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and

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Stress and disturbance in benthic diatom assemblages

Examples from lakes and streams and from the field and laboratory studies

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Photo by Edina Lengyel

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Ph.D. Dissertation

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Stress and disturbance in benthic diatom assemblages

Készült a Pannon Egyetem **Kémiai és Környezettudományi Doktori Iskolája** keretében

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Elfogadásra javaslom (igen / nem) ....

(aláírás)

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Elfogadásra javaslom (igen / nem) ....

(aláírás)

A jelölt a doktori szigorlaton ....%-ot ért el,

Az értekezést bírálóként elfogadásra javaslom:

Bíráló neve: …………………………. igen / nem

....

(aláírás)

Bíráló neve: …………………………. igen / nem

....

(aláírás)

A jelölt az értekezés nyilvános vitáján ....%-ot ért el.

Veszprém, ……………………….... ....

a Bíráló Bizottság elnöke

A doktori (PhD) oklevél minősítése...................................

....

Az EDHT elnöke

Abbreviations

DO	Dissolved oxygen
DO%	Dissolved oxygen saturation
TP	Total phosphorus
COD	Chemical oxygen demand
SRSi	Soluble reactive silica
SRP	Soluble reactive phosphorus
$\mathbf{P_{max}}$	Maximal carbon uptake
$\mathbf{I_k}$	Photoadaptation parameter
$\mathbf{P_s}$	Biomass specific photosynthetic activity
R	Growth rate
$\boldsymbol{\alpha}$	Initial slope of the P-I curve
$\boldsymbol{\beta}$	Photoinhibition parameter
IDH	Intermediate disturbance hypothesis
PAR	Photosynthetically active radiation
DIC	Dissolved inorganic carbon
DOC	Dissolved organic carbon
TN	Total nitrogen

Contributions to the research

The sampling of saline lakes was carried out with some assistance, such as Dr. Csilla Stenger-Kovács, Dávid Németh, István Kacsala and Beáta Szabó. On the field, Attila Pellinger, Dr. András Ambrus, Péter Kugler and Gábor Takács, as the colleagues of Fertő-Hanság National Park helped us during the whole study period. The samplings in Torna-streams were also teamwork with the assistance of many students and colleagues, such as Csaba Kálmán, Dr. Csilla Stenger-Kovács, Dr. Kata Karádi-Kovács and Dr. Tamás Kucserka.

The preparations of the samples collected from saline lakes were carried out by Dávid Németh in 2014. Additionally, the accurate identifications of some diatom species were required electron microscopic analysis which was carried out by Dr. Csilla Stenger-Kovács and Dr. Krisztina Buczkó’s helps.

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For *Nitzschia aurariae*, the processes of photosynthetic activity and the other necessary laboratory works were carried out mainly by Diána Lázár.

The calculation of AVTD values was carried out by Dr. Éva Hajnal.

Content

Kivonat

A stressz és a bolygatás fogalmát a mai napig gyakran összekeverik, mivel elkülönítésük nehéz köszönhetően annak, hogy a környezeti faktorok nem sorolhatók be egyszerűen az egyes csoportokba. Pedig a megkülönböztetésük fontos lenne a helyes tudományos következtetések levonása miatt. A jelen kutatás alapvető célja a stressz és bolygatás hatásának vizsgálata bentikus kovaalga közösségekben mind terepi, mind kísérletes körülmények között, specifikusan:

(i) feltárni három kis szikes tó bentikus kovaalga flóráját, amelyeknek többszörös stresszt kell elviselniük;

(ii) meghatározni két kovaalga faj optimumát és toleranciáját fény, hőmérséklet és vezetőképesség gradiens mentén;

(iii) megvizsgálni a stressz és bolygatás komplex hatását három szikes tóban referencia helyek bevonásával; valamint

(iv) meghatározni a lehetséges egyensúlyi állapotok kialakulását folyóvízi környezetben.

Ennek érdekében két éves terepi gyűjtésekből származó adatsort (bevonat, fizikai és kémiai paraméterek) használtam fel, valamint tisztatenyészetet hoztam létre az ökofiziológiai kísérletekhez. Az alábbi fő megállapításokra jutottam:

(i) Az eredmények a tudomány számára új információt nyújtanak a Fertő-Hanság három szikes tavának bentikus kovaalga flórájáról, melyet fotókkal részletesen dokumentáltam. A tavakban a kovaalga közösség térbeli eloszlására nincs hatással a szubsztrát típusa köszönhetően a többszörös stressznek. Tekintve az egyes konstanciával jellemezhető fajok magas számát, az alacsony fajszámot, a lehetséges új fajokat és a számos Vörös listás fajt, a vizsgált tavak bentikus kovaalga flórája egyedi és jelentős természetvédelmi értékkel rendelkezik.

(ii) Mindét faj, a *Nitzschia frustulum* és *N. aurariae* is magas vezetőképesség optimummal és széles sótartalom toleranciával jellemezhető, ami ökológiai előnyt jelenthet számukra más fajokkal szemben. Habár a két faj niche-e átfed egymással, a *N. aurariae* kedvezőbb helyzetben van, mivel magasabb szalinitás stresszt képes elviselni. A fajok ionpreferenciája és alacsony-közepes fényigénye lehet a magyarázat az elterjedésükre és dominanciájukra. Habár a fajok magas hőmérsékleti optimummal és széles toleranciával rendelkeznek, a fotoszintetikus aktivitásuknak a csökkenése várható a klímamodellek által

jelzett növekvő, egyes esetekben extrém értékeket elérő hőmérsékletnek köszönhetően.

(iii) A kezdeti, ígéretes eredmények után, a Borsodi-dűlő és Nyéki-szállás jelenlegi ökológiai állapota mérsékeltté romlott: a természetes fizikai, kémiai és biológiai jellemzőik még mindig nem megfelelőek köszönhetően az erősen szabályozott vízszintjüknek és a Fertő felöl alkalomszerűen érkező vízutánpótlásnak. Ezzel szemben a Legény-tó állapota messze elmarad a természetestől köszönhetően a természetes hidrológiai háttér hiányának. Az említett bolygatások olyan váratlan változásokat okoznak a közösség szukcessziójában ún. “shiftek” és “reverziók” formájában, amelyek megakadályozzák a szikes tavakra jellemző természetes közösség vagy egy lehetséges alternatív stabil állapot kialakulását. A vizsgált tavak florisztikai szempontból hot-spotoknak számítanak, ezért szükséges lenne a jó ökológiai állapotuknak a megőrzése, mely elérhető a természetes hidrológiai és diszturbancia rendszerük helyreállításával.

(iv) A vizsgált folyóvízi ökoszisztémában kapott konklúziók hasonlóak, mint amit a mérsékelt övi tavaknál tapasztaltak: az egyensúlyi állapotok ritkák (csupán három időszakra szűkíthetők: 2008 júliusa, 2009 májusa, és 2010 januárja), megjósolhatatlanok, ideig-óráig tartóak és leginkább egy faj monodominanciájával jellemezhetők (*Cocconeis placentula sensu lato* és *Navicula lanceolata*). A kialakult egyensúlyi állapot rugalmassága biztosíthatja a biotikus állandóságot a környezeti háttérparaméterek nagymértékű fluktuálásának ellenére is. Néhány paraméternél olyan küszöbértékek állapíthatók meg, melyek önmagukban elegendő mértékűek a steady-state állapot kialakulásának megelőzésére. Mindazonáltal viszonylagosan stabil környezetben is kialakulhat egyensúlyi állapot, amelyhez a fitoplanktonnál tapasztaltakhoz képest hosszabb időre van szükség.

Abstract

The term of stress is often confused with the definition of disturbance, probably because none of the environmental variables can be clearly claimed as stressor or disturbance. The clarification and the differentiation of these factors are very important, because their impacts need different approaches. The basic aim of present dissertation is to study the effects of stress and disturbance in benthic diatom communities in the field and laboratory studies, specifically:

(i) to identify what kind of diatom species can tolerate multiple stress in three alkaline, saline, shallow soda pans;

(ii) to recognize the optimum and tolerance of two diatom species along light, temperature and conductivity gradients;

(iii) to investigate the complexity of three impacts (natural, and human disturbances, stress) in three saline pans using reference sites; and

(iv) to determine the potential establishment of equilibrium state of benthic diatom assemblages in a stream ecosystem.

For these purposes, two-year datasets (phytobenthos, physical and chemical parameters) were applied from the field and cultures were grown for laboratory ecophysiological experiments. The major conclusions are the following:

(i) New information is provided with detailed photo-documentation about the diatom flora of three pans in the Fertő-Hanság region. In these ecosystems, the spatial distribution of diatoms is not affected by the substrates due to the multiple stresses. Regarding the high number of constancy-one species, the low species richness, the possible new species and many Red-list species, the benthic diatom flora of the studied pans are unique and have significant conservation value.

(ii) Both *Nitzschia frustulum* and *N. aurariae* have high salinity optimum with broad tolerance, which represents an ecological advantage against other species. However, the niche of the species is overlapped: *N. aurariae* have higher ecological advantages tolerating high level stress. The ion preference and the low-medium irradiance demand of the species may explain their distribution and dominance. The species have high temperature optima and broad tolerance, but their photosynthetic activity will decrease under increasing, sometimes extreme temperatures, as predicted by the climate change models.

(iii) After the initial, promising results, the current ecological status of Borsodi-dűlő and Nyéki-szállás fall into the moderate category: their natural physical, chemical and biological features are still unsatisfactory due to the strongly manipulated water level and the occasional water supply originating from Lake Fertő. Regarding the Legény-tó, this pan was far from the natural conditions due to the lack of the natural hydrological regime. The disturbance events cause unpredictable and repeated shifts or reversions in the natural succession of the community preventing the developments of characteristic communities for soda pans or the possible alternative stable states. These pans are diversity hot-spots, so their good ecological status should be completely reached by restoring their natural hydrological and disturbance regimes.

(iv) The conclusions in the studied lotic ecosystem are similar to those found in temperate lakes: equilibrium states are rare (can be restricted to three separate months: July 2008, May 2009 and January 2010), unpredictable, ephemeral, and are mostly characterized by monodominance (*Cocconeis placentula sensu lato* and *Navicula lanceolata*). The resilience of a developed equilibrium phase may ensure biotic constancy even though the underpinning environmental background fluctuates at higher amplitude. Regarding some parameters, threshold values could be defined, where the degree of change alone was enough to prevent the development of an equilibrium phase. But the equilibrium state may occur in relatively-stable environments, too. Contrary to the phytoplankton, their establishment requires a longer time to develop corresponding to difference in generation times.

Resumé

Les concepts du stress et de la perturbation sont souvent confondus, en raison de la difficulté à classer les facteurs environnementaux dans l'un ou l'autre de ces concepts. Pourtant, leur distinction permettrait l'émission de conclusions plus fiables. L'objectif principal de cette étude est d'examiner les effets du stress et de la perturbation dans les communautés de diatomées benthiques par l'intermédiaire d'études expérimentales et de terrain.

Pour cela, il convient:

(i) d'identifier les flores de diatomées benthiques tolérant les stress multiples, dans 3 lacs salins;

(ii) de déterminer les conditions optimales et de tolérance de deux espèces diatomées selon un gradient de lumière, de température et de conductivité;

(iii) d'examiner la complexité de trois effets (perturbations naturelles, humaines et stress) dans trois bassin salins, en utilisant des sites de référence;

(iv) de définir la formation possible de l'état d'équilibre des communautés diatomées benthiques dans l'écosystème aquatique.

Dans ce but, les données collectées durant deux années de terrain (revêtement, paramètres physiques et chimiques) ont été utilisées, associées à la mise en place de cultures pures pour les expériences écophysiologiques.

Les principales conclusions sont les suivantes:

(i) La génération de nouvelles données sur la flore de diatomées benthiques des trois bassins salins de la région de Fertő-Hanság, agrémentés de nombreuses photographies. Dans cet écosystème, la distribution spatiale des communautés de diatomées ne semblent pas influencées par le type de substrat induit par le stress multiple. En raison du grand nombre d'espèces caractérisées avec le constance 1, la faible richesse spécifique, le potentiel de nouvelles espèces et les nombreuses espèces classées en liste rouge, la flore unique de diatomées benthiques des bassins salins montre une valeur de conservation importante.

(ii) Toutes les espèces (*Nitzschia frustulum* et *N. aurariae* aussi) ont un haut optimum et une large tolérance à la conductivité, leur conférant un avantage écologique remarquable face aux autres espèces. Bien que les niches écologiques des deux espèces se recouvrent, *N. aurariae* est favorisée par rapport *N. frustulum* en raison de sa tolérance face au stress de salinité. La

préférence ionique des espèces et leur besoin de lumière faibles à modérés peuvent expliquer leur distribution et dominance. Malgré l’optimum haut et la large tolérance des espèces face à la température, la diminution de l'activité photosynthétique peut être expliquée par l’atteinte possible de valeurs extrêmes, comme le suggèrent les modèles climatiques.

(iii) Après des premiers résultats prometteurs, les états écologiques actuels de Borsodi-dűlő et Nyéki-szállás sont devenus plutôt modérés : les caractéristiques naturelles biologiques, physiques et chimiques ne sont pas satisfaisantes en raison d’étiages fortement régulés et le prélèvement d’eau occasionnel provenant du lac Fertő (Neusiedlersee). L'état écologique de Legény-tó est loin des conditions naturelles en raison du manque de système hydrologique naturel. Ces perturbations entrainent des changements imprévisibles et récurrents dans la succession naturelle des communautés, et empêchent la mise en place de communautés caractéristiques de milieux salins ou la mise en place d’un possible état d’équilibre. Ces bassins sont de véritables hotspots de diversité ce qui suggère la possible atteinte d’un bon état écologique par la restauration des régimes hydrologiques naturels, soumis aux perturbations.

(iv) Les conclusions obtenues dans cet écosystème lotique sont similaires à celles obtenues dans les lacs tempérés : les conditions d'équilibre sont rares (réduites à trois périodes: juillet 2008, mai 2009 et janvier 2010), imprévisibles, éphémères et caractérisées par la dominance d'une espèce (*Cocconeis placentula sensu lato* et *Navicula lanceolata*). La résilience de l'état d'équilibre peut donc assurer la stabilité biotique malgré l’importante fluctuation des paramètres environnementaux. Concernant certains paramètres, des valeurs limites peuvent être définies, se suffisant à elles-mêmes pour empêcher la formation d’un état d’équilibre. Cependant, l’état d'équilibre peut également s’observer dans des environnements relativement stables. Contrairement au phytoplancton, son installation requiert plus de temps en raison de temps de génération différents.

1. General introduction

1.1. Definition and synonyms of phytobenthos

According to Wetzel (1979), the term of "Aufwuchs" includes organisms, which are attached to or move upon any submerged substratum without penetrating into it. In contrast, the benthos including fungal, bacterial, protozoan and other attached animal components is closely related to the substratum. Periphyton, as one of the subcategory of the benthos involves fungi, bacteria or microscopic algae which are growing on plant or any kind of substrate, phytobenthos refers to only the algal communities (Wetzel, 1983). Often, the unattached organisms are associated with the periphyton assemblages, which leads to further classification: euperiphyton (immobile organisms attached to the substrates), pseudoperiphyton or metaphyton (free-living, motile organisms creeping among or within the periphyton; Wetzel, 1979). In some cases the term biofilm is also used as a synonym of periphyton, but it is rather preferred in other scientific fields and refers largely to bacteria and protozoa (O'Toole et al., 2000). As it was concluded earlier by several researchers, the type of substrate is an important factor, and based on the available habitats, several further terms are used in freshwater lentic ecosystem (Goldsborough and Robinson, 1996; Azim et al., 2005): epilithon (on rocks or other inorganic matter), epipelon (on fine sediment), epiphyton (on macrophytes), episammon (on sand), epizoon (on aquatic animals).

1.2. Taxonomic composition and diversity of phytobenthos

On any submerged substrate, colonization processes immediately start and periphyton layer develops within a short period (Azim et al., 2005). As the first step of primary succession, the deposition of a coating of organic substance is assumed. Within hours, bacteria attach to the substrates by mucilaginous strands ensuring suitable binding site for other components, as colloidal, organic and inorganic elements (Flemming, 1995). After a few days, the colonization of small pennate diatoms (e.g. *Navicula*) and other single celled or coenobial species (e.g. *Scenedesmus*) start and is followed by short- and long-stalked species and diatoms with rosettes and mucilage pads (e.g. *Achnanthidium*, *Cymbella*, *Ulothrix*, *Oscillatoria*) (Stevenson, 1996; Azim et al., 2005).

These benthic algal growth forms can mean competitive advantages for the species in the different environments. Adnate algae can avoid the shear stress of severe currents, be resistant to grazing, but become nutrient and light limited (McCormick and Stevenson, 1989; Stevenson, 1996; Passy, 2007). Apically attached algae have competitive advantage in slow current environment and can overgrow the adnate forms. Stalked and filamentous forms can access to the light and nutrient sources, but they are threatened by the sudden disturbances such as shear forces and grazing (Stevenson, 1996; Passy, 2007). Motile species have the ability to change their position within the benthos, but they are sensitive to the flood velocity due to the lack of any stabilizing aid (Passy, 2007).

In freshwater ecosystems, most benthic algae are Cyanophyta, Chlorophyta, Bacillariophyta and Rhodophyta (Stevenson, 1996). In shallow lentic environments, the phytobenthos is dominated by *Achnanthidium*, *Amphora*, *Diatoma*, *Fragilaria*, *Navicula* and *Nitzschia* (Bacillariophyceae). *Lyngbya* and *Oscillatoria* species from Cyanophyta, *Spirogyra* and *Mougeotia* species from Chlorophyceae are also dominant taxa in wetland ecosystems (Goldsborough and Robinson, 1996; Azim et al., 2005). Usually, the phytobenthos of streams consist of diatoms, cyanophytas, chlorophytes, rhodophytes and xantophytes. *Achnanthidium*, *Cocconeis*, *Cymbella*, *Diatoma*, *Fragilaria*, *Gomphonema*, *Meridion*, *Navicula*, *Planothidium*, *Rhoicosphenia* and *Ulnaria* genus make up the phytobenthos as the components of Bacillariophyceae. *Phormidium*, *Oscillatoria*, *Calothrix* species from Cyanophyta, *Closterium*, *Oedogonium*, *Scenedesmus*, *Spirogyra*, *Stigeoclonium*, *Ulothrix* species as the members of Chlorophyceae may also dominate in lotic ecosystems (Azim et al., 2005).

The taxonomical diversity, the abundance of the species and the time to reach the phytobenthos' maximal biomass peak depend on several abiotic and biotic factors, such as the available nutrient content and light intensity. Development of the biomass can peak lasts for a few days to months, but according to the generally accepted concept, mature phytobenthos layer can occur within 4 weeks after the start of the colonization (Azim et al., 2005).

1.3. Application of diatoms

Diatom assemblages themselves are typically used instead of the entire phytobenthos for assessing the ecological status of the ecosystems (Stevenson and Pan, 1999). Stevenson and Pan (1999) summarized the three most important features of the diatoms, which qualify them to be the ideal indicators for determining ecological conditions. These are:

(i) their importance in ecosystems: the most widespread and diverse group; roles in the food webs, water oxygenation and biogeochemical cycle;

(ii) their utility as indicators: direct, fast and sensitive response to the changing environmental conditions and

(iii) their easy examination: cleaning, preparation, preservation, exchange and reanalysis are easy; a number of publication are available for their identification.

In view of the above, the role and the usefulness of diatoms are unquestionable. According to Vannote et al. (1980) the dominance of phytoplankton is expected in larger lotic and deeper lentic ecosystems against to the periphyton that is more abundant in shallow systems. These two groups are affected by different environmental factors and the opinions of the scientists who work in this field are divided. One group of the scientists recommends working with the planktonic diatoms (e.g. Reavie et al., 2010; Kireta et al., 2012), and the other group prefers benthic forms (e.g. Hill et al., 2000; Lane and Brown, 2007; Kireta et al., 2012). Applying the benthic form of diatoms, further problem presents itself: the exclusion or inclusion of the embedded planktonic and entrained benthic species. Similarly to the Potapova and Charles (2007), present dissertation applied the use of the phytobenthos including the entrained species too.

1.4. Primary environmental factors in lentic and lotic environments

The phytobenthos are affected by several abiotic factors, such as light intensity, temperature, nutrients, hydrodynamics and substrate specificity. Additionally, the herbivory is dominant biotic factor (Hodgkiss and Law, 1985; Goldsborough and Robinson, 1996; Azim et al., 2005).

1.4.1. Light

As consisted of photolithoautotrophic organisms, the phytobenthos requires sufficient available light to develop. The available light is related to both physiology (photosynthesis) and ecology (competitive interactions) of the algae (Azim et al., 2005).

There is a widely accepted model to describe the relationship between photosynthetic activity and light intensity, which is called as P-I curve (photosynthesis-irradiance, Webb et al., 1974; Platt et al., 1981; Hill, 1996). According to this model, three phases of the ecophysiological process are distinguished:

(i) light-limited phase: positive linear relationship between the photosynthesis and irradiance; α (initial slope of the P-I curve) is its typical parameter;

(ii) light-saturated phase: the photosynthetic activity reaches its maximum (P_{max}) at given irradiance (I_k);

(iii) photoinhibated phase: after the maximal photosynthetic activity, the photosynthesis can decrease ($\beta>0$) or it can more or less constant ($\beta=0$) with further increases in irradiance (Hill, 1996).

The photosynthesis mainly depends directly on the pH/available inorganic carbon source, irradiance and temperature, and indirectly on the nutrient content (Kirk, 1994).

The light quality (as spectral composition) and the light quantity (as intensity) are equally important (Azim et al., 2005). Only the PAR range of the global radiation is useful for the algae, which includes the light between 400 and 700 nm (Kirk, 1994). In lentic ecosystems, the vertical light extinction is critical regarding the the primary production as it determines the useful photosynthetic wavelengths and their intensity. The vertical light extinction in the littoral zone depends on the macrophyte and metaphyton density, turbulence, sediment resuspension and the water depth. In contrast, the light quality and quantity in streams mainly depend on the canopy of the ecosystem (Azim et al., 2005).

Every species has an optimal irradiance range for their growth. Thus, the available light intensity can affect the taxonomic composition of phytobenthos by selecting the species based on their different ecological demands. For example, many cyanobacteria and diatoms can tolerate low light availability (10-231 μmol $m^{-2}s^{-1}$) (Reynolds, 1988; Padisák, 2004; de Tezanos Pinto and Litchman, 2010) and can grow at 5-6 μmol $m^{-2}s^{-1}$ (Richardson et al., 1983; Langdon, 1988) making them good competitors for light. In contrast, most green algae can utilize higher irradiance intervals (85-510 μmol $m^{-2}s^{-1}$) (Pillsbury and Reynolds, 1988; Hill, 1996; Lowe, 1999; Padisák, 2004). The ecological light preferences of the species are in accordance with the seasonal succession patterns of the phytobenthos, since diatoms are the dominant members in spring when the global radiation is lower, green algae dominate in summer associated with higher light intensity (Azim et al., 2005). Furthermore, the available light regime can determine the algal assemblages by selecting the different life forms. In general, non-motile, adnate species (such as *Cocconeis*) can tolerate strong light limitation, motile (such as *Nitzschia*) and epiphytic attached species (such as *Epithemia*) can avoid it by altering their position within the phytobenthos layer (Passy, 2007).

1.4.2. Nutrients

According to Epstein's (1972) definition, the 17 life-essential elements can be sorted into two groups based on their concentrations: macro- and micronutrients (or trace elements). Macronutrients, such as hydrogen, carbon, oxygen, nitrogen, potassium, calcium, magnesium, phosphorous, sulphur, magnesium are required in higher concentrations (10^{-2} - 10^{-4} mol L^{-1}). The most significant determinants are carbon, nitrogen and phosphorous, which might be available in limiting concentrations for the growth of algae. The optimal Redfield molar ratio for phytobenthos is 119C:17N:1P (Redfield et al., 1963). Silicate can also be essential for diatoms or silica-scaled chrysophytes (Hopkins and Hüner, 2004b), it is generally required in a ratio of 16Si:16N:1P (Brzezinski, 1985). Contrary to the macronutrients, trace elements are sufficient in low levels (<10^{-5} mol L^{-1}) and include the chlorine, boron, iron, manganese, zinc, copper, nickel and molybdenum (Hopkins and Hüner, 2004b).

The nutrient accumulation and uptake are different in lotic and lentic environments (Stevenson, 1996; Azim et al., 2005). In lotic ecosystems, the increased nutrient loading is not necessarily associated with the higher nutrient uptake rate. It depends also on the flow rate, periphyton composition and condition. In lentic ecosystems, the nutrient uptake of benthic algae is related rather to the sediment-surface interactions, than the water column. Thus, the nutrient uptake depends on the conditions of the lake bottom (e.g. oxygen supply, redox potential). Whenever wetlands or shallow lakes are in focus, the states of the sediment and water column are equally important.

Eutrophication is the most widespread form of water pollution causing changes in primary production, biochemical cycles and biological communities (Hall and Smol, 1999). The process of eutrophication is easy to follow by the changes in the composition of diatom communities. Diatoms are good competitors for P, cyanobacteria for N (Sommer, 1983; Tilman et al., 1986). Thus, the changes of N:P ratio involve the shift from diatoms to cyanobacteria in the assemblages (Tilman et al., 1986). Some diatom species, such as *Amphora pediculus* (Kützing) Grunow ex A.Schmidt, *Aulacoseira granulate* (Ehrenberg) Simonsen, *Nitzschia palea*, *Rhoicosphenia abbreviata*, *Surirella brebissonii* and *Stephanodiscus hantzschii* can be reliable indicators of eu- or hypertrophic waters, contrary to *Cyclotella ocellata*, *Encyonopsis subminuta*, which usually are abundant in oligotrophic conditions (Hall and Smol, 1992; Van Dam et al., 1994; Reavie et al., 1995).

1.4.3. Temperature

Temperature has major role in many biological processes (e.g. enzymatic processes, photosynthesis) (DeNicola, 1996). Not only the lower, but the higher temperature also can cause serious damage in these processes. For example, low temperatures may cause irreversible changes in membrane fluidity (Falkowski and Raven, 1997), and high temperature results in higher dark reaction rate and respiration, reduced photosynthetic efficiency due to the denaturation of enzymes (Hopkins and Hüner, 2004b). However, often the effects of temperature and light cannot be separated from each other due to the strong collinearity observed in situ measurements (Azim et al., 2005).

Similarly to the light intensity, species have different temperature optima. For example *Nitzschia* species prefer higher temperature (~30 °C) (Barker, 1935), contrary to *Navicula lanceolata* which typically occurs in cold waters (Hofmann et al., 2011).

1.4.4. Salinity

The distributions of diatoms are highly correlated not only with the salinity, but also with the ionic composition (Servant-Vildary and Roux, 1990; Blinn, 1993; Cumming and Smol, 1993). Contrary the ionic composition, the effects of salinity are well-known. It can affect directly or indirectly the communities by affecting nutrients, controlling the cellular processes, causing osmotic and ionic stress, regulating the photosynthesis and the growth of the species (Hasegawa et al., 2000; Sullivan and Currin, 2000; Munns, 2002; Sudhir and Murthy, 2004).

Salinity originated from the product of the source waters hence a wide range of salinity is represented in aquatic ecosystems. There are some classifications to categorize the ecosystems based on their conductivity. According to Williams (1967), three categories were distinguished:

(i) freshwaters: salinity < 500 mg L^{-1} (<0.5 $^{\circ}/_{\circ\circ}$; ~ 670 µS cm^{-1})
(ii) subsaline waters: salinity 500 - 3000 mg L^{-1} (0.5 - 3 $^{\circ}/_{\circ\circ}$; 670-5500 µS cm^{-1})
(iii) saline waters: salinity > 3000 mg L^{-1} (> 3 $^{\circ}/_{\circ\circ}$; ~ 5500 µS cm^{-1})

Based on Hammer's (1986) classification, another three categories can be used:

(i) hyposaline waters: 3000 - 20000 g L^{-1} (3-20 $^{\circ}/_{\circ\circ}$; 5500-30000 µS cm^{-1})
(i) mesosaline waters: 20000 - 50000 g L^{-1} (20-50 $^{\circ}/_{\circ\circ}$; 30000-70000 µS cm^{-1})
(i) hypersaline waters: > 50000 g L^{-1} (>50 $^{\circ}/_{\circ\circ}$; >70000 µS cm^{-1})

The strong correlation between the distribution of diatom species and salinity range is well documented (Blinn, 1993; Fritz et al., 1993). The freshwater species have distribution limits about the 3000 mg L^{-1} concentration of salinity. Based on paleolimnological datas (Fritz et al., 1999), *Stephanodiscus minutulus*, *Fragilaria capucina* var. *mesolepta* (Rabenhorst) Grunow are rare or missing above this threshold, contrary to *Navicula fonticola* which occur only under saline conditions. As a result of recent studies (Blinn, 1993; Veres et al., 1995; Żelazna-Wieczorek et al., 2015), *Nitzschia commutata*, *Hippodonta hungarica* or *Fragilaria vauchariae* are associated with low salinity range, *Anomoeoneis costata*, *Halamphora dominici* have high salt tolerance, some species, such as *Navicula veneta* is “salt generalist” having broad tolerance. However, ecophysiological laboratory experiments could provide detailed and more accurate information about the optimum and tolerance of the species. Many of such investigations were carried out with the phytoplankton (mainly fast-growing easy to culture species) (e.g. Grant and Horner, 1976; Stramski et al., 2002; Roubeix and Lancelot, 2008), but those with benthic forms have been missing.

1.4.5. Substrate

The abundance of the algae is affected on a wide scale from climate- and landscape through the nutrient sources until the micro scale (Biggs, 1996; Stevenson, 1997). The type of substrates affects the algae communities on micro-scale as found in severe studies including lotic and lentic environments too (Biggs, 1996; Stevenson, 1997; Winter and Duthie, 2000; Townsend and Gell, 2005; King et al., 2006; Bere and Tundisi, 2011; Wojtal and Sobczyk, 2012; Dalu et al., 2014). In such habitats, where the environmental conditions reach extreme values causing multiple stresses on their biota, the effect of substrates is less noticeable, as it was concluded by several researchers (Jüttner et al., 1996; Kitner and Poulícková, 2003; Soininen and Eloranta, 2004; Potapova and Charles, 2005).

When nutrient availability is low, the substrate specificity can be more profound. Many taxa showed strong affinity to sediments, mosses or rocks. *Cocconeis placentula*, *Denticula elegans* Kützing prefer moss, and, for example, *Navicula salinarum* or *Caloneis schumanniana* (Grunow) Cleve are associated with sediment (Douglas and Smol, 1995; Lim et al., 2001). But sometimes this relationship is more complex, than it was originally thought. Based on a study of *Cyclotella pseudostelligera* Hustedt, this species was identified also as moss- (Michelutti et al., 2003) and rock-specific (Lim et al., 2001).

Several investigations concluded that epiphytic communities are substrate-specific (Gough and Gough, 1981; Jones et al., 2000). Blindow (1987) found that some species can migrate between preferred and less preferred habitats. Macrophytes can be positive (e.g. mutualism, symbiosis), negative (e.g. competition) and neutral substrata for epiphytic algae (Azim et al., 2005).

Beside the habitat specificity, the age of substrate, the season, the position and the stability are also very important (Azim et al., 2005). According to these parameters the lentic and lotic ecosystems can be different for the phytobenthos.

1.4.6. pH

pH is an important environmental parameter because many algae grow only within a narrow pH range. pH prevents the formation of precipitates, influences the available C source for photosynthesis (Hopkins and Hüner, 2004b). The dissociation of carbon dioxide is pH-dependent: under low pH the main form is CO_2, around neutral circumstances the available form is HCO_3^-, and in alkaline conditions CO_3^{2-}. This is very important for the algae, because they can utilize only free CO_2 or HCO_3^- (Hopkins and Hüner, 2004b). pH of natural waters varies commonly between 7 and 8 serving sufficient available inorganic carbon.

Acidification and alkalinisation of natural aquatic habitats is one of the contemporary problems, and has been observed worldwide (Battarbee et al., 1999). The changes in pH can be indicated by the appearance and disappearance of diatom species, since most taxa have definite pH preferences. Hustedt (1939) suggested a classification system based on the optimal pH ranges, which is adopted and applied by most diatomists after some modification (Renberg, 1976; Van Dam et al., 1994).

i) alkalibiontic: species occurring at pH > 7, such as: *Rhopalodia gibba*
(ii) alkaliphilous: species occurring mainly at pH > 7, such as *Hippodonta hungarica*
(iii) circumneutral: species occurring at pH ~ 7, such as *Encyonema silesiacum*
(iv) acidophilous: species occurring at mainly pH < 7, such as: *Fragilaria tenera*
(v) acidobiontic: species occurring at pH < 7, optimal occurrence at pH < 5.5, such as: *Gomphonema micropus* var. *micropus*
(vi) indifferent: no apparent optimum, such as *Eunotia bilunaris.*

1.4.7. Grazing

There are a wide variety of the herbivores grazing on phytobenthos (Azim et al., 2005). The gastropods, crustaceans, insect larvae as the most important invertebrates, but fish and tadpoles among the vertebrate organisms can also feed on phytobenthos. The herbivores can be strong selectors of the species in the phytobenthos (e.g. Cattaneo, 1983; Vermaat, 1994) which can be measured with an electivity coefficient. Underwood and Thomas (1990) concluded that using such coefficients, some taxa are under-represented in the diet, others are over-represented based on their efficiency (the rate of the invested energy and the nutritional value). The adnata forms need higher effort to remove than their nutritional value, contrary to the penduculate or filamentous forms which are easy to remove. The selectivity is rather depends on the interplay of some factors: pre-contact, post-contact and post-ingestion factors (e.g. visual camouflaging, release of chemicals, Underwood and Thomas, 1990).

1.5. Stress and disturbance

As it was concluded earlier by Professor János Selye (1976), "Stress is the spice of the life". Though this statement originated from the human psychology, it is not so different in the field of hydrobiology. According to that definition, stress is a quite ambiguous concept: it is necessary in a manner to a healthy and meaningful life, but its great extent could be very dangerous. Based on Professor Selye's investigation, there are three phases of the stress (GAS: General Adaptation Syndrome), which could be adapted for the aquatic organisms, as it is known from the biochemistry/physiology fields.

1. Alarm reaction;
2. Adaptation, resistance;
3. Depletion.

Despite stress is one of the most thoroughly studied topics in science, the term is not so clear and often confused with the definition of disturbance. According to the Science Direct database, and especially to the agricultural and biological sciences, there are 125197 articles after searching for the stress in the titles and 895 for the disturbance up to now (up to 20.02.2016). However, different definitions were developed for stress and disturbance during the last decades (Table 1), the use of these terms is still ambiguous.

Grime (1979) divided the ecological factors which determine the growth and reproduction of the organism into two groups for the clear discrimination of the two terms.

1. Stressors: sources (e.g. nutrients, light), physical and chemical factors (e.g. temperature, pH)
2. Disturbance: e.g. grazing, flooding.

However, the application of this approach needs careful consideration, because none of the environmental variables can be clearly claimed as stressors or disturbances. Disturbance has two components, which are equally important: frequency and intensity (Sommer et al., 1993). Thus, in every time, the frequency, the intensity of the impact and the resilience of the studied ecosystem are required to take into consideration for the determination of these factors. For example, high and intermediate disturbances as it was defined in Connel's IDH, can also be stressors, if these parameters are kept in mind.

The clarification and the differentiation of the two factors are very important, because both the disturbances and stress can be used to investigate the effects of climate change, but their impacts need different approaches. The climate change has strong effects on the hydrosphere by affecting the ecological structure and functioning of the communities. The impacts of global climate change can be measured through changes in the frequency and intensity of the events impacting the ecosystems (e.g. floods) (Whetton et al., 1993; Fowler and Hennessy, 1995). However, establishment of the correct conclusions are not possible without the unequivocal definitions of these factors. In present paper, the definitions described by Borics et al. (2013) are accepted and applied for the investigation of stress and disturbance.

Shallow ecosystems, such as wetlands and soda pans are especially vulnerable by climate change, because the stability of their hydrological budget is very sensitive (Winter, 1990; Mason et al., 1994a) to alterations in water level and hence water chemistry. The fluctuation of water level, the increased nutrient concentrations, conductivity and temperature, the altered light regime poses multiple stresses on the biota affecting the physiological responses and species composition. In these habitats, only a few species can tolerate the extreme conditions. Many species could disappear and replaced by other species with special adaptations (Padisák, 1998b). The aim of the first Chapter of the present dissertation is to determine the benthic diatom flora of three alkaline, saline, shallow pans for recognizing what kind of species can survive in highly stressed ecosystems.

The diatom communities, as other organisms, can adapt to the environmental stress on different levels. The acclimation and adaptation should be distinguished. The term of acclimation refers to the physiological processes and phenotypic adjustment, adaptation rather to evolutional processes and genotypic changes (Falkowski and LaRoche, 1991). Physiological acclimation (for example to light regime) has effects on photosynthetic processes and growth rates (e.g. Richardson et al., 1983; Cullen, 1990) or on cellular level through changes in pigment- and lipid content and composition (Perry et al., 1981). Unambiguous acclimation can be assessed only when the cells are in balanced growth (Beardall and Morris, 1976). The acclimation is species-specific and very important process by having effect on the biomass and species compositions (Stevenson, 1997). Every species has ecological preferences, sensitivities and tolerances, which determine their dispersal area. The best way to identify these parameters of the species is to use cultures in laboratory experiments. The second chapter of this dissertation deals with the growth response of two diatom species along several gradients by ecophysiological measurements to understand their potential response to climate change.

The stress and disturbance can originate not only from natural processes (such as climate change), but also from human activity. For example, incorrect water management tools can be viewed as human impact, which can regulate the hydrological regimes of the lakes (e.g. water level, hydrological basin). Aquatic ecosystems often suffer from both natural and human impact. In saline lakes, these effects are straightened with extreme stress gradients, such as high salinity and phosphorous content (Stenger-Kovács et al., 2014b). In the third chapter of this dissertation, the complexity of these three impacts (natural, and human disturbances, stress) was investigated in three saline pans using reference sites.

In lotic environments, different chemical and physical parameters determine the algal assemblages, than in lentic systems. Lotic environments are complex and dynamic systems, where these parameters fluctuate in a wide range along spatial and temporal scales (Stevenson and Pan, 1999). Several studies deal with the effect of physical disturbance on benthic algae in streams, as drought and flood events (Peterson, 1987; Steinman and McIntire, 1990; Ledger et al., 2008). The recovery of the phytobenthos after flooding can be slow or prevented depending on the intensity and frequency of the impacts (Lake, 2000). Thus, the equilibrium phase of the communities strongly depends on the stress and disturbance events. The fourth chapter of present dissertation focuses on the potential establishment of equilibrium state of benthic diatom assemblages in a stream ecosystem based on two-year dataset.

Table 1 *The historical development of the definitions of stress and disturbance*

	Stress	Disturbance
Barrett et al., 1976	perturbation (stressor) applied to a system	
Connell, 1978		IDH (Intermediate Disturbance Hypothesis), any event that interrupts the approach toward the eventual exclusion. (e.g. decrease in biomass, increase in the availability resources). It was originated from internal processes.
Bormann and Likens, 1979		disturbance as disruption of the pattern of the ecosystem, principally by external physical forces
Grime	stress, consist of factors that place prior restriction on plant production	the mechanisms which limit plant biomass by causing its partial or total destruction
Odum et al., 1979	unfavourable deflections	as a deviation or displacement from the nominal state in structure or function at any level of organization
Odum, 1985	detrimental or disorganizing influence	
Pickett and White, 1985		Any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment
Rykiel, 1985	stress indicates tension or emphasis, as in placing weight upon something	disturbance suggests disorderly ‘stirring’ or disruption as in stirring up trouble
Rapport et al., 1985	external force or factor, or stimulus that causes changes in the ecosystem	
Grime, 1989	external constraints limiting the rates of resource acquisition, growth or reproduction of organism	
Crawford, 1989	any environmental factor which restricts growth and reproduction of an organism or population	

Larcher, 1991	exposure to extraordinarily unfavourable conditions	
Olrik and Nauwerck, 1993		disturbance is a natural environment is defined by its effects on the biotic community
Reynolds et al., 1993		primarily non-biotic, stochastic events that results in distinct and abrupt changes in the composition and which interfere with internally-driven progress towards self-organization and ecological equilibrium
Townsend and Hildrew, 1994		any relatively discrete event that removes organisms and opens up space and other resources that can be used by individuals of the same or different species
Freedman, 1995	environmental influences that cause measurable ecological changes	
Nilsen and Orcutt, 1996	conditions that cause an aberrant change in physiological processes resulting eventually in injury	
Bartha et al., 1997		a multi-species, spatiotemporal pattern of mortality of non-competitive origin
Lake, 2000		a disturbance occurs when potentially damaging forces are applied to habitat space occupied by a population, community, or ecosystem
Roelofs et al., 2008	stress is evoked in organism living at the edges of their ecological niches, where environmental conditions may exceed the ranges required for normal growth and development	
Borics et al., 2013	frequently occurring or continuous event, when as a result of the impact the system does not recover, therefore, value of the system variable does not reach the basic level	occasionally occurring or periodic event, that result in an abrupt change of the system, with the possibility of recovery

2. Diatom flora under stress conditions[1]

2.1. Introduction

Saline lakes can be found almost in each continent (Bauld, 1981; Hammer, 1986; Goudie, 2003; Williams, 2005; Boros et al., 2006;): Central-Europe (Carpathian basin, Romania, Serbia), Africa (Kenya, Tanzania, Egypt), North-America, Australia and Asia. These lakes are mostly found in the continental zone far from the Sea vapor source (Slaymaker and Spencer, 1998). The inland saline lakes occur in semi-arid (200-500 mm) and arid (25-200 mm) areas, where the annual amount of the precipitation is lower than the potential evapotranspiration (Mainguet, 1999). These ecosystems have closed basins without outflows, their water budget depends largely on the precipitation and evaporation (Noy-Meir, 1973). These lakes can completely dry out for years (astatic), or they could be filled by water (eustatic), or their water level may fluctuate strongly (semi-astatic). Consequently, these closed-basin saline lakes are intricately tied to the climate system (Mason et al., 1994a).

