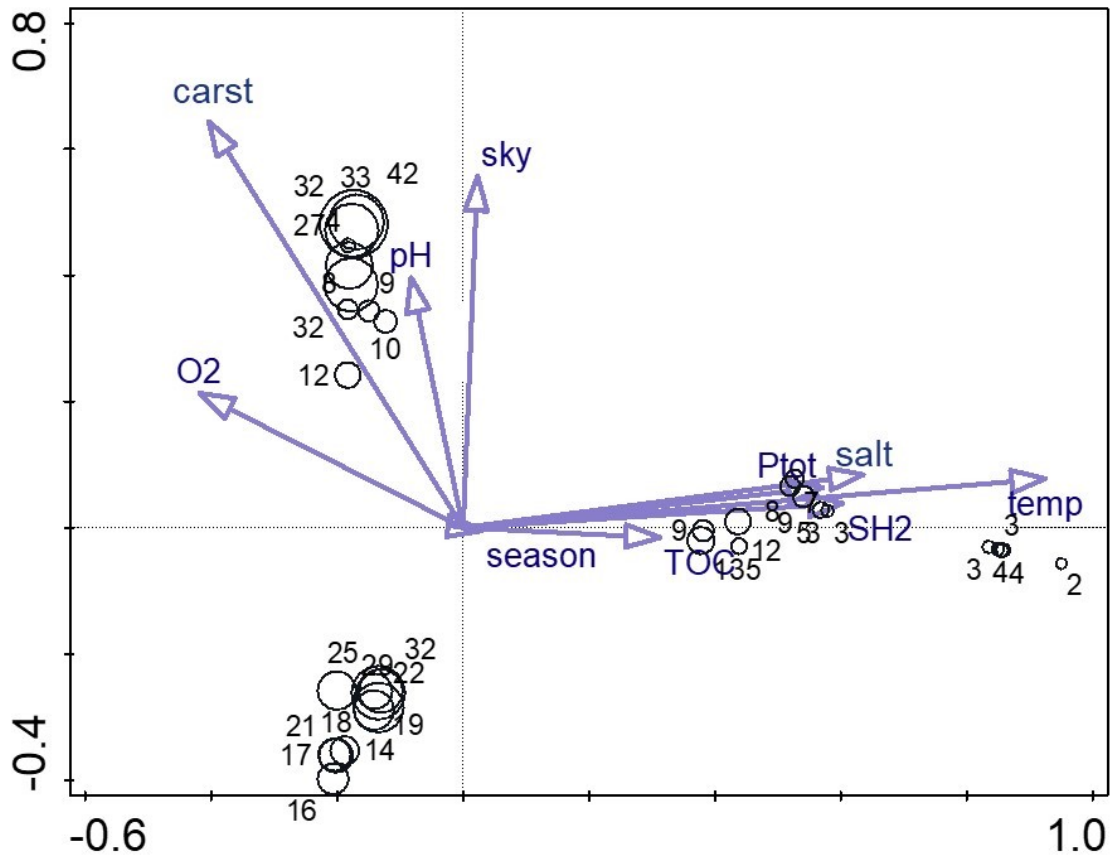
**Fig. 19.** Algae species at MA: *Cocconeis pediculus* (1, mid), *Nitzschia fonticola* (1, top right), *Chroodactylon ornatum* (2) and *Frustulia vulgaris* (3).



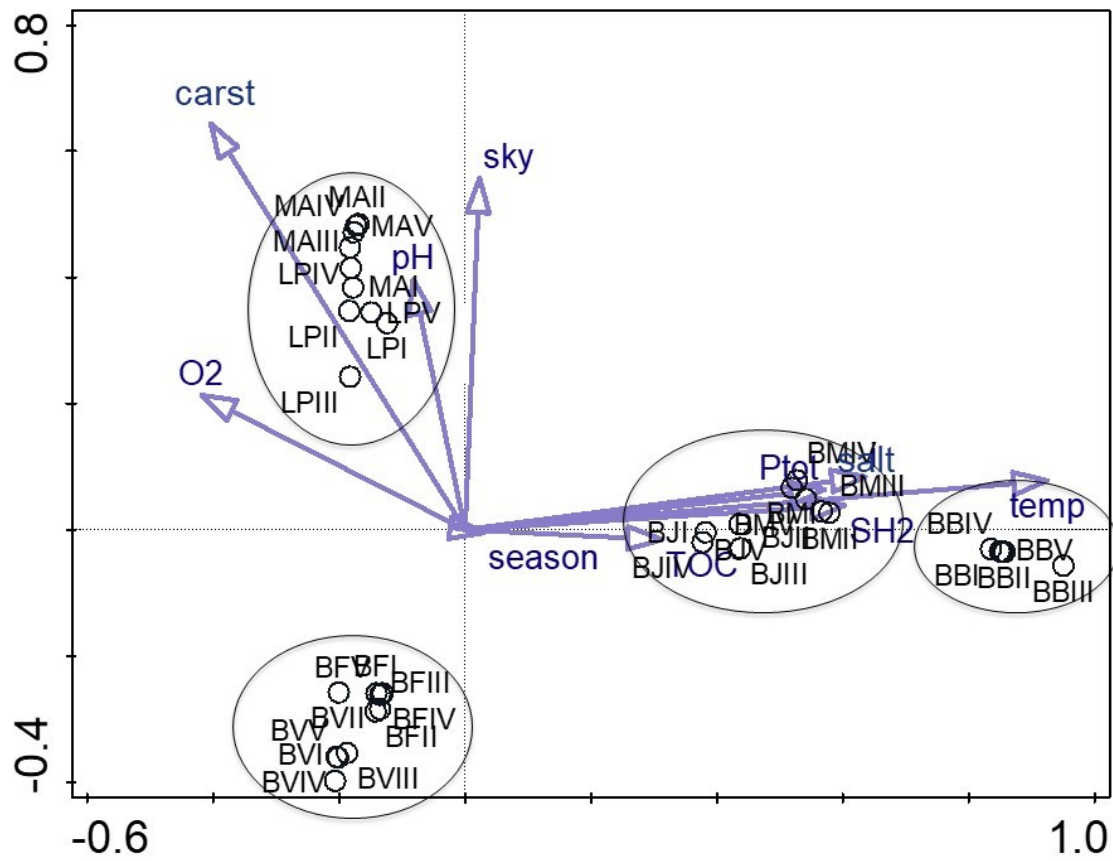
**Fig. 20.** Algae species at the thermal spring of LP: *Halamphora normanii* (1), *Diploneis krammeri* (2) and *Pinnularia appendiculata* (3).



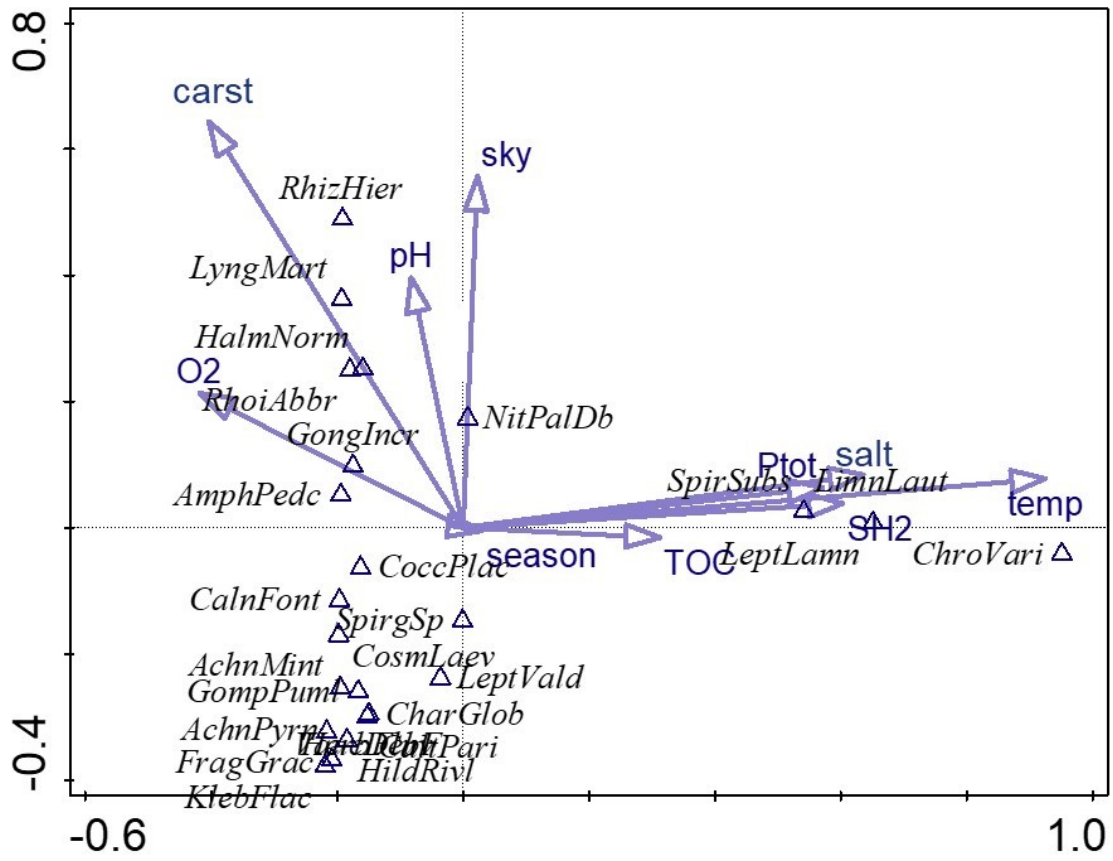
**Fig. 21.** Algae species at BB: *Nitzschia pusilla* (1), *Leptolyngbya laminosa* (2) and *Chroococcus varius* (3).