Intermittent soda pans (lakes that can be filled with water or totally dried with predictable annual cycle; Williams, 2005) represent a special type of wetland ecosystems and they are extreme habitats having special chemical and physical features. They are dominated by Na^+, CO_3^{2-}/HCO_3^- ions, and characterized by high levels of conductivity, day-night temperature variation, turbidity, pH, alkalinity and TP (total phosphorus) concentration (Boros et al., 2014; Stenger-Kovács et al., 2014b). Based on their secchi transparency, soda pans can be turbid, colored or transparent. Such aquatic habitats occur in Central Europe (Keresztes et al., 2012; Horváth et al., 2014; Somogyi et al., 2014) especially in two regions of Hungary and Austria: the Danube-Tisza Interfluve and the Fertő-Hanság region (Stenger-Kovács et al., 2014b). Despite of the significant number of these habitats, the benthic algal vegetation of the bigger shallow lakes (Lake Fertő/Neusiedlersee and Lake Velencei) were mostly studied in Hungary (Grunow 1860, 1862, 1863; Pantocsek, 1912; Hustedt, 1959b, 1959c; Tevanné, 1981; Padisák, 1982, 1984; Buczkó, 1986, 1989; Buczkó and Padisák, 198788; Khondker and Dokulil, 1987, 1988; Buczkó and Ács, 1997, 1998; Ács et al., 1994, 2003, 2005; Ács, 2007).

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[1] A part of this chapter was published in Studia Botanica Hungarica:
Stenger-Kovács, C. & E. Lengyel, 2015. Taxonomical and distribution guide of diatoms in soda pans of Central Europe. Studia Botanica Hungarica 46: 3-203.

The algological investigations of the soda pans situated around Lake Fertő started very early, but focused mainly on the Austrian side (Legler, 1941; Hustedt, 1959a, 1959c). Contrary to the Danube-Tisza Interfluve, the studies of the pans located in the Fertő-Hanság region started in the last years (Lengyel and Stenger-Kovács, 2012; Boros et al., 2013a; Lázár et al., 2015; Stenger-Kovács and Lengyel, 2013; 2015; Stenger-Kovács et al., 2014a, 2014b, 2016), because these habitats were previously entirely disappeared due to the draining activities in the 19th and 20th centuries and just were reconstructed in 1989 (Pellinger, 2013).

According to the previous complex study focusing on their benthic diatoms (Stenger-Kovács et al., 2014b), the pans in the two Hugarian regions have different chemical and physical features and diatom flora. The differences appeared markedly in anion concentrations (HCO_3^-, SO_4^{2-}, and Cl^-), platinum (Pt) units (color), and oxygen saturation. The lakes situated in the Fertő-Hanság region can be characterized by lower HCO_3^- and Cl^- concentrations, higher SO_4^{2-} content, increased Pt color and oxygen saturation, then pans found in the other region. The description of algological differences has just been published: the 93 most abundant and widely distributed diatom species were characterized by light- and electron microscopic photos, morphological and distributional parameters, and references (Stenger-Kovács and Lengyel, 2015). However, the publication of the whole diatom flora has been missing.

2.2. Aims

The aim of the present chapter was to identify the whole benthic diatom flora of three shallow, alkaline, saline pans situated in the Fertő-Hanság region, especially their epipelic and epiphytic diatoms.

2.3. Material and methods

2.3.1. Study areas

The present study focused on three saline pans situated in the Fertő-Hanság Region in the Hungarian site of Lake Fertő (Neusiedlersee): Borsodi-dűlő, Legény-tó, Nyéki-szállás (Fig. 1). These lakes are ex-lege protected and can be found in the territory of Natura 2000 and Fertő-Hanság National Park.

These soda pans, as extreme habitats have special chemical and physical features. They are very shallow ecosystems, their average water depth is less than 23 cm (Boros et al., 2013a). All of them is alkaline (pH: 7.8-9.8) and hypertrophic because of their high TP content. The Borsodi-dűlő is transitional, the Nyéki-szállás and Legény-tó are turbid based on their secchi transparency. Their salinity varied along a wide range within the hyposaline category, but they have similar ionic composition (Na^{+}>Mg^{2+}>HCO_3^{-}>SO_4^{2-}) (Boros et al., 2013a; Stenger-Kovács et al., 2014b).

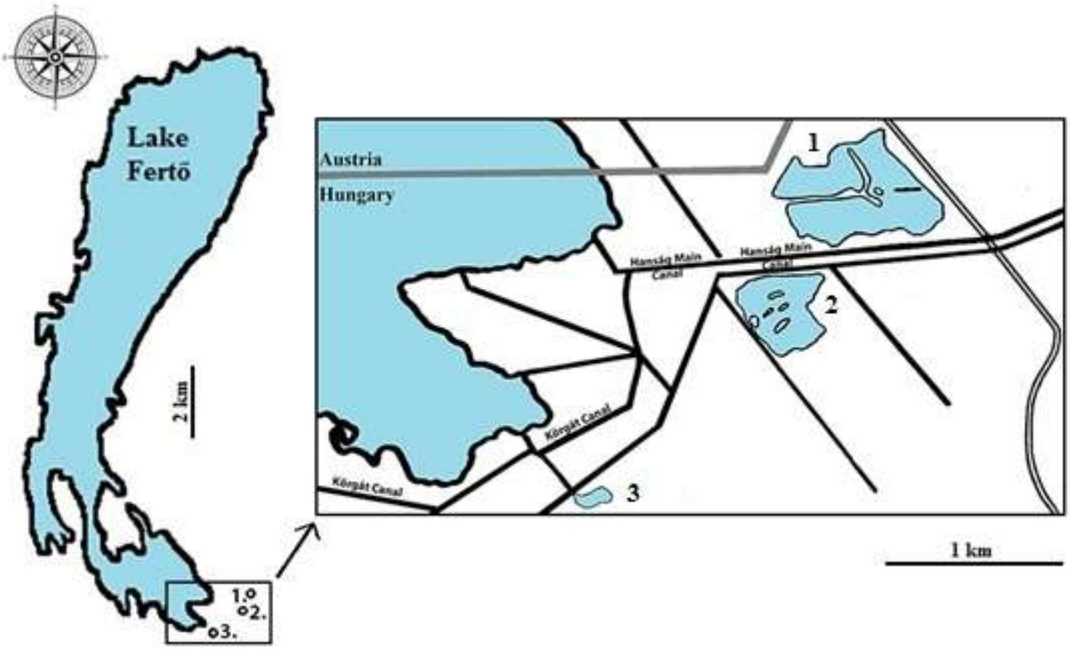

Fig. 1 *Location of the saline pans (1: Borsodi-dűlő; 2: Nyéki-szállás; 3: Legény-tó)*

2.3.2. Sampling process and diatom analyses

In the three pans, altogether 128 phytobenthos samples were collected from mud (79) and macrophytes (49) between January 2012 and August 2014.

The samples were cleaned by hot hydrogen-peroxide methods and embedded in Zrax resin (CEN, 2003). Diatom valves were identified at least to species level under SEM electron- (Hitachi S-2600 N) and light microscopy (Zeiss, Axio A1) at 1000× magnification using immersion oil and taxonomical guides (Bey and Ector, 2010; Hofmann et al., 2011; Krammer, 2000; Krammer, 2002; Krammer, 2003; Krammer and Lange-Bertalot, 1991; Krammer and Lange-Bertalot, 1997; Krammer and Lange-Bertalot, 1999a; Krammer and Lange-Bertalot, 1999b; Lange-Bertalot, 2001; Levkov, 2009; Taylor et al., 2007; Witkowski et al., 2000). The relative abundance and constancy of each diatom species were calculated.

The categories of the constancy values:

- Constancy 5: the species were present in the 80-100% of the samples;
- Constancy 4: the species were present in the 60-80% of the samples;
- Constancy 3: the species were present in the 40-60% of the samples;
- Constancy 2: the species were present in the 20-40% of the samples;
- Constancy 1: the species were present in less then 20 % of the samples.

The pH, salinity, trophic and saprobic preferences of the individual taxa were determined according to Van Dam et al. (1994). Correspondence analysis (CA) was applied to ordinate the samples for exploring differences in the diatom communities of the samples.

2.4. Results

Altogether 200 diatom species were identified during the study period belonging to 60 genera according to the currently valid taxonomic system. Most of the species were the members of the genera *Nitzschia* (34), *Navicula* (16) and *Gomphonema* (10); 6-6 taxa belonged to the genera *Cyclotella, Cymbella, Fragilaria* and *Halamphora,* and the other genera were represented by less than 5 species. Altogether 474 photo documentations are presented and arranged on 18 photo tables (Appendix, Table 1-18).

Table 2 summarizes the species numbers found in epiphyton and epipelon samples of the studied pans. The highest number of species was found in Legény-tó, where the mean species number was 36±11. Borsodi-dűlő and Nyéki-szállás showed close similarity; their mean species number were 28±10 and 27±11, respectively.

Table 2: *The species richness of the three studied pans*

	Legény-tó			**Borsodi-dűlő**			**Nyéki-szállás**		
	Total	Epiphyton	Epipelon	Total	Epiphyton	Epipelon	Total	Epiphyton	Epipelon
Min.	15	18	15	3	3	13	8	8	8
Max.	59	59	56	55	55	45	55	43	55
Mean	36	37	35	28	29	28	27	23	29
SD	11	11	11	10	12	9	11	11	11

Independently of the pans, no significant difference was observed between the epipelic and epiphytic communities in the soda pans as confirmed by CA. Based on the species pools, the CA analysis showed significant separation of the saline pans (Fig. 2).

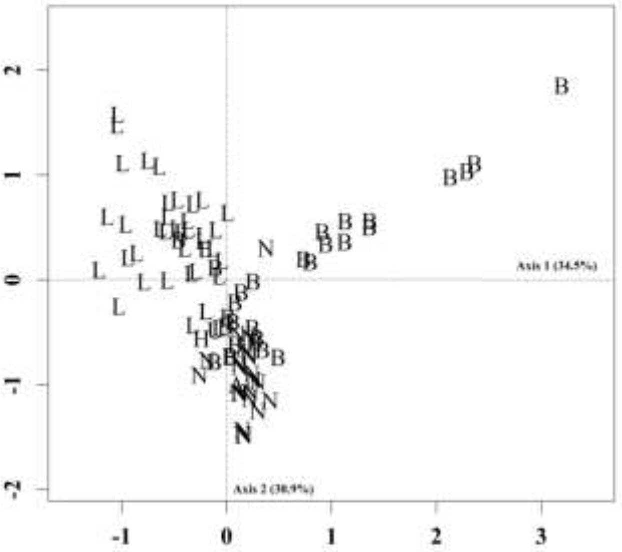

Fig. 2 *Correspondence analysis of the diatom communities (B: Borsodi-dűlő; L: Legény-tó; N: Nyéki-szállás)*

2.4.1. Legény-tó

Altogether 162 diatom species were identified in the Legény-tó, the dominant species (>5%) were *Achnanthidium minutissimum* var. *minutissimum*, *Ctenophora pulchella*, *Entomoneis paludosa* var. *subsalina*, *Navicula veneta*, *Nitzschia frustulum* and *N. palea* var. *palea* based on their mean annual relative abundances. In certain seasons, another 40 species became occasionally dominant, such as *Amphora copulata* (max.: 17.2%), *Cyclotella meneghiniana* (max.: 28.3%), *Cymbella neocistula* (max.:10.4%), *Navicula oblonga* (max.:19.6%), *Nitzschia paleaceae* (max.: 33.8%).

Six species (*Achnanthidium minutissimum* var. *minutissimum*, *Ctenophora pulchella*, *Cyclotella meneghiniana, Navicula veneta, Nitzschia frustulum*, *N. palea* var. *palea*) belonged to constancy category 5; 10 species (e.g. *Nitzschia supralitorea*, *Surirella brebissonii*, *Tryblionella apiculata*) were present in 60-80% of the samples (Constancy 4). Another 17 species (e.g. *Nitzschia solita, Pseudostaurosira brevistriata, Rhopalodia gibba*) were characterized by constancy 3, and further 26 taxa with constancy 2. The remaining 103 diatom species were rare: observed only in less than 20% of the samples (Appendix 4).

There were 48 diatom taxa of the total flora, which were found only in Legény-tó, such as *Nitzschia elegantula*, *Tryblionella gracilis* and *Ulnaria ulna*. The parameters (relative abundance, constancy and photos) of 15 species which are not included in Stenger-Kovács and Lengyel's study (2015) are detailed in Table 3.

Based on the pH preferences, 0.5% of the taxa were acidophilous, 26.8% circumneutral, 38.4% alkaliphilous, 17.9% alkalibiontic and 0.2% pH indifferent The pH preferences of 16.1% of the diatom species were unknown. As to salinity, 4.3% of the species were fresh, 45.1% fresh-brackish, 24.8% brackish-fresh, 10.6% brackish species and 15.2% of the species had no salinity preference. As to organic matter demand/tolerance, 12.4% of the diatom community indicated oligosaprobic conditions associated with high oxygen saturation (>85%), 22.1% of the species were β-mesosaprobic, 23.0% α-mesosaprobic, 10.5% alpha-béta meso/polysaprobic and only 5.3% α-mesopolysaprobic, and the saprobic preferences of 26.7% of the species were not available. Regarding the trophic preferences, 1.6-1.6-1.6 % of the diatom species indicated oligotrophic, oligo-mesotrophic and mesotrophic environment; 4.8% of the species were meso-eutrophic, 40.3% eutrophic, 9.5% hypereutrophic and 10.4% indifferent. The trophic preferences of the 30.2% of the diatom species remained unidentified.

2.4.2. Borsodi-dűlő

Altogether 165 diatom species were identified in the Borsodi-dűlő. The dominant species were *Navicula veneta*, *Nitzschia frustulum*, *N. palea* var. *palea*, *Stephanodiscus parvus* and *Tryblionelly apiculata*. Occasionally another 31 species became dominant, such as *Anomoeoneis sphaerophora* (max.: 42.3 %), *Hantzschia abundans* (max.: 79.6 %).

Three species (*Navicula veneta*, *Nitzschia frustulum*, *Tryblionella apiculata*) belonged to constancy category 5. Eight species (e.g. *Craticula ambigua*, *Cyclotella meneghiniana*) were present in 60-80% of the samples; 13 species (e.g. *Ctenophora pulchella*, *Halamphora kevei*, *Tabularia fasciculata*) were characterized by constancy 3. Additionally, 25 taxa belonged to constancy category 2, and 116 diatom species were observed in less than 20 % of the samples (Appendix 5).

Of the total flora, 43 diatom taxa were found only in Borsodi-dűlő, such as *Gyrosigma obtusatum*, *Halamphora paraveneta* and *Nitzschia acicularis*. The relative abundance, constancy and photos of that 25 species which are not included in Stenger-Kovács and Lengyel’s study (2015) are detailed in Table 3.

Based on the pH preferences of the taxa, 0.1% was acidophilous, 22.2% circumneutral, 45.2% alkaliphilous and 21.0% alkalibiontic. The pH preference of 11.4% of the diatom species has been unknown. As to salinity, 3.5% of the species were fresh, 50.9% fresh-brackish, 25.6% brackish-fresh, and 10.6% brackish species. For 9.5% of the species salinity preference has not been known. As to preference/tolerance organic matter, 7.6% of the diatom species indicated oligosaprobic conditions, 19.1% of the species were β-mesosaprobic, 28.9% α-mesosaprobic, 18.4% alpha-beta meso/polysaprobic, 6.3 % α-mesopolysaprobic, and the saprobic preferences of 19.7% of the species were not available. Concerning trophic preferences, 2.6% of the diatom species indicated oligotrophic, 1.3% oligo-mesotrophic, 1.0% mesotrophic, 7.4% meso-eutrophic, 46.2% eutrophic, 18.5% hypereutrophic and 8.5% indifferent. The trophic preference of the 14.5% of the diatom species has not been known.

2.4.3. Nyéki-szállás

Only 126 diatom species were identified in the Nyéki-szállás. The dominant species were *Navicula veneta*, *N. wiesneri*, *Nitzschia frustulum*, *Tryblionella apiculata* and *T. hungarica*. On certain sampling occasions another 27 species became dominant, such as *Hippodonta hungarica* (max.: 15.8%), *Nitzschia paleaceae* (max.: 7.4%).

Five species (*Navicula veneta*, *N. wiesneri*, *Nitzschia frustulum, Tryblionella apiculata, T. hungarica*) belonged to constancy 5. Five species (*Anomoeoneis sphaerophora*, *Ctenophora pulchella*, *Fallacia pygmaea* ssp. *subpygmaea*, *Navicula salinarum*, *Nitzschia inconspicua*) fall to constancy category 4; 12 species (e.g. *Achnanthes brevipes* var. *intermedia*, *Nitzschia solita*) to constancy category 3. Additionally, 23 taxa belonged to constancy 2, and 81 diatom species were observed in less than 20% of the samples (Appendix 6).

Only 12 diatom taxa of the total flora were found only in Nyéki-szállás, such as *Aulacoseira ambigua*, *Gomphonema micropus* and *Nitzschia capitellata*. The relative abundance, constancy and photos of that two species which are not included in Stenger-Kovács and Lengyel's study (2015) are detailed in Table 3.

In the Nyéki-szállás, 0.1% of the species was acidophilous, 11.2% circumneutral, 59.6% alkaliphilous and 12.8% alkalibiontic. The pH preferences of 16.4% of the diatom species have been unknown. As to salinity, 7.4% of the species were fresh, 46.7% fresh-brackish, 23.3% brackish-fresh, 9.1% brackish species and 13.5% of the species had no predetermined salinity preference. As to saprobity, 9.1% of the diatom species indicated oligosaprobic conditions, 14.5% were β-mesosaprobic, 28.7% α-mesosaprobic, 12.2% alpha-beta meso/polysaprobic and 4.1% α-mesopolysaprobic, and the saprobic preferences of 31.3% of the species has been unknown. Considering the trophic preferences, 0.7% of the diatom species indicated oligotrophic, 0.3% oligo-mesotrophic, 6.5 mesotrophic, 4.0% of the species meso-eutrophic, 49.3% eutrophic, 7.4% hypereutrophic conditions and 5.6%

was indifferent. The trophic preferences of 26.0% of the diatom species have not been known.

Table 3 *The relative abundance, constancy and habitat of the identified benthic diatoms (B: Borsodi-dűlő; L: Legény-tó; Ny: Nyéki-szállás; Table: See photo tables and figures in Appendix)*

Taxon	Relative abumdance (%)			Constancy		Lakes	Table
	Min.	Max.	Mean	%	category		
Achnanthes exigua	0.2	0.2	0.2	0.9	1	B	T1:18
Achnanthidium sp.	0.2	7.3	0.2	10.7	1	B, L	T1:1-14
Achnanthidium straubianum	0.5	0.5	<0.1	0.9	1	L	T1:15-17
Amphipleura pellucida	0.2	0.5	<0.1	2.7	1	L	T1:19-20
Amphora commutata	0.2	0.5	<0.1	3.6	1	L	T1:21-24
Asterionella formosa	1.0	1.0	<0.1	0.9	1	L, Ny	T1:25
Aulacoseira ambigua	0.3	1.1	<0.1	3.6	1	Ny	T2:1-5
Berkeleya rutilans	0.2	0.2	<0.1	0.9	1	B, L	T1:26-30
Brachysira neoexilis	0.2	0.2	<0.1	0.9	1	B, L	T2:6
Brachysira procera	0.2	0.9	<0.1	1.8	1	B	T2:7
Brachysira vitrea	0.2	0.2	<0.1	0.9	1	B, L	T2:8
Caloneis lancettula	0.2	0.5	<0.1	1.8	1	B, L	T2:9-10
Caloneis molaris	1.5	1.5	<0.1	0.9	1	L	T2:11-12
Cocconeis neothumensis	0.2	0.7	<0.1	3.6	1	L, Ny	T2:13-17
Cocconeis pediculus	0.2	0.5	<0.1	1.8	1	L	T2:18-21
Craticula cuspidata	0.2	0.5	<0.1	8.0	1	B, L	T3:1-3
Craticula molestiformis	0.2	3.4	<0.1	6.3	1	B, L, Ny	T3:4-12
Cyclostephanos dubius	0.2	0.5	<0.1	5.4	1	B, L, Ny	T4:1-3
Cyclostephanos invisitatus	0.2	1.2	0.1	9.8	1	B, L	T4:4-11
Cyclotella atomus	0.2	0.7	<0.1	1.8	1	B, L	T4:12-15
Cyclotella distinguenda	0.2	0.2	<0.1	0.9	1	B	T4:22-25
Cyclotella ocellata	0.2	2.8	0.1	8.9	1	B, L, Ny	T4:26-31
Cyclotella praetermissa	0.2	1.1	<0.1	1.8	1	B	T4:16-21
Cymbella cymbiformis	0.7	0.7	<0.1	0.9	1	B	T5:1-2
Cymbella excisa	0.5	3.0	0.1	4.5	1	B, L, Ny	T5:3-10
Cymbella hustedtii **var.** ***hustedtii***	0.2	1.8	0.1	9.8	1	B, L, Ny	T5:11-16
Cymbella parva	0.2	0.2	<0.1	0.9	1	B	T5:18-19
Cymbella subhelvetica	0.2	0.9	<0.1	1.8	1	B	T5:17
Cymatopleura elliptica	0.2	0.2	<0.1	0.9	1	B	T6:1
Delicata delicatula	0.2	0.2	<0.1	0.9	1	B	T6:2-3
Denticula tenuis	0.2	24.8	0.2	2.7	1	L, Ny	T6:4-7
Diatoma ehrenbergii	0.5	0.5	0.5	0.9	1	B	T6:8-9
Diatoma moniliformis	0.2	2.0	0.1	7.1	1	B, L, Ny	T6:10-15
Diatoma vulgaris	0.5	1.2	<0.1	1.8	1	B, L	T6:16-19
Diploneis sp.	0.5	0.5	0.5	0.9	1	B	T6:20-21
Encyonema caespitosum	0.3	1.4	<0.1	3.6	1	L, Ny	T7:1-6
Encyonema lacustre	0.2	1.7	<0.1	3.6	1	L, Ny	T7:7-14
Encyonema prostratum	0.3	0.3	<0.1	0.9	1	B	T7:15-16
Encyonema silesiacum	0.5	1.7	<0.1	2.7	1	B, L, Ny	T7:17-22
Encyonopsis caesatti	1.5	1.5	<0.1	0.9	1	B	T8:1-5
Encyonopsis krammeri	0.2	0.2	<0.1	1.8	1	B	T8:6-8
Encyonopsis microcephala	0.2	0.2	<0.1	0.9	1	L	T8:9-12
Encyonopsis minuta	0.2	1.4	<0.1	3.6	1	B, L	T8:13-19
Encyonopsis subminuta	0.2	1.7	<0.1	5.4	1	B, L	T8:20-25
Entomoneis alata	0.2	16.9	0.8	20.5	2	B, L	T8:26-27
Entomoneis costata	0.2	0.7	<0.1	7.1	1	B, L, Ny	T8:28-29
Eolimna minima	0.2	0.2	<0.1	1.8	1	L, Ny	T8:30
Eolimna subminuscula	1.6	1.6	<0.1	0.9	1	B	T8:31-35
Epithemia adnata	0.2	2.4	0.1	8.9	1	B, L, Ny	T9:1-3
Eunotia mucophila	0.2	0.5	<0.1	1.8	1	L	T9:4-7
Fragilaria dilatata	0.2	0.3	<0.1	1.8	1	B, L	T9:8-10
Fragilaria nanana	0.2	1.1	<0.1	5.4	1	B, L	T9:11-14
Fragilaria perminuta	1.2	1.2	<0.1	0.9	1	L	T9:15-18
Fragilaria tenera	1.2	1.2	<0.1	0.9	1	L, Ny	T9:19-23
Fragilaria vaucheriae	0.2	2.5	0.1	8.9	1	B, L, Ny	T9:24-28

Table 3 (continuation) *The relative abundance, constancy and habitat of the identified benthic diatoms (B: Borsodi-dűlő; L: Legény-tó; Ny: Nyéki-szállás; Table: See photo tables and figures in Appendix)*

Taxon	Relative abumdance (%)			Constancy		Lakes	Table
	Min.	Max.	Mean	%	category		
Gomphonema italicum	0.2	0.5	<0.1	3.6	1	L	T10:1-4
Gomphonema micropus	0.2	0.2	<0.1	0.9	1	Ny	T10:5-7
Gomphonema pseudoaugur	0.2	0.3	<0.1	1.8	1	B	T10:8-10
Gomphonema pumilum	0.2	2.2	<0.1	1.8	1	B, Ny	T10:11-13
Gyrosigma obtusatum	0.2	7.5	0.3	12.5	1	B, L, Ny	T10:14-16
Halamphora oligotrophenta	0.2	0.7	<0.1	8.0	1	B, L, Ny	T11:1-6
Halamphora tumida	0.2	4.4	0.1	10.7	1	B, L, Ny	T11:7-14
Hantzschia vivax	0.2	0.2	<0.1	3.6	1	B, L, Ny	T11:15-16
Hippodonta capitata	0.7	0.7	<0.1	0.9	1	B	T11:17-19
Lemnicola hungarica	0.3	0.3	<0.1	0.9	1	L	T11:20-22
Luticola mutica	0.2	0.7	<0.1	4.5	1	B, L	T11:25-29
Luticola dismutica	0.3	0.3	<0.1	1.8	1	B, L	T11:23-24
Mastogloia elliptica	0.2	1.1	<0.1	8.9	1	B, L	T12:1-6
Melosira varians	0.2	1.7	<0.1	2.7	1	B, L, Ny	T12:17-12
Meridion circulare	0.5	0.5	<0.1	0.9	1	B	T12:13
Navicula antonii	0.2	0.3	<0.1	2.7	1	B, L	T12:14
Navicula capitatoradiata	0.2	1.2	<0.1	3.6	1	B, L, Ny	T12:15-20
Navicula cryptocephala	0.2	5.4	0.6	36.6	2	B, L, Ny	T13:1-5
Navicula gregaria	0.7	0.7	<0.1	0.9	1	L	T13:6-10
Navicula kotschyi	0.2	0.6	<0.1	2.7	1	B, L	T11:11-15
Navicula lanceolata	0.2	0.7	<0.1	1.8	1	B, L	T13:16-18
Navicula subrhynocephala	0.2	1.7	<0.1	4.5	1	B, L	T13:19-21
Navicula tripunctata	0.2	1.2	0.5	6.3	1	B, L	T13:22-26
Nitzschia acicularis	0.2	1.6	<0.1	5.4	1	B, Ny	T14:1-7
Nitzschia angustata	0.2	0.2	<0.1	0.9	1	B	T14:8
Nitzschia calida	0.2	0.7	<0.1	3.6	1	B, L	T14:9-11
Nitzschia capitellata	0.5	1.0	<0.1	1.8	1	Ny	T14:12-17
Nitzschia dissipata	0.2	2.4	<0.1	3.6	1	B, L, Ny	T14:18-26
Nitzschia fonticola	0.2	0.7	<0.1	8.0	1	B, L, Ny	T15:1
Nitzschia liebetruthii	0.2	0.7	<0.1	5.4	1	B, L, Ny	T15:2-9
Nitzschia sp.	0.2	0.3	<0.1	1.8	1	B	T15:10-11
Nitzschia obtusa* var. *obtusa	0.2	0.3	<0.1	2.7	1	B, L	T15:12-15
Nitzschia palea* var. *debilis	0.2	16.2	0.4	17.0	1	B, L, Ny	T16:1-6
Nitzschia radicula	0.2	0.5	<0.1	2.7	1	L	T16:7-14
Nitzschia salinarum	0.2	0.7	0.5	5.4	1	L,B	T16:15-18
Nitzschia sigma	0.2	0.5	<0.1	3.6	1	L, Ny	T16:19-24
Pinnularia borealis* var. *borealis	0.5	0.5	<0.1	0.9	1	B	T17:1-6
Planothidium frequentissimum	0.2	1.6	<0.1	7.1	1	B, L	T17:7-13
Planothidium rostratum	0.2	0.2	0.2	0.9	1	L	T17:14-15
Pseudostaurosira brevistriata	0.2	4.6	0.4	28.6	2	B, L, Ny	T17:16-22
Rhoicosphenia abbreviata	0.2	1.6	0.1	13.4	1	B, L, Ny	T17:23-29
Rhoicosphenia adriatica	0.2	7.8	0.3	33.0	2	B, L, Ny	T17:30-36
Sellaphora capitata	0.2	2.1	0.1	16.1	1	B, L, Ny	T17:37-42
Staurophora tackei	0.2	0.2	<0.1	0.9	1	L	T17:43
Staurosira binodis	0.5	0.5	<0.1	0.9	1	B	T18:1-5
Staurosira construens	10.6	10.6	0.1	0.9	1	B	T18:6-13
Staurosira venter	0.2	21.1	0.3	8.9	1	B, L, Ny	T18:14-19
Staurosirella lapponica	0.5	0.5	<0.1	0.9	1	B	T18:20-23
Staurosirella ovata	0.2	1.0	<0.1	6.3	1	B, L	T18:24-28
Staurosirella pinnata	0.3	0.8	<0.1	2.7	1	B, L	T18:29-30
Stephanodiscus hantzschii f. tenuis	0.5	19.4	0.5	11.6	1	B	T4:32-38
Stephanodiscus hantzsii	0.5	6.3	0.2	8.0	1	B	T4:39-46
Stephanodiscus minutulus	0.2	3.3	0.1	10.7	1	B, Ny	T4:47-54
Surirella brightwelli	0.2	0.6	<0.1	6.3	1	B, L, Ny	T18:31-32
Surirella minuta	0.2	0.2	<0.1	0.9	1	L	T18:33

2.5. Discussion

Altogether 200 benthic diatom species were identified in 128 samples. Many species (108) were illustrated in 18 photo tables by light microscopy photos. This iconographic work provides new scientific information for the national and international science about the special diatom flora of three pans situated in the Fertő-Hanság region including detailed quantitative and qualitative datas**.** Based on the many unequivocally difference in their main morphological features (such as stria density, width, length), some of the 200 species is presumably new to the science: *Achnanthidium* sp., *Mastogloia* sp., *Nitzschia* sp. 1 and *Nitzschia* sp. 3.

Diatom species are commonly associated with special microhabitats, such as substrates (Biggs, 1996; Stevenson, 1997; Winter and Duthie, 2000; Townsend and Gell, 2005; King et al., 2006; Bere and Tundisi, 2011; Wojtal and Sobczyk, 2012; Dalu et al., 2014) both in lentic and lotic ecosystems, but sometimes other environmental factors (e.g. nutrients, catchment scale) can override it (Jüttner et al., 1996; Kitner and Poulícková, 2003; Potapova and Charles, 2005; Soininen and Eloranta, 2004; Żelazna-Wieczorek, 2011). In intermittent, shallow, alkaline soda pans, where the environmental parameters can reach extreme values representing multiple stresses on the biota, the diatom species have to tolerate a broad range of physical and chemical changes. In these ecosystems, the spatial distribution of diatoms was related to the pans and their characteristic limnological features, and the effect of substrates was less noticeable. The low taxon number is in accordance with the special chemical and physical features of the habitats. The species living in such ecosystems have to tolerate and adapt to high level stress resulting in a very special and low-diversity community (e.g. Pálffy et al., 2014; Stenger-Kovács et al., 2014b). Contrary, the shallow ecosystems usually have broader species pool, as it was found in the littoral zone of shallow water bodies in the Czech Republic too, where altogether 119 species were identified in 45 samples (Kitner and Poulícková, 2003). Based on a previos study focusing Hungarian shallow lakes, altogether 361 diatom species were found in 83 samples (Stenger-Kovács et al., 2007).

Based on the ecological preferences of the individual species (Van Dam et al., 1994), the diatom communities were not completely in accordance with the natural features of the inland saline pans. The diatom flora consists mainly of alkaliphilous species indicating the typical high pH level of the pans (Stenger-Kovács et al., 2014b). According to the salinity preferences, many diatom species were present in all the salinity categories (from fresh to brackish) as a result of seasonality. Many of the species were fresh-brackish indicating the lower annual salinity of the studied pans that can be supposed in the typical inland saline pans, where the hypersaline conditions are not outstanding. In the saline lakes, where higher conductivity can be measured, the typical diatom flora consists of e.g. *Denticula elegans* Kützing, *Surirella striatula* Turpin, *Amphora ovalis* (Kützing) Kützing, *Halamphora coffeaeformis* (C.Agardh) Levkov, which are missing from the studied pans (Blinn, 1993). The studied pans are well oxygenated, however with seasonal fluctuation. These results are in accordance with the diatom flora, which consists of taxa representing wide range of saprobic spectrum (from oligo- to mesopolysaprobic). The hypertophic conditions are typical in these ecosystems due to the high P loading by the water birds (Boros et al., 2008). The diatom flora represented a wide range of trophic spectrum due to the seasonal variation of the TP, but most species were only eutrophic, which is worse than it can be supposed in the typical soda pans.

Concerning the total species pool of the studied pans, an overlap (50%) can be observed that of Lake Fertő, indicating its proximity (Grunow 1860, 1862, 1863; Pantocsek, 1912; Hustedt, 1959b; Tevanné, 1981; Padisák, 1982, 1984; Buczkó, 1986, 1989; Buczkó and Padisák, 1987/88; Khondker and Dokulil, 1987, 1988; Buczkó and Ács, 1997): e. g. *Achnanthes breviceps* var. *intermedia*, *Caloneis silicula*, *Navicula cryptocephala*, *N. gregaria*, *Nitzschia fonticola*, *N. obtusa*. Regarding the Austrian shallow soda pans, 46% of the benthic diatom flora is common, such as *Amphora copulata*, *Caloneis lancettula*, *Cymbella excisa*, *Halamphora subcapitata*, *Nitzschia solita*, *Staurophora wislouchii* (Legler, 1941; Hustedt, 1959a, 1959c; Grunow 1860, 1862, 1863; Stenger-Kovács and Lengyel, 2016). Based on the checklists of diatoms found in the Danube-Tisza Interfluve, 59% of the species is overlapped, such as *Hippodonta capitata*, *Navicula tripunctata*, *Nitzschia inconspicua*, *Pinnularia oriunda*, *Rhopalodia operculata* (Cholnoky, 1929; Hortobágyi, 1956a, 1956b, 1956c; Uherkovich, 1965, 1969, 1970a, 1970b, 1972; Kiss, 1971, 1974, 1975, 1978a, 1978b; V-Varga, 1971; Hegewald et al., 1975; Schmidt, 1976, 1978, 1996, 2003; Schmidt and Uherkovich, 1979; Schmidt and Kiss, 1989; Komáromy and Padisák, 1999; Padisák, 1999; Ponyi and Dévay, 1999; Stenger-Kovács et al., 2014; Stenger-Kovács and Lengyel, 2016). Altogether 31% of the species can be found in all the three regions, such as *Anomoeoneis sphaerophora*, *Campylodiscus bicostatus*, *Cocconeis placentula*, *Craticula halophila*, *Nitzschia vitrea*, *Scoliopleura peisonis*. Nevertheless, a remarkable part (29%) of the benthic diatom species can be found only in the studied pans (e.g. *Achnanthidium straubianum*, *Brachysira* *neoexilis*, *Cocconeis neothumensis*, *Diploneis parma*, *Encyonopsis caesatti*, *Navicula antonii*), to which may contribute to the development of the taxonomy: new species are described, existing species are renamed and divided into different taxon. The present study provides new scientific information about 108 species of the total diatom flora, which were not included in the taxonomical and distribution guide for saline pans in the Carpathian basin (Stenger-Kovács and Lengyel 2015).

The uniqueness of the pans was also confirmed by the constancy numbers, as most of the identified species can be characterized by the category 1, which supports the existence of unique diatom flora in the pans, as it was also concluded by an earlier study (Lengyel and Stenger-Kovács, 2012). Many environmental gradients mean stresses for the biota which do not allow recover the diatom flora and force it towards continuous compositial changes, as it was showed in the high number of constancy-one species and low diversity. Padisák et al. (2003) also found that most of the equilibriated lakes were under stress factors and have low species number concluding that environmental stress can force algal communities towards equilibrium.

The present study provided significant floristical information for nature conservation since these pans provide habitats for a number of vulnerable species (VU), like *Caloneis silicula*, *Cocconeis neothumensis*, *Cylindrotheca gracilis*, *Delicata delicatula*, *Encyonema lacustre*, *Scoliopleura peisonis*, *Surirella peisonis*, or for presumably threatened (PR) species, like *Bacillaria paxillifera*, *Craticula halophila*, *Fragilaria tenera* according to the Hungarian Red list (Németh, 2005).

3. Stress tolerance along light-, temperature-, sulfate- and chloride gradients [2]

3.1. Introduction

Most climate change models (Christensen and Christensen, 2007; George et al., 2007) predict substantial changes in hydrological balance and ecological functioning in both rivers and lakes (Jarman and Jones, 1982) projecting increasing summer temperatures, decreasing groundwater level and annual precipitation, changes in the duration of the ice-free period and stratification patterns of the lakes (Dokulil, 2013). These models also predict decreasing water levels and a reduction of wetland areas (Dokulil, 2013), as a consequence of misbalance in the hydrological regimes (Williams, 1981; Hammer et al., 1983; Fritz et al., 1993; Mason et al., 1994b).

Consequently, endorheic shallow saline lakes are highly influenced by climate variables since their water level (practically: their existence) largely depends on the evaporation and rainfalls. Changes caused by the climate change cascade to their chemical and physical variables, and to their flora and fauna (Wilhelm et al., 2006; Dokulil, 2013). Climate was demonstrated to be an important predictor of zooplankton biomass, community composition and food-web dynamics (Gyllström et al., 2005); it may change overall abundance and community composition of bacteria and fungi (Castro et al., 2010), cladocerans (Molinero et al., 2007), marine and estuarine fish (Roessig et al., 2004) and algal assemblages (Harley et al., 2006; Anneville et al., 2015).

Diatom communities have been widely used to assess long-term changes in lakes due to the shift in climate (Smol et al., 1991). According to the paleolimnological studies, diatom species distributions are highly correlated with salinity and the anion composition (Servant-Vildary and Roux, 1990; Roux et al., 1991; Blinn, 1993; Cumming and Smol, 1993; Wilson et al., 1994; Gasse et al., 1995), however, the underlying ecophysiological processes have been unknown (Saros and Fritz, 2002). Salinity, temperature, pH and conductivity have both direct and indirect effects on the composition and biomass of phytoplankton and phytobenthos (Hasegawa et al., 2000; Sullivan and Currin, 2000; Munns, 2002; Sudhir and Murthy, 2004). Diatoms are a major group of photoautotrophic

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[2] A part of this chapter was published in Aquatic Ecology and Hidrológiai Közlöny:
Lengyel, E., A.W. Kovács, J. Padisák & C. Stenger-Kovács, 2015. Photosynthetic characteristics of the benthic diatom species *Nitzschia frustulum* (Kützing) Grunow isolated from a soda pan along temperature-, sulfate- and chloride gradients. Aquatic Ecology 49: 401-416.
Lázár, D., E. Lengyel & C. Stenger-Kovács, 2015. *Nitzschia aurariae* Cholnoky (Bacillariophyceae) fotoszintetikus aktivitásának vizsgálata szulfátion gradiens mentén. Hidrológiai Közlöny 95: 39-41.

organisms in alkaline saline lakes (Servant Vildary, 1984; De Deckker, 1988; Ionescu et al., 1998) similar to oceans (Nelson et al., 1995; Mann, 1999; Sarthou et al., 2005).

The bulk of the photosynthetic measurements were carried out with phytoplankton species, mainly fast-growing species easy to culture (Stramski et al., 2002; Radchenko and Il'Yash, 2006; Sobrino and Neale, 2007; Roubeix and Lancelot, 2008) and only along temperature, irradiance and NaCl gradients (Pinckney and Zingmark, 1991; Brotas and Catarino, 1995). No photosynthetic rate measurements are available on species preferring lakes with high HCO_3^- and SO_4^{2-} concentrations. Two of the dominant benthic diatoms in the soda pans of the Carpathian basin are *Nitzschia frustulum* and *N. aurariae.* Their dominance within the diatom assemblage is typically higher than 10% in pans where the conductivity (mean: 5300 µS cm^{-2}), temperature (mean: 30°C), light irradiance (mean: 490 µmol m^{-2} s^{-1}) and SO_4^{2-} concentration (mean: 604 mg L^{-1}) was relatively high, and Cl^- was relatively low (mean: 94 mg L^{-1}) (Stenger-Kovács et al., 2014b). Due to the projected effect of climate change in endorheic lakes, the increase of these ionic contents, temperature and the alteration of the light regime can be assumed as a consequence of increasing air temperature and evaporation parallel with decreasing amount of precipitation.

3.2. Aims

In this chapter, cultures of *N. frustulum and N. aurariae* were used to explore their ecophysiological response to changing environmental conditions generated by climate change. We hypothesize that (i) the photosynthetic activity of the species will increase parallel with the salinity along both ionic gradients. We suppose that (ii) they need at least medium irradiance to optimize their photosynthesis, (iii) and at high light intensities photoinhibition will occur. The species are assumed (iv) to tolerate temperature stress. Based on the photosynthetic characteristics of the species, (v) environmental conditions set by climate change in soda pans will be a beneficiary for these species. To support or reject these hypotheses, photosynthetic activity of the species was measured along temperature, light, SO_4^{2-} and Cl^- gradients using an *in vitro* device and monoclonal cultures.

3.3. Material and methods

3.3.1. Study areas

N. aurariae was collected from Legény-tó (GPS coordinates: N 47º 39,793’, E 16º 48,802’) on 27th May in 2013, and *N. frustulum* from Borsodi-dűlő (GPS coordinates: N 47º 06,815’, E 16º 84,000’) on 20th January in 2012, respectively (Fig. 3).

Fig. 3 *Habitat images of the sampling sites (A-C: Borsodi-dűlő; D-E: Legény-tó; A,D: spring; B,E: summer; C,F: autumn)*

3.3.2. Isolation and culturing

Both diatom species were isolated using a micromanipulator (Narishige) and one-cell isolation method under a light microscopy (Zeiss, Axio Invert 40 C) (Andersen and Kawachi, 2005). *N. frustulum* and *N. aurariae* are illustrated on Fig. 4. The species were first identified in light microscopy (Krammer and Lange-Bertalot, 1997; Trobajo et al., 2012) and subsequently with scanning electron microscopy (Hitachi S-2600N).

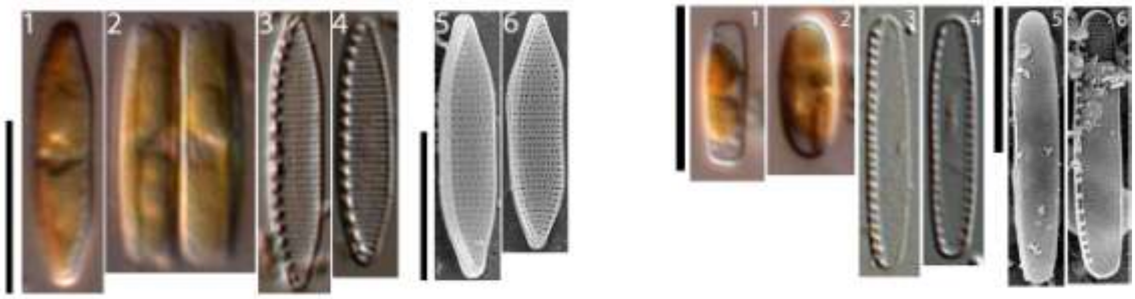

Fig. 4 *Light (1–4) and electron microscopic (5, 6) photographs of* N. frustulum *(left side) and* N. aurariae *culture (right side) (scales 10 µm)*

The species were grown in batch culture maintained in DIAT medium (Schlösser, 1994) after some modifications using glass beads as substrate (Fig. 5B). To avoid HCO_3^- limitation of photosynthesis, to reach the natural ionic straight of the lake (HCO_3^- range: 30-3000 mg L^{-1}) and to attain the minimum conductivity threshold (3000 μS cm^{-1}) of saline conditions, 5.5 g $NaHCO_3$ per liter was added to the culture medium. The applied soil extract and micronutrient solution were previously purified with $Ba(NO_3)_2$ to eliminate its sulphate content via precipitation. The media were replaced by fresh medium in every 2nd-3rd week. The cultures were maintained at 23 °C under photosynthetic active radiation (PAR) of 15 μmol $m^{-2}s^{-1}$ and a 14:10 light:dark cycle was applied by cool white and daylight (1:1) fluorescent tubes.

3.3.3. Laboratory experiments

The study was carried out in a photosynthetron illustrated on Fig. 5A (Üveges et al., 2011). This incubation system consists of nine cells with nine different irradiances (0 - 8 - 35 - 70 - 110 - 200 - 400 - 800 - 1200 μmol m^{-2} s^{-1}). The PAR was provided by daylight fluorescent tubes (Tungsram F74) at both sides of the photosynthetron and measured by a LI 1400 (LI-COR) equipped with a spherical (4π) quantum micro sensor (US-SQS/L, Heinz Walz GmbH). The mirror inner walls multiplied and uniformed the irradiance. Permanent temperatures were kept constant by a circulating water bath (Neslab RTE-211).

Fig. 5 *The applied photosynthetron (A), the cultures (B) and the Karlsruhe flasks (C)*

The cultures were starved in sulphate and chloride-free modified DIAT medium for 2-3 weeks prior to the experiments for emptying cellular stocks of ions. After the starving, the cultures were incubated in fresh modified DIAT medium and the experiments were started just after the cultures reached the log phase of the growth curve, which was followed by optical density measurements. On the fifth day, the cultures were homogenized and divided into Karlsruhe flasks (Fig. 5C). Three replicates were placed in each cells of the photosynthetron. The experiment was started at 5°C and after a one-hour pre-incubation in dark, the homogenous samples were further incubated for one or two hours depending on the density of the cultures (Wetzel and Likens, 2000). The dissolved oxygen concentration was measured at the beginning and at the end of the incubation period to determine photosynthetic activities (Wetzel and Likens, 2000) using LDO sensor (HQ-20, Hach Lange) (Fig. 2). The chlorophyll-*a* was measured in acetone extracts (Wetzel and Likens, 2000).

After the initial measurement, the cultures were re-homogenized and re-divided into the flasks and the temperature was raised up to 10 °C in the photosynthetron, and after the repeated pre-incubation, the dissolved oxygen and chlorophyll-*a* was measured again.

This process was repeated six times at different (15 - 20 - 25 - 30 - 35 - 40 °C) temperatures. After that, the diatom medium was replaced and the similar experimental design was applied for the two ionic gradients (Appendix 1). The gradients of the two anions (Cl^-, SO_4^{2-}) were established by adding $MgSO_4$ and $MgCl_2$ to the modified DIAT medium (Appendix 2-3). Accordingly, 0 - 50 - 600 - 1200 - 2400 - 3600 - 4800 - 7200 mg L^{-1} SO_4^{2-} and 0 - 36 - 437.5 - 875 - 1750 - 3500 - 5250 mg L^{-1} Cl^- concentrations were used by taking into consideration the mean and the full concentration ranges of the anions measured in the soda pans.

Concentrations of the anions were checked by titrimetric (Cl^-) and spectrophotometric (SO_4^{2-}) methods (APHA, 1998). The surplus of the anions and the short incubation time ensured stable concentrations, furthermore, no precipitation was observed during the experiment. The pH was kept constant between 8-9 to provide sufficient carbon source for the photosynthesis. The conductivity of the medium was measured with multimeter (HQ40d Hach Lange).

3.3.4. Statistical analyses

Respiration, net and gross photosynthetic activities were calculated according to Wetzel and Likens (2000). For characterizing photosynthesis, the initial slope (α), the photoinhibition parameter (β) and the photosynthetic rate (P_s) were estimated by a formula described by Platt et al. (1981) in GraFit program (Leatherbarrow, 2009). The I_k (photoadaptation parameter: the irradiance representing the onset of photosaturation) and P_m (maximal photosynthetic rate) were scored. Spearman's rank correlation was applied to describe the relationships between the photoadaptation parameter (I_k), the temperature and the ionic (Cl^-, SO_4^{2-}) concentrations using R Statistic program (Team, 2010). Multiway ANOVA analyses were used to characterize the effects of the studied environmental factors on the photosynthetic activity. To determine the optimum and tolerance ranges, the skewed normal distribution was used since it is widely applied in algal ecophysiological studies (Dauta et al., 1990; Lehman et al., 1975). The photosynthetic activity was normalized to unit chl-*a*. Variables of the photosynthetic activity along the temperature and anions were plotted using the Surfer Surface Mapping System v. 9.0 with the Kriging gridding transformation methods.

3.4. Results

3.4.1. P-I characteristics

The mean values of photosynthetic activity were plotted as a function of the irradiances (P-I). Saturation curves were obtained in all cases and no photoinhibition (β) was observed at any conductivities or temperatures within the applied light interval. The gross photosynthetic activity measured in the sulphate and chloride-free medium were close to zero. The initial slope (α) of the P-I curve of *N. frustulum* changed from 0.0010 to 0.0061 and from 0.0022 to 0.0233 along Cl^- and SO_4^{2-} gradient (Fig. 6). In the regard of *N. aurariae*, this parameter varied between 0.0007 and 0.0242, 0.0005 and 0.0153 respectively (Fig. 7). The initial slope increased parallel with the conductivity, but in the most concentrated media there were remarkable decline, which approached 50% in most cases (independently of the ionic composition and the diatom species). This relationship was confirmed statistically and showed a significant correlation between this parameter (α) and the ionic gradients ($p>0.01$). No remarkable significant correlations were found between the α and the temperature.

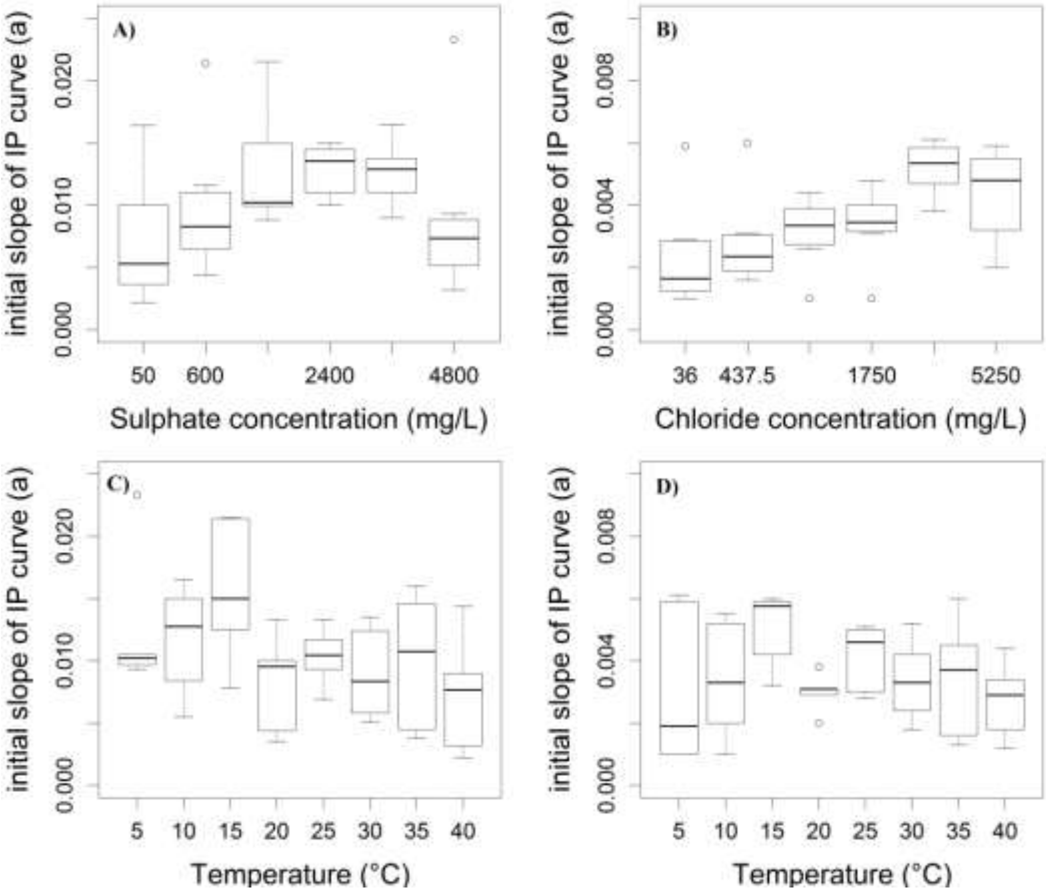

Fig. 6 *The initial slope of PI curve of* N. frustulum *measured in the different ion concentration (A,B) and temperatures (C,D)*

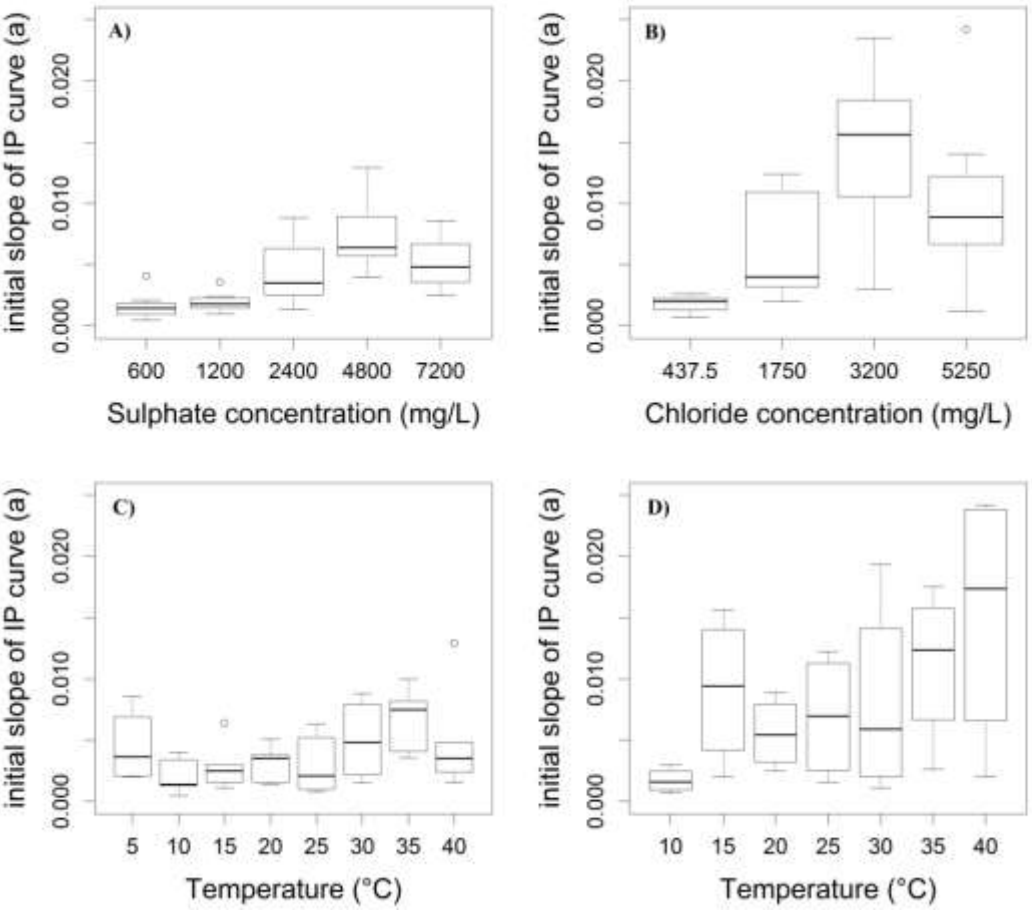

Fig. 7 *The initial slope of PI curve of* N. aurariae *measured in the different ion concentration (A,B) and temperatures (C,D)*

The photoadaptation parameter (I_k) of *N. frustulum* ranged between 3 and 305 μmol m^{-2} s^{-1} along both ion gradients. In contrary, the interval of this parameter of *N. aurariae* was broader: it varied from 7 to 435. In general, lower I_k values were estimated at the low temperatures and conductivities. Based on the mean values, the photoadaptation parameter (I_k) showed an increasing tendency (r^2=0.97) up to 30-35 °C in all media. A similar relation was found between the I_k and the conductivity gradients. Up to these values, the I_k increased exponentially along the SO_4^{2-} and linearly along the Cl^- gradient. Above these concentrations a setback was measured. A strong positive correlation (r^2=0.82) was confirmed between the maximum photosynthetic rate and the photoadaptation parameter.

Studying the SO_4^{2-} gradient, the gross photosynthetic rate (P) of *N. frustulum* ranged between 0.02 and 3.48, regarding the *N. aurariae* it changed from 0.02 to 3.85 mg C mg Chl-*a*$^{-1}$ h^{-1} (Fig. 8). Along the Cl^- gradient this parameter varied between 0.01 and 1.52, 0.12 and 5.26 mg C mg Chl-*a*$^{-1}$ h^{-1} respectively (Fig. 8). The photosynthetic activity was always lower in the diluted medium than in media characterized with high conductivity. At the highest ion concentration a decline of the photosynthesis was measured at each irradiance level and incubation temperature independently of the species.

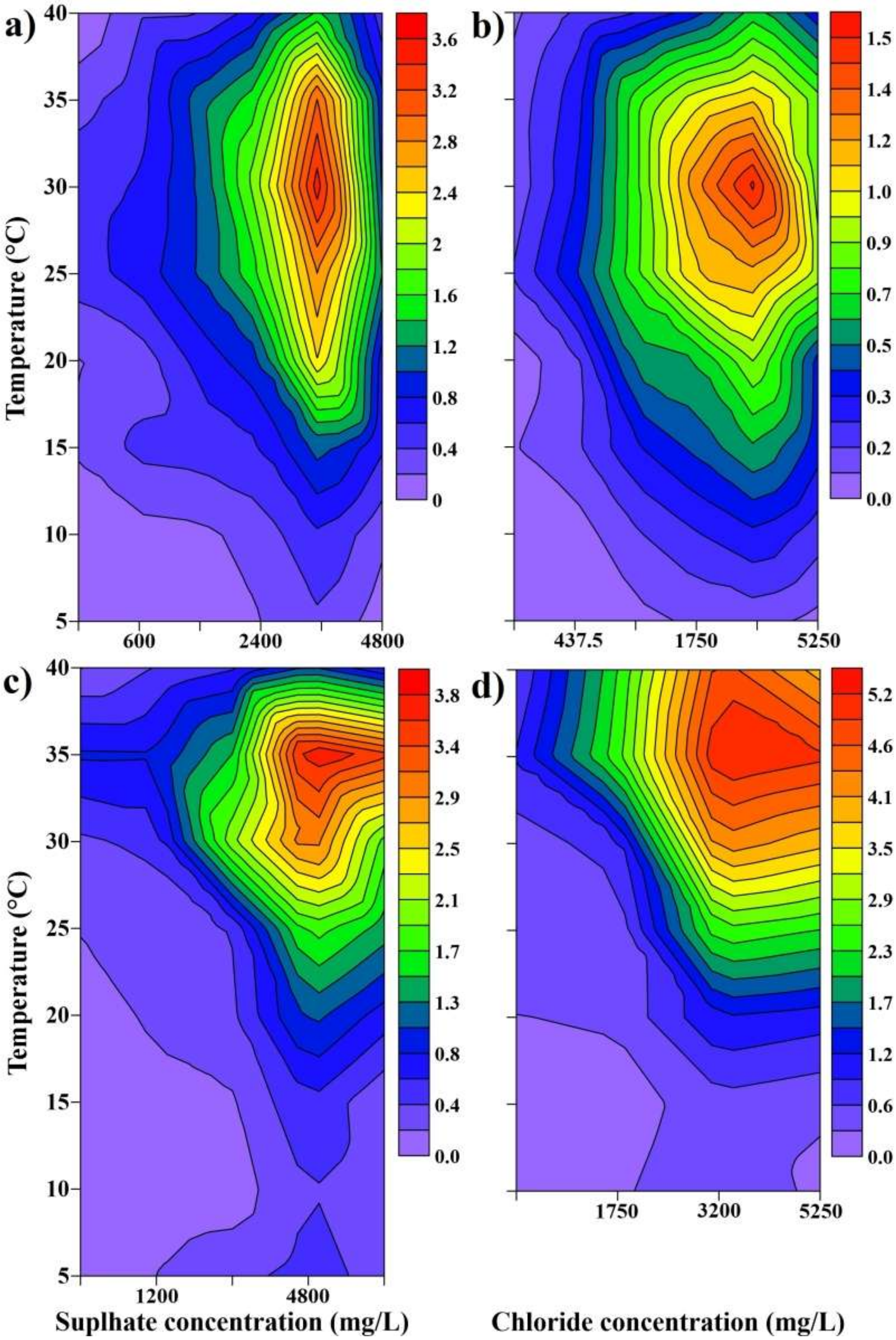

Fig. 8 *Variations of the gross photosynthetic rate of* N. frustulum *(A,C) and* N. aurariae *(B,D) measured along the temperature (A,B) and the ions gradients (C,D)*

3.4.2. P_{max}*-temperature-conductivity linkage*

The photosynthetic activity increased up to 30-35°C independently from the species or ionic composition. At the low temperatures (5-10°C), lower photosynthetic rates were measured than at higher incubation temperatures. The photosynthetic activity was augmented parallel with the increasing temperature up to 30 °C. At higher temperatures, a decrease of the photosynthesis was observed at each conductivity level. The maximum photosynthesis-temperature curve of *N. frustulum* had a peak at 28.5 ± 0.5 °C that appeared to be independent of the ion content of the media and the irradiance (Fig. 9). In the regard of *N. aurariae*, the photosynthetic activity reached its maxima at 34.5 ± 2.5 °C (Fig. 9).

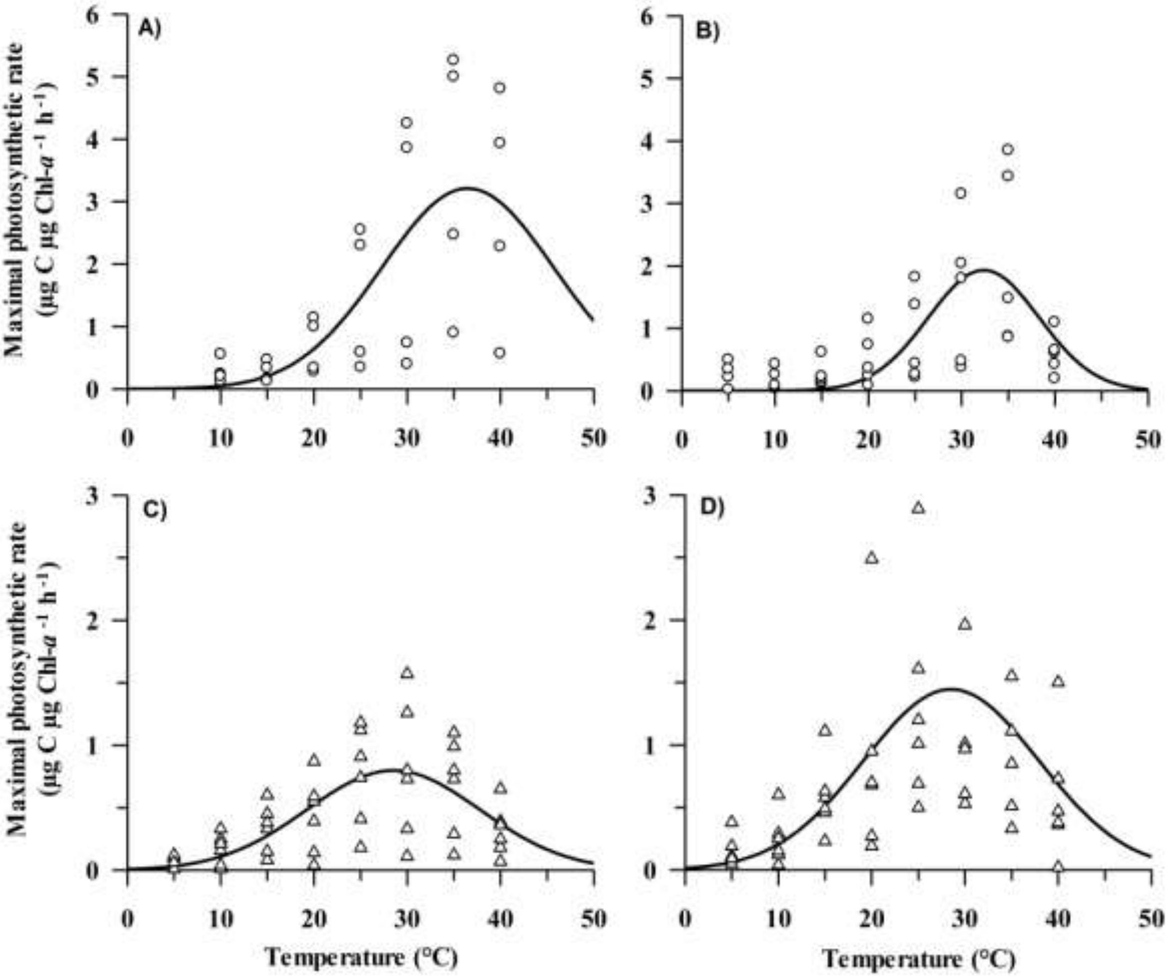

Fig. 9 *The optimal temperature of the N. aurariae (A,B) and N. frustulum (C,D) measured along the chloride (A,C) and sulphate ion (B,D) gradients*

Similarly, the lowest photosynthetic activity was measured in the most diluted and the most concentrated media. There were positive correlations between the maximal photosynthesis of *N. frustulum* and the ion gradients up to 3600 mg L^{-1} SO_4^{2-} and 3500 mg L^{-1} Cl^- content, beyond which reduced values were measured again (Fig. 10). For *N. aurariae* these values were 4800 and 3500 mg L^{-1} (Fig. 10). These relations were independent of the temperature. The photosynthetic activity of *N. frustulum* reached its maxima at 3253±106 mg L^{-1} chloride and 3332±120 mg L^{-1} SO_4^{2-} concentration which means a conductivity of approximately 8700 µS cm^{-1}. As to *N. aurariae*, the photosynthetic activity reached its maxima at 4182±474 mg L^{-1} chloride and 5255±460 mg L^{-1} SO_4^{2-} concentrations which correspond to approximately 10500 µS cm^{-1} conductivity.

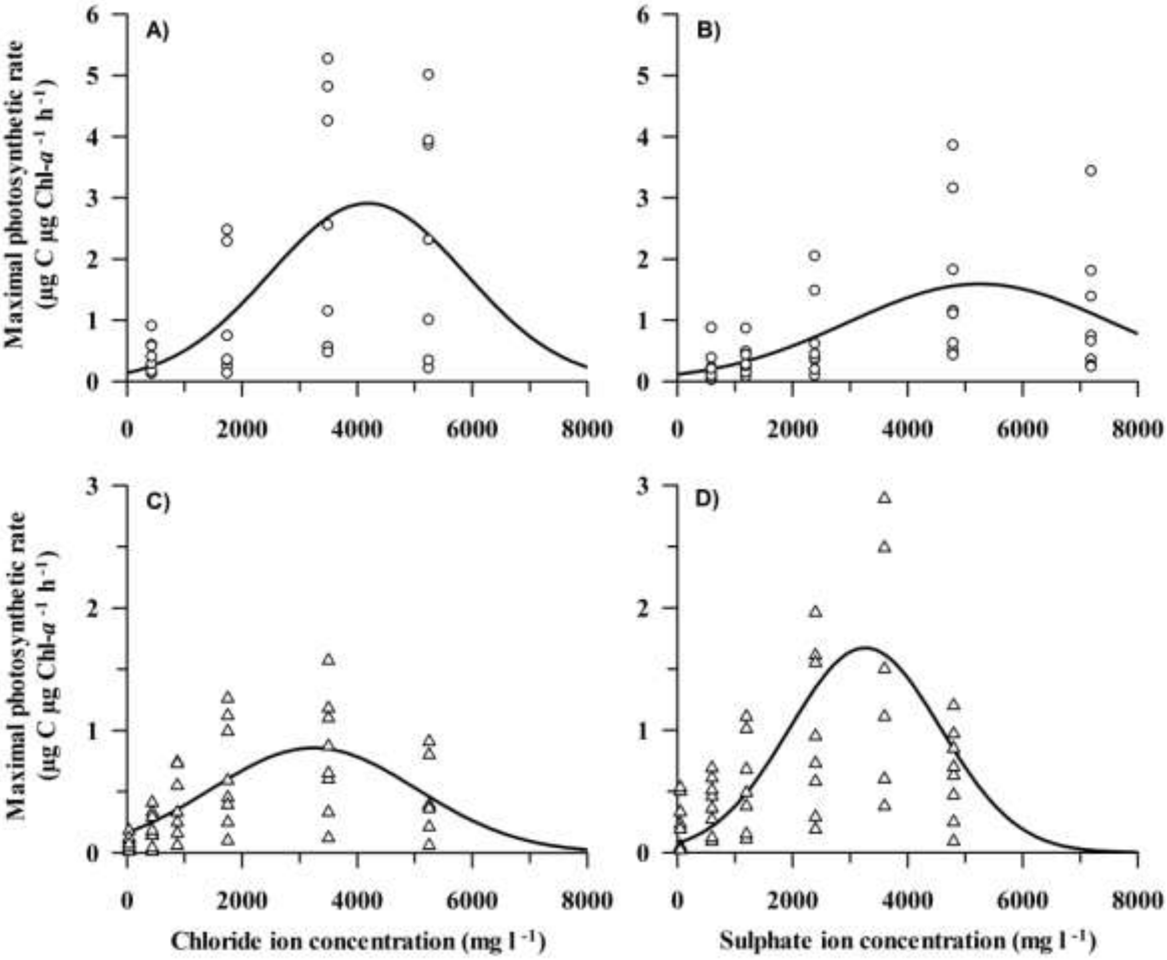

Fig. 10 *The optimal chloride and sulphate concentrations of* N. aurariae *(A,B) and* N. frustulum *(C,D) measured along the temperature gradients*

3.5. Discussion

In 2006 and 2008, approximately 100 diatom samples were collected for a compositional survey from altogether 31 Hungarian and Austrian shallow, alkaline, saline lakes (Stenger-

Kovács et al. 2014). According to the redundancy analyses (RDA) *N. frustulum* and *N. aurariae* were both constant species in the lakes of Fertő-Hanság region, where besides HCO_3^-, SO_4^{2-} dominance is characteristic, the Cl^- concentration is low (Boros et al., 2014; Stenger-Kovács et al., 2014b). Due to climate change, increasing conductivity, Cl^- and SO_4^{2-} concentrations as well as higher temperature records and changing light depending on the water level can be predicted in saline, shallow lakes.

3.5.1. Ion preference

N. frustulum prefers more SO_4^{2-} than Cl^- supporting the results of the ecological analyses of diatom assemblages in shallow saline lakes (Stenger-Kovács et al., 2014b), and in contrast, *N. aurariae* did not show considerable difference in its growth response to these two ions. The observed difference can be explained with the roles of these two major anions. The biochemical role of sulphur is more important and diversified than that of chloride. Sulphur is an important constituent of proteins (cysteine and methionine), coenzymes and vitamins (thiamine and biotin), which facilitate uptake of the divalent ions, and the coenzymes have important role of the respiration and fatty acid metabolism. Furthermore, sulfur has a main role in the electron transfer reaction of photosynthesis (ferredoxin) and in the nitrogen fixation (Hopkins and Hüner, 2004b). However, SO_4^{2-} is a competitive inhibitor of molibdenate uptake (Cole et al., 1986), which has an important role of the NO_3^- uptake by being a component of enzymes involved in its intracellular reduction.

Based on this process, the inhibition of the photosynthetic activity of the species were also expected under higher SO_4^{2-} content similarly as supposed by Cole et al. (1986) for phytoplankton communities. In contrast, Cl^- has two key roles, one is the photosynthetic oxygen evolution and the other is the maintenance of charge balance across cellular membranes. Cl^- is a counterion to several diffusible cations and, due to its mobility, can maintain electrical neutrality across cellular membranes. It is very important in habitats where the salinity is high. In the Hungarian small saline lakes, Na^+, K^+, Mg^{2+} and Ca^{2+} are the main cations that need to be countervailed by Cl^-. In summary, the Cl^- is one of the principal osmotically active solutes in the vacuole (Hopkins and Hüner, 2004b), however, at high amounts of this ion, it becomes a toxic element (Hopkins and Hüner, 2004b). Survival of organisms and their photosynthetic activity under salinity stress implies effective osmoregulation (Bauld, 1981). However, salt stress increases the accumulation of toxic Cl^- in chloroplasts causing decrease in photosynthetic electron transport activities (Boyer, 1976; Kirst, 1990). In the present study, concentrations higher than 3300 and 5000 mg L^{-1} appeared to be toxic.

3.5.2. The optimal ion concentrations and conductivity

In regard of *N. frustulum*, the maximum photosynthetic rate was detected at 3253±106 mg L^{-1} Cl^- and 3332±120 mg L^{-1} SO_4^{2-} concentration independently from the temperature, and this parameter of *N. aurariae* peaked at 4182±474 mg L^{-1} chloride and 5255±460 mg L^{-1} SO_4^{2-} concentrations. The above values can be considered as optima of the species. At high salinity levels, inhibition of photosynthetic activity was observed in our study. Available floristic studies report on dominance of *N. frustulum* at low salinities (3000-4000 $\mu S\ cm^{-1}$) (Veres et al., 1995) and in mesohaline conditions above 3000 mg L^{-1} Cl^- (Ziemann, 1971; Ziemann, 1982; Busse et al., 1999), and there is no information about the occurrence of this species along SO_4^{2-} gradient. In contrast, there is no available ecological preference for *N. aurariae,* except it could be abundant in electrolyte rich waters. An interesting strategy of *N. frustulum* was demonstrated by Trobajo et al. (2004) that may contribute to its tolerance of higher conductivity levels. The species can alter its length-width ratio parallel with the alteration of the salinity range. Similarly, longer frustules were found at higher conductivity levels in another study (Busse et al., 1999). The variation of the frustules shape, cell size or colony size regarding the salinity stress is not unique: it is a well-known strategy among the unicellar algae (Kirk, 1994). However, these papers are based on floristic surveys and monitoring investigations, but the ecophysiological experiments have been missing.

In response to osmotic stress, the present species may have strategy by synthesizing a co-soluted, osmoregulation metabolites to avoid the damage (Sudhir and Murthy, 2004), which was not investigated in the present study. According to our study, both diatom species can tolerate the gradually increasing conductivity thus gaining ecological benefit in hyposaline waters.

3.5.3. Light preference

Sediment surfaces of the shallow lakes can be excellent habitats for the epipelic algal assemblages since adequate light is available (Hill, 1996). Our results may provide another possible explanation why these species are abundant only in the Fertő-Hanság region. In this region, the suitable light intensity always persists, contrary to the lakes situated in the Danube-Tisza Interfluve, where low light levels can be measured during most of the time

(V.-Balogh et al., 2009). The photosynthetic rates of the two species become light-saturated already at medium light intensities (<300 μmol $m^{-2}s^{-1}$). Based on the photoadaptation parameter (I_k), along increasing temperature and conductivity the species needs higher light intensity to maximize its photosynthetic processes similarly to other algae like *Chlorella*, *Synechocystis*, *Fragilaria* as well as *Staurastrum* sp. (Dauta et al., 1990). This condition (as the required medium irradiance) is sufficed in the field, since as summer progresses, salts in the soda pans are concentrating, their water levels lower and their transparency increases. Based on the medium I_k (range from 5 to 305 μmol $m^{-2}s^{-1}$), *N. frustulum* and *N. aurariae* can be good light competitors similarly to many cyanobacteria (10-231 μmol $m^{-2}s^{-1}$) and most green algae (85-510 μmol $m^{-2}s^{-1}$) (Reynolds, 1988; Padisák, 2004). Similarly, *Anabaena minderi* and *A. torques* as the members of the phytobenthos exhibited the highest growth rates at low irradiances (75 μmol $m^{-2}s^{-1}$) indicating their adaptation to low light conditions (de Tezanos Pinto and Litchman, 2010). However, acclimation to low irradiances is often combined with photoinhibition at high irradiances (Belay and Fogg, 1978). A benthic community growing in shallow water is exposed to high irradiance, which causes photooxidative decay of chlorophyll pigments in presence of oxygen (Kirk, 1994). Despite these environmental conditions can prevail in the Fertő-Hanság region (30-2300 μmol $m^{-2}s^{-1}$ irradiance and 1.5-18 mg L^{-1} dissolved oxygen was measured), photoinhibition was not observed in our study, which can contribute to the success of these species. Based on several studies carried out on sand flat and planktonic diatoms, photosynthesis is usually inhibited at moderate light intensities around 600-1200 μmol $m^{-2}s^{-1}$, or at higher levels (>1200 μmol $m^{-2}s^{-1}$) (Taylor, 1964; Whitney and Darley, 1983).

There are different strategies of algal species to avoid the photooxidative damage. Physiologically, they may synthesize more secondary photoprotective pigments, like carotenoids (Krumbein et al., 1977) in the form of fukoxantin. The function of these secondary pigments is to cover the chlorophylls protecting them from the direct light (Kirk, 1994). The life form of the species can serve another way to avoid this damage. The genus *Nitzschia* belongs to the motile guild (they do not attach to the substrates), and these species are able to change their position in the benthic layer to find the most adequate habitats (Passy, 2007). Thus, in seasons with high irradiation and low water levels, motility enables motile species to find microrefuges with lower light. However, in some seasons low solar radiation and high turbidity seriously reduce underwater light availability. Besides the good light harvesting efficiency (net photosynthesis occur around 20 μmol m^{-}

$^{2}s^{-1}$), the life forms of the species are also helpful in these environments. Additionally, those taxa, which are adapted to low-light conditions may exhibit diurnal vertical movements thus regulating their position in the benthos (Hill, 1996). Therefore, phototaxis may play a major role in their primary production (Kemp et al., 2000) under reduced light conditions. The high turbidity of shallow, saline lakes is originating from the high inorganic seston content (V.-Balogh et al., 2009) restricts light intensity, but by altering carotenoid:chlorophyll ratio (Jorgensen 1979) or changing location, *N. frustulum* and *N. aurariae* can tolerate or survive the unfavorable environmental conditions, which confirms the flexibility of the *Nitzschia* species under stressed conditions.

3.5.4. Temperature preference

For *N. frustulum,* the optimal temperature of the photosynthesis was found at 27-28 °C, and it was 34-35 °C for *N. aurariae*. The observed normal distribution is characteristic for temperate diatoms rather than for the polar populations where the optimum curve is less symmetric (Fiala and Oriol, 1990). Other *Nitzschia* species like *N. closterium* reached its maximal photosynthesis at about 27 °C, *N. palea* found in soil or in small water bodies was able to survive high temperatures (35 °C) (Barker, 1935). Sensitivity of *N. frustulum* and *N. aurariae* to cold water temperatures is demonstrated by parallel decrease in a photosynthetic activity. Low temperatures may cause irreversible changes, for example in membrane fluidity (Falkowski and Raven, 1997). On the other side of the optimum curve (>35 °C) photosynthetic efficiency is a reduced because of denaturation of enzymes at high temperatures (Hopkins and Hüner, 2004a). The photosystem II and the oxygen evolving complex inactivate and the fluidity of the thylakoid membranes (Falkowski and Raven, 1997; Hopkins and Hüner, 2004a). Salinity, light and temperature are important environmental variables influencing species abundance *via* affecting the photosynthetic process (Oppenheim, 1991; Underwood et al., 1998; Underwood, 1994). Based on the ANOVA analyses, the main photosynthetic parameters of the two *Nitzschia* species are principally determined by temperature rather than conductivity and light, contrary to *Pseudo-Nitzschia granii* (El-Sabaawi and Harrison, 2006).