**Fig. 22.** DCA ordination diagram for thermal springs sites (samplings I-V) and explanatory variables (vectors); numbers and diameter represent number of algae taxa.



**Fig. 23.** DCA ordination diagram for thermal springs sites (samplings I-V) and explanatory variables (vectors).



**Fig. 24.** DCA ordination diagram for species with greatest contribution to the pattern (>25% of maximum value) and explanatory variables (vectors).



## Appendix

### Zusammenfassung

Quellbiotop sind Biodiversitäts-Hotspots, doch unzureichende Schutzgesetzgebung und hoher Nutzungsdruck gefährden diese sensiblen Lebensräume. Thermalquellen repräsentieren einen besonderen Fall (charakterisiert durch erhöhte Temperatur und oft auch hohen Mineralstoffgehalt). Wir konzentrierten uns auf die Algenvegetation, da das Phytobenthos eine essentielle Komponente photoautotropher Biofilme darstellt und auch zur Bioindikation genutzt wird. Trotz seiner Bedeutung als Nahrungsgrundlage für Tiere (darunter einige stark gefährdete und geschützte) gibt es nahezu keine Information zum Phytobenthos gemäßigter Thermalquellen. Diese Studie liefert Einblicke in einige ausgewählte Standorte dieser Mikrohabitate und richtet dabei den Fokus auf Algenbestände entlang der 'Thermenlinie' in Ost-Österreich. Wir fanden einige signifikante Unterschiede bezüglich Wassertemperatur und Mineralstoffgehalt bzw. -zusammensetzung, welche sich auch in der Phytobenthoszusammensetzung widerspiegeln. Wir unterschieden sowohl hoch temperierte Standorte ( $>25^{\circ}\text{C}$ ) mit hohem Gehalt an Sulfid oder auch Natriumhydrogencarbonat und Chlorid, also auch karstische, schwach thermale Quellen ( $>18^{\circ}\text{C}$ ) mit vergleichsweise niedrigen Mineralstoffgehalten. Die Temperaturverhältnisse blieben das Jahr über wie erwartet sehr stabil, weshalb auch keine Änderung in den Algenzusammensetzung zu erkennen war. An hohe Wassertemperatur angepasste Taxa konnten vorwiegend innerhalb der Cyanobakterien festgestellt werden. An den am Höchsten temperierten Standorten waren diese dominant anzutreffen. Diatomeen beanspruchten in Summe den größten Anteil an der Gesamtartenzahl aller Quellen. Es konnte eine negative Korrelation der Artenzahl zwischen den jeweiligen Standorten in Bezug auf Temperatur und Hemerobie festgestellt werden. Gemäßigte Thermalquellen (mit den höchsten Artenzahlen) beherbergten auch ein paar Rote Liste Arten, welche auf besondere und schützenswerte Lebensräume hinweisen. Das Fehlen des zu erwartenden thermalen Cyanobakteriums *Mastigocladus laminosus* war überraschend. Dies konnte durch den Einfluss von Sulfid an zwei der hoch temperierten Standorte erklärt werden. Basierend auf ihrer Phytobenthoszusammensetzung konnten die Standorte bestimmten Quelltypen zugeordnet werden. Außerdem konnten Ansätze für einen geeigneten Schutz der Quelllebensräume ermittelt werden: die Nutzung von Thermalwasser für Badeanstalten erfordert nicht zwangsläufig Eingriffe in Quellhabitats.

Tatsächlich lassen sich der strikte Schutz von Quellen und eine nachhaltige Nutzung des Wassers quellabwärts mit einander vereinbaren.

### **Danksagung**

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