In summary, *Nitzschia frustulum* prefers high temperature (28.5 °C) and conductivity (8700 µS cm^{-1}), but *N. aurariae* can tolerate hihger values (34.5 °C and 10500 µS cm^{-1}), which are typical characteristics of the shallow soda pans. *N. frustulum* showed more intensive photosynthetic activity in HCO_3^{-}-SO_4^{2-}, than in HCO_3^{-}-Cl^{-} dominated media, in the regard of *N. aurariae* negligible difference was observed. The ion preference and the medium irradiance demand of *N. frustulum* may explain its dominance in the Fertő-Hanság region, the reason of the significant abundance of *N. aurariae* in this region could be only the available irradiance level. Both species is tolerant to a broad range of salinities, which can be observed due to the extreme weather events (e.g. droughts or sudden and heavy rainfalls). It can occupy a broad niche (Reynolds, 1988; Reynolds and Kinne, 1997), which represents an ecological advantage against other diatom species (Litchman and Klausmeier, 2008). However, the niche of these species is overlapped: *N. aurariae* have higher ecological advantages tolerating high level stress. Nevertheless, their photosynthetic transport chain will slow down resulting in a decrease in the photosynthetic activity under increasing, sometimes extreme temperatures (observed in the field (Vörös and Boros, 2010)) as predicted by the climate change models.

4. Stress and disturbances in soda pans[3]

4.1. Introduction

Nowadays, the degradation and loss of wetlands raise worldwide concern (Mitsch and Jørgensen, 2004; Bugenyi, 2005; Mitsch and Gosselink, 2007; Mitsch, 2013). All lakes, including the large and deep ones are threatened by climate change and human activities (e.g. land use, water regulation), but shallow endorheic aquatic ecosystems are especially vulnerable due to their hydrological sensitivity. Intermittent soda pans are lakes that can be filled with water or totally dried with predictable annual cycle (Williams, 2005) represent a special type of wetland ecosystems characterized by shallowness, pH of 9-10, high conductivity with mainly Na^+-HCO_3^- ionic dominance and high daily temperature variation (Stenger-Kovács et al., 2014b). These pans are inhabited by unique flora and fauna, which can tolerate these extreme environmental conditions (Pálffy et al., 2014). In recent decades, the number of soda pans decreased all over the world (Williams, 1992; Zulka and Milasowszky, 1998; Williams, 2005) and their conservation should be urgently forced.

Despite of the comprehensive knowledge about the saline lakes, the lack of management plans for these habitats has been emergent worldwide (Comin et al., 1999). The difference between freshwater and saline ecosystems makes their restoration management difficult. In freshwater ecosystems the goal of the restoration is mainly to reduce the phosphorous and nitrogen input for controlling eutrophication (e.g. Crisman et al., 2005; Jeppesen et al., 2007), the high trophic level is an inherent and natural feature of the soda pans since nutrient loading is attributable to the presence of thousands of migrating and nesting waterfowl (Boros et al., 2008). The management plans of these habitats need different approaches and criteria. In general, the conservation efforts shifted from the preservation and protection of aquatic habitats to the restoration of degraded systems or even establishment of new ones (Dobson et al., 1997). The main aim of the conservation practice of the soda pans should focus on sustaining their natural hydrological cycle, drying-filling phase and consequently their good ecological status (Ecsedi and Boros, 2013; Stenger-Kovács et al., 2014b).

In Hungary, the area of natural soda pans decreased by 86% in the Danube-Tisza Interfluve and by 78% in Fertő-Hanság region by the end of the 20th century (Boros et al.,

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[3] This chapter was published in Hydrobiologia:
Lengyel, E., J. Padisák, É. Hajnal, B. Szabó, A. Pellinger & C. Stenger-Kovács, 2016. Application of benthic diatoms to assess efficiency of conservation management: a case study on the example of three reconstructed soda pans, Hungary. Hydrobiologia 777: 95-110.

2013b; Dick et al., 1994). Nowadays, all the soda pans are under "*ex lege*" protection. According to an extensive survey in Carpathian basin including 148 soda pans, 37 % of the habitats is in natural, 58% in degraded, 5% in restored or rehabilitated status in Hungary (Boros et al., 2013a). In contrast, 94% of Austrian soda pans are in natural status, only 6% is degraded. The natural and degraded pans can be found mainly in the Danube-Tisza Interfluve, in Mezőföld and in the Tiszántúl region, all the soda pans around Lake-Fertő were reconstructed in 1989 to provide suitable habitat for the breeding and feeding waterfowl populations (Fertő-Hanság National Park, 2001) and protected mammals. For this purpose, the water level of these pans is regulated by a constructed drainage system.

The restoration success of the soda pans was studied in detail in 2000-2001 focusing on four groups of biota (zooplankton, macroscopic zoobenthos, birds and macrophytes) and the results were very encouraging (Fertő-Hanság National Park, 2001; Tóth et al., 2014). However, after more than 10 years a comprehensive survey of the effects of conservational management has been still missing apart from a recent study focusing on their zooplankton communities (Tóth et al., 2014).

Despite algal vegetation plays a significant role both in the structural and functional integrity of these pans (Lebo et al., 1992; Ionescu et al., 1998), their application in the restoration monitoring as bioindicator has been neglected. In soda pans, photoautotrophic picoplankton dominance is characteristic; they exhibit summer and winter chlorophyll-a maxima contributing 74-100 % of the phytoplankton community (Felföldi et al., 2009; Pálffy et al., 2014; Somogyi et al., 2014). Besides picoalgae, genera such as *Euglena*, *Phacus*, *Trachelomonas*, *Nautococcus*, *Oocystis*, *Cladophora*, *Oedogonium*, *Nodularia*, *Gongrosira*, *Tribonema* and *Vaucheria* are also important components of the phytoplankton and the phytobenthos, sometimes occurring as blooms (Vörös, 2013). A recent study (Stenger-Kovács et al., 2014b) emphasized the significance of the benthic diatom communities in these habitats as diatoms may have competitive advantage against other algae owing to their ecophysiological plasticity: good osmoregulation (Bauld, 1981), phenotypic plasticity (Kirk, 1994) or the secondary photoprotective pigments (Krumbein et al., 1977), thereby they can survive and tolerate the prevalent extreme environmental conditions. Furthermore, their application as bioindicators in the ecological status assessment cannot be neglected, since they have strong relation with the typical chemical and physical features of the soda pans (Stenger-Kovács et al., 2014b).

4.2. Aims

The aim of present research was to measure vital environmental attributes (VEA, Noble and Slatyer, 1980) as diatom composition and its environmental descriptors using more than one reference site for assessing the ecological status of three reconstructed soda pans with the evaluation of the conservation practices

4.3. Material and methods

4.3.1. Study areas

As a consequence of draining activities in the 19th and 20th centuries (Pellinger, 2013) migrating birds almost completely disappeared in the Fertő-Hanság region. In 1989, some soda pans were restored in order to re-establish the high population densities of migrating bird species especially in the breeding season. This chapter focuses on three restored soda pans:

1. Borsodi-dűlő is situated directly on the left site of the Hanság Main Canal (GPS coordinates: N 47.6815, E 16.8400), close to Lake Fertő (Neusiedlersee) (Fig. 1). Sluices built on the Canal ensure the water supply from Lake Fertő to increase the water level and surface area of the pan. Through this canal, the water level and surface area can also be reduced. The timing of the applied flush-through water management (to prevent the expansion of the reed-belt) changes year by year depending on the weather conditions and on the requirements of the water fowls and mammal populations (Pellinger, 2013).
2. Nyéki-szállás is located directly on the right bank of the Hanság Main Canal (GPS coordinates: N 47.6771, E 16.8328). The management of this pan is similar to that applied for the Borsodi-dűlő (Fig. 1).
3. Legény-tó can be found on the right site of one of the numerous drainage canals on the area (GPS coordinate is N 47.6632, E 16.8134) (Fig. 1). This drainage runs parallel with the Körgát Canal joining to the Hanság Main Channel. There is a fixed linkage with the channel. Contrary to the other two pans, hydrological management was not applied.
4. Reference pans: Three natural soda pans were selected for the comparisons, and the composite samples were considered as a reference category. Kirschsee (N 47.7574, E 16.7883), Albersee (N 47.7742, E 16.7696) and Untersee (N 47.8000, E 16.7833) can be found by side of Lake Fertő, in Austria.

4.3.2. Sampling process and diatom analyses

Epipelic and epiphytic diatom samples were collected monthly between January 2012 and December 2013 from all representative microhabitats. Altogether, 90 phytobenthos samples were taken: 36 from macrophytes and 54 from mud. The preparation and analyses of the samples followed the methods described in Chapter 2.3.2. The species were classified into four salinity groups: brackish, brackish fresh, fresh brackish and freshwater species (Van Dam et al., 1994). Among the community metrics, Shannon diversity (H), species number (Sp) and Average Taxonomic Distinctness (AvTD) were calculated (Clarke and Warwick, 2001) due to their strong relation with the characteristic features of the soda pans (Stenger-Kovács et al., 2016).

4.3.3. Chemical and physical analyses

In the field, water temperature, pH, conductivity, oxygen saturation (DO%) were measured with portable multimeter (HQ40d Hach Lange). The irradiance (LI) was measured directly above the diatom communities by a LI 1400 (LI-COR) apparatus equipped with a spherical (4π) quantum micro sensor (US-SQS/L, Heinz Walz GmbH). The concentration of nitrogen forms, as nitrite (NO_2^-), nitrate (NO_3^-) and ammonium (NH_4^+), phosphorus forms, as total phosphorous and soluble reactive phosphorus, soluble reactive silica and water color (Cuthbert and del Giorgio, 1992) were determined by spectrophotometric methods (APHA, 1998). The chemical oxygen demand (COD), carbonate (CO_3^{2-}), hydrogen-carbonate (HCO_3^-), chloride (Cl^-) and sulphate (SO_4^{2-}) content were measured titrimetrically (APHA, 1998).

4.3.4. Statistical analyses

Only phytobenthos taxa with a relative abundance >2% were included in the statistical analyses. The relative abundance values were root square transformed ($\sqrt{x}$) to stabilize variance. The version 3.1.2 of R program (Team, 2010) was used to the statistical analyses loading Vegan (Oksanen et al., 2012) and Indicspecies packages (De Cáceres and Jansen, 2014). Correspondence analysis (CA) was run to ordinate the samples exploring the differences in the diatom communities of the samples based on the substrate types and the sampling sites. Canonical correspondence analysis (CCA) was applied to examine the relationship between the environmental variables and the diatom composition. To determine the most associated diatom species to the different pans ($p<0.05$), indicator species analysis (IndVal) was performed including its two components: Component ‘A’ (specificity or positive predictive value; the probability that the species belongs to the target site group) and Component 'B' (fidelity or sensitivity; the probability of finding the species in the given group). Spearman rank correlation was used to analyse the relationship between the environmental variables and community metrics. Based on the significant environmental factors, multivariate linear models were developed and reduced applying backward selection. Multi-way ANOVA was performed to describe whether the cumulative relative abundances show differences between the salinity groups and the seasons. T-test was used to examine the differences between the environmental variables and the community metrics among the pans.

4.4. Results

Environmental variables (mean, range, SD) are summarized in Appendix 7. All the pans were well-oxygenated (around 100 %). The mean pH was 8.9 with only slight fluctuation (SD: 0.4). The irradiance level observed directly above the phytobenthos changed along a wide range: it varied between 15 and 2200 µmol $m^{-2}s^{-1}$. As to conductivity, Legény-tó separated from the other pans ($p=0.05$) based on the t-test. Its mean and standard deviation (1967±410 µS cm^{-1}) was the lowest, in Borsodi-dűlő and Nyéki-szállás the average value was 2590±1310 µS cm^{-1}. All the reconstructed pans had significantly lower conductivity compared to the reference dataset ($p<0.05$), which varied between 3120 and 13650 µS cm^{-1}. Among the reconstructed pans, the Nyéki-szállás and Borsodi-dűlő were more colored with averages of 211 and 145 mg Pt^{-1} unit, and in Legény-tó the water color was moderate (87 Pt^{-1}). Regarding the water color, this separation of Legény-tó from the other pans was statistically confirmed ($p<0.02$). The water color of reference sites was similar to the reconstructed pans. All the pans were dominated by hydrogen-carbonate (mean: 497.4 mg L^{-1}), sulphate (mean: 344.8 mg L^{-1}) and chloride (mean: 209.7 mg L^{-1}) ions. The concentrations of phosphorus were high, contrary to the nitrogen forms (mean TN:TP = 1:4). High TP values were measured in Nyéki-szállás (mean: 919 µg L^{-1}) and Borsodi-dűlő (mean: 526 µg L^{-1}), which did not differ significantly from values of the reference sites (mean: 766 µg L^{-1}). The lowest TP values were observed in Legény-tó (mean: 246 µg L^{-1}), which difference was statistically confirmed ($p=0.03$).

According to the three axes of the CCAs, the diatom communities of all the studied pans were driven mainly by conductivity (Cond) ($r = 0.73$) and pH ($r = -0.94$). Based on the second axis, the explanatory variables were Cl^- ($r = -0.29$) and DO% ($r = 0.61$). According to the third axis, the most important variables were SO_4^{2-} ($r = -0.54$) and SRP (r

= 0.07) (Appendix 8). Borsodi-dűlő and Legény-tó are clearly separated according to the second axis, while in the reference pans and Nyéki-szállás are close to each other due to the main explanatory variable, which is the conductivity.

Altogether 170 diatom taxa were identified. The CA analysis showed significant separation of the reconstructed pans (Fig. 11), but the diatom communities of Nyéki-szállás were close to the reference ones.

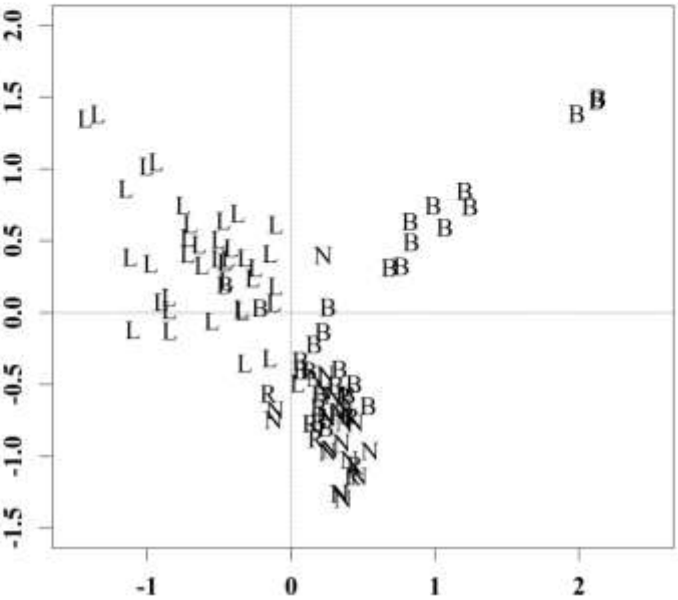

Fig. 11 *Correspondence analysis (CA) of the diatom community (B: Borsodi-dűlő; L: Legény-tó; N: Nyéki-szállás; R: references)*

Different indicator species were identified in the three reconstructed pans and the reference pans by IndVAL analysis (Appendix 9). In the Legény-tó, 13 indicator species were determined, in the Borsodi-dűlő eight species, five in the Nyéki-szállás and three species in the reference sites. *Amphora copulata*, *Ulnaria ulna*, *Fragilaria famelica*, *Gomphonema olivaceum*, *Hippodonta hungarica*, *Navicula cryptotenelloides* and *Rhopalodia gibba* species occurred only in Legény-tó (Component A>0.90), but not in all samples (Component B<1) contrary to *Achnanthidium minutissimum* var. *minutissimum*, which was present in almost all samples (Component B=0.97). *Gyrosigma obtusatum*, *Hantzschia abundans*, *Nitzschia acicularis*, *N. gracilis*, *Cyclostephanos invisitatus*, *Stephanodiscus parvus*, *S. hantzschii*, *S. hantzschii* var. *tenuis* preferred only Borsodi-dűlő (Component A>0.90), and *Gomphonema parvulum* f. *saprophilum*, *Nitzschia commutata* or *Rhopalodia operculata* only in Nyéki-szállás (Component A=1). Three diatom species (*Craticula buderi*, *Halamphora dominici*, *H. subcapitata*) appeared only in the reference sites. Many indicator species overlapped between the reconstructed pans. Seven species

(*Cyclotella meneghiniana, Entomoneis paludosa* var. *subsalina, Surirella brebissonii, Nitzschia palea* var. *tenuirostris, N. thermaloides, N. aurariae, Pseudostaurosira brevistriata*) were characteristic for Legény-tó and Borsodi-dűlő ($0.5<r<0.84$), *Navicula salinarum* var. *salinarum* had a strong affinity to Legény-tó and Nyéki-szállás ($r=0.72$), three species (*Tryblionella hungarica*, *Craticula ambigua*, *Achnanthes brevipes* var. *intermedia*) were common in Borsodi-dűlő and Nyéki-szállás ($0.66<r<0.79$) and further three species (*Tryblionella apiculata*, *Fallacia pygmaea*, *F. pygmaeae* ssp. *subpygmaea*) had affinity to all three reconstructed pans. Altogether the reconstructed pans had six common diatom species with the reference sites, such as *Halamphora veneta, Diatoma tenuis, Scoliopleura peisonis*.

Concerning the community metrics (Table 4), no significant differences were found between the substrate types. The pans had different diversity, species richness and AvTD values according to the multi-way ANOVA analyses ($p<0.005$). Borsodi-dűlő and Nyéki-szállás showed higher similarity, Legény-tó mostly separated from the other pans ($p = 0.00014$). The reconstructed pans did not separate significantly from the reference sites regarding the AvTD, contrary to the other metrics. The species number and the diversity were significantly lower in the reference sites ($p <0.05$) than at the reconstructed pans.

Table 4 *The statistical parameters of common community metrics measured on the basis of episammic and epiphytic diatom assemblages in the reconstructed and reference pans (H: diversity; S: species number; AvTD: Average Taxonomic Distinctness)*

	Legény-tó			**Borsodi-dűlő**			**Nyéki-szállás**			**Reference**		
	H	**S**	**AvTD**	**H**	**S**	**AvTD**	**H**	**S**	**AvTD**	**H**	**S**	**AvTD**
Min.	1.5	14	57	1.5	11	56	0.6	8	51	0.6	8	54
Max.	4.7	53	69	4.2	44	73	4.1	35	67	3.5	19	65
Mean	3.3	31	64	3.2	25	64	2.6	21	61	1.7	13	60
SD	0.8	10	3	0.7	8	4	1.0	8	5	1.2	5	3

Both diversity and species richness had seasonal fluctuation ($p<0.006$), and AvTD was more or less constant during the years (Fig. 12) independently of the habitats. In Borsodi-dűlő and Nyéki-szállás, the diversity and species number started increasing in winter, reached their peak in spring or summer, and their lowest values were found in autumn. In Legény-tó, the highest values were observed in summer, the lowest in winter. In the reference sites, the mean diversity (H) was 1.7, the species number (S) varied between 8 and 19. The AvTD varied between 51 and 73 (between species and family), its average standard deviation was 4.

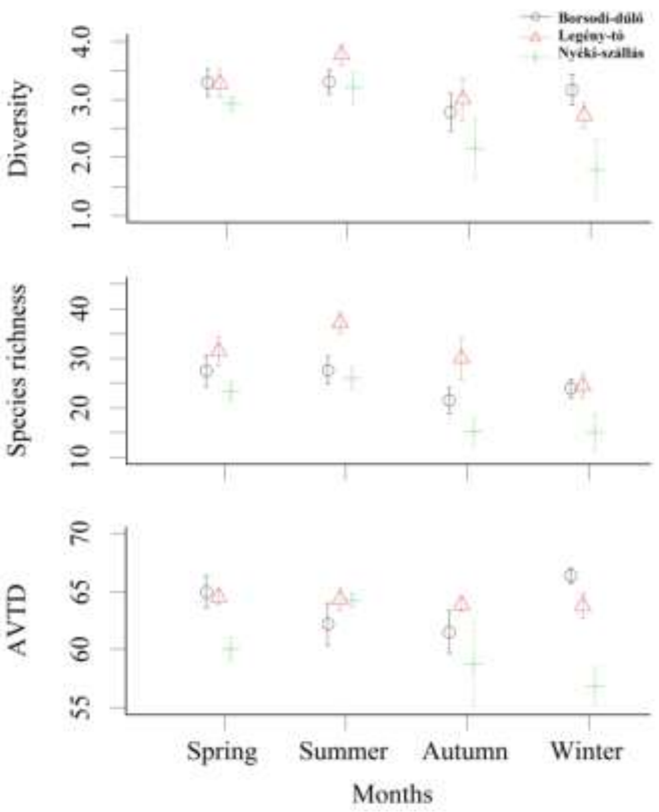

Fig. 12 *The fluctuation of the diversity, species richness and AvTD in the three studied pans and reference sites*

The cumulative relative abundance of the species within each salinity group differed among the pans. According to the multi-way ANOVA analyses, in Borsodi-dűlő and Nyéki-szállás the cumulative relative abundance showed fluctuation in accordance with the season and the salinity groups ($p<0.0001$) (Fig. 13). The total relative abundance of freshwater taxa was more or less constant, it varied between 0 and 8% in Borsodi-dűlő, 0 and 2% in Nyéki-szállás. In summer, the abundance of brackish and brackish-fresh species (on the average 18-17 species) became dominant (their relative abundance >20%) contrary to the fresh-brackish diatoms (average 47 species with lower relative abundance). In autumn and winter, the relative abundance of the brackish-fresh and brackish species started to decrease and the fresh-brackish diatom species overcame them. Contrary to Borsodi-dűlő and Nyéki-szállás, in Legény-tó the cumulative relative abundance of the species had significant difference ($p<0.0001$) between the salinity groups, without seasonal fluctuation (Fig. 13). The number of fresh-brackish species was high (68): they were constantly dominant in all seasons. The number of brackish species was low (20) and their occurrence was sporadic with low relative abundance. In the reference sites, the contribution of brackish species was 14.6% at average, which was similar to the studied pans (p>0.05).

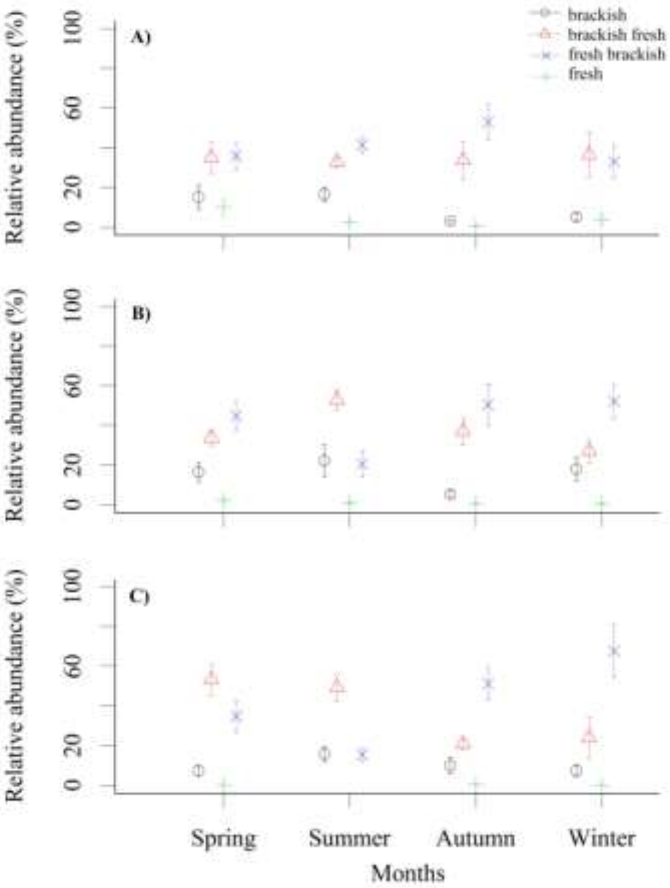

Fig. 13 *The relative abundances of the salinity groups in the three studied pans (A: Legény-tó; B: Borsodi-dűlő; C: Nyéki-szállás)*

The relative abundance of brackish-fresh species was significantly higher in the reference (mean: 67.9%) than in the reconstructed pans (p<0.05) (Fig 14). In contrast, the relative abundance of fresh-brackish species was significantly lower in the reference pans (mean: 5.5%), and their abundance was high in the reconstructed pans (Fig 14). The contribution of freshwater diatom species was very low in the reference sites (mean: 1.1%) similarly to Borsodi-dűlő and Nyéki-szállás (p>0.05), and it was significantly higher in Legény-tó (p<0.05) (Fig. 14).

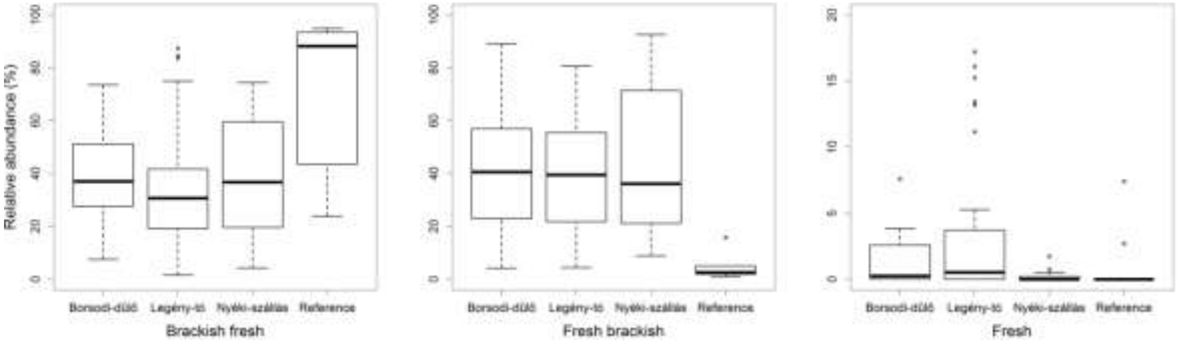

Fig. 14 *The boxplots of the relative abundance of the salinity groups calculated in the reconstructed and reference pans*

The AvTD was related to six environmental parameters in Nyéki-szállás, to three in Legény-tó and to zero in Borsodi-dűlő (Table 5). In the reduced linear model AvTD was influenced by five environmental variables in Nyéki-szállás (DO%, pH, temperature, irradiance level, CO_3^{2-}) (Table 5). Six variables had effects on the diatom diversity in Legény-tó, three in Nyéki-szállás and two in Borsodi-dűlő, which were reduced to only one in every pan: TP in Borsodi-dűlő and temperature in the others (Table 5), similarly to the species richness.

Table 5 *The coefficients of Spearman rank correlation ($p<0.05$) measured between the population metrics and environmental parameters (AvTD: Average Taxonomic Distinctness) indicating with bold italics the results of linear modell ($lm(Y \sim X_1+X_2+...)$*

	Legény-tó			**Borsodi-dűlő**			**Nyéki-szállás**		
	AvTD	**Diversity**	**Species richness**	**AvTD**	**Diversity**	**Species richness**	**AvTD**	**Diversity**	**Species richness**
Oxygen saturation							***0.47***		
pH		0.30	0.31			-0.41	***0.51***		
Conductivity		0.44	0.45						
Temperature		***0.53***	***0.6***				***0.75***	***0.63***	***0.58***
Irradiance level							***0.51***		
COD		0.50	0.42						
SO_4^{2-}						-0.40			
NO_2^-							0.40		0.40
NH_4^+	-0.33							0.39	0.41
SRSi		0.30							
SRP	-0.32					-0.36			
TP	-0.37				***-0.37***	***-0.61***			
Colour					-0.37				
CO_3^{2-}		0.56	0.53				***0.67***	0.44	0.42

4.5. Discussion

The key in management success are (i) measurements of adequate number of vital environmental attributes (VEA) (Aronson et al., 1993; Ruiz-Jaen and Mitchell Aide, 2005, (ii) application of more than one reference site {Mayer, 1999) and (iii) allowing sufficient time to recovery (Mitsch and Wilson, 1996). In practice, three major attributes are used to assess the success of such practices: diversity, vegetation structure and ecological processes (Ruiz-Jaen and Mitchell Aide, 2005) after at least 3-5 years of the beginning of the management measures (Mitsch and Wilson, 1996; Montalvo et al., 1997; Campbell et al., 2002; Ruiz-Jaen and Mitchell Aide, 2005). In this research, the temporal distribution of diatoms was applied for the judgment of the success of the management after reconstruction using reference sites. The term of "success" refers to the prevalence of the natural structural and functional features of soda pans, and the "failure" refers to its absence. In general, the primary aim of the restoration is to establish a self-supporting ecosystem with high degree of resilience against perturbation without further assistance (SER, 2004) by returning a system that is functionally and structurally close to its pre-disturbed condition (Palmer et al., 1997).

4.5.1. Main drivers in diatom composition of the reconstructed pans

In the reconstructed soda pans of the Fertő-Hanság region the main environmental parameters, which determined the diatom composition were temperature, pH, oxygen saturation, ionic composition and salinity similarly to the other soda pans of Central Europe (Stenger-Kovács et al., 2014b) and contrary to most freshwater ecosystems at the same latitude, where the benthic diatom communities are mostly related to TP, water depth, DIC (dissolved inorganic carbon), DOC (dissolved organic carbon), TN (total nitrogen) and alkalinity (Reavie and Smol, 2001; Schönfelder et al., 2002; Soininen, 2007).

4.5.2. The response of diatoms to the typology and the water management of the pans

Borsodi-dűlő and Nyéki-szállás

According to the survey in 2001 (Fertő-Hanság National Park, 2001), the chemical and physical parameters and the fauna (zooplankton, macroscopic zoobenthos, migrating waterfowls) were close to the typical features of natural soda pans. An opposite conclusion was raised by Tóth et al. (2014) 13 years later describing Nyéki-szállás and Borsodi-dűlő with typical soda pan species and low Conservation Index resulting in weak and moderate ecological status based on the zooplankton communities.

According to the present study, a high level of similarity was observed between Borsodi-dűlő and Nyéki-szállás presumably because of the similar limnological features (e.g. Secchi transparency, ion composition) and hydrological management. As the reference pans, they are characterized by similar ion dominance (HCO_3^-, SO_4^{2-}, Cl^-), turbidity (Boros et al., 2014; Burgenland, 2012; Tóth et al., 2014) and morphology. The pH above 9, which is in accordance with the natural status of the soda pans, increases the NH_3/NH_4^+ ratio and the denitrification leading low NO_3^- and TN concentration in spite of the high dissolved oxygen content (Hopkins and Hüner, 2004b; Boros et al., 2013b).

The irradiance level ranged from strongly shaded to close to the direct sunlight depending on the filling-drying phase, the actual weather conditions and the degree of the sedimentation of suspended inorganic solids. The presence of planktonic forms (e.g. *Stephanodiscus* sp., *Nitzschia acicularis*) and aerophilic species (e.g. *Gyrosigma* sp., *Hantzschia* sp.) in the benthic community indicates the fluctuating water levels of the pans. Accordingly, the mean conductivity and its standard deviation are also relatively high in the reconstructed habitats (2500±1300 $\mu S\ cm^{-1}$, max. 6000 $\mu S\ cm^{-1}$), but these values were still far below those in the reference pans (4000-14000 $\mu S\ cm^{-1}$) due to the water management resulting shifts in their natural hydrological cycling and consequently in communities not characteristic for soda pans (Zulka and Milasowszky, 1998). It was confirmed by most of the indicator species, like *Hantzschia abundans* (autecology: neutral pH, aerophilic and fresh-brackish species), *Stephanodiscus* spp. (littoral and pelagic, fresh-brackish species in eutrophic waters) and *Gomphonema parvulum* f. *saprophilum* (fresh-brackish species in α-mesosaprobic to polisaprobic waters) (Van Dam et al., 1994). Furthermore, the main indicator species of the reference pans were missing, like *Craticula buderi* or *Halamphora dominici* and *H. subcapitata*, which occur in pristine, saline environments (Levkov, 2009). Despite the water level and the salinity are the main filters that determine the abundance of the species (Keddy, 1999), the water management practice did not try to simulate the natural dynamics of these parameters in the studied pans.

Most taxa, including alkaliphilic species in the two reconstructed pans occur in eutrophic and hypertrophic water bodies of β-mesosaprobic to polysaprobic conditions (Van Dam et al., 1994). Most of the species were fresh-brackish (53%), the others were brackish-fresh (20%), brackish (20%) and freshwater (<10%) (Van Dam et al., 1994). The most abundant (>5%) halophilic or brackish species were e.g. *Achnanthes brevipes* var. *intermedia*, *Anomoeoneis sphaerophora*, *Ctenophora pulchella*, *Navicula salinarum* var. *salinarum*, *Nitzschia vitrea*, *Tabularia fasciculata*, *Tryblionella gracilis*, which are characteristic members of the diatom communities under hypersaline conditions (Blinn, 1993; Asencio, 2013; Żelazna-Wieczorek et al., 2015). The general species pool indicates the proximity and periodical linkage with Lake Fertő (Neusiedlersee), where similar species can be found (e.g. (Padisák, 1982; Buczkó, 1989; Buczkó and Ács, 1997), like *Achnanthes brevipes, Bacillaria paxillifera, Navicula oblonga, Surirella peisonis.* The relative abundance of brackish and brackish-fresh species peaked at summer or autumn, directly before the drying period indicating a shift from the dominance of fresh-brackish diatoms. Although this succession trend is associated with the natural features of soda pans, the proportion of the brackish-fresh species low, and the relative abundance of fresh-brackish species is too high. The reason is the moderate conductivity of the pans resulted by the water management and the periodical water supply from Lake Fertő. Lake Fertő can be characterized with lower conductivity range (1500-3500 μS cm^{-1}; (Padisák and Dokulil, 1994; Padisák, 1998a), which contributes to the lower salinity degree of the reconstructed saline pans. The prevailing wind direction is northern or northwestern in parallel with the longitudinal axis of Lake Fertő inducing strong water movements (seiching) towards the southern parts (Berczik, 2012). Consequently, when the water level of Lake Fertő is relatively high, strong wind can provide occasional water supply in the direction of the small saline pans.

Contrary to (Van Dam, 1982; Blanco et al., 2012)'s suggestions, the key in monitoring of the success of water management in soda pans can be to measure the diversity or species richness due to their significant correlations with the typical features, like conductivity, of these ecosystems (Stenger-Kovács et al., 2016). The AvTD values (mean: 63, between the genus and family) were similar to those in the reference sites and it was constant during the whole study may due to the stable pH level (Stenger-Kovács et al., 2016). The species richness and diversity were different from those in the reference pans where lower species richness (mean: 13) and diversity (mean: 1.7) were typical. Though the community metrics have seasonal fluctuation, these parameters did not show correlation with the conductivity and pH of soda pans, which could be considered as a result of regulation of the water level and the periodic water supply originated from Lake Fertő.

The applied conservation managements and the occasional water supply originated from Lake Fertő cause unpredictable and repeated shift or reversion in the natural succession of the community preventing the developments of possible alternative stable states that can be typical for shallow and created lakes (Aronson et al., 1993; Suding et al., 2004). To reach the good ecological status and natural conditions of the pans, the conductivity should be high associated with high number of brackish and brackish-fresh species, low species number and diversity similarly to (Por, 1980)‘s criteria. Some of the general principles of ecological engineering applied to the restoration ecology (Zedler, 2000; Mitsch and Jørgensen, 2004) did not prevail in these pans, like multiple goals, landscape context or natural regimes. If the ecological principles, as establishment of the natural disturbance regime, are kept in mind and applied, the natural succession process may lead to the original or new, alternative states (Keddy, 1999; Young et al., 2001; Suding et al., 2004).

Legény-tó

According to the survey in 2001 (Fertő-Hanság National Park, 2001), the typical chemical features of the soda pans have not been reached, but the zooplankton and macroscopic zoobenthos composition were similar to the typical natural soda pans (halophilic species pool and low diversity).

Based on our results, Legény-tó was separated the most from the other reconstructed and reference habitats. This pan differed the most from the reference sites, which was confirmed not only by the significantly different chemical and physical features, but also by the high number of indicator species. The main ionic composition of the pan was similar to the other two pans, but due to the permanent linkage of Legény-tó to a drainage canal, its basin is open. Consequently, its water level is more or less constant and the drying-filling periods are not apparent resulting in a salinity level, which did not reach the limit of saline category (threshold: 3000 μS cm^{-1}; Hammer, 1986). Indicating the disadvantageous effect of the canal, many of the indicator species (like *Achnanthidium minutissimum* var. *minutissimum*) are cosmopolitan and lotic taxa are associated with moderate conductivity and eutrophic conditions (Van Dam et al., 1994). Furthermore, the irradiance level is lower (15-1500 μmol m^{-2} s^{-1}) than that of the other lakes due to a deeper water body and higher turbidity. The hypertrophic conditions associated with low N/P ratio was supported by the success of the *Rhopalodia gibba* and *Epithemia sorex*. These species might support N-fixing cyanobacterial endosymbionts, which is successful strategy in N deficient saline aquatic habitats (Alvarez et al., 2006; Reuter et al., 1993).

Since the conductivity did not exceed the salinity limit (annual mean 1967 μS cm^{-1}), it falls in the freshwater category during the whole study. Correspondingly, the diatom assemblages of this pan were dominated by fresh or fresh-brackish species (e.g. *Amphora* *copulata*, *Gomphonema olivaceum*, *Ulnaria acus*) and the diatom vegetation was more diverse (the species richness ~32; diversity ~3.3), than expected in soda lakes (Alvarez et al., 2006; Flöder et al., 2010). The high degree of fluctuation of the diversity can be explained with the lower halophilic level, similarly to the phytoplankton studied under stress gradients (Flöder et al., 2010). Due to less severe environmental conditions, the members of low- and high profile guilds (Passy, 2007; Rimet and Bouchez, 2011) were abundant (e.g. *Amphora*, *Achnanthidium*, *Cymbella*, *Epithemia*, *Fragilaria*, *Gomphonema*, *Rhopalodia*, *Ulnaria*) contrary to the natural conditions, where the motile guild was dominant.

Based on our results, it is apparent that the conservation activity was not successful in Legény-tó. For the complete restoration, some of the ecological principles (e.g. multiple goals, landscape and time contexts) (Zedler, 2000; Mitsch and Jørgensen, 2004) have already been applied at Legény-tó. In October of 2012, there was a further attempt at restoring the natural hydrological system by terminating the connection with the canal, thus the success of the reconstruction is presumable accords to the assembly rules (Keddy, 1999; Young et al., 2001; Suding et al., 2004).

As the main conclusion of the study, we provided an overview on the success of water management after reconstruction of three soda pans in the Fertő-Hanság region by analysing the diversity of benthic diatoms. After the initial, promising results, the current ecological status of Borsodi-dűlő and Nyéki-szállás fall into the moderate category, but their natural physical, chemical and biological features have been still unsatisfactory due to the strongly manipulated water level. Legény-tó was far from the natural conditions, because its conductivity was constantly low and the diversity was high with the dominance of freshwater species due to the lack of the natural hydrological regime. As being diversity hot-spots and having effects on the nation's biodiversity (Whigham, 1999), good ecological status of the soda pans should be completely restored. Considering the assembly rules (Young et al., 2001) and the general principles of restoration ecology (Zedler, 2000; Mitsch and Jørgensen, 2004), the absolute success of their reconstruction could be predicted after the restoration of natural hydrological and disturbance regimes. According to the definition of restoration ecology, the restored community is self-regulated and self-maintaining, so based on the Field of Dreams hypothesis (Palmer et al., 1997), ("If you build it, they will come") and Mitsch and Wilson's (1996) theory ("Mother Nature and Father Time") the good ecological status of alkaline, shallow soda pans will be reached without any external intervention.

5. Equilibrium states of benthic diatoms in a lotic ecosystem[4]

5.1. Introduction

Implementation of the Water Framework Directive (WFD, 2000) initiated a number of phytobenthos surveys in European countries (King et al., 2006; Kelly et al., 2008; Kelly et al., 2009; Várbíró et al., 2012). One of the most robust arguments for using diatoms in ecological status assessment is their high species number. Though methods of status assessment from sampling to data analyses, and including the applied indices improved markedly, the underlying ecological knowledge has remained incomplete (Kelly, 2013). Until now, process based research on relationships between environmental factors, population dynamics and community attributes have largely been missing. For example, except for a very early study (Ács and Kiss, 1993) the effect of disturbances is poorly understood, especially in relation to the opportunity of development equilibrium states. In phytoplankton, prevalence of equilibrium states is authoritative and basically determines the sampling period (Padisák et al., 2006) for WFD status assessment.

Hardin's (1960) Competitive Exclusion Principle (only as many species may co-exist as the number of limiting resources) predicts equilibrial plant communities with low species number. However, plant communities typically consist of many species in Nature. This contradiction is well known as the Paradox of Plankton (Hutchinson, 1961). For its explanation a number of equilibrium and non-equilibrium theories were proposed (Hutchinson, 1961; Richerson et al., 1970; Wilson, 1990). The non-equilibrium theories attribute basic role to disturbances (e.g., current velocity) preventing competitive exclusion. According to Connell's (1978) Intermediate Disturbance Hypothesis (IDH), in absence of disturbance diversity will be reduced by competitive exclusion. When disturbance is very frequent only pioneer species can establish resulting also in low diversity. This hypothesis predicts that the communities reach maximal diversity at disturbances with intermediate frequency and intensity. Considering the relatively high number of diatom species in phytobenthos samples, logic suggests that we monitor disturbed, non-equilibrium diatom communities where separation of causes and consequences is doubtful (Reynolds et al., 1993).

Disturbance can be measured as response of the association to alternating forces (Juhász-Nagy, 1993). It is a complex variable: the origin of the disturbance is less

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important than its presence, frequency, and intensity (Sommer et al., 1993). After any kind of disturbance the recovery of community is strongly controlled by the succession processes (Odum, 1969; Odum et al., 1971).

A number of case studies evidenced that in natural phytoplankton communities it is very difficult to delimit equilibrium phases mostly because of the insufficient sampling frequency and absence of physical and chemical background data. As recommended for phytoplankton communities by Sommer et al. (1993), in the equilibrium phase (i) a maximum of three species contribute more than 80% of the total biomass, (ii) for at least 2 weeks, (iii) without significant variation in total biomass. These conditions were widely tested by the scientists, but as these criterions proved to be too strict, some modifications were allowed. Based on several studies (Morabito et al., 2003; Naselli-Flores et al., 2003; Nixdorf et al., 2003), increasing the number of co-dominating species to 4-5 was necessary. Furthermore, the generation time of the species in a phytoplankton and in a periphyton community is different. For this reason, the 2 weeks constancy required for phytoplankton have to be increased to 4-5 weeks for attached diatoms. Mischke and Nixdorf (2003) allowed ±15% variation in constancy of the total biomass.

Investigations of the equilibrium phases of stream benthic diatoms are missing. Since environmental parameters of a stream ecosystem often change suddenly and significantly, we hypothesize that the equilibrium communities cannot develop or occur only very rarely.

5.2. Aims

The aims of this study were (i) to investigate whether the equilibrium phase can develop or not under highly fluctuating conditions, such as what streams are exposed to; (ii) to determine the potential numbers of these states and (iii) to define such threshold limits of the environmental parameters, which certainly prevent the equilibrium phase.

5.3. Material and methods

5.3.1. Study areas

Fig. 15 *The situation of Torna-stream*

The sampling site for this study was the midland Torna-stream, in the area of the town Devecser, Hungary (N 47º 06,612’, E 17º 26,154’, altitude 170 m (Stenger-Kovács et al., 2013) (Fig. 15). According to the Hungarian national typology system, Torna-stream at the sampling point is a hilly stream with calcareous hydrogeochemistry and rough bedrock. Contrary to the upper region of the stream, the section at the study point is strongly modified. The riparian vegetation is missing due to the agricultural activity observed in the surrounding areas. The stream bed is straight and concreted.

5.3.2. Sampling process and diatom analyses

Semi-natural limestone bricks were used as substratum. The size of the bricks is 10x10x3 cm, the surface is flat with low roughness. Prior to the experiments the stones were sterilized (cc. hydrogen-peroxide, heat treatment, UV light). From April 2008 to May 2009, 62 phytobenthos samples were taken (first period), and further 50 samples were collected between April 2009 and May 2010 (second period). The limestone bricks were fixed to the bottom of the bed (Fig. 16) and were collected randomly one by one every third day in the first month, and then weekly.

Fig. 16 *The applied substrates and the sampling site in the stream*

Diatom valves were cleaned and identified on the same way as described in Chapter 2.3.2. Three parameters (length, breadth, and girdle) of ten specimens were measured, and their volumes were calculated following the formulas in the NAWQA program (2001). Biomass data were obtained as the product of relative individual numbers among the 400 valves and biovolume data, which could result stronger alga-based metrics contrary to the relative abundance (Reavie et al. 2010; Lavoie et al. 2011). Establishment of equilibrium phases was based on data expressing relative contribution to total biomass, and these data were used to separate

- dominants (>5%),
- frequent species (1-5%),
- and rare species (<1 %).

The net growth rates of the species were calculated based on the exponential equation of population growth described by Malthus (2013) and Turchin (2001).

In present study, equilibrium phase was assumed to occur, when maximum of five species contribute more than 80% of the total biomass for at least 4 weeks without significant variation (<15%) in total biomass.

5.3.3. Chemical and physical analyses

Water temperature (ºC), pH, dissolved oxygen (DO, mg l^{-1}), oxygen saturation (DO%) and conductivity (µS cm^{-1}) were measured on the field by HQd 40 Field Case mobile set. NO_2^-, NO_3^-, SRP, TP, SRSi, and NH_4^+ were quantified with spectrophotometer (APHA, 1998; Wetzel and Likens, 2000), and Cl^-, SO_4^{2-}, COD, and alkalinity with titrimetry (APHA, 1998). The regional Water Authority provided daily discharge data. The chlorophyll-*a* content of the epilithon was measured according to Wetzel and Likens (2000) using a

Metertech UV/VIS Spektrophotometer, SP8001). To avoid the impact of pheopigments, the acid method was applied (Lorenzen, 1967; Tett et al., 1975).

5.4. Results

Altogether 100 diatom species were identified. The average number of the species was 25±5 in the first year and it was 28±9 in the second year. In the first year arithmetic mean of Shannon-Weaver diversity was 3.41±0.5 and in the second year it was 2.99±1.05.

5.4.1. Fulfillment of the first and second condition of equilibrium state

The following species constituted equilibrium assemblages: *Gomphonema olivaceum* (GOLI), *Gomphonema parvulum* (GPAR), *Diatoma tenuis* (DITE), *Fragilaria vaucheriae* (FCVA), *Navicula cryptotenella* (NCRY), *Navicula gregaria* (NGRE), *Navicula lanceolata* (NLAN), *Surirella brebissonii* (SBRE), *Cocconeis placentula sensu lato* (CPLI), *Planothidium frequentissimum* (PLFR), *Ulnaria ulna* (FULN), and *Nitzschia linearis* (NLIN). CPLI, FCVA, and NLAN were most frequently the dominant species during almost the whole first year (Fig. 17). In January *Gomphonema parvulum* was replaced by *Gomphonema olivaceum*. *Ulnaria ulna*, *Diatoma tenuis*, and *Planothidium frequentissimum* were abundant only occasionally.

In the second year, *Diatoma tenuis*, *Ulnaria ulna*, and *Planothidium frequentissimum* did not appear among the dominant species; *Navicula cryptotenella* and *Nitzschia linearis* appeared as new members in the assemblage. *Gomphonema olivaceum* showed a similar seasonal dynamics as in the first period (Fig. 17).

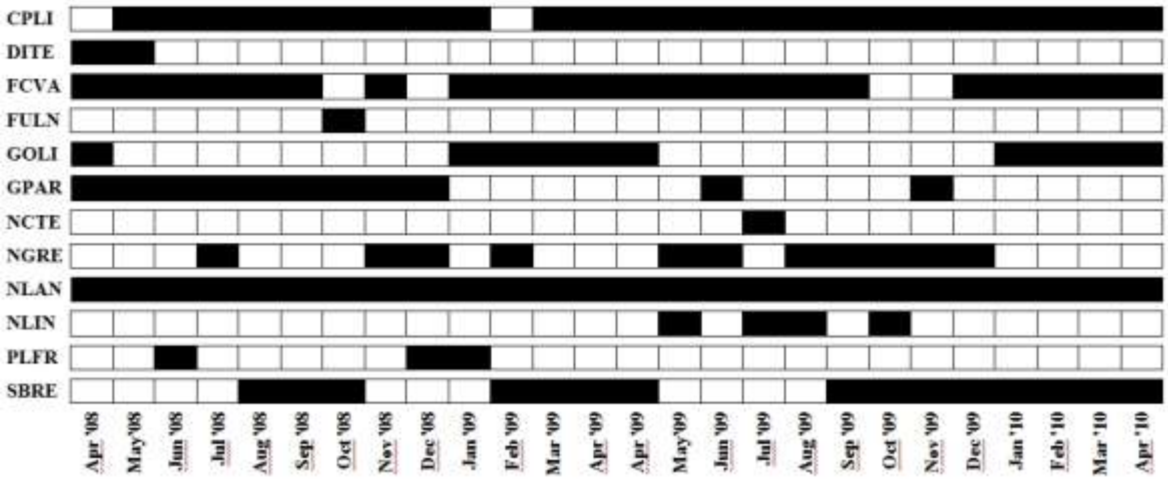

Fig. 17 *Species compositions of the diatom community considering no more than five species (cumulative contribution to total biomass > 80%)*

According to the first assumption, 80 ± 10% of the biomass should consist of no more than 5 species (Fig. 18). In 2008 the cumulative values of the 5 dominant species usually reached 72% of the biomass, except in October and February. Diversity did not change significantly (its variation did not exceed 10%) from June to December: It varied commonly between 3.46 and 3.96. In the first month, and from January to April, the diversity was lower (average 2.95). Next year there was a long period (from June to October 2009) when this cumulative contribution did not reach this limit value (<72%). The diversity was high (more than 3.28) during this period. When the cumulative biomass of the five species reached 72% of the total biomass, the diversity significantly decreased (r = -0.81); it was lower than 2.72.

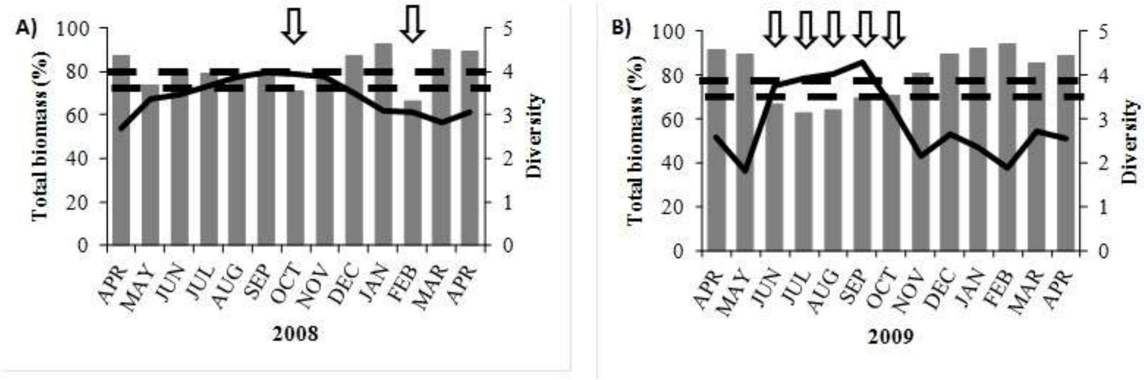

Fig. 18 *Contribution of the five most dominant species to the total biomass (grey bars), and Shannon diversity (black line) during the first (A) and second (B) year (line: 80%, broken line: 72%, arrow: month where the first condition did not occur)*

5.4.2. Third condition of equilibrium state

Chlorophyll-*a* content increased during the vegetation period in both years (Fig. 19). Annual average chlorophyll-*a* was higher in the second year. In the first period there were two significant peaks: one in late summer (94 µg cm^{-2}), and the other in the next April (69 µg cm^{-2}). In the second year, the chlorophyll-*a* content reached its maximum amounts in November (42 µg cm^{-2}) and in January (37 µg cm^{-2}).

In the first year (Fig. 19), monthly biomass was constant (biomass variation < 15%) only in July, when the average value of chlorophyll-*a* was 7 µg cm^{-2}. In the second year (Fig. 20), monthly biomass did not change significantly in May (average chlorophyll *a*: 6 µg cm^{-2}), July (20 µg cm^{-2}), August (21 µg cm^{-2}), and January (30 µg cm^{-2}).

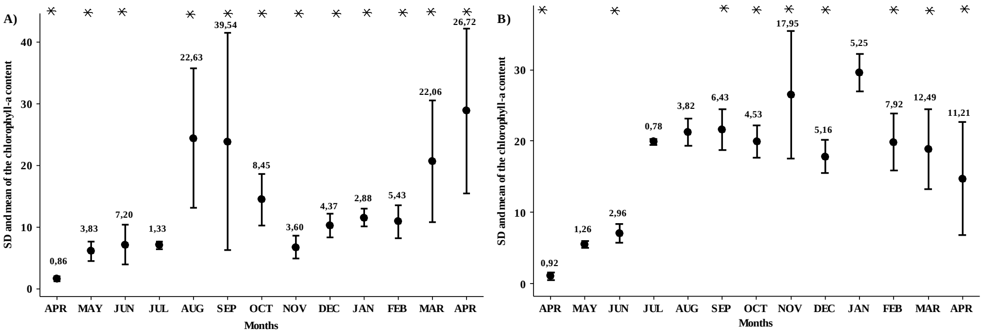

Fig. 19 *Mean and the SD of chlorophyll a content in the first (A) and the second period (B) (star: month when the biomass changed significantly)*

5.4.3. Chemical and physical parameters

Table 6 summarized the coefficients of variation (CV) of the parameters. The most balanced factors (<20%) were the DO, DO% and pH. Temperature, conductivity, alkalinity, Cl^- concentration and discharge were also mainly homogeneous except some shorter intervals. The measured phosphorus and nitrogen forms, SO_4^{2-}, SRSi concentration and COD were extremely variable (>20%) during the entire period.

Table 6 *Percentage coefficient of variation of the parameters (grey marked cells indicate higher variations of the given environmental parameter than in the equilibrium phase, bold numbers indicate the strong and extreme variability)*

	2008									2009												2010			
	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR
DO	12.6	8.1	8.7	2.1	13.3	11.7	4.2	4.4	5.9	6.0	1.0	3.0	4.1	4.6	12.2	4.5	2.4	5.8	9.5	9.7	7.8	4.2	14.3	9.8	7.1
DO%	10.8	10.2	6.1	8.4	7.9	9.2	7.3	7.9	1.6	2.3	1.2	4.3	4.0	9.6	11.7	7.0	1.9	6.0	3.2	3.0	1.5	2.1	6.1	7.3	2.5
Temperature (°C)	17.5	14.5	12.5	14.5	15.2	19.5	13.8	**41.3**	**28.2**	**80.1**	**23.2**	17.5	9.1	18.9	11.9	6.4	9.8	7.5	**21.6**	**27.1**	**54.4**	**43.1**	**82.7**	**45.0**	**29.7**
pH	9.6	0.4	1.6	3.2	1.4	4.5	2.4	1.2	2.5	2.1	2.2	0.7	0.7	3.1	3.2	3.9	2.4	2.0	2.3	1.5	2.0	1.3	3.0	0.7	2.3
Conductivity (µS cm^{-1})	12.5	3.2	**28.1**	5.0	15.0	**27.2**	2.5	**25.9**	18.0	5.4	9.4	11.5	13.9	11.1	10.5	11.5	4.0	2.5	6.5	10.2	4.1	1.1	4.4	2.9	14.0
NO_2^- (mg l^{-1})	**24.9**	**32.7**	**48.6**	**66.4**	**60.9**	**67.4**	**64.2**	**54.8**	**61.1**	**28.2**	14.3	11.9	15.2	**50.7**	**42.0**	**38.5**	**66.5**	**31.6**	**53.3**	**49.1**	**41.6**	**21.6**	19.4	**28.0**	**68.1**
NO_3^- (mg l^{-1})	**40.0**	**52.3**	**48.5**	**36.3**	**29.9**	**38.8**	**47.9**	8.9	**29.5**	**20.7**	**34.9**	8.7	12.1	**29.6**	**21.4**	8.1	2.7	8.0	6.9	13.3	8.0	4.8	2.2	3.0	8.8
NH_4^+ (mg l^{-1})	**63.3**	**103.5**	**96.7**	**151.6**	**61.9**	**25.5**	**158.2**	**127.5**	**84.3**	**69.1**	**40.9**	**32.1**	**148.5**	**90.1**	**115.0**	**77.2**	**98.3**	13.5	**68.3**	**74.1**	**118.9**	**39.7**	**33.6**	**74.8**	**21.0**
COD (mg O_2 l^{-1})	**70.9**	**117.1**	**61.1**	**51.5**	7.5	11.6	**96.3**	12.2	**198.4**	**28.6**	**135.4**	**111.2**	**101.8**	**196.4**	18.6	10.2	**48.8**	16.6	**31.6**	4.0	**37.1**	17.7	5.5	**34.7**	**65.0**
SRP (µg l^{-1})	**72.4**	**170.4**	**34.3**	**26.0**	**41.1**	**22.7**	**129.3**	**115.5**	**136.9**	**68.2**	**40.3**	**100.6**	**21.1**	**38.4**	**60.8**	**33.0**	11.7	11.2	11.3	**26.7**	19.6	**38.9**	13.1	**36.7**	**33.7**
TP (µg l^{-1})	**90.3**	**80.3**	**51.4**	**102.4**	**180.6**	**129.8**	**69.6**	**138.5**	**146.0**	**113.8**	**49.7**	**64.9**	16.1	**75.6**	17.3	**26.9**	**50.2**	**41.7**	**72.1**	**73.1**	18.3	**24.6**	**22.0**	**31.0**	**82.1**
SRSi (mg l^{-1})	10.2	**50.6**	**44.6**	**51.2**	**29.9**	17.1	3.5	**20.7**	**47.8**	5.8	16.5	6.6	11.9	8.7	11.1	7.5	7.3	12.3	**20.9**	**23.0**	7.9	**45.1**	**45.8**	**22.2**	12.7
SO_4^{2-} (mg l^{-1})	16.9	14.5	**34.1**	**107.6**	6.1	**96.6**	**56.7**	**26.0**	**27.2**	13.7	10.7	12.1	19.1	**33.8**	19.1	**32.5**	9.8	19.0	**31.6**	**25.9**	17.2	5.4	**30.3**	18.0	**37.2**
HCO_3^- (mg l^{-1})	17.1	14.4	**24.0**	**24.3**	8.8	15.9	**21.7**	9.5	14.2	16.0	11.0	12.6	7.3	12.1	2.0	14.2	3.9	6.2	3.1	11.7	**42.8**	8.5	11.2	**81.5**	8.6
Cl^- (mg l^{-1})	**24.1**	**20.3**	**40.6**	**35.0**	**48.7**	**37.9**	**31.7**	18.3	10.9	17.6	6.0	8.8	9.7	19.1	10.3	**20.1**	3.3	14.0	9.1	4.6	6.7	7.9	2.2	**25.4**	12.6
Discharge (m^3 s^{-1})	6.2	6.8	6.8	7.1	9.6	15.2	14.9	13.4	**20.9**	**20.3**	17.0	16.4	8.0	4.8	5.8	10.1	11.1	10.5	6.8	14.8	14.9	14.0	14.0	13.9	11.3

In the first year (2008-2009) the DO, conductivity, discharge and SRP fluctuated (compared to the equilibrium state) mostly (7-9 out of 13), but the changes of NO_3^- ion and TP were also important (5-6 out of 13). The CV of NH_4^+, SRSi, SO_4^{2-} and alkalinity did not exceed the values measured in the supposed equilibrium states. If we consider each month, most of the parameters fluctuated at the same time in September (8 variables out of 16), in April, August, December and January (5-6 out of 16). Mostly, three or four variables fluctuated at the same time. In the second year DO (8 months out of 13) fluctuated mostly, but the other environmental parameters did not change or not significantly (1-3 out of 13) compared to the steady states. Contrary to the previous year, commonly 1-3 parameters fluctuated a lot together in the month and the highest number of variables (4 out of 16) changed together in December.

Taking all the three conditions of establishment of the equilibrium status into consideration (Tables 7 and 8), mostly (10 times out of 13) only two conditions, in October and February none of the conditions were fulfilled at the same time. Equilibrium state (when all of the conditions were realized) was found only in July. In the second year, three times (June, September, October) none of the conditions were fulfilled. In July and August just one condition, in six further months two conditions were fulfilled. The three equilibrium conditions were realized at the same time only in May and January. The species compositions in the equilibrium phases were different:

1. *Cocconeis placentula sensu lato*, *Fragilaria vauchariae, Navicula lanceolata, Gomphonema parvulum*, *Navicula gregaria*;
2. *Cocconeis placentula sensu lato*;
3. *Navicula lanceolata*

Table 7 Equilibrium conditions in the first year (+ fulfilled, - not fulfilled)

	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR
1st condition (max. 5 species contribute more than 80% of total biomass)	+	+	+	+	+	+	-	+	+	+	-	+	+
2nd condition (for at least 4 weeks)	+	+	+	+	+	+	-	+	+	+	-	+	+
3rd condition (without significant variation in total biomass)	-	-	-	+	-	-	-	-	-	-	-	-	-

Table 8 Equilibrium conditions in the second year (+ fulfilled, - not fulfilled)

	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR
1st condition (max. 5 species contribute more than 80% of total biomass)	+	+	-	-	-	-	-	+	+	+	+	+	+
2nd condition (for at least 4 weeks)	+	+	-	-	-	-	-	+	+	+	+	+	+
3rd condition (without significant variation in total biomass)	-	+	-	+	+	-	-	-	-	+	-	-	-

5.5. Discussion

Heraclitus's evergreen wisdom "*One cannot step into the same river twice*" goes to philosophical depths, but even in its most immediate meaning it expresses the continuously changing nature of running waters. Here the word "river", small to large, cannot be replaced by the word "lake". Variability of running waters can be observed by naked eyes especially through changes in discharge, flow velocity, and suspended solids.

Many diatom species were identified early as good indicators of some major variables (for example salinity or conductivity) or the entire habitat (Hustedt, 1930). After recognizing a number of important properties of diatoms useful for monitoring water quality (like occurrence in almost all inland waters, high species number, relatively standard taxonomy, easy-to-archive slides, etc.), development of diatom indices started blossoming (see Whitton, 2012 for a summary), and this kind of research has been accelerating since issuing of the Water Framework Directive (WFD, 2000) that designated benthic microalgae as one of the five major biological quality elements. During the last 25 years most studies on river diatoms were directly or indirectly related to application of the WFD including elaboration of national metrics, selection of relevant indices, improving assessments by intercalibration exercises, etc. (e.g. Kelly et al., 2009 and references cited therein). As case- and comparative studies accumulated, doubts started to emerge about the overall applied methods and their appropriateness in assessing real ecological status. In his seminal paper, Kelly (2013) concluded that more knowledge is needed about traits of phytobenthos, with deep roots in functional ecology to achieve a better coupling of cause and effect, similarly as has been done for benthic macroinvertebrates.

During the last 25 years, phytoplankton ecologists focused rather on coupling habitat properties with morphological and/or physiological traits of phytoplankton that resulted in three functional classifications (Reynolds et al., 2002; Salmaso and Padisák, 2007; Kruk et al., 2010). Two of them are applied for the ecological status assessment according to the WFD (Padisák et al., 2006; Phillips et al., 2010). Additionally, much effort was dedicated to the understanding of the diversity-disturbance relationship (Reynolds et al., 1993; Sommer et al., 1993), and the closely related emergence of equilibrium states (Naselli-Flores et al., 2003).

According to the original assumptions (Sommer et al., 1993), progress towards an equilibrium state requires environmental constancy during a sufficiently long time for allowing selection of the best-fit species or species complexes (up to 5 according to reasons and considerations detailed in the introduction). In statistical models elaborated for explaining relationships between compositions of attached diatom assemblages and environmental variables, the following determinant groups were selected repeatedly (present results, references listed in Appendix 10):

- Variables describing a temporal scale (season), like temperature, DO;
- Nutrient conditions and ratios (nitrate, ammonium, SRP, SRSi) or trophic state;
- Variables describing ionic composition;

- Acidity-alkalinity (pH, alkalinity, calcium concentration);
- Organic content (BOD, COD, color, TOC, PON, etc.);
- Light conditions (turbidity, suspended solids);
- Spatial and land use descriptors and in some special cases;
- Toxic agents.
- Interestingly, probably the most important physical variable (measured as discharge or flow velocity) is largely neglected.

Therefore, it seems reasonable to analyze constancy of such variables during the equilibrium phases found in this study. During the first equilibrium state (July, 2008) the most important variables determined by the PCA and CCA (Stenger-Kovács et al., 2013) changed significantly (>20%): Nitrogen forms showed approximately 36-152%, COD 50%, and Cl^- exhibited 35% CV. Furthermore, extremely variable concentrations of phosphorus forms were recorded (SRP: 26%, TP: 102.5%). In the second one similar trends were observed, but instead of Cl^-, the SO_4^{2-} concentration had higher CV. A decreasing fluctuation of these variables was detected in the third equilibrium phase (January, 2010), but the correlations of variation of these factors still remained significant (20-40%). Additionally in this month the temperature, as another main environmental parameters determined by PCA and CCA showed higher CV (43%). Analyses of environmental constancy during equilibrium phases are not available in the literature; however, these data allow concluding that resilience of a developed equilibrium phase may ensure biotic constancy even though the underpinning environmental background fluctuates at higher amplitude.

The number of coexisting species varied between one and five (1st equilibrium state: *Cocconeis placentula sensu lato*, *Fragilaria vaucheriae*, *Gomphonema parvulum*, *Navicula gregaria*, and *Navicula lanceolata*; 2nd: *Cocconeis placentula sensu lato*; 3rd: *Navicula lanceolata*). This observation is similar to findings for phytoplankton: monodominance is more likely in such phases than coexistence of more than one species (Padisák et al., 2003). However, mechanisms resulting in equilibrium are more diverse than competitive exclusion (Rojo and Alvarez-Cobelas, 2003). For example, during the second equilibrium phase disturbance intensities were rather high. *Cocconeis placentula sensu lato* is fresh-brackish water diatom. It is a non-motile species, attaching by the valve face and mucilage to the substratum. *C. placentula sensu lato* is associated with low organic matter content (Lange-Bertalot, 1979; Gómez, 1998; Kelly, 1998), and it is favored by moderate or high nutrient concentrations (Gómez and Licursi, 2001; Yallop et al., 2009). This is confirmed also by the IPS (Specific Pollution Index) indicator values (1.0) and taxon sensitivities (4.0), which mean that *C. placentula sensu lato* tolerates elevated concentrations of organically bound nitrogen. According to its autecological features, the high relative contribution to total biomass of this pioneer species (Hofmann et al., 2011) might be the result of its stress tolerance (*sensu* Borics et al., 2013) rather than of competitive exclusion.

During the 3rd equilibrium phase *N. lanceolata* built up 78.4% of the total biomass, and this period was characterized by highest environmental constancy. According to the slow net growth rates of the species, *N. lanceolata* can be characterized as a climax species. It is also a fresh-brackish species but typically occurs in cold waters, and it is motile (Hofmann et al., 2011; Stenger-Kovács et al., 2013) allows the species to resist against moderate water discharge. According to Kelly (1998) *N. lanceolata* is an organic-matter-pollution-tolerant species. As indicated in many works (e.g., (Lange-Bertalot, 1979), this species is more abundant at lower temperatures (the end of autumn, winter, and early spring). The IPS indicator value is 1.0, the taxon sensitivity is 3.8, and in this month the concentration of the nutrients were moderate or high, which also contributed to the increase of this species. In the absence of nutrient limitation, temperature was the primary factor allowing emergence of *N. lanceolata*. The species found in equilibrium states in this study are either stress-tolerant or K-selected ones with low net growth rates in agreement with observations on phytoplankton (Padisák et al., 2003; Stoyneva, 2003). In our study, steady state did not occur during the colonization periods (when the diversity was low) in contrast of Hameed's (2003) study, where, paradoxically, the equilibrium state was suggested during the colonization period.

Overall, non-equilibrium states of the diatom assemblage were characteristic during this study. The Torna-stream is a fast-changing ecosystem like non-stratified lakes, with discharge as the major regulating environmental factor by affecting nutrient supplies and the light regime (Descy, 1993). Though there was no nitrogen or phosphorus limitation during the entire study, in the non-equlibrial phases 3 or more environmental parameters (mainly the conductivity, SRP, DO, discharge) changed significantly or the amplitudes of variation of fewer parameters were high at the same time.

Contrary to Reynolds' (1984) theoretical presumptions (river phytoplankton should be dominated by r, fast-growing species which are able to develop in a strongly-disturbed and light-limited environment), Shannon diversity remained high during almost the entire first year, because disturbance reached intermediate intensities and frequencies, allowing smaller, fast growing species to co-occur with the K strategist species as described in the IDH. In the second period after the steady-state in May the diversity was high due to intensive disturbances which excluded the equilibrium phase. This maximal diversity collapsed in September, probably due to the Si depletion. After it, despite that the environmental conditions were sufficient for the developing of the steady-state, there was no sufficiently long undisturbed period which is necessary to reach it. Naselli-Flores et al. (2003) also concluded that, in the absence of disturbance, there should be enough time to progress towards the equilibrium state. For phytoplankton 35-60 days were required to achieve equilibrium (Sommer, 1985; Sommer, 1989; Reynolds, 1993; Padisák, 1994), but it appears reasonable that it should be longer for the periphyton because of the different (longer) generation times.

In most of the cases, changes in biomass prevented detection of the equilibrium phases. In both years, chlorophyll-*a* concentration continued increasing until autumn (September in the first year and November) then restarted again in approximately February in both years which could hardly be explained by Si utilization.

Similar to lakes in the temperate regions, equilibrium phases in the diatom assemblage occurred only occasionally and were ephemeral but could develop both in relatively-permanent and in highly-variable environments (Mischke and Nixdorf, 2003; Naselli-Flores et al., 2003; O'Farrell et al., 2003; Rojo and Alvarez-Cobelas, 2003; Stoyneva, 2003). Regarding some water chemical parameters, threshold values could be defined: if the CV of conductivity > 14%, pH> 4%, NO_2^- > 66.5% and DO > 5.8%, equilibrium state could not develop. The degree of change in these parameters alone was enough to prevent the development of an equilibrium phase. However, in other cases lower amplitude of variance was observed for two-three variables and their combined effect led to the non-equilibrium phase. Experiences on phytoplankton assemblages report on the climate determination of the probability of development of equilibrium states: they are more likely to occur and last longer in warmer climates (Komárková and Tavera, 2003; Becker et al., 2008; Li et al., 2011). Such relationship is to be explored for stream diatoms.

As to the ecological status according to the WFD, there were no significant differences between the equilibrium and non-equilibrium phases since the IPS values varied between 3 and 4 independently from the equilibrium status.

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8. The most significant result in thesis points

The term of stress is often confused with the definition of disturbance, probably because none of the environmental variables can be clearly claimed as stressor or disturbance. The clarification and the differentiation of these factors are very important, because their impacts need different approaches. The basic aim of present dissertation is to study the effects of stress and disturbance in benthic diatom communities in the field and laboratory studies:

(i) to identify what kind of diatom species can tolerate multiple stress in three alkaline, saline, shallow soda pans;

(ii) to recognize the optimum and tolerance of two diatom species along light, temperature and conductivity gradients;

(iii) to investigate the complexity of three impacts (natural, and human disturbances, stress) in three saline pans using reference sites; and

(iv) to determine the potential establishment of equilibrium state of benthic diatom assemblages in a stream ecosystem.

For these purposes, two-year datasets (phytobenthos, physical and chemical parameters) were applied from the field and cultures were grown for laboratory ecophysiological experiments. The most important results are the following:

8.1. DIATOM FLORA UNDER STRESS CONDITIONS

8.1.1. Altogether 200 epiphytic and epipelic diatom species were identified in 128 samples collected from three soda pans (Borsodi-dűlő, Legény-tó, Nyéki-szállás) between January in 2012 and August in 2014. 108 species were documented in 18 photo tables including 474 light microscopy photos. Regarding the surrounding areas (Lake Fertő, Seewinkel and Danube-Tisza Interfluve), 29% of the benthic diatom species can be found only in the studied pans and the other taxon were common with the other regions. **The present study provides new scientific information about the special and unique diatom flora of three pans in the Fertő-Hanság region, which is still missing in the national and international literature. Furthermore, this iconographic work is supplemented not only with detailed photo-documentation, but presents quantitative datas including one of the four presumably new species.**

8.1.2. Regarding the epiphyton and epipelon assemblages, the mean species number was 37 and 35 in Legény-tó, 29 and 28 in Borsodi-dűlő, 23 and 29 in Nyéki-szállás. The CA analysis supported that there is no significant difference between the epipelic and epiphytic diatom communities, independently of the pans. **As conclusion, in these ecosystems, the spatial distribution of diatoms is related to the pans and their characteristic limnological features, and the effect of substrates is less noticeable. The physical and chemical parameters (TP, pH, conductivity, temperature, transparency) can reach extreme values representing multiple stresses on the biota, thus the diatom species have to tolerate a broad range of physical and chemical changes which override the effects of substrates.**

8.1.3. Only few species (e.g. *Achnanthidium minutissimum* var. *minutissimum, Navicula veneta*, *Nitzschia palea* var. *palea*, *Tryblionella hungarica*) can be characterized with constancy 5, and most of the species belonged to the constancy 1 category. Based on the annual mean relative abundances, altogether only 10 species (e.g. *Ctenophora pulchella*, *Navicula veneta*, *N. wiesneri*, *Nitzschia frustulum*) were dominant (>5%), and many species had only occasional dominance. **Based on the high number of constancy-one species and low species richness, the benthic diatom flora of the studied pans can be characterized with uniqueness. The diatom assemblages can not recover and are forced towards continuous compositial changes due to the many environmental gradients which represent multiple stresses for the biota.**

8.1.4. A number of vulnerable species (VU) were identified, such as *Caloneis silicula*, *Cocconeis neothumensis*, *Cylindrotheca gracilis*, *Delicata delicatula*, *Encyonema lacustre*, *Scoliopleura peisonis*, *Surirella peisonis*. Furthermore, presumably threatened (PR) species were also found, like *Bacillaria paxillifera*, *Craticula halophila, Fragilaria tenera*. **These aquatic habitats have significant conservation value, since they provide habitats for several Red-list species. The studied pans are diversity hot-spots which may have effects on the nation's biodiversity, so their protection and good ecological status has to be maintained.**

8.2. STRESS TOLERANCE ALONG LIGHT-, TEMPERATURE-, SULFATE- AND CHLORIDE GRADIENTS

8.2.1. *Nitzschia frustulum* preferred SO_4^{2-} more than Cl^- contrary to *N. aurariae*, which did not show considerable difference for different concentrations of these two ions. The maximum photosynthetic rate of *N. frustulum* was detected at 3253±106 mg L^{-1} Cl^- and 3332±120 mg L^{-1} SO_4^{2-} concentration (approximately 8700 µS cm^{-1}), this parameter of *N. aurariae* peaked at 4182±474 mg L^{-1} Cl^- and 5255±460 mg L^{-1} SO_4^{2-} concentrations (~10500 µS cm^{-1}) independently from the temperature. **As conclusion, *N. frustulum* and *N. aurariae* are tolerant to a broad range of salinity, and can occupy a broad niche providing ecological advantage against other species. However, the niche of the species is overlapped, *N. aurariae* have higher competitive advantages tolerating higher level stress.**

8.2.2. The light compensation point of *N. frustulum* and *N. aurariae* was very low, and their photosynthetic rates became light-saturated already at low-medium light intensities (I_k <440 µmol $m^{-2}s^{-1}$), independently from the studied gradients. No photoinhibition was detected at any temperatures or concentrations. **As conclusion, *N. frustulum* and *N. aurariae* can tolerate low light availability making them good competitors for light and beside their ion preferences, their irradiance demand may explain their distributions and dominances in the Fertő-Hanság region. Both species can tolerate and survive unfavorable light conditions gaining ecological benefit in stressed environments.**

8.2.3. The photosynthetic activity increased parallel with the temperature up to 30-35 °C. Above it, a decrease of the photosynthesis was observed at each conductivity level. The maximum photosynthetic activity of *N. frustulum* peaked at 28.5 ± 0.5 °C, and of *N. aurariae*, it maximized at 34.5 ± 2.5 °C that appeared to be independent of the ion content of the media. Based on the ANOVA, the temperature was the principal determining factor among the studied gradients. **Based on the results, *N. frustulum* and *N. aurariae* have high temperature optimum with broad tolerances, which provide advantages in the shallow soda pans, where the high day-night temperature variation is typical. Nevertheless, their photosynthetic activity will decrease under increasing, sometimes extreme temperatures predicted by the climate change models.**

8.3. STRESS AND DISTURBANCES IN SODA PANS

8.3.1. All the studied pans can be characterized by the similar ion composition (HCO_3^-, SO_4^{2-}, Cl^-), pH, COD, high TP:TN ratio. All the reconstructed pans had significantly lower conductivity (754-5920 μS cm^{-1}) compared to the reference dataset (3120-13650 μS cm^{-1}). According to the TP, Nyéki-szállás, Borsodi-dűlő and the reference sites were statistically similar, contrary to Legény-tó, which had the lowest TP values. **However, many chemical and physical features of the reconstructed pans are similar to the reference sites but their conductivity values are still considerably lower indicating that the conservation activity is not successful due to the purposive regulation of the water level by the National Park, the periodic water supply originating from Lake Fertő and the permanent linkage to a drainage canal. The final success of their reconstruction is expectable only after the restoration of natural hydrological and disturbance regimes.**

8.3.2. Regarding the applied community metrics, Borsodi-dűlő and Nyéki-szállás showed high similarity, and Legény-tó mostly separated from them. The reconstructed pans did not separate significantly from the reference sites as revealed by the AvTD, contrary to the species number and the diversity, which were significantly lower in the reference sites. The diversity and species richness had seasonal fluctuation, but AvTD remained more or less constant. AvTD was influenced by five environmental variables in Nyéki-szállás (DO%, pH, temperature, irradiance level, CO_3^{2-}). Only one variable had effects on the diatom diversity and species richness: TP in Borsodi-dűlő and temperature in Nyéki-szállás and Legény-tó. **As conclusion, the diversity metrics indicate unequivocally moderate ecological status of the Borsodi-dűlő and Nyéki-szállás, but the ecological status of the Legény-tó is far from the natural conditions. These parameters do not show correlation with the conductivity as one of the main ecological filter, which could be considered as a result of their unnatural disturbance regimes.**

8.3.3. Different indicator species were identified in the studied pans: 13 diatom species in Legény-tó, eight in Borsodi-dűlő, five in Nyéki-szállás and three in the reference sites. The chemical and physical difference between the reconstructed and reference were in accordance with the autecological features of the indicator species. In Borsodi-dűlő and Nyéki-szállás, the number of freshwater taxa was low and more or less constant, but in summer the brackish and brackish-fresh species became dominant. In Legény-tó, the number of fresh-brackish species was high and constant in all seasons contrary to the brackish species, which was low and sporadic. In the reference sites, the relative abundance of brackish-fresh species was significantly higher, the fresh-brackish and freshwater species were lower than in the reconstructed pans. **Based on the results, the biological features of the reconstructed pans are still unsatisfactory. The modified disturbance regimes cause unpredictable and repeated shifts or reversions in the natural succession of the community preventing the development of the typical-soda-pan communities and the possible alternative stable states that can be typical for shallow and reconstructed lakes.**

8.4. EQUILIBRIUM STATES OF BENTHIC DIATOMS IN A LOTIC ECOSYSTEM

8.4.1. Taking all the three conditions of establishment of the equilibrium status into consideration in the first year, equilibrium state was found only in July. In the second year, the three equilibrium conditions were realized at the same time in May and January. **As conclusion, equilibrium phases in the diatom assemblage are rare, unpredictable, occurred only occasionally and are ephemeral similar to lakes in the temperate regions.**

8.4.2. Altogether 100 diatom species were identified during the two years in Torna-stream, out of which only 5 species contributed to equilibria. The species compositions in the developed equilibrium phases were different and consisted of *Cocconeis placentula sensu lato, Fragilaria vauchariae, Gomphonema parvulum, Navicula gregaria, N. lanceolata* in July (2008), *C. placentula sensu lato* in May (2009) and *N. lanceolata* in January (2010). **The conclusions of present study are similar to those found in phytoplankton of lentic habitats: in lotic environment, the equilibrium states in benthic diatom communities are mostly characterized by monodominance**. **However, according to their autecological features, their high relative contribution to total biomass might be the result of their stress tolerance rather than of competitive exclusion.**

8.4.3. Almost in the entire first year, the diversity was high (>3.4) associated with strongly fluctuating chlorophyll-*a* (>15%). In the second year, the diversity was mainly low (<2.9), except from June to October. Regarding the biomass, despite the higher chlorophyll-*a* content, more constant periods were observed in the second year than in the first year. **The results supported that mechanisms resulting in equilibria are quite diverse. As the IDH predicts, Shannon diversity remained high during almost the entire first year, because disturbance reached intermediate intensities and frequencies. In the second**

period after the steady-state, the intensive disturbances resulted high diversity excluding the equilibrium phase that requires sufficiently longer undisturbed period than it was supposed for the phytoplankton.

8.4.4. Eight environmental variables were identified as the most balanced factors: DO, DO%, pH, temperature, conductivity, alkalinity, Cl^- concentration, discharge. In contrast, another eight determining parameters (the phosphorus- and nitrogen forms, SO_4^{2-}, SRSi concentration, COD) were highly variable during the entire period. During almost the entire first year, mostly 8-10 parameters fluctuated together at the same time. In the second year, the alteration of 4-7 parameters was rather characteristic. **Though Torna-stream is a fast-changing ecosystem, the equilibrium states could develop both in relatively-permanent and in highly-variable environments. Regarding some parameters, threshold values could be defined: if the CV of conductivity > 14%, pH > 4%, NO_2^- > 66.5% and DO > 5.8%, the degree of change alone was enough to prevent the development of an equilibrium phase. In other cases lower amplitude of variance was observed for two-three variables, but their combined effect led to the non-equilibrium phase.**

9. List of publications

9.1. Cumulative

Number of the international conference with oral presentation: 7
Number of the international conference with poster presentation: 8
Number of the national conference with oral presentation: 20
Number of the national conference with poster presentation: 11
Number of the international publication: 7
Number of the national publication: 17
Impact factors: 13.629
Independent citations: 46
Dependent citations: 26

9.2. Papers directly related to the dissertation

Lengyel, E., C. Stenger-Kovács & J. Padisák, 2010. Köztes diszturbancia és az egyensúlyi állapot vizsgálata a Torna – patak kovaalga közösségeiben. Hidrológiai Közlöny 90: 91-93.

Lengyel, E. & C. Stenger-Kovács, 2012. Hazai és osztrák kis szikes tavak különleges jellemzői és kovaalga flórája. Hidrológiai Közlöny 92: 52-54.

Lengyel, E., K. Buczkó & C. Stenger-Kovács, 2012. A Fertő-tó környéki és a Duna-Tisza közi kis szikes tavak különleges jellemzői és kovaalga flórája. Magyar Hidrológiai Társaság, XXX. Országos Vándorgyűlés, Kaposvár, 2012. július 4-6., CD:ISBN 978-963-8172-29-7.

Stenger-Kovács, C., **E. Lengyel**, L.O. Crossetti, V. Üveges & J. Padisák, 2013. Diatom ecological guilds as indicators of temporally changing stressors and disturbances in the small Torna-stream, Hungary. Ecological Indicators 24: 138–147. ***IF: 3.230, SJR: Q1.***

Stenger-Kovács, C. & **E. Lengyel**, 2014. Egy mexikópusztai szikes tó (Borsodi-dűlő) diatómái és fizikai, kémiai jellemzői. Szélkiáltó 16: 32-34.

Stenger-Kovács, C., **E. Lengyel**, K. Buczkó, M.F. Tóth, L.O. Crossetti, A. Pellinger, Z, Zámbóné Doma & J. Padisák, 2014. Vanishing world: alkaline, saline lakes in Central Europe and their diatom assemblages. Inland Waters 4:383-396. ***IF: 1.310, SJR: Q2.***

Stenger-Kovács C**, E. Lengyel** & K. Buczkó , 2014. Kovaalga összetétel és ökológiai guildek kis szikes tavainkban. Hidrológiai Közlöny 94: 28-30.

Lengyel, E., J. Padisák & C. Stenger-Kovács, 2015. Establishment of equilibrium states and effect of disturbances on benthic diatom assemblages of the Torna-stream, Hungary. Hydrobiologia 750: 43-56. ***IF: 2.051, SJR: Q1.***

Padisák, J., C. Stenger-Kovács, D. Lázár,K. E. Hubai, Y. Němcová, D. Magyar, M. Vass, A. J. Trájer, B. Tánczos, T. Hammer & **E. Lengyel,** 2015. A kisvizes

ökoszisztémák prediktív értéke a klímaváltozás hatásainak megértésében és jelentőségük a biodiverzitás megőrzésében. Magyar Tudomány 5: 559-567.

Lázár, D., **E. Lengyel** & C. Stenger-Kovács, 2015. *Nitzschia aurariae* Cholnoky (Bacillariophyceae) fotoszintetikus aktivitásának vizsgálata szulfátion gradiens mentén. Hidrológiai Közlöny 95: 39-41.

Lengyel, E., A. W Kovács, J. Padisák & C. Stenger-Kovács, 2015. Photosynthetic characteristics of the benthic diatom species *Nitzschia frustulum* (Kützing) Grunow isolated from a soda pan along temperature-, sulfate- and chloride gradients. Aquatic Ecology 49: 401-416. ***IF: 1.797, SJR: Q2.***

Stenger-Kovács, C. & **E. Lengyel**, 2015. Taxonomical and distribution guide of diatoms in soda pans of Central Europe. Studia Botanica Hungarica 46: 3-203.

Lengyel, E., J. Padisák, É. Hajnal, B. Szabó, A. Pellinger & C. Stenger-Kovács, 2016. Application of benthic diatoms to assess efficiency of conservation management: a case study on the example of three reconstructed soda pans, Hungary. Hydrobiologia 777: 95-110. ***IF: 2.051, SJR: Q1.***

9.3. Other papers

Biró, R., É. Ács, **E. Lengyel** & C. Stenger-Kovács, 2011. A Csigere-patak kovaalga biótája. Hidrológiai Közlöny 91:22-24.

Teke, G., É. Hajnal, E. **Lengyel**, C. Stenger-Kovács & J. Padisák, 2011. Fajgazdagság és mintavétel összefüggésének vizsgálata a Peridat on-line perifiton adatbázis segítségével. Hidrológiai Közlöny 91: 98-100.

Üveges, V., V. Andirkó, A. Ács, R. Bíró, E. Drávecz, É. Hajnal, M. Havasi, K.E. Hubai, I. Kacsala, K. Kovács, N. Kováts, T. Kucserka, **E. Lengyel**, A. Matulka, G.B. Selmeczy, C. Stenger-Kovács, B. Szabó, G. Teke, M. Vass & J. Padisák, 2011. A vörösiszap katasztrófa hatása a Torna-patak és a Marcal élővilágára, a regeneráció első időszaka. Economica 12: 95-139.

Biró, R., B. Szabó, **E. Lengyel** & C. Stenger-Kovács, 2012. A Torna-patak bevonatalkotó kovaalgáinak kolonizációja a vörösiszap katasztrófa után. Hidrológiai Közlöny 92: 9-11.

Biró, R., B. Szabó, E. **Lengyel** & C. Stenger Kovács, 2012. A Torna-patak bevonatalkotó kovaalgáinak kolonizációja a vörösiszap-katasztrófa után. Magyar Hidrológiai Társaság, XXX. Országos Vándorgyűlés, Kaposvár, 2012. július 4-6., CD:ISBN 978-963-8172-29-7.

Lengyel, E. & C. Stenger-Kovács, 2013. Szikes tóból izolált *Nitzschia fonticola* SRP tolerancia vizsgálata. Magyar Hidrológiai Társaság, XXXI. Országos Vándorgyűlés, Gödöllő, 2013. július 3-5., CD:ISBN 978-963-8172-31-0.

Lengyel, E., A.W. Kovács, H.M. Shafik, & C. Stenger-Kovács, 2014. *Nitzschia supralitorea* (Bacillariophyceae) fotoszintetikus aktivitásának vizsgálata eltérő szulfát koncentrációk esetén. Hidrológiai Közlöny 94:59-61.

Lengyel, E., 2014. Mikroszkopikus algáink jelentősége és lehetséges alkalmazása a környezetpedagógiában. Iskolakultúra 11-12: 87-95.

Lengyel, E., K. E. Hubai & J. Padisák, 2015. Kab-hegyi időszakos sekély tavak hidrobiológiai kutatásának története. Hidrológiai Közlöny 95: 42-44.

Körmendi, K., **E. Lengyel**, K. Buczkó & C. Stenger-Kovács, 2015. A Kiskunsági Nemzeti Park néhány szikes tavának kovavázas algái. Hidrológiai Közlöny 95:36-38.

Stenger-Kovács C, É. Hajnal, **E. Lengyel**, K. Buczkó & J. Padisák, 2016. A test of traditional diversity measures and taxonomic distinctness indices on benthic diatoms of soda pans in the Carpathian basin. Ecological Indicators 64: 1-8. ***IF: 3.190, SJR: Q1.***

9.4. Congress Attendances directly related to the dissertation

Lengyel, E., L. O. Crossetti, & C. Stenger-Kovács, 2011. Diatom assemblages and special features of small saline lakes in Hungary. In Witkowski, A., M. Wroniecki, M. Bąk, G. Daniszewska-Kowalczyk, A. Kierzek, D. Krawczyk (eds) 5th Central European Diatom Meeting and 25. Treffen Deutschsprachiger Diatomologen mit Internationaler Beteiligung, Szcezin (Poland), 24-27 March 2011, ***oral presentation***

Lengyel, E., L. O. Crossetti, & C. Stenger-Kovács, 2011. Unique diatom flora of the Hungarian small saline lakes. In Matuła, J., D. Richter, J. Urbaniak, B. Matuła (eds) 30th International Conference of the Polish Phycological Society, Wroclaw (Poland), 19-22 May 2011, ***oral presentation***

Stenger-Kovács, C. & **E. Lengyel**, 2011. Hazai és osztrák kis szikes vízterek kovaalga összetétele. In Magyar Hidrológiai Társaság (eds) Szikes Vízi Munkacsoport éves találkozója, Pusztaszer (Hungary), 17-18 June 2011, ***oral presentation***

Lengyel, E. & C. Stenger-Kovács, 2011. Osztrák és hazai kis szikes tavak különleges jellemzői és kovaalga flórája. In Magyar Hidrológiai Társaság (eds) LIII. Hidrobiológus Napok, Tihany (Hungary), 5-7 October 2011, ***oral presentation***

Lengyel, E. & C. Stenger-Kovács, 2011. Kis szikes tavak különleges diatóma flórája és tulajdonságai. In Lengyel, S., A. Báldi, D. Cserhalmi, B. Czúcz, Z. Hanga, Z. Illyés, A. Kovács, N. Vili (eds) VII. Magyar Természetvédelmi Biológiai Konferencia, Debrecen (Hungary), 3-6 November 2011, ***poster presentation***

Lengyel, E., L. O. Crossetti, & C. Stenger-Kovács, 2012. Diatom composition of Hungarian and Austrian small saline lakes. In Rott, E., G. Gärtner, D. Gesierich, K. Koinig, R. Psenner, P.Pfister, E. Carli, P. Tschaikner, W. Kofler (eds) 6th Central European Diatom Meeting and 26. Treffen Deutschsprachiger Diatomologen, Innsbruck (Austria), 22-25 March 2012, ***oral presentation***

Stenger-Kovács, C., **E. Lengyel**, L.O. Crossetti, V. Üveges & J. Padisák, 2012. Diatom ecological guilds as indicators of temporally changing stressors and disturbances in the small Torna-stream, Hungary. In Rott, E., G. Gärtner, D. Gesierich, K. Koinig, R. Psenner, P.Pfister, E. Carli, P. Tschaikner, W. Kofler (eds) 6th Central European Diatom Meeting and 26. Treffen Deutschsprachiger Diatomologen, Innsbruck (Austria), 22-25 March 2012, ***poster presentation***

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Appendix

Table 1

Figs 1-14:	***Achnanthidium sp.***
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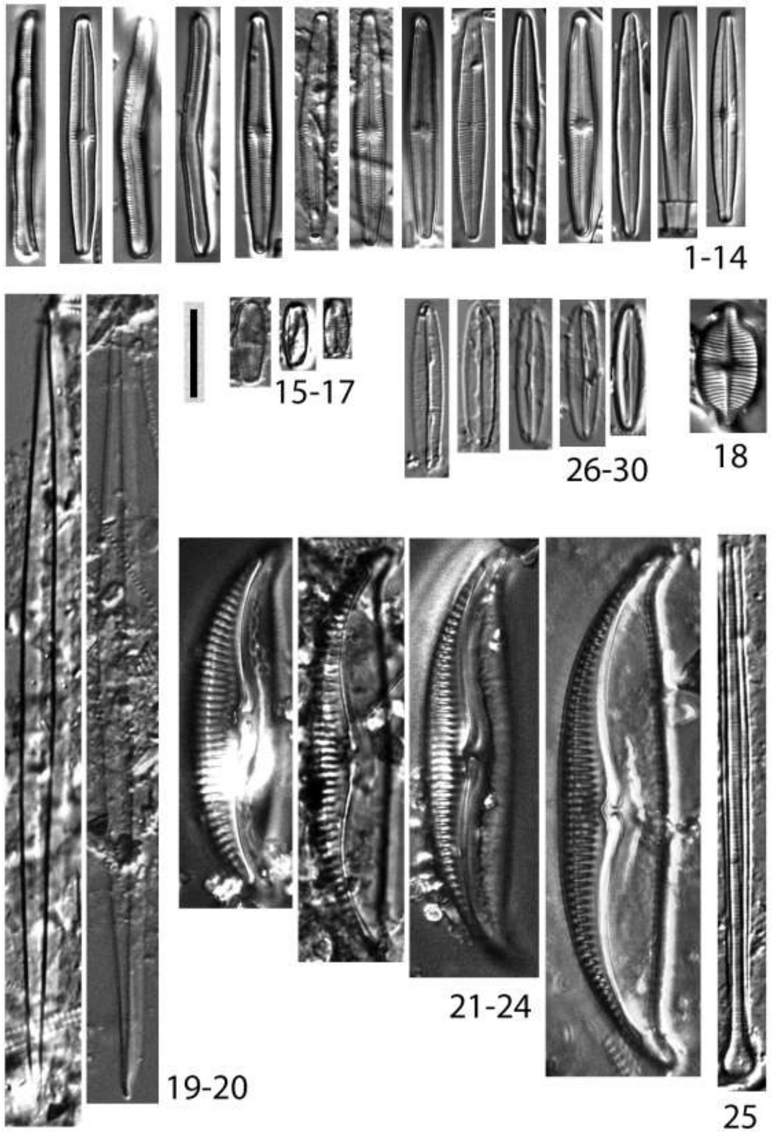
Fig. 18:	***Achnanthes exigua*** Grunow
Figs 19-20:	***Amphipleura pellucida*** (Kützing) Kützing
Figs 21-24:	***Amphora commutata*** Grunow
Fig. 25:	***Asterionella formosa*** Hassall
Figs 26-30:	***Berkeleya rutilans*** (Trentepohl ex Roth) Grunow

Figs 1-17, 19-20, 21-24, 26-30: Legény-tó
Fig. 18: Borsodi-dűlő
Fig. 25: Nyéki-szállás



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Figs 1-5: ***Aulacoseira ambigua*** (Grunow) Simonsen

Fig. 6: ***Brachysira neoexilis*** Lange-Bertalot

Fig. 7: ***Brachysira procera*** Lange-Bertalot & Moser

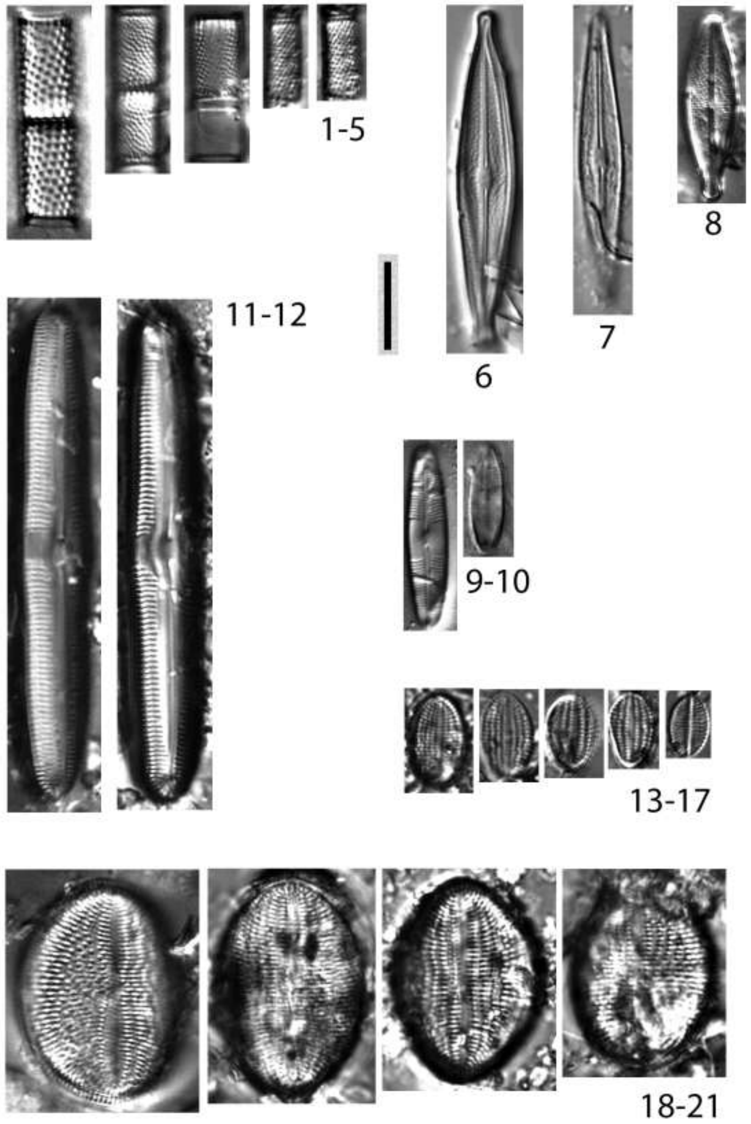
Fig. 8: ***Brachysira vitrea*** (Grunow) Ross

Figs 9-10: ***Caloneis lancettula*** (Schulz-Danzig) Lange-Bertalot & Witkowski

Figs 11-12: ***Caloneis molaris*** (Grunow) Krammer

Figs 13-17: ***Cocconeis neothumensis*** Krammer

Figs 18-21: ***Cocconeis pediculus*** Ehrenberg

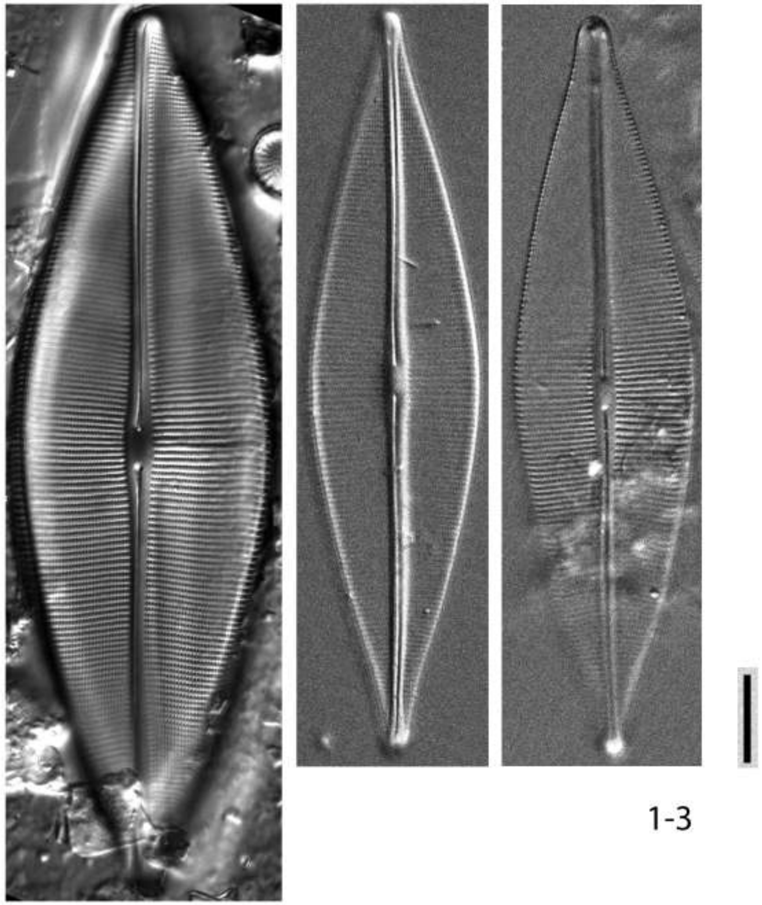


Figs 1-8, 9: Borsodi-dűlő
Fig. 10, 15-17: Nyéki-szállás
Fig. 11-14, 18-21: Legény-tó

Table 3

Figs 1-3: ***Craticula cuspidata*** (Kützing) D.G. Mann

Figs 4-14: ***Craticula molestiformis*** (Hustedt) Lange-Bertalot



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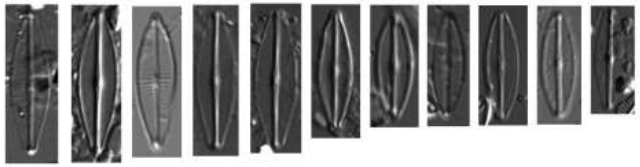

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Figs 1-3: Borsodi-dűlő
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Figs 1-3: ***Cyclostephanos dubius*** (Hustedt) Round

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Figs 16-21: ***Cyclotella praetermissa*** (Lund) T. Nakov

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Figs 1, 28: Nyéki-szállás
Figs 3, 13, 26-27, 29-30: Legény-tó

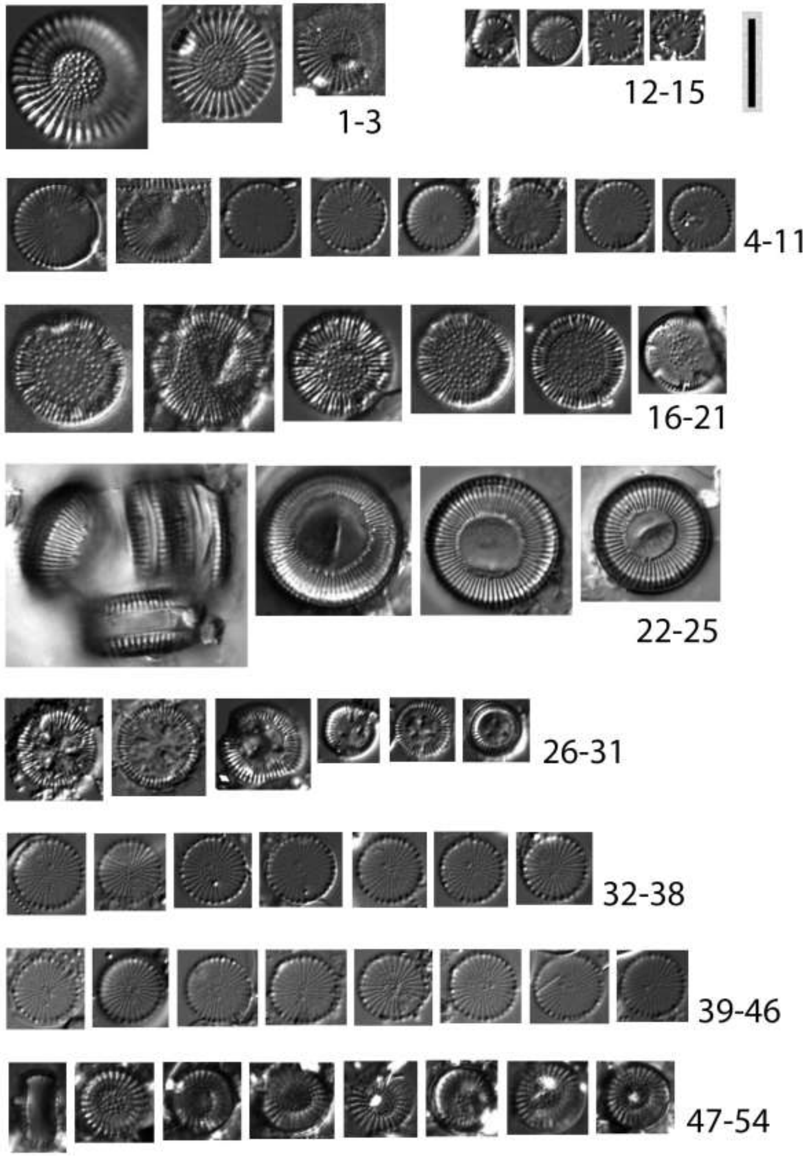


Table 5

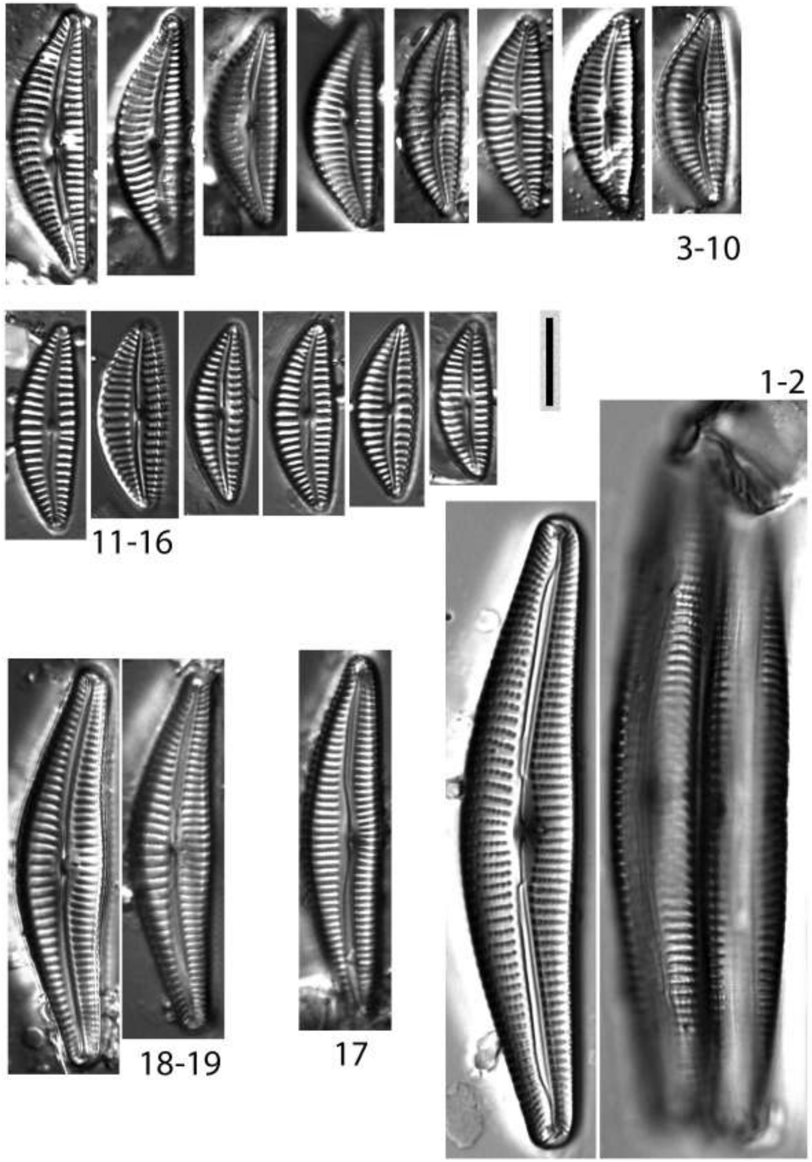
Figs 1-2: ***Cymbella cymbiformis*** C. Agardh

Figs 3-10: ***Cymbella excisa*** Kützing

Figs 11-16: ***Cymbella hustedtii*** Krasske **var. *hustedtii***

Fig. 17: ***Cymbella subhelvetica*** Krammer

Figs 18-19: ***Cymbella parva*** (W. Smith) Kirchner



Figs 1-2, 17-19: Borsodi-dűlő
Figs 3-7, 9-10: Nyéki-szállás
Figs 8, 11-16: Legény-tó

Table 6

Fig. 1: ***Cymatopleura elliptica*** (Brébisson) W. Smith **var. *elliptica***

Figs 2-3: ***Delicata delicatula*** (Kützing) Krammer

Figs 4-7: ***Denticula tenuis*** Kützing

Figs 8-9: ***Diatoma ehrenbergii*** Kützing

Figs 10-15: ***Diatoma moniliformis*** Kützing ***ssp. moniliformis***

Figs 16-19: ***Diatoma vulgaris*** Bory

Figs 20-21: ***Diploneis parma*** Cleve sensu Krammer & Lange-Bertalot

Figs 1-3, 8-9, 20-21: Borsodi-dűlő
Figs 4-7, 10-19: Legény-tó

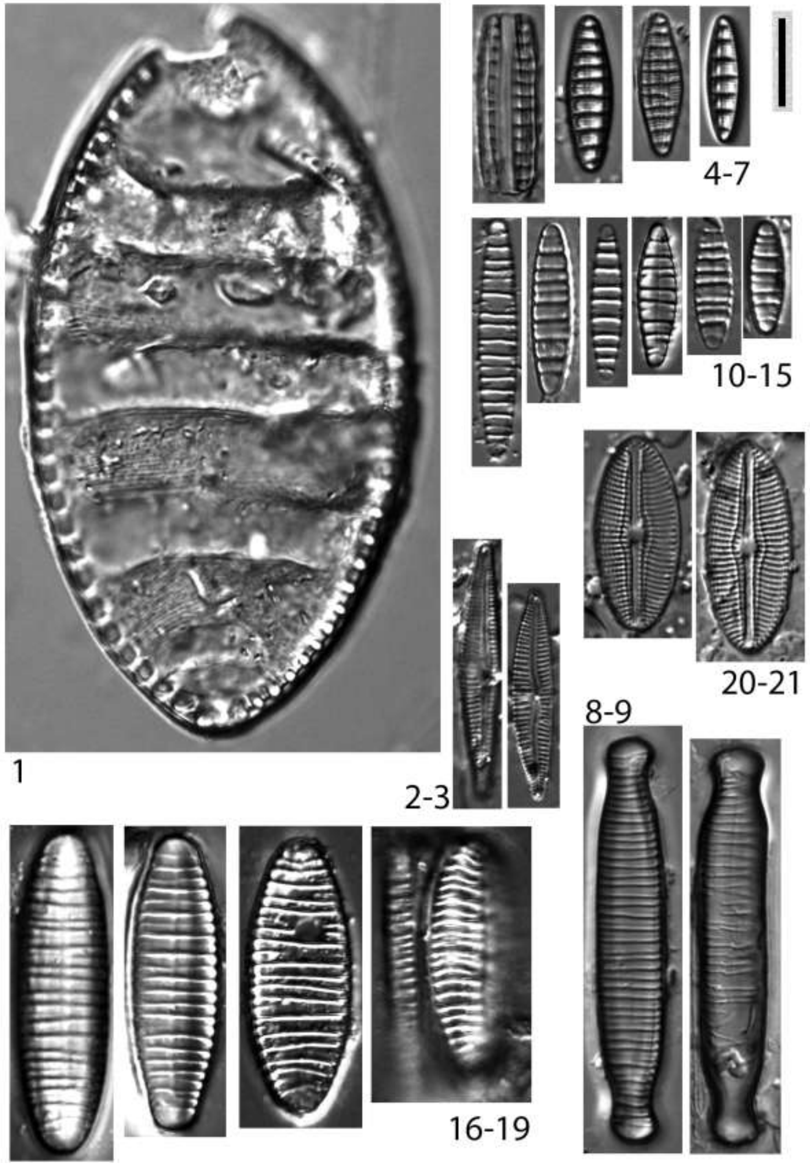


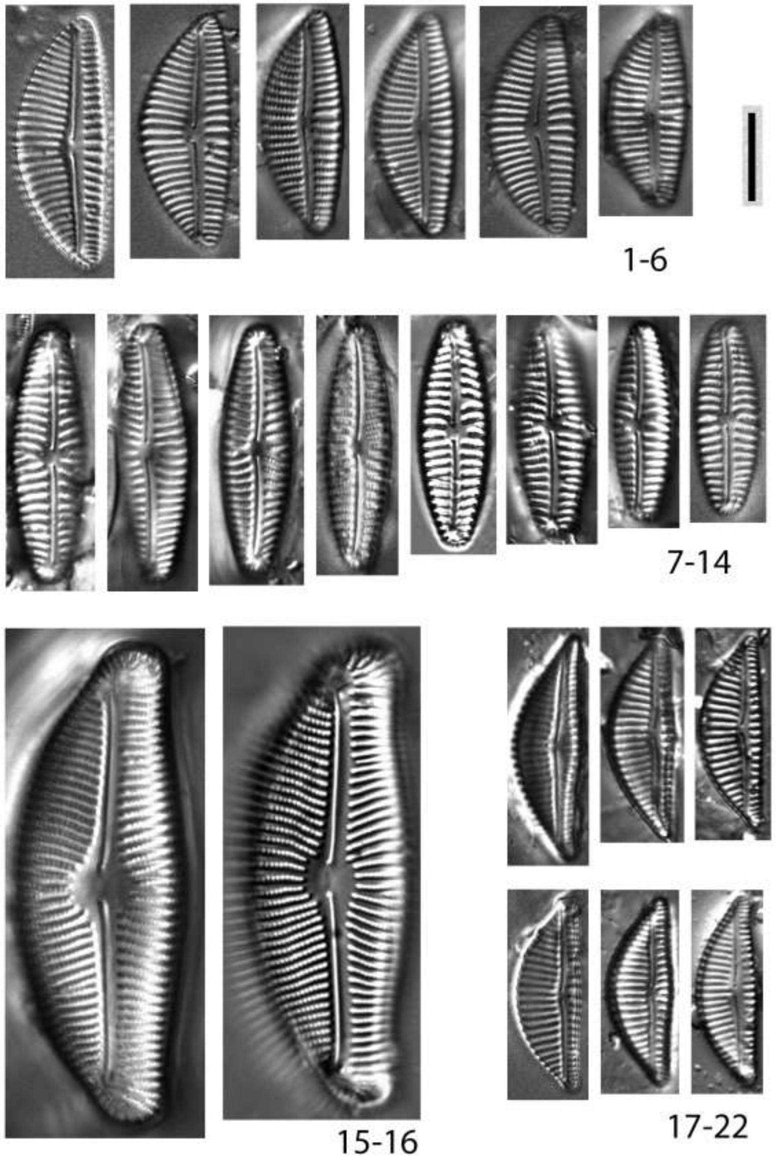
Table 7

Figs 1-6: ***Encyonema caespitosum*** Kützing **var.** ***caespitosum***

Figs 7-14: ***Encyonema lacustre*** (C. Agardh) Mills

Figs 15-16: ***Encyonema prostratum*** (Berkeley) Kützing

Figs 17-22: ***Encyonema silesiacum*** (Bleisch) D.G. Mann



Figs 1-14, 17-18, 20-22: Legény-tó
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Table 8

Figs 1-5: ***Encyonopsis cesatii*** (Rabenhorst) Krammer

Figs 6-8: ***Encyonopsis krammeri*** Reichardt

Figs 9-12: ***Encyonopsis microcephala*** (Grunow) Krammer

Figs 13-19: ***Encyonopsis minuta*** Krammer & Reichardt

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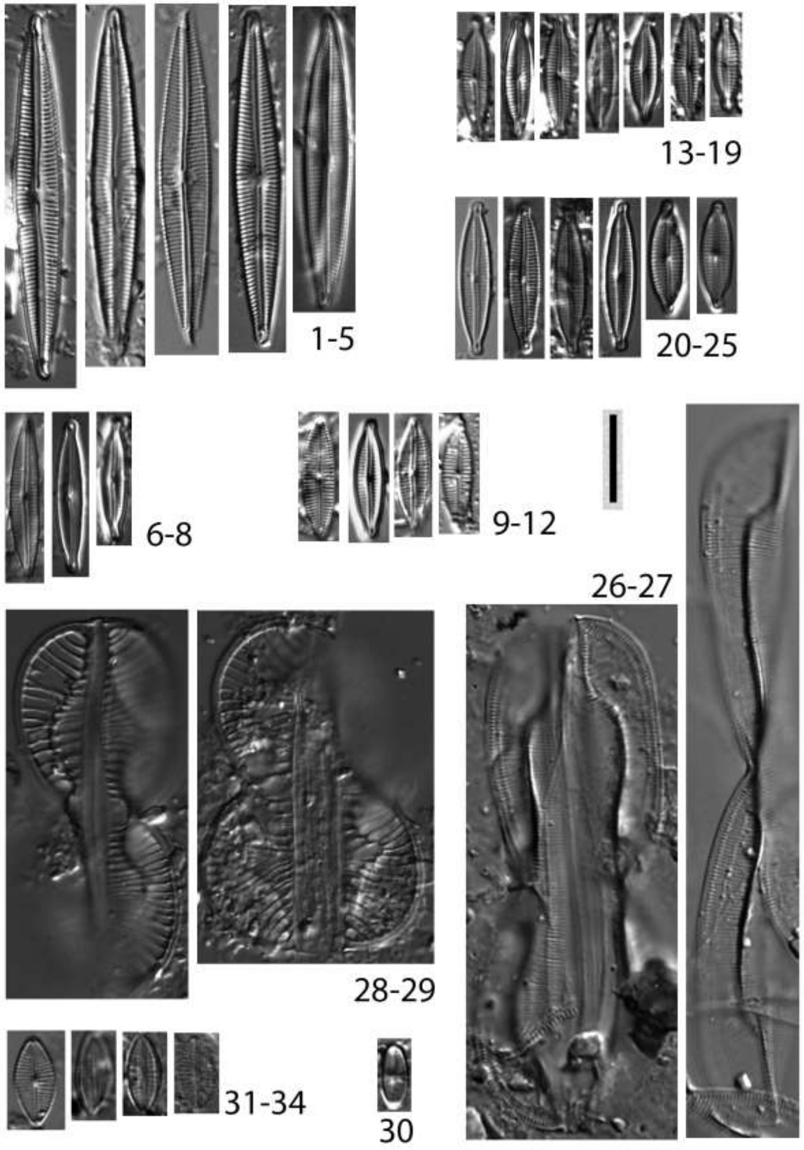
Figs 30: ***Eolimna minima*** (Grunow) Lange-Bertalot & W.Schiller

Figs 31-34: ***Eolimna subminuscula*** (Manguin) Moser, Lange-Bertalot & Metzeltin



Figs 1-5, 7-8, 14, 19-21, 23, 26, 31-34: Borsodi-dűlő
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Figs 1-3: ***Epithemia adnata*** (Kützing) Brébisson

Figs 4-7: ***Eunotia mucophila*** (Lange-Bertalot & Nörpel) Lange-Bertalot

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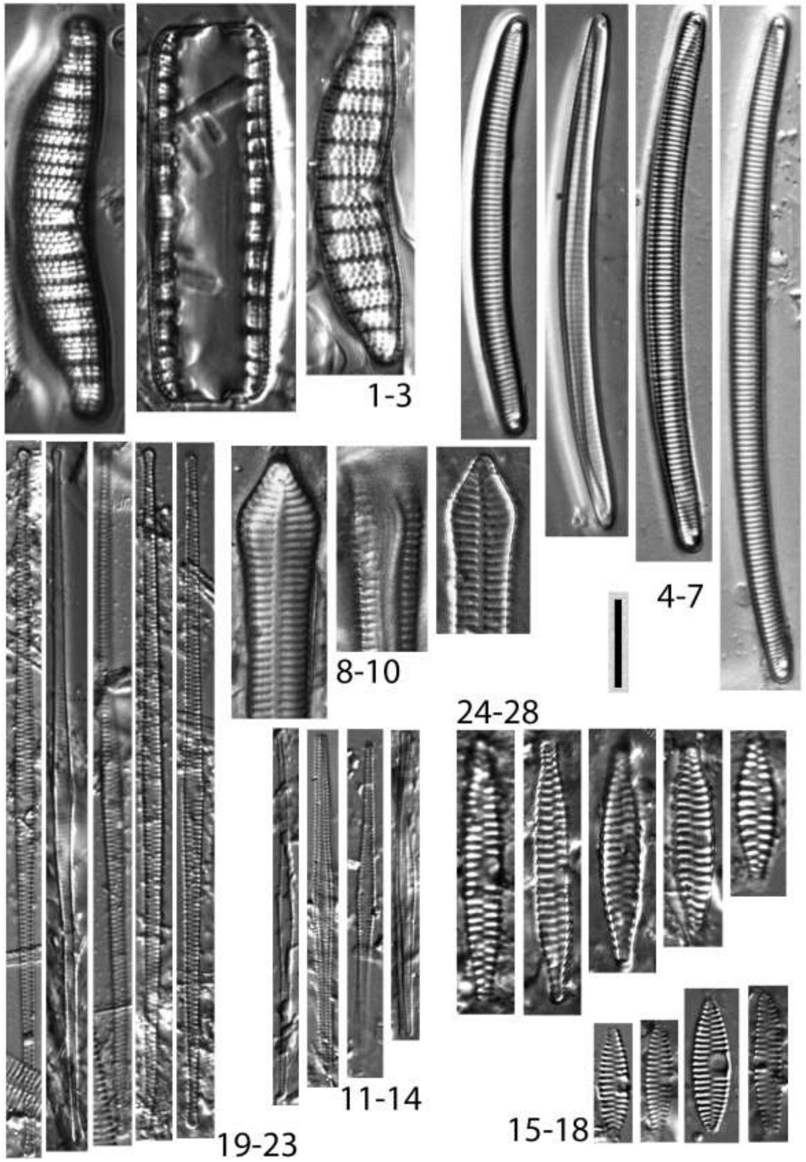
Figs 11-14: ***Fragilaria nanana*** Lange-Bertalot

Figs 15-18: ***Fragilaria perminuta*** (Grunow) Lange-Bertalot

Figs 19-23: ***Fragilaria tenera*** (W. Smith) Lange-Bertalot

Figs 24-28: ***Fragilaria vaucheriae*** (Kützing) Petersen



Figs 1-28: Legény-tó

Table 10

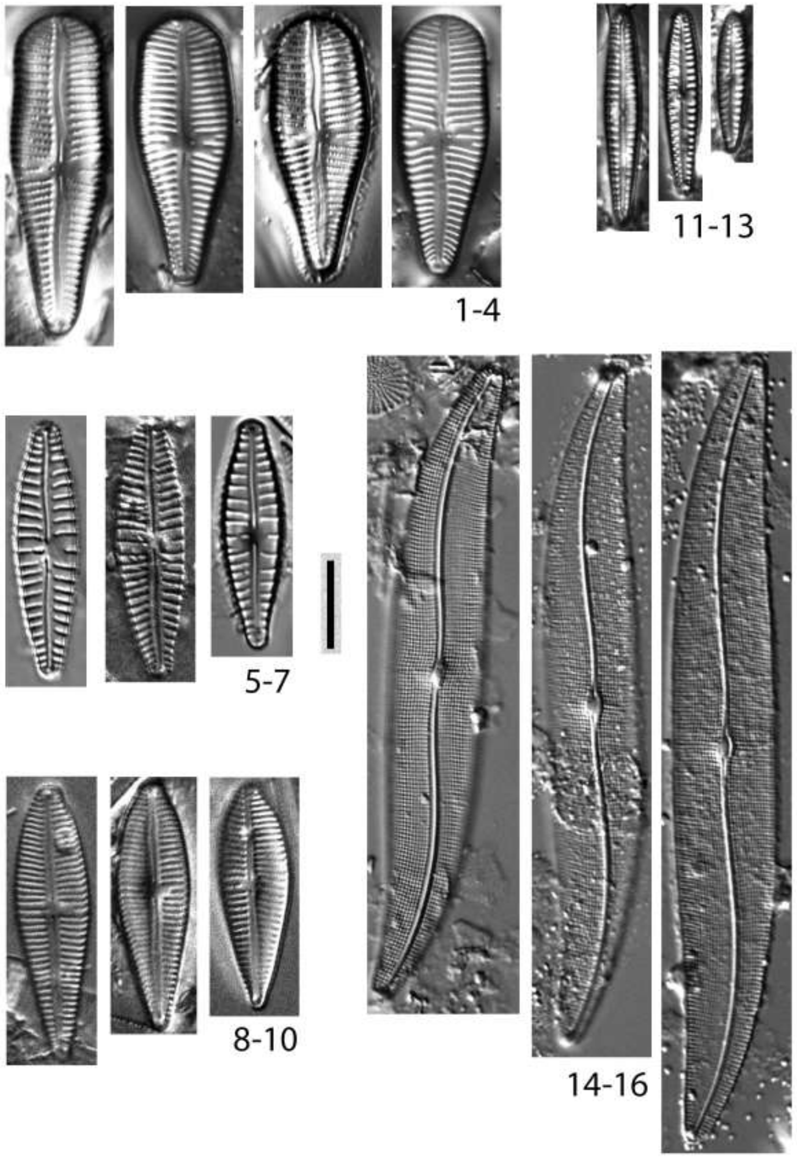
Figs 1-4: ***Gomphonema italicum*** Kützing

Figs 5-7: ***Gomphonema micropus*** Kützing

Figs 8-10: ***Gomphonema pseudoaugur*** Lange-Bertalot

Figs 11-13: ***Gomphonema pumilum*** (Grunow) Reichardt & Lange-Bertalot

Figs 14-16: ***Gyrosigma obtusatum*** (Sullivant & Wormley) C.S. Boyer



Figs 1-4: Legény-tó
Figs 5-16: Borsodi-dűlő

Table 11

Figs 1-6: ***Halamphora oligotrophenta* (**Lange-Bertalot) Levkov

Figs 7-14: ***Halamphora tumida*** (Hustedt) Levkov comb. nov.

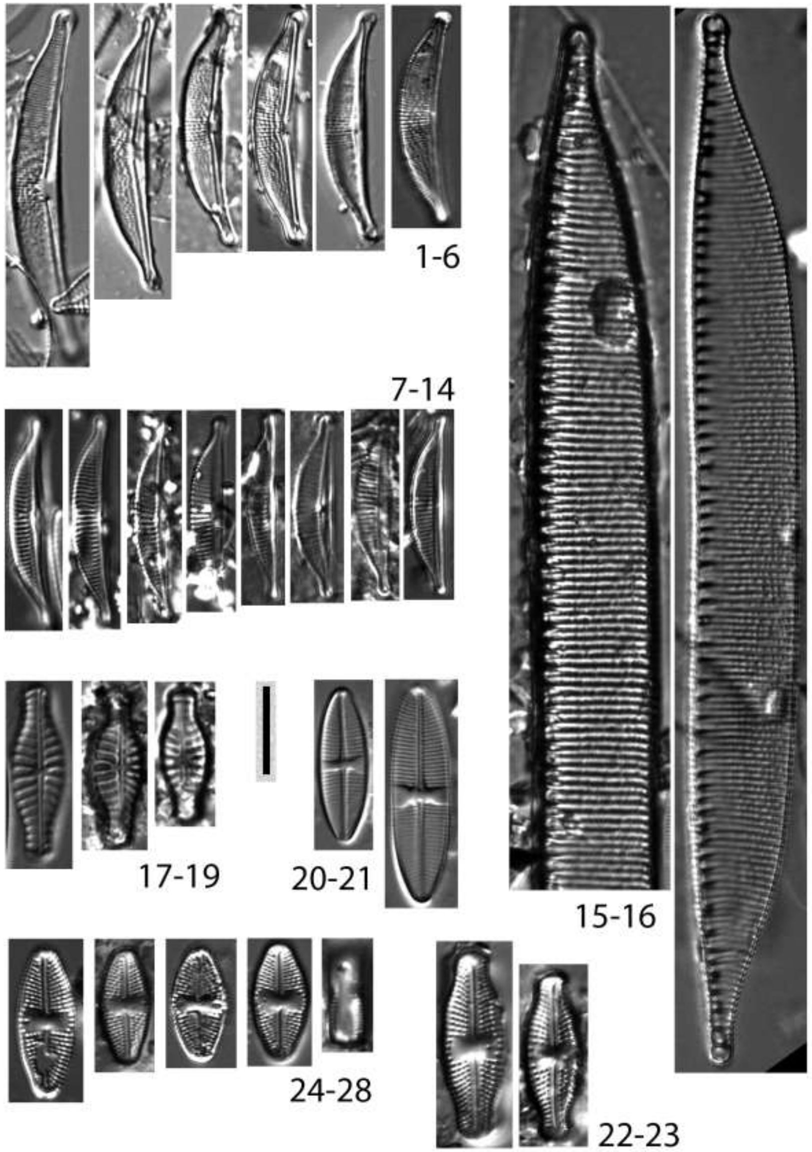
Figs 15-16: ***Hantzschia vivax*** (W. Smith) Peragallo var. *vivax*

Figs 17-19: ***Hippodonta capitata*** (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski

Figs 20-21: ***Lemnicola hungarica*** (Grunow) Round & Basson

Figs 22-23: ***Luticola dismutica*** (Hustedt) D.G. Mann

Figs 24-28: ***Luticola mutica*** (Kützing) D.G. Mann



Figs 1-7, 11-14, 20-21, 27-28: Legény-tó
Figs 15-19, 22-26: Borsodi-dűlő
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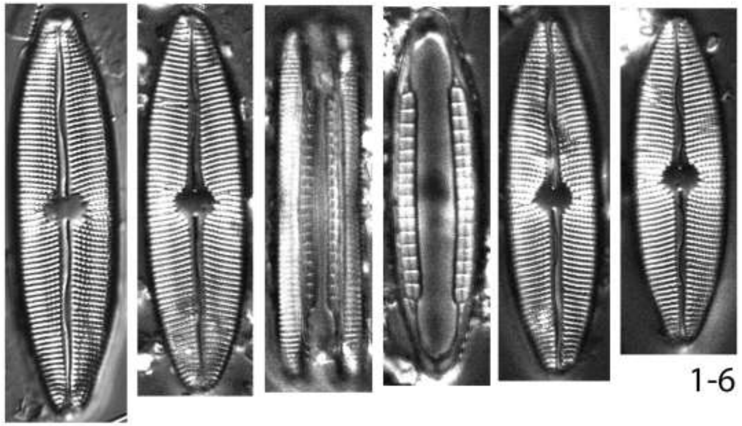
Figs 1-6: ***Mastogloia elliptica*** (C. Agardh) Cleve

Figs 7-12: ***Melosira varians*** C. Agardh

Fig. 13: ***Meridion circulare*** (Gréville) C. Agardh **var. *circulare***

Fig. 14: ***Navicula antonii*** Lange-Bertalot

Figs 15-20: ***Navicula capitaoradiata*** Germain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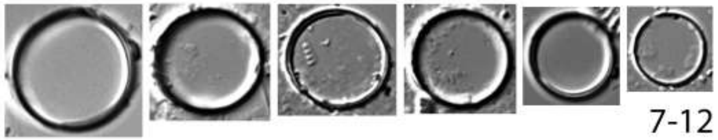
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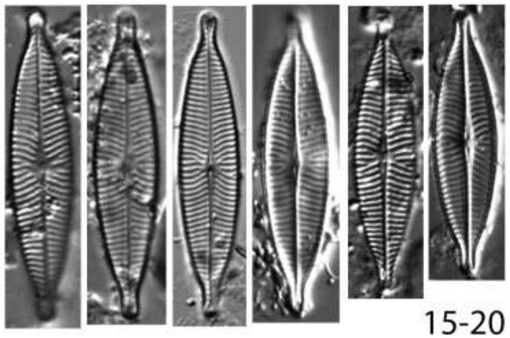
14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Figs 1-6, 14: Legény-tó
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Figs 1-5:	***Navicula cryptocephala*** Kützing
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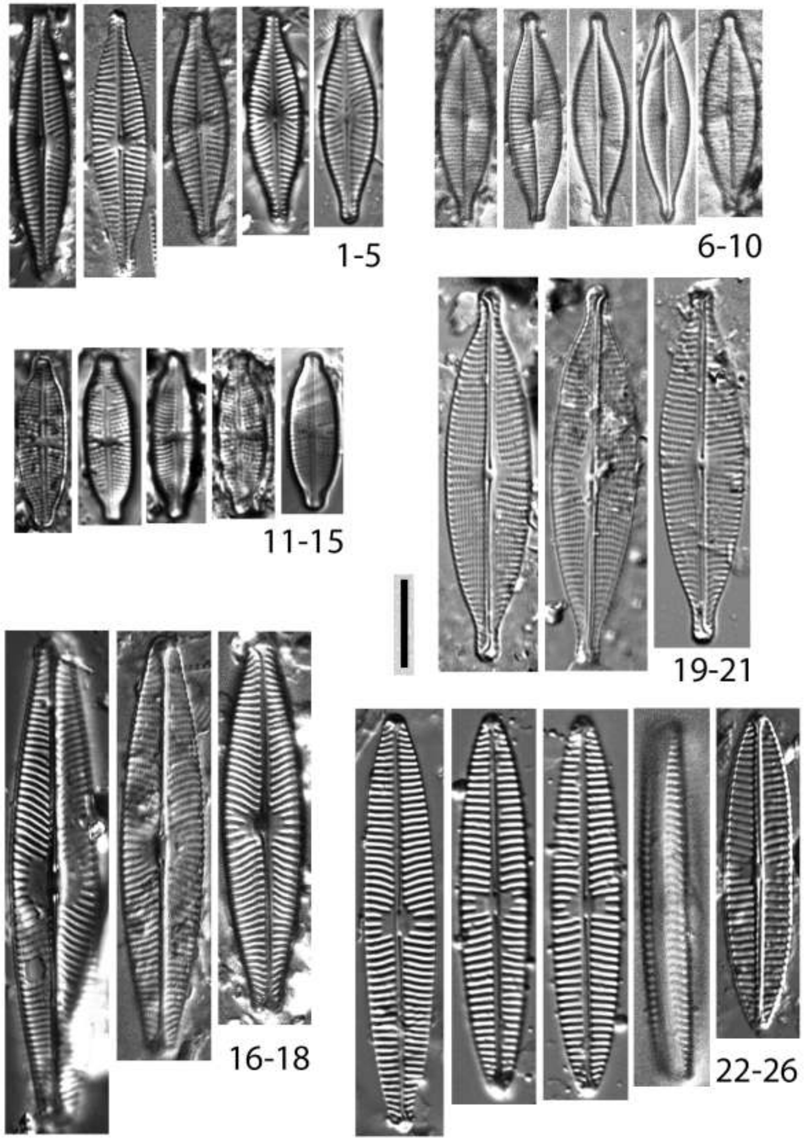
Figs 11-15:	***Navicula kotschyi*** Grunow
Figs 16-18:	***Navicula lanceolata*** (C. Agardh) Ehrenberg
Figs 19-21:	***Navicula subrhynchocephala*** Hustedt
Figs 22-26:	***Navicula tripunctata*** (O.F. Müller) Bory



Figs 1-3, 5- 11, 13, 16-21, 25-26: Legény-tó
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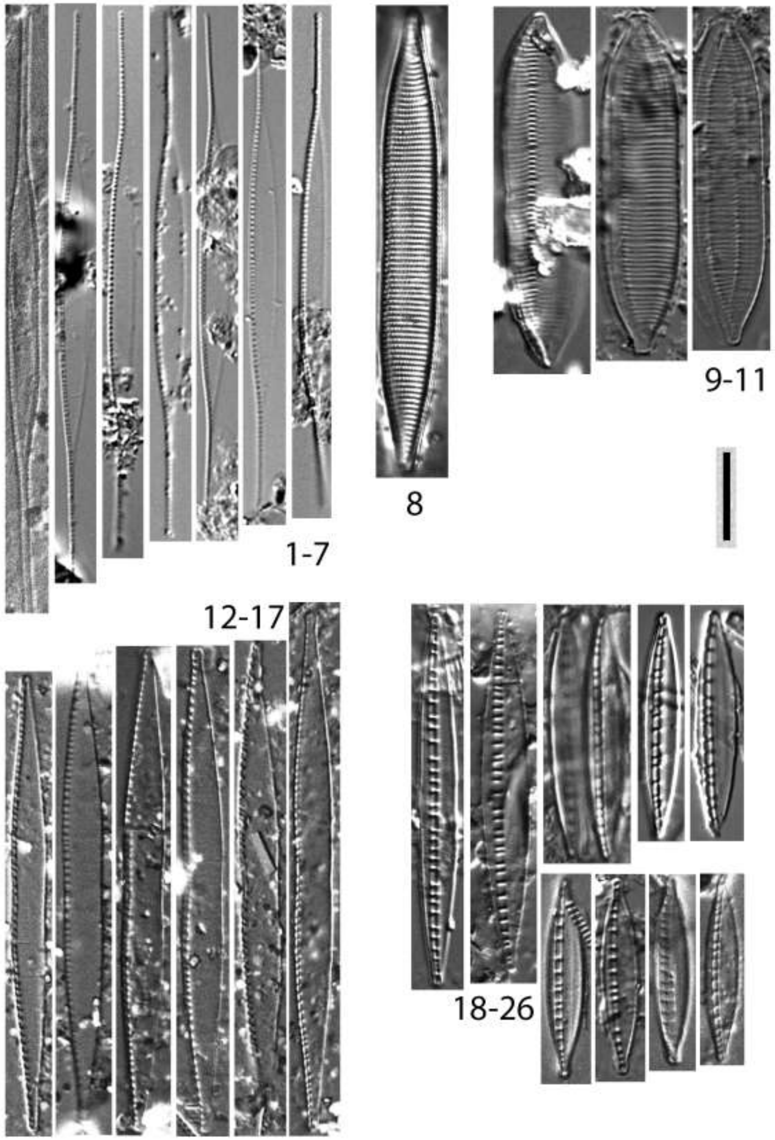
Figs 8: ***Nitzschia angustatula*** Lange-Bertalot

Figs 9-11: ***Nitzschia calida*** Grunow

Figs 12-17: ***Nitzschia capitellata*** Hustedt

Figs 18-26: ***Nitzschia dissipata*** (Kützing) Grunow **ssp. *dissipata***



Figs 1-26: Borsodi-dűlő

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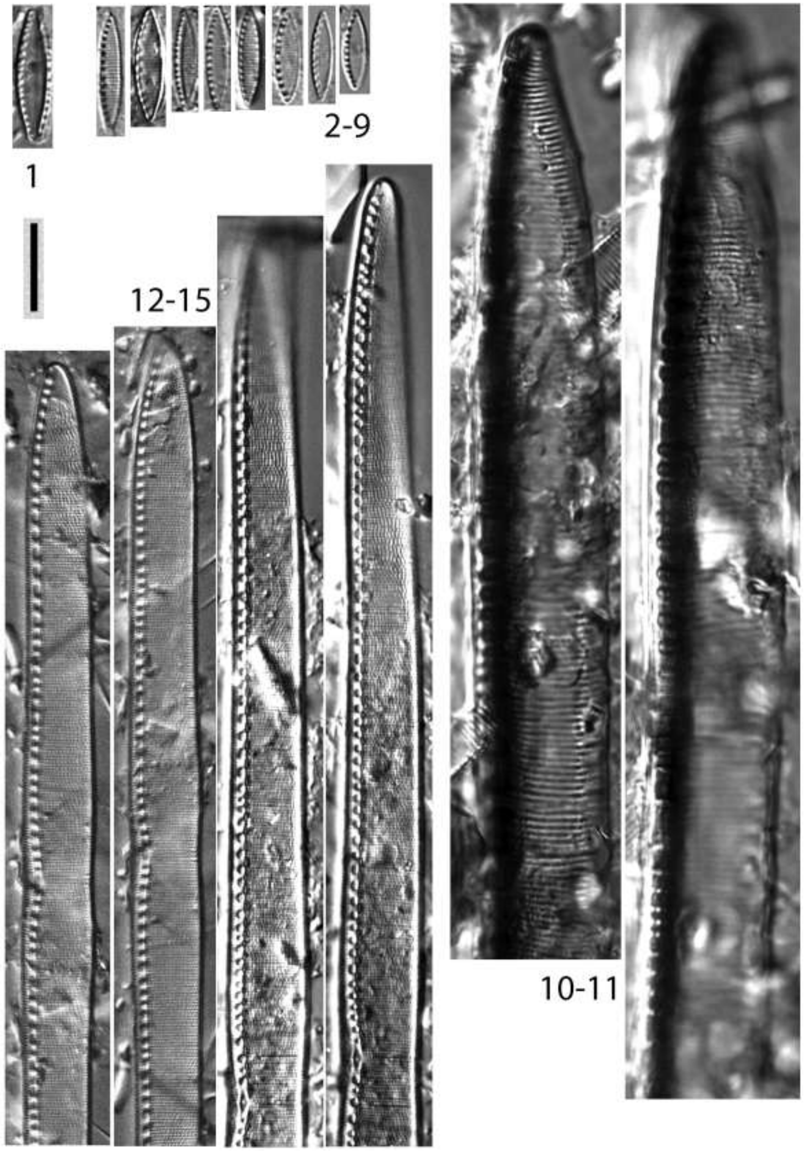
Fig. 1: ***Nitzschia fonticola*** Grunow

Figs 2-9: ***Nitzschia liebetruthii*** Rabenhorst

Figs 10-11: ***Nitzschia* sp.**

Figs 12-15: ***Nitzschia obtusa*** W. Smith **var. *obtusa***



Figs 1-2, 4-5, 7-11: Borsodi-dűlő
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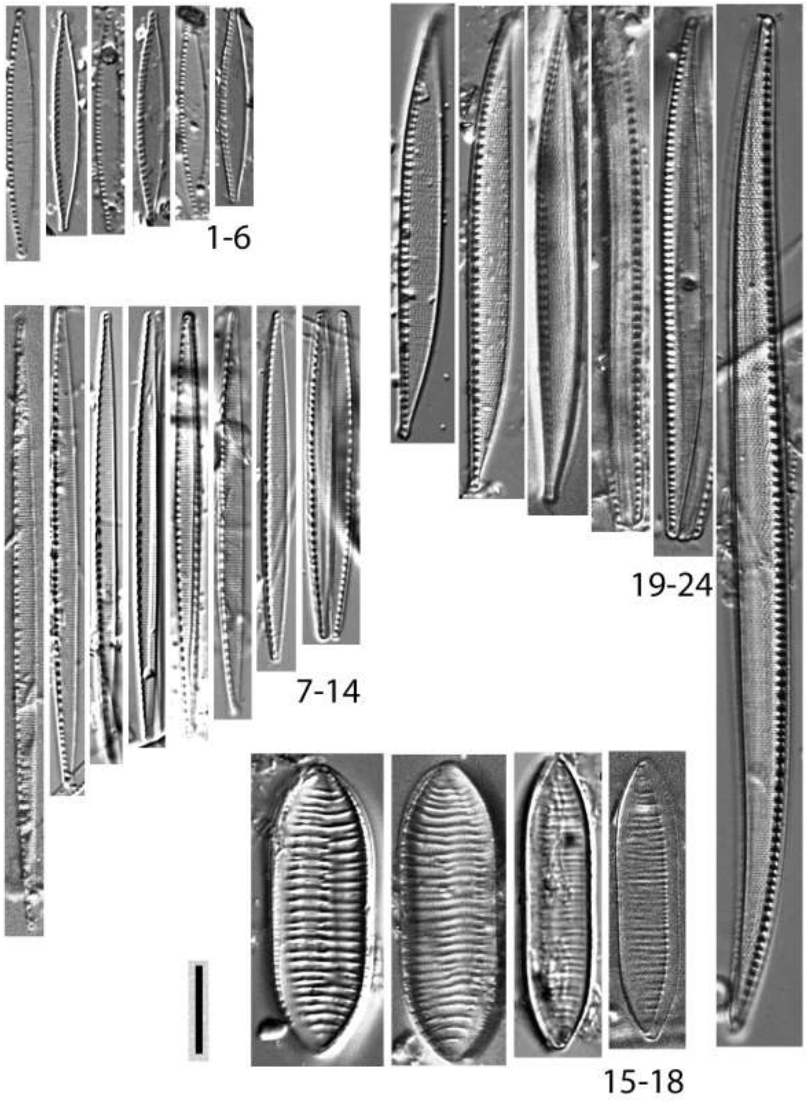
Figs 1-6: ***Nitzschia palea* var. *debilis*** (Kützing) Grunow

Figs 7-14: ***Nitzschia radicula*** Hustedt

Figs 15-18: ***Nitzschia salinarum*** Grunow

Figs 19-24: ***Nitzschia sigma*** (Kützing) W. Smith



Figs 1-14, 18-24: Legény-tó
Figs 15-17: Borsodi-dűlő

Table 17

Figs 1-6: ***Pinnularia borealis*** Ehrenberg **var. *borealis***

Figs 7-13: ***Planothidium frequentissimum*** (Lange-Bertalot) Lange-Bertalot

Figs 14-15: ***Planothidium rostratum*** (Østrup) Lange-Bertalot

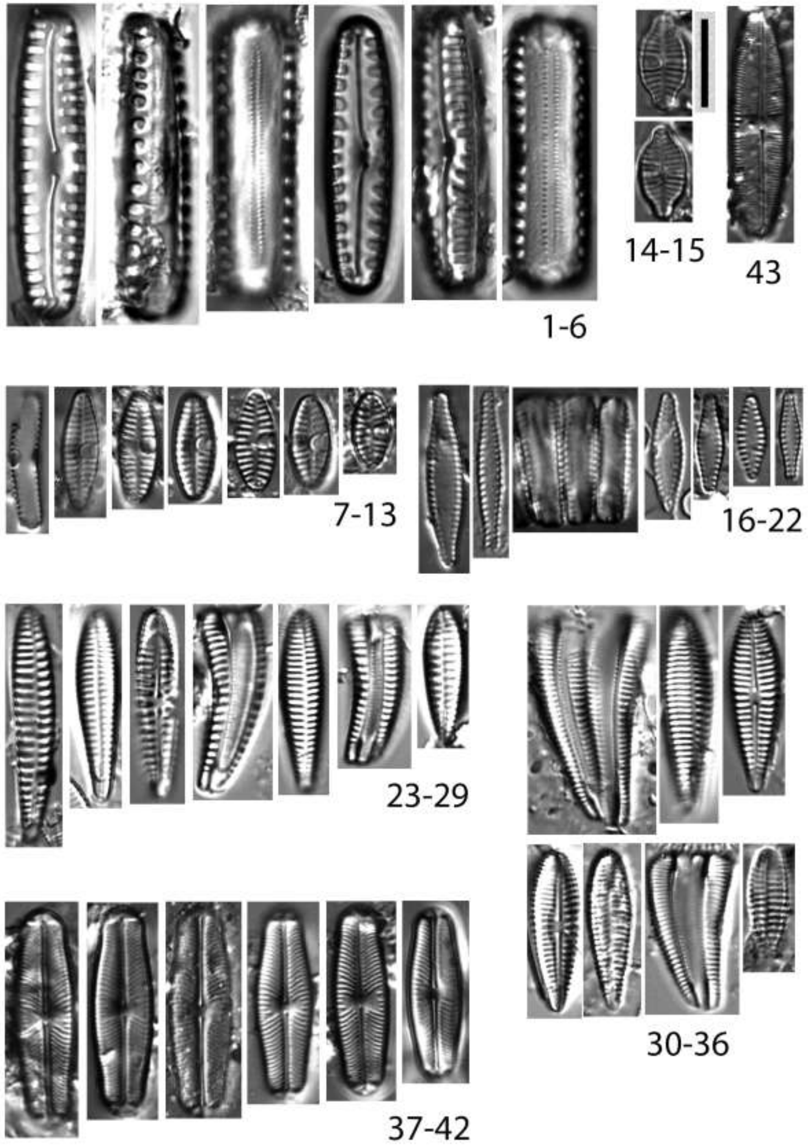
Figs 16-22: ***Pseudostaurosira brevistriata*** (Grunow) D.M. Williams & Round

Figs 23-29: ***Rhoicosphenia abbreviata*** (C. Agardh) Lange-Bertalot

Figs 30-36: ***Rhoicosphenia adriatica*** Caput Michalic & Levkov

Figs 37-42: ***Sellaphora capitata*** D.G.Mann & McDonald, S.M.

Figs 43: ***Staurophora tackei*** (Hustedt) L.Bahls



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Figs 7-8, 12-15, 17, 20, 22, 24, 26-29, 31-33, 35, 40-43: Legény-tó
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Table 18

Figs 1-5: ***Staurosira binodis*** (Ehrenberg) Lange-Bertalot

Figs 6-13: ***Staurosira construens*** Ehrenberg

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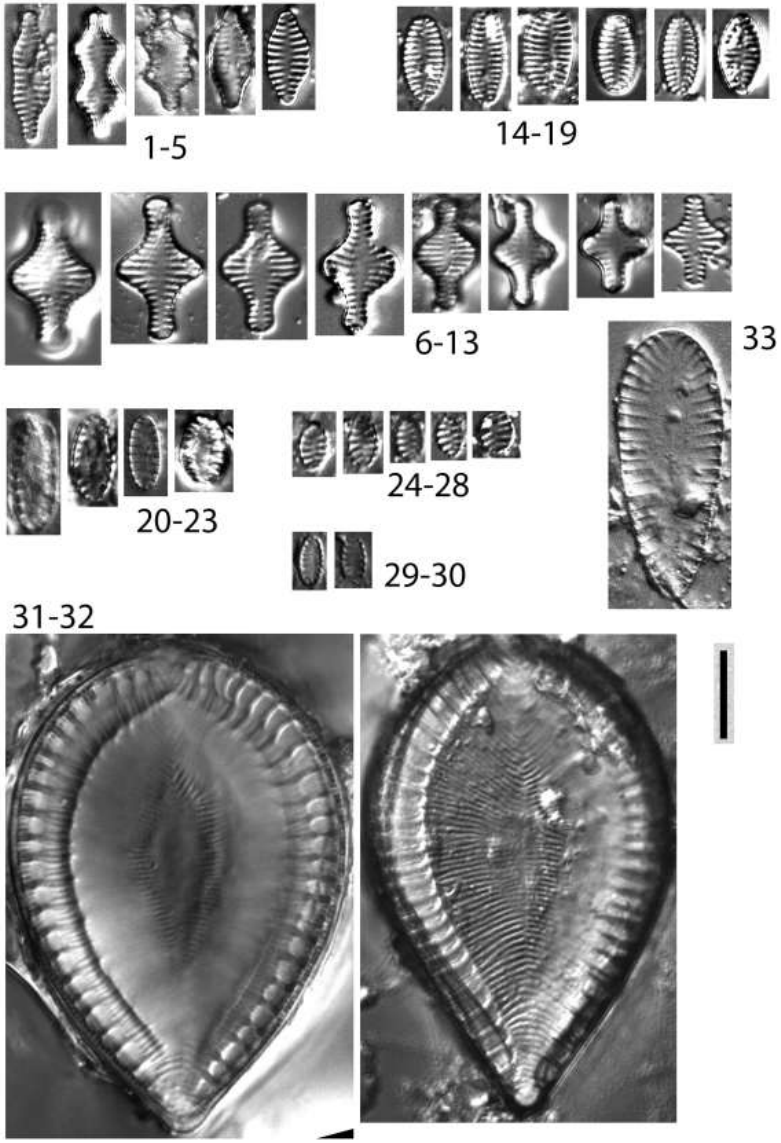
Figs 20-23: ***Staurosirella lapponica*** (Grunow) D.M.Williams & Round

Figs 24-28: ***Staurosirella ovata*** E. Morales

Figs 29-30: ***Staurosirella pinnata*** (Ehrenberg) D.M. Williams & Round

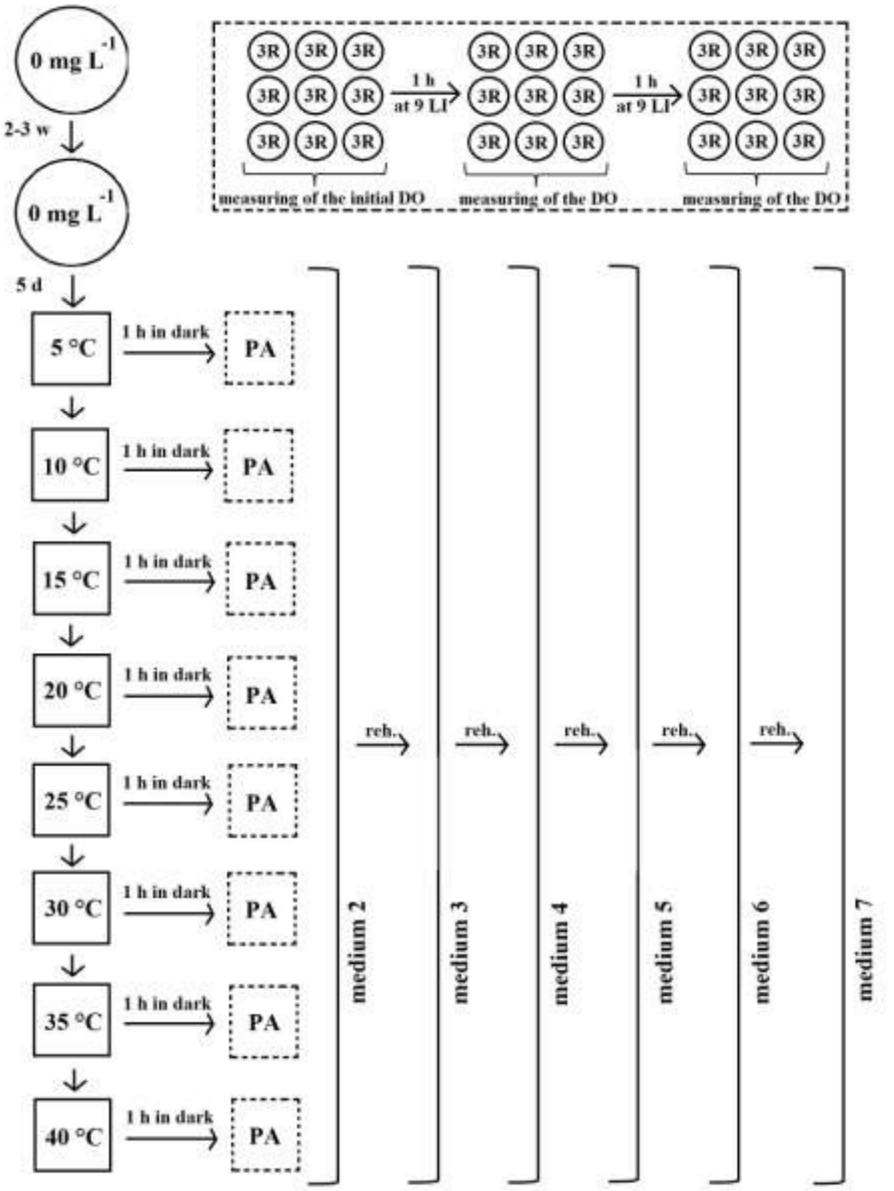
Figs 31-32: ***Surirella brightwellii*** W.Smith

Fig. 33: ***Surirella minuta*** Brébisson ex Kützing



Figs 1-13, 28-30: Borsodi-dűlő
Figs 14-27, 31-33: Legény-tó

Appendix 1 *A schematic flow chart of the laboratory experiments (3R: three replicates; PA: the measurements of the photosynthetic activity; LI: irradiance; reh.: rehomogenization; w: week; d: day; h: hour)*



Appendix 2 *The composition of the applied mediums (DIAT: Bacillariophycean Medium) along the sulphate gradient*

	Basic DIAT		**Modified medium 1 (0 mg L^{-1} SO_4^{2-})**		**Modified medium 2 (50 mg L^{-1} SO_4^{2-})**		**Modified medium 3 (600 mg L^{-1} SO_4^{2-})**		**Modified medium 4 (1200 mg L^{-1} SO_4^{2-})**		**Modified medium 5 (2400 mg L^{-1} SO_4^{2-})**		**Modified medium 6 (3600 mg L^{-1} SO_4^{2-})**		**Modified medium 7 (4800 mg L^{-1} SO_4^{2-})**		**Modified medium 8 (7200 mg L^{-1} SO_4^{2-})**	
	Stock solution (g/100 ml)	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**
$Ca(NO_3)_2 \times 4\ H_2O$	0.4	10	0.4	10	0.4	10	0.4 g	10	0.4	10	0.4	10	0.4	10	0.4	10	0.4	10
K_2HPO_4	0.1	10	0.1	10	0.1	10	0.1 g	10	0.1	10	0.1	10	0.1	10	0.1	10	0.1	10
$MgSO_4 \times 7\ H_2O$	0.1	25	-	-	30.75	0.4	30.75	5	30.75	10	30.75	20	30.75	30	30.75	40	30.75	60
$NaCO_3$	0.1	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
$NaHCO_3$	-	-	-	5.5 g	-	5.5 g	-	5.5 g	-	5.5 g	-	5.5 g	-	5.5 g	-	5.5 g	-	5.5 g
$Na_2SiO_3 \times 9\ H_2O$	0.5	10	0.5	10	0.5	10	0.5 g	10	0.5	10	0.5	10	0.5	10	0.5	10	0.5	10
Fe-citrate	0.1	10	0.1	10	0.1	10	0.1 g	10	0.1	10	0.1	10	0.1	10	0.1	10	0.1	10
Citric acid	0.1	10	0.1	10	0.1	10	0.1 g	10	0.1	10	0.1	10	0.1	10	0.1	10	0.1	10
Soil extract	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Soil extract (SO_4^{2-} - free)	-	-	-	15	-	15	-	15	-	15	-	15	-	15	-	15	-	15
Micronutrient solution: **Stock solution (g/100 ml)** **Applied solution (ml)** $ZnSO_4 \times 7\ H_2O$ 0.1 1 $MnSO_4 \times 4\ H_2O$ 0.1 2 H_3BO_3 0.2 5 $Co(NO_3)_2 \times 6\ H_2O$ 0.02 5 $Na_2MoO_4 \times 2\ H_2O$ 0.0.2 5 $CuSO_4 \times 5\ H_2O$ 0.005 1 de-ionized water (MilliQ) - 981 $FeSO_4 \times 7\ H_2O$ - 0.7 EDTA (Titriplex III) - 0.8	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Micronutrient solution (SO_4^{2-} - free; purified with $Ba(NO_3)_2$)	-	-	-	5	-	5	-	5	-	5	-	5	-	5	-	5	-	5
de-ionized water (MilliQ)	-	885	-	930	-	929.6	-	925	-	920	-	910	-	900	-	890	-	870

Appendix 3 *The composition of the applied mediums (DIAT: Bacillariophycean Medium) along the chloride gradient*

	Basic DIAT		Modified medium 1 (0 mg L^{-1} SO_4^{2-})		Modified medium 2 (36 mg L^{-1} Cl^-)		Modified medium 3 (437.5 mg L^{-1} Cl^-)		Modified medium 4 (875 mg L^{-1} Cl^-)		Modified medium 5 (1750 mg L^{-1} Cl^-)		Modified medium 6 (3500 mg L^{-1} Cl^-)		Modified medium 7 (5250 mg L^{-1} Cl^-)	
	Stock solution (g/100 ml)	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**	**Stock solution (g/100 ml)**	**Nutrient solution (ml)**
$Ca(NO_3)_2 \times 4\ H_2O$	0.4	10	0.4	10	0.4	10	0.4 g	10	0.4	10	0.4	10	0.4	10	0.4	10
K_2HPO_4	0.1	10	0.1	10	0.1	10	0.1 g	10	0.1	10	0.1	10	0.1	10	0.1	10
$MgSO_4 \times 7\ H_2O$	0.1	25	0.1	25	0.1	25	0.1	25	0.1	25	0.1	25	0.1	25	0.1	25
$MgCl_2 \times 6\ H_2O$	-	-	-	-	50.75	0.2	50.75	2.5	50.75	5	50.75	10	50.75	20	50.75	30
$NaCO_3$	0.1	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
$NaHCO_3$	-	-	-	5.5 g	-	5.5 g	-	5.5 g	-	5.5 g	-	5.5 g	-	5.5 g	-	5.5 g
$Na_2SiO_3 \times 9\ H_2O$	0.5	10	0.5	10	0.5	10	0.5 g	10	0.5	10	0.5	10	0.5	10	0.5	10
Fe-citrate	0.1	10	0.1	10	0.1	10	0.1 g	10	0.1	10	0.1	10	0.1	10	0.1	10
Citric acid	0.1	10	0.1	10	0.1	10	0.1 g	10	0.1	10	0.1	10	0.1	10	0.1	10
Soil extract	-	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Soil extract (SO_4^{2-} - free)	-	-	-	15	-	15	-	15	-	15	-	15	-	15	-	15
Micronutrient solution: **Stock solution (g/100 ml)** / **Applied solution (ml)** $ZnSO_4 \times 7\ H_2O$ 0.1 1 $MnSO_4 \times 4\ H_2O$ 0.1 2 H_3BO_3 0.2 5 $Co(NO_3)_2 \times 6\ H_2O$ 0.02 5 $Na_2MoO_4 \times 2\ H_2O$ 0.0.2 5 $CuSO_4 \times 5\ H_2O$ 0.005 1 de-ionized water (MilliQ) - 981 $FeSO_4 \times 7\ H_2O$ - 0.7 EDTA (Titriplex III) - 0.8	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Micronutrient solution (SO_4^{2-} - free; purified with $Ba(NO_3)_2$)	-	-	-	5	-	5	-	5	-	5	-	5	-	5	-	5
de-ionized water (MilliQ)	-	885	-	905	-	904.8	-	902.5	-	900	-	895	-	885		875

Appendix 4 *The relative abundance and constancy of the diatom species in Legény-tó (Cat: Category)*

Species	Relative abundance (%)			Constancy	
	Mean	Min.	Max.	%	Cat
Achnanthes brevipes Agardh var. *intermedia* (Kützing) Cleve	0.1	0.2	5.6	3.8	1
Achnanthidium minutissimum (Kützing) Czarnecki var. *minutissimum*	10.7	0.3	47.9	92.5	5
Achnanthidium sp.	0.4	0.2	7.3	20.8	2
Achnanthidium straubianum (Lange-Bertalot) Lange-Bertalot	<0.1	0.5	0.5	1.9	1
Amphipleura pellucida (Kützing) Kützing	<0.1	0.2	0.5	3.8	1
Amphora commutata Grunow	<0.1	0.2	0.2	5.7	1
Amphora copulata (Kützing) Schoeman et Archibald	1.7	0.2	17.2	71.7	4
Amphora indisctincta Levkov	0.3	0.2	3.7	30.2	2
Anomoeoneis sphaerophora Pfitzer f. *sphaerophora*	0.8	0.2	20.8	47.2	3
Anomoeoneis sphaerophora f. *sculpta* (Ehrenberg) Krammer	<0.1	0.6	0.9	3.8	1
Aulacoseira ambigua (Grunow) Simonsen	<0.1	0.3	0.3	1.9	1
Bacillaria paxillifera (Müller) Hendey	0.2	0.2	5.3	13.2	1
Berkeleya rutilans (Trentepohl ex Roth) Grunow	<0.1	0.2	0.2	3.8	1
Brachysira neoexilis Lange-Bertalot	<0.1	0.3	0.3	1.9	1
Caloneis amphisbaene (Bory) Cleve	<0.1	0.2	1.4	9.4	1
Caloneis lancettula (Schulz-Danzig) Lange-Bertalot & Witkowski	<0.1	0.2	0.2	1.9	1
Caloneis molaris (Grunow) Krammer	<0.1	1.5	1.5	1.9	1
Caloneis silicula (Ehrenberg) Cleve	0.1	0.2	1.6	30.2	2
Campylodiscus bicostatus W. Smith	0.1	0.2	2.3	13.2	1
Cocconeis neothumensis Krammer	<0.1	0.5	0.5	1.9	1
Cocconeis pediculus Ehrenberg	<0.1	0.2	0.5	3.8	1
Cocconeis placentula Ehrenberg	0.4	0.2	4.8	50.9	3
Craticula ambigua (Ehrenberg) D. G: Mann	0.1	0.2	1.7	28.3	2
Craticula buderi (Hustedt) Lange-Bertalot	0.1	0.2	0.9	26.4	2
Craticula cuspidata (Kützing) D.G. Mann	<0.1	0.2	0.2	1.9	1
Craticula halophila (Grunow) D. G. Mann	0.1	0.2	2.2	11.3	1
Craticula molestiformis (Hustedt) Lange-Bertalot	0.1	0.2	1.2	9.4	1
Ctenophora pulchella (Ralfs ex Kützing) D. M. Williams	5.1	0.2	53.7	88.7	5
Cyclostephanos dubius (Hustedt) Round	<0.1	0.2	0.2	1.9	1
Cyclostephanos invisitatus (Hohn & Hellermann) Theriot, Stoermer & Håkasson	<0.1	0.2	0.2	1.9	1
Cyclotella atomus Hustedt	<0.1	0.2	0.2	1.9	1
Cyclotella meneghiniana Kützing	2.5	0.2	28.3	81.1	5
Cyclotella ocellata Pantocsek	<0.1	0.2	1.7	5.7	1
Cylindrotheca gracilis (Brébisson) Grunow	<0.1	0.2	0.2	3.8	1
Cymatopleura solea (Brébisson) W. Smith var. *apiculata* (W. Smith) Ralfs	<0.1	0.2	0.7	13.2	1
Cymbella excisa Kützing	<0.1	1.0	1.0	1.9	1
Cymbella hustedtii Krasske *var. hustedtii*	0.1	0.2	1.8	15.1	1
Cymbella neocistula Krammer	0.9	0.2	10.4	56.6	3
Denticula tenuis Kützing	<0.1	0.3	0.3	1.9	1
Diatoma moniliformis Kützing ssp. *moniliformis*	0.1	0.2	2.0	9.4	1
Diatoma tenuis Agardh	3.0	0.2	50.8	54.7	3
Diatoma vulgaris Bory	<0.1	0.5	0.5	1.9	1
Encyonema caespitosum Kützing var. *caespitosum*	<0.1	0.3	1.4	5.7	1
Encyonema lacustre (C. Agardh) Mills	<0.1	0.2	1.7	5.7	1
Encyonema silesiacum (Bleisch) D.G. Mann	<0.1	0.7	0.7	1.9	1
Encyonopsis krammeri Reichardt	<0.1	0.2	0.2	1.9	1
Encyonopsis microcephala (Grunow) Krammer	<0.1	0.2	0.2	1.9	1
Encyonopsis minuta Krammer & Reichardt	0.1	0.2	1.4	7.5	1
Encyonopsis subminuta Krammer & Reichardt	<0.1	0.2	0.5	9.4	1
Entomoneis alata (Ehrenberg) Ehrenberg	1.5	0.2	16.9	34.0	2
Entomoneis costata (Hustedt) Reimer	<0.1	0.2	0.7	11.3	1
Entomoneis paludosa (W. Smith) Reimer var. *subsalina* (Cleve) Krammer	7.0	0.2	57.7	69.8	4
Eolimna minima (Grunow) Lange-Bertalot & W.Schiller	<0.1	0.2	0.2	1.9	1
Epithemia adnata (Kützing) Brébisson	0.1	0.2	2.4	13.2	1
Epithemia sorex Kützing	0.3	0.2	1.9	39.6	2
Eunotia mucophila (Lange-Bertalot & Nörpel) Lange-Bertalot	<0.1	0.2	0.5	3.8	1
Fallacia pygmaea ssp. *subpygmaea* Lange-Bertalot, Cavicini, Tagliaventi et Alfinito	0.2	0.2	2.7	37.7	2
Fallacia pygmea (Kützing) A. J. Stickle et D. G. Mann	0.5	0.2	5.2	73.6	4
Fragilaria acus (Kützing) Lange-Bertalot	0.9	0.2	11.7	50.9	3
Fragilaria dilatata (Brébisson) Lange-Bertalot	<0.1	0.2	0.2	1.9	1
Fragilaria famelica (Kützing) Lange-Bertalot	0.4	0.2	4.8	28.3	2
Fragilaria nanana Lange-Bertalot	0.1	0.2	1.1	11.3	1
Fragilaria perminuta (Grunow) Lange-Bertalot	<0.1	1.2	1.2	1.9	1
Fragilaria tenera (W. Smith) Lange-Bertalot	0.1	0.2	1.4	11.3	1
Fragilaria vauchariae (Kützing) Petersen	<0.1	0.2	0.7	11.3	1
Gomphonema brebissonii Kützing	<0.1	0.2	0.2	1.9	1
Gomphonema clavatum Ehrenberg	<0.1	0.5	0.5	1.9	1
Gomphonema italicum Kützing	<0.1	0.2	0.5	7.5	1
Gomphonema olivaceum (Hornemann) Brébisson	2.1	0.2	36.1	56.6	3
Gomphonema parvulum (Kützing) Kützing var. *parvulum* f. *parvulum*	0.2	0.2	5.9	18.9	1
Gyrosigma acuminatum (Kützing) Rabenhorst	0.1	0.2	2.2	28.3	2
Gyrosigma obtusatum (Sullivant & Wormley) C.S. Boyer	<0.1	0.7	0.7	1.9	1
Halamphora dominici Ács et Levkov	<0.1	0.2	0.5	5.7	1
Halamphora kevei Ács et Levkov	<0.1	0.2	0.6	7.5	1
Halamphora oligotrophenta (Lange-Bertalot) Levkov	0.1	0.2	0.7	17.0	1
Halamphora subcapitata (Kisselew) Levkov	<0.1	0.7	0.7	1.9	1
Halamphora tumida Hustedt) Levkov comb. nov.	0.1	0.2	1.2	15.1	1
Halamphora veneta (Kützing) Levkov	0.1	0.2	1.7	13.2	1
Hantzschia abundans Lange-Bertalot	<0.1	0.2	0.7	9.4	1
Hantzschia vivax (W. Smith) Peragallo var. *vivax*	<0.1	0.2	0.2	1.9	1
Hippodonta hungarica (Grunow) Lange-Bertalot, Metzeltin et Witkowski	1.3	0.2	21.0	67.9	4
Lemnicola hungarica (Grunow) Round & Basson	<0.1	0.3	0.3	1.9	1
Luticola dismutica (Hustedt) D.G. Mann	<0.1	0.3	0.3	1.9	1
Luticola mutica (Kützing) D.G. Mann	<0.1	0.4	0.4	1.9	1
Mastogloia elliptica (C. Agardh) Cleve	0.1	0.2	1.1	18.9	1
Mastogloia sp.	0.5	0.2	4.3	32.1	2
Mayamaea atomus (Kützing) Lange-Betralot var. *permitis* (Hustedt) Lange-Bertalot	0.4	0.2	8.6	13.2	1
Melosira varians C. Agardh	<0.1	0.2	0.2	1.9	1
Navicula antonii Lange-Bertalot	<0.1	0.2	0.2	3.8	1
Navicula capitatoradiata Germain	<0.1	1.1	1.1	1.9	1
Navicula cryptocephala Kützing	1.0	0.2	5.4	58.5	3
Navicula cryptotenella Lange-Bertalot	0.1	0.2	3.3	13.2	1
Navicula cryptotenelloides Lange-Bertalot	0.2	0.2	5.2	24.5	2
Navicula duerrenbergiana Hustedt	0.1	0.3	5.4	7.5	1
Navicula gregaria Donkin	<0.1	0.7	0.7	1.9	1
Navicula kotschyi Grunow	<0.1	0.2	0.3	3.8	1
Navicula lanceolata (C. Agardh) Ehrenberg	<0.1	0.2	0.2	1.9	1
Navicula oblonga (Kützing) Kützing	0.7	0.2	19.6	32.1	2
Navicula radiosa Kützing	0.1	0.2	2.3	18.9	1
Navicula salinarum Grunow var. *salinarum*	0.8	0.2	17.3	45.3	3
Navicula subrhynocephala Hustedt	0.1	0.2	1.7	7.5	1
Navicula tripunctata (O.F. Müller) Bory	<0.1	0.2	0.9	5.7	1
Navicula veneta Kützing	5.8	0.2	20.2	96.2	5
Navicula wiesneri Lange-Bertalot	3.3	0.2	24.3	77.4	4
Navicymbula pusilla (Grunow) Krammer	2.4	0.2	18.2	73.6	4
Nitzschia amphibia Grunow	0.2	0.2	3.7	26.4	2
Nitzschia aurariae Cholnoky	2.8	0.2	43.6	30.2	2
Nitzschia calida Grunow	<0.1	0.2	0.2	1.9	1
Nitzschia communis Rabenhorst	0.1	0.2	2.5	5.7	1
Nitzschia commutata Grunow	<0.1	0.3	0.5	3.8	1
Nitzschia dissipata (Kützing) Grunow ssp. *dissipata*	<0.1	0.5	0.5	1.9	1
Nitzschia elegantula Grunow	0.3	0.2	4.3	26.4	2
Nitzschia fonticola Grunow	<0.1	0.2	0.5	9.4	1
Nitzschia frustulum (Kützing) Grunow	5.8	0.3	32.1	94.3	5
Nitzschia gracilis Hantzsch	0.1	0.5	1.7	7.5	1
Nitzschia inconspicua Grunow	0.3	0.2	4.2	24.5	2
Nitzschia liebetruthii Rabenhorst	<0.1	0.2	0.5	3.8	1
Nitzschia obtusa W. Smith var. *obtusa*	<0.1	0.2	0.3	3.8	1
Nitzschia palea var. *tenuirostris* sensu Lange-Bertalot	2.9	0.2	58.5	56.6	3
Nitzschia palea var. *debilis* (Kützing) Grunow	0.5	0.2	16.2	17.0	1
Nitzschia palea (Kützing) W. Smith var. *palea*	5.4	0.2	56.1	81.1	5
Nitzschia paleaceae Grunow	1.3	0.5	33.6	32.1	2
Nitzschia pusilla Grunow	0.4	0.2	2.5	35.8	2
Nitzschia radicula Hustedt	<0.1	0.2	0.5	5.7	1
Nitzschia reversa W. Smith	<0.1	0.2	0.2	1.9	1
Nitzschia salinarum Grunow	<0.1	0.2	0.7	3.8	1
Nitzschia sigma (Kützing) W. Smith	<0.1	0.2	0.5	5.7	1
Nitzschia solita Hustedt	0.8	0.2	9.1	58.5	3
Nitzschia sp. 1	<0.1	0.3	0.3	1.9	1
Nitzschia sp. 3	0.4	0.2	8.4	47.2	3
Nitzschia supralitorea Lange-Bertalot	0.6	0.2	3.8	60.4	4
Nitzschia thermaloides Hustedt	0.7	0.2	6.9	43.4	3
Nitzschia valdecostata Lange-Bertalot et Simonsen	2.9	0.2	76.3	22.6	2
Nitzschia vitrea G. Norman var. *vitrea*	0.1	0.2	1.8	11.3	1
Pinnularia brebissonii (Kützing) Rabenhorst	1.4	0.2	16.2	66.0	4
Pinnularia kneuckerii Hustedt	0.1	0.2	1.0	20.8	2
Planothidium frequentissimum (Lange-Bertalot) Lange-Bertalot	<0.1	0.2	0.5	7.5	1
Planothidium rostratum (Østrup) Lange-Bertalot	<0.1	0.2	0.2	1.9	1
Pseudostaurosira brevistriata (Grunow) D.M. Williams & Round	0.5	0.2	4.6	43.4	3
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot	<0.1	0.2	0.7	11.3	1
Rhoicosphenia adriatica Caput Michalic & Levkov	0.2	0.2	1.4	32.1	2
Rhoicosphenia lacustris Levkov	0.2	0.2	2.4	26.4	2
Rhopalodia gibba (Ehrenberg) Müller	1.5	0.2	16.6	50.9	3
Rhopalodia operculata (Agardh) Håkansson	0.1	0.2	1.0	20.8	2
Scoliopleura peisonis Grunow	0.1	0.2	0.8	18.9	1
Sellaphora capitata D.G.Mann & McDonald, S.M.	0.1	0.2	2.0	18.9	1
Staurophora tackei (Hustedt) L.Bahls	<0.1	0.2	0.2	1.9	1
Staurophora wislouchii (Poretzsky et Anisimowa) D. G. Mann	1.1	0.2	20.9	35.8	2
Staurosira venter (Ehrenberg) Grunow	0.5	0.2	21.1	15.1	1
Staurosirella ovata E. Morales	<0.1	0.2	1.0	9.4	1
Staurosirella pinnata (Ehrenberg) D.M. Williams & Round	<0.1	0.3	0.5	3.8	1
Stephanodiscus parvus Stoermer et Håkansson	1.2	0.2	50.9	13.2	1
Surirella brebissoii Krammer et Lange-Bertalot	3.9	0.2	30.0	73.6	4
Surirella brightwelli W.Smith	<0.1	0.2	0.6	9.4	1
Surirella minuta Brébisson ex Kützing	<0.1	0.2	0.2	1.9	1
Surirella ovalis Brébisson	0.1	0.2	0.9	18.9	1
Surirella peisonis Pantocsek	0.1	0.2	0.5	17.0	1
Tabularia fasciculata (Agardh) D. W. Williams et Round	1.1	0.2	17.3	50.9	3
Tryblionella apiculata W. Gregory	1.7	0.2	10.4	77.4	4
Tryblionella gracilis W. Smith	0.4	0.2	9.0	35.8	2
Tryblionella hungarica (Grunow) Frenguelli	0.9	0.2	8.7	58.5	3
Ulnaria ulna (Nitzsch) Compère	0.3	0.2	2.7	41.5	3

Appendix 5 *The relative abundance and constancy of the diatom species in Borsodi-dűlő (Cat: Category)*

Species	Relative abundance (%)			Constancy	
	Mean	Min.	Max.	%	Cat
Achnanthes brevipes Agardh var. *intermedia* (Kützing) Cleve	0.3	0.2	2.7	30.8	2
Achnanthes exigua Grunow	<0.1	0.2	0.2	2.6	1
Achnanthidium minutissimum (Kützing) Czarnecki var. *minutissimum*	1.1	0.2	9.8	33.3	2
Achnanthidium sp.	<0.1	1.2	1.2	2.6	1
Amphipleura pellucida (Kützing) Kützing	<0.1	0.3	0.3	2.6	1
Amphora copulata (Kützing) Schoeman et Archibald	0.1	0.2	0.7	12.8	1
Amphora indisctincta Levkov	0.4	0.2	8.9	23.1	2
Anomoeoneis sphaerophora Pfitzer f. *sphaerophora*	3.7	0.2	42.6	61.5	4
Anomoeoneis sphaerophora f. *costata* (Kützing) Schmid	0.1	0.2	2.1	15.4	1
Anomoeoneis sphaerophora f. *sculpta* (Ehrenberg) Krammer	0.6	0.2	17.0	20.5	2
Aulacoseira ambigua (Grunow) Simonsen	0.1	0.5	1.1	7.7	1
Bacillaria paxillifera (Müller) Hendey	<0.1	0.2	1.0	7.7	1
Brachysira neoexilis Lange-Bertalot	<0.1	0.2	0.2	2.6	1
Brachysira procera Lange-Bertalot & Moser	<0.1	0.2	0.9	5.1	1
Brachysira vitrea (Grunow) Ross	<0.1	0.2	0.2	2.6	1
Caloneis amphisbaene (Bory) Cleve	<0.1	0.5	0.5	2.6	1
Caloneis lancettula (Schulz-Danzig) Lange-Bertalot & Witkowski	<0.1	0.5	0.5	2.6	1
Caloneis silicula (Ehrenberg) Cleve	<0.1	0.2	0.3	7.7	1
Campylodiscus bicostatus W. Smith	0.1	0.2	1.1	10.3	1
Cocconeis placentula Ehrenberg	0.1	0.2	1.0	23.1	2
Craticula ambigua (Ehrenberg) D. G: Mann	0.8	0.2	4.9	74.4	4
Craticula buderi (Hustedt) Lange-Bertalot	0.5	0.2	6.6	30.8	2
Craticula cuspidata (Kützing) D.G. Mann	0.1	0.2	0.5	20.5	2
Craticula halophila (Grunow) D. G. Mann	0.1	0.2	1.6	17.9	1
Craticula molestiformis (Hustedt) Lange-Bertalot	<0.1	0.2	0.2	2.6	1
Ctenophora pulchella (Ralfs ex Kützing) D. M. Williams	3.5	0.5	28.1	51.3	3
Cyclostephanos dubius (Hustedt) Round	<0.1	0.2	0.5	7.7	1
Cyclostephanos invisitatus (Hohn & Hellermann) Theriot, Stoermer & Håkasson	0.2	0.2	1.2	25.6	2
Cyclotella atomus Hustedt	<0.1	0.7	0.7	2.6	1
Cyclotella praetermissa (Lund) T. Nakov	<0.1	0.2	1.1	5.1	1
Cyclotella distinguenda (Hustedt) var. *distinguenda*	<0.1	0.2	0.2	2.6	1
Cyclotella meneghiniana Kützing	3.4	0.4	35.6	71.8	4
Cyclotella ocellata Pantocsek	0.1	0.2	2.8	12.8	1
Cylindrotheca gracilis (Brébisson) Grunow	<0.1	0.3	0.3	2.6	1
Cymatopleura elliptica (Brébisson) W. Smith var. *elliptica*	<0.1	0.2	0.2	2.6	1
Cymbella cymbiformis C. Agardh	<0.1	0.7	0.7	2.6	1
Cymbella excisa Kützing	0.1	0.5	1.7	5.1	1
Cymbella hustedtii Krasske var. *hustedtii*	<0.1	0.2	0.2	5.1	1
Cymbella neocistula Krammer	<0.1	0.2	0.2	7.7	1
Cymbella parva (W. Smith) Kirchner	<0.1	0.2	0.2	2.6	1
Cymbella subhelvetica Krammer	<0.1	0.2	0.9	5.1	1
Delicata delicatula (Kützing) Krammer	<0.1	0.2	0.2	2.6	1
Diatoma ehrenbergii Kützing	<0.1	0.5	0.5	2.6	1
Diatoma moniliformis Kützing ssp. *moniliformis*	<0.1	0.2	0.5	5.1	1
Diatoma tenuis Agardh	0.3	0.2	5.8	28.2	2
Diatoma vulgaris Bory	<0.1	1.2	1.2	2.6	1
Diploneis parma Cleve sensu Krammer & Lange-Bertalot	<0.1	0.5	0.5	2.6	1
Encyonema prostratum (Berkeley) Kützing	<0.1	0.3	0.3	2.6	1
Encyonema silesiacum (Bleisch) D.G. Mann	<0.1	0.5	0.5	2.6	1
Encyonopsis cesatti (Rabenhorst) Krammer	<0.1	1.5	1.5	2.6	1
Encyonopsis krammeri Reichardt	<0.1	0.2	0.2	2.6	1
Encyonopsis minuta Krammer & Reichardt	<0.1	0.5	0.5	2.6	1
Encyonopsis subminuta Krammer & Reichardt	<0.1	1.7	1.7	2.6	1
Entomoneis alata (Ehrenberg) Ehrenberg	0.2	0.2	4.0	17.9	1
Entomoneis costata (Hustedt) Reimer	<0.1	0.2	0.2	2.6	1
Entomoneis paludosa (W. Smith) Reimer var. *subsalina* (Cleve) Krammer	1.5	0.2	22.7	56.4	3
Eolimna subminuscula (Manguin) Moser, Lange-Bertalot & Metzeltin	<0.1	1.6	1.6	2.6	1
Epithemia adnata (Kützing) Brébisson	<0.1	1.3	1.3	2.6	1
Epithemia sorex Kützing	<0.1	0.2	0.2	5.1	1
Fallacia pygmea (Kützing) A. J. Stickle et D. G. Mann	0.6	0.2	3.7	48.7	3
Fallacia pygmaea ssp. *subpygmaea* Lange-Bertalot, Cavicini, Tagliaventi et Alfinito	1.1	0.2	10.5	64.1	4
Fragilaria acus (Kützing) Lange-Bertalot	<0.1	0.8	0.8	2.6	1
Fragilaria dilatata (Brébisson) Lange-Bertalot	<0.1	0.3	0.3	2.6	1
Fragilaria famelica (Kützing) Lange-Bertalot	<0.1	0.2	0.2	5.1	1
Fragilaria nanana Lange-Bertalot	<0.1	0.2	0.2	2.6	1
Fragilaria vauchariae (Kützing) Petersen	0.1	0.2	2.1	5.1	1
Gomphonema olivaceum (Hornemann) Brébisson	<0.1	0.2	0.2	7.7	1
Gomphonema parvulum (Kützing) Kützing var. *parvulum* f. *parvulum*	0.1	0.2	1.2	20.5	2
Gomphonema pseudoaugur Lange-Bertalot	<0.1	0.2	0.3	5.1	1
Gomphonema pumilum (Grunow)cReichardt & Lange-Bertalot	<0.1	0.2	0.2	2.6	1
Gyrosigma acuminatum (Kützing) Rabenhorst	<0.1	0.2	0.5	5.1	1
Gyrosigma obtusatum (Sullivant & Wormley) C.S. Boyer	0.7	0.2	7.5	30.8	2
Halamphora dominici Ács et Levkov	0.2	0.2	1.9	35.9	2
Halamphora kevei Ács et Levkov	0.8	0.2	17.6	43.6	3
Halamphora oligotrophenta (Lange-Bertalot) Levkov	<0.1	0.4	0.4	2.6	1
Halamphora paraveneta (Lange-Bertalot, Cavacini, Tagliaventi et Alfinito) Levkov	0.2	0.2	3.4	15.4	1
Halamphora subcapitata (Kisselew) Levkov	<0.1	0.4	0.8	5.1	1
Halamphora tumida Hustedt) Levkov comb. nov.	<0.1	0.2	0.2	5.1	1
Halamphora veneta (Kützing) Levkov	0.8	0.2	6.6	56.4	3
Hantzschia abundans Lange-Bertalot	2.5	0.2	79.5	43.6	3
Hantzschia amphioxys (Ehrenberg) Grunow	0.1	0.2	2.0	10.3	1
Hantzschia vivax (W. Smith) Peragallo var. *vivax*	<0.1	0.2	0.2	2.6	1
Hippodonta capitata (Ehrenberg) Lange-Bertalot, Metzeltin & Witkowski	<0.1	0.7	0.7	2.6	1
Hippodonta hungarica (Grunow) Lange-Bertalot, Metzeltin et Witkowski	0.1	0.2	2.7	12.8	1
Luticola dismutica (Hustedt) D.G. Mann	<0.1	0.3	0.3	2.6	1
Luticola mutica (Kützing) D.G. Mann	<0.1	0.2	0.7	10.3	1
Mastogloia sp.	<0.1	1.5	1.5	2.6	1
Mayamaea atomus (Kützing) Lange-Betralot var. *permitis* (Hustedt) Lange-Bertalot	<0.1	0.2	0.2	2.6	1
Melosira varians C. Agardh	<0.1	0.2	0.2	2.6	1
Meridion circulare (Gréville) C. Agardh var. circulare	<0.1	0.5	0.5	2.6	1
Navicula antonii Lange-Bertalot	<0.1	0.3	0.3	2.6	1
Navicula capitatoradiata Germain	<0.1	0.2	1.2	5.1	1
Navicula cryptocephala Kützing	0.2	0.2	4.3	15.4	1
Navicula cryptotenella Lange-Bertalot	<0.1	0.2	0.2	2.6	1
Navicula cryptotenelloides Lange-Bertalot	<0.1	0.2	0.2	5.1	1
Navicula duerrenbergiana Hustedt	<0.1	0.2	0.2	2.6	1
Navicula kotschyi Grunow	<0.1	0.6	0.6	2.6	1
Navicula lanceolata (C. Agardh) Ehrenberg	<0.1	0.7	0.7	2.6	1
Navicula oblonga (Kützing) Kützing	0.1	0.4	1.5	12.8	1
Navicula radiosa Kützing	0.1	2.1	2.1	2.6	1
Navicula salinarum Grunow var. *salinarum*	0.3	0.3	5.7	15.4	1
Navicula subrhynocephala Hustedt	<0.1	0.2	0.2	2.6	1
Navicula tripunctata (O.F. Müller) Bory	0.1	0.2	1.2	10.3	1
Navicula veneta Kützing	14.7	1.2	60.5	100.0	5
Navicula wiesneri Lange-Bertalot	1.3	0.2	8.9	61.5	4
Navicymbula pusilla (Grunow) Krammer	0.2	0.2	5.9	17.9	1
Nitzschia acicularis (Kützing) W. Smith	0.1	0.2	1.6	12.8	1
Nitzschia angustatula Lange-Bertalot	<0.1	0.2	0.2	2.6	1
Nitzschia aurariae Cholnoky	1.7	0.5	18.8	35.9	2
Nitzschia calida Grunow	<0.1	0.2	0.7	7.7	1
Nitzschia commutata Grunow	0.1	0.2	3.5	10.3	1
Nitzschia dissipata (Kützing) Grunow ssp. *dissipata*	0.1	0.5	2.4	5.1	1
Nitzschia elegantula Grunow	<0.1	0.6	0.6	2.6	1
Nitzschia fonticola Grunow	<0.1	0.2	0.7	7.7	1
Nitzschia frustulum (Kützing) Grunow	8.3	0.5	39.6	89.7	5
Nitzschia gracilis Hantzsch	0.4	0.2	2.6	38.5	2
Nitzschia inconspicua Grunow	0.8	0.2	6.0	38.5	2
Nitzschia liebetruthii Rabenhorst	<0.1	0.2	0.7	5.1	1
Nitzschia obtusa W. Smith var. *obtusa*	<0.1	0.2	0.2	2.6	1
Nitzschia palea var. *debilis* (Kützing) Grunow	0.3	0.4	2.7	17.9	1
Nitzschia palea (Kützing) W. Smith var. *palea*	6.8	0.2	47.7	71.8	4
Nitzschia palea var. *tenuirostris* sensu Lange-Bertalot	2.3	0.2	42.4	61.5	4
Nitzschia paleaceae Grunow	2.5	0.3	23.8	41.0	3
Nitzschia pusilla Grunow	0.1	0.2	1.1	23.1	2
Nitzschia reversa W. Smith	<0.1	0.3	0.3	2.6	1
Nitzschia salinarum Grunow	<0.1	0.5	0.7	7.7	1
Nitzschia solita Hustedt	0.1	0.2	1.2	28.2	2
Nitzschia sp.	<0.1	0.2	0.3	5.1	1
Nitzschia sp. 1	<0.1	0.2	0.8	5.1	1
Nitzschia sp. 3	0.7	0.2	12.0	23.1	2
Nitzschia supralitorea Lange-Bertalot	1.3	0.2	8.6	59.0	3
Nitzschia thermaloides Hustedt	0.1	0.2	1.0	25.6	2
Nitzschia valdecostata Lange-Bertalot et Simonsen	<0.1	0.2	0.5	5.1	1
Nitzschia vitrea G. Norman var. *vitrea*	0.3	0.2	4.0	23.1	2
Pinnularia borealis Ehrenberg var. *borealis*	<0.1	0.5	0.5	2.6	1
Pinnularia brebissonii (Kützing) Rabenhorst	0.5	0.2	4.8	43.6	3
Pinnularia kneuckerii Hustedt	<0.1	0.2	0.2	2.6	1
Planothidium frequentissimum (Lange-Bertalot) Lange-Bertalot	0.1	0.3	1.6	10.3	1
Pseudostaurosira brevistriata (Grunow) D.M. Williams & Round	0.2	0.2	4.3	17.9	1
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot	0.1	0.2	1.6	17.9	1
Rhoicosphenia adriatica Caput Michalic & Levkov	0.4	0.2	7.8	30.8	2
Rhoicosphenia lacustris Levkov	1.0	0.2	29.8	28.2	2
Rhopalodia gibba (Ehrenberg) Müller	<0.1	0.5	0.5	2.6	1
Sellaphora capitata D.G.Mann & McDonald, S.M.	<0.1	0.4	1.2	5.1	1
Staurophora wislouchii (Poretzsky et Anisimowa) D. G. Mann	1.8	0.2	40.9	43.6	3
Staurosira binodis (Ehrenberg) Lange-Bertalot	<0.1	0.5	0.5	2.6	1
Staurosira construens Ehrenberg	0.3	10.6	10.6	2.6	1
Staurosira venter (Ehrenberg) Grunow	0.1	3.2	3.2	2.6	1
Staurosirella lapponica (Grunow) D.M.Williams & Round	<0.1	0.5	0.5	2.6	1
Staurosirella ovata E. Morales	<0.1	0.2	0.5	5.1	1
Staurosirella pinnata (Ehrenberg) D.M. Williams & Round	<0.1	0.8	0.8	2.6	1
Stephanodiscus hantzschii Grunow	0.6	0.5	6.3	23.1	2
Stephanodiscus hantzschii f. *tenuis* (Hustedt) H.Håkansson & E.F.Stoermer	1.6	0.5	19.4	33.3	2
Stephanodiscus minutulus (Kützing) Krieger	0.2	0.2	3.3	20.5	2
Stephanodiscus parvus Stoermer et Håkansson	10.0	0.2	60.1	59.0	3
Surirella brebissoii Krammer et Lange-Bertalot	1.3	0.2	15.2	59.0	3
Surirella brightwelli W.Smith	<0.1	0.2	0.2	2.6	1
Surirella ovalis Brébisson	0.1	0.2	1.6	15.4	1
Surirella peisonis Pantocsek	<0.1	0.2	0.3	12.8	1
Tabularia fasciculata (Agardh) D. W. Williams et Round	2.8	0.2	28.2	56.4	3
Tryblionella apiculata W. Gregory	8.0	0.2	44.0	94.9	5
Tryblionella gracilis W. Smith	0.2	0.7	5.3	5.1	1
Tryblionella hungarica (Grunow) Frenguelli	3.1	0.4	16.2	61.5	4
Ulnaria ulna (Nitzsch) Compère	<0.1	0.2	0.4	5.1	1

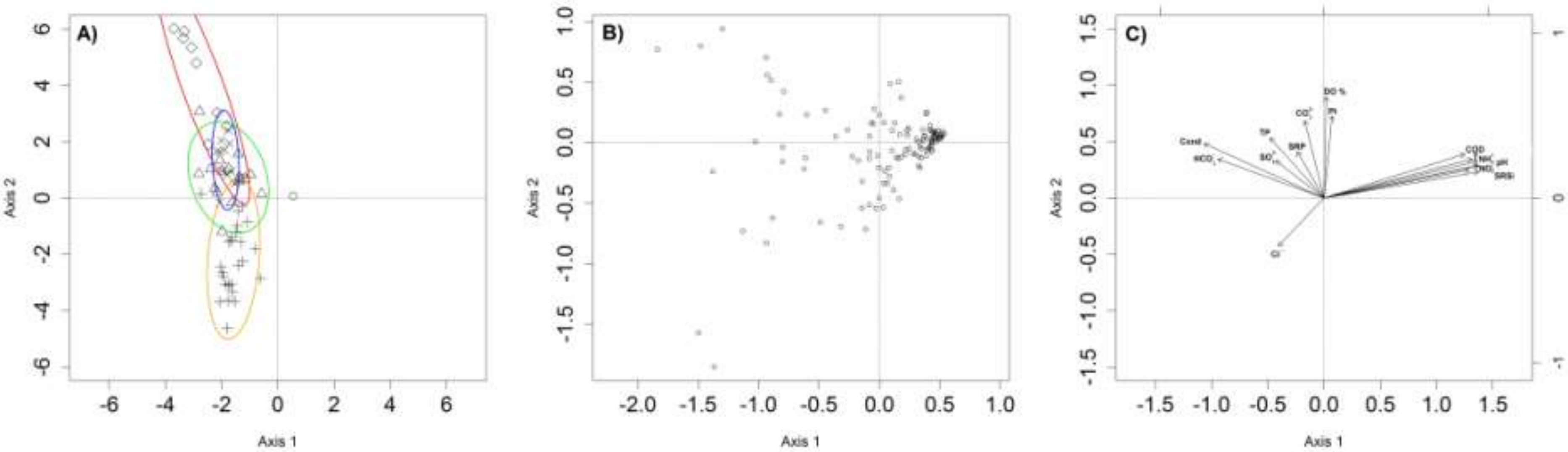
Appendix 6 *The relative abundance and constancy of the diatom species in Nyéki-szállás (Cat: Category)*

Species	Relative abundance (%)			Constancy	
	Mean	Min.	Max.	%	Cat
Achnanthes brevipes Agardh var. *intermedia* (Kützing) Cleve	0.5	0.2	4.3	48.5	3
Achnanthidium minutissimum (Kützing) Czarnecki var. *minutissimum*	0.8	0.2	9.5	36.4	2
Amphora commutata Grunow	<0.1	0.5	0.5	3.0	1
Amphora copulata (Kützing) Schoeman et Archibald	0.3	0.2	5.8	21.2	2
Amphora indisctincta Levkov	0.3	0.2	4.0	24.2	2
Anomoeoneis sphaerophora Pfitzer f. *sphaerophora*	1.7	0.2	13.0	60.6	4
Anomoeoneis sphaerophora f. *costata* (Kützing) Schmid	<0.1	0.2	0.2	3.0	1
Anomoeoneis sphaerophora f. *sculpta* (Ehrenberg) Krammer	<0.1	0.2	0.3	6.1	1
Asterionella fromosa Hassall	<0.1	1.0	1.0	3.0	1
Aulacoseira ambigua (Grunow) Simonsen	<0.1	0.2	0.2	3.0	1
Bacillaria paxillifera (Müller) Hendey	0.3	0.3	2.4	27.3	2
Caloneis amphisbaene (Bory) Cleve	<0.1	0.2	0.2	6.1	1
Caloneis silicula (Ehrenberg) Cleve	0.1	0.2	1.2	9.1	1
Campylodiscus bicostatus W. Smith	<0.1	0.2	0.2	3.0	1
Cocconeis neothumensis Krammer	<0.1	0.2	0.7	9.1	1
Cocconeis placentula Ehrenberg	0.2	0.2	2.5	18.2	1
Craticula ambigua (Ehrenberg) D. G: Mann	2.0	0.2	29.8	51.5	3
Craticula buderi (Hustedt) Lange-Bertalot	0.2	0.2	1.6	21.2	2
Craticula halophila (Grunow) D. G. Mann	<0.1	0.2	0.5	12.1	1
Craticula molestiformis (Hustedt) Lange-Bertalot	0.1	0.2	3.4	6.1	1
Ctenophora pulchella (Ralfs ex Kützing) D. M. Williams	2.6	0.2	24.8	63.6	4
Cyclostephanos dubius (Hustedt) Round	<0.1	0.2	0.5	6.1	1
Cyclotella meneghiniana Kützing	0.8	0.2	7.6	57.6	3
Cyclotella ocellata Pantocsek	<0.1	0.2	0.7	6.1	1
Cymbella excisa Kützing	0.2	2.7	3.0	6.1	1
Cymbella hustedtii Krasske var. *hustedtii*	<0.1	0.5	0.5	3.0	1
Cymbella neocistula Krammer	0.2	0.2	4.0	15.2	1
Denticula tenuis Kützing	0.8	0.2	24.8	6.1	1
Diatoma moniliformis Kützing ssp. *moniliformis*	<0.1	1.3	1.3	3.0	1
Diatoma tenuis Agardh	2.0	0.3	35.9	30.3	2
Encyonema caespitosum Kützing var. *caespitosum*	<0.1	0.5	0.5	3.0	1
Encyonema lacustre (C. Agardh) Mills	<0.1	0.2	0.2	3.0	1
Encyonema silesiacum (Bleisch) D.G. Mann	0.1	1.7	1.7	3.0	1
Entomoneis costata (Hustedt) Reimer	<0.1	0.2	0.2	3.0	1
Entomoneis paludosa (W. Smith) Reimer var. *subsalina* (Cleve) Krammer	0.2	0.2	1.9	27.3	2
Eolimna minima (Grunow) Lange-Bertalot & W.Schiller	<0.1	0.2	0.2	3.0	1
Epithemia adnata (Kützing) Brébisson	0.1	0.5	1.2	6.1	1
Epithemia sorex Kützing	0.6	0.5	15.1	21.2	2
Fallacia pygmea (Kützing) A. J. Stickle et D. G. Mann	0.8	0.2	7.4	51.5	3
Fallacia pygmaea ssp. *subpygmaea* Lange-Bertalot, Cavicini, Tagliaventi et Alfinito	0.5	0.2	3.4	60.6	4
Fragilaria acus (Kützing) Lange-Bertalot	0.3	0.2	5.4	18.2	1
Fragilaria famelica (Kützing) Lange-Bertalot	0.1	0.2	2.2	15.2	1
Fragilaria tenera (W. Smith) Lange-Bertalot	<0.1	0.2	0.2	6.1	1
Fragilaria vauchariae (Kützing) Petersen	0.1	0.5	2.5	6.1	1
Gomphonema micropus Kützing	<0.1	0.2	0.2	3.0	1
Gomphonema olivaceum (Hornemann) Brébisson	0.1	0.2	2.2	15.2	1
Gomphonema parvulum (Kützing) Kützing var. *parvulum* f. *parvulum*	0.2	0.2	2.8	39.4	2
Gomphonema parvulum Lange-Bertalot & Reichardt var. *parvulum* f. *saprophilum*	0.1	0.2	2.2	12.1	1
Gomphonema pumilum (Grunow)cReichardt & Lange-Bertalot	0.1	2.2	2.2	3.0	1
Gyrosigma acuminatum (Kützing) Rabenhorst	0.1	0.2	2.4	15.2	1
Gyrosigma obtusatum (Sullivant & Wormley) C.S. Boyer	<0.1	0.7	0.7	3.0	1
Halamphora dominici Ács et Levkov	<0.1	0.2	0.2	3.0	1
Halamphora kevei Ács et Levkov	0.2	0.2	1.2	30.3	2
Halamphora oligotrophenta (Lange-Bertalot) Levkov	<0.1	0.2	0.2	3.0	1
Halamphora paraveneta (Lange-Bertalot, Cavacini, Tagliaventi et Alfinito) Levkov	<0.1	0.2	0.5	6.1	1
Halamphora tumida Hustedt) Levkov comb. nov.	0.2	1.5	4.4	6.1	1
Halamphora veneta (Kützing) Levkov	0.4	0.2	1.7	48.5	3
Hantzschia abundans Lange-Bertalot	0.0	0.2	0.5	18.2	1
Hantzschia vivax (W. Smith) Peragallo var. *vivax*	<0.1	0.2	0.2	6.1	1
Hippodonta hungarica (Grunow) Lange-Bertalot, Metzeltin et Witkowski	0.5	0.2	15.8	15.2	1
Mayamaea atomus (Kützing) Lange-Betralot var. *permitis* (Hustedt) Lange-Bertalot	0.1	0.5	2.0	9.1	1
Melosira varians C. Agardh	0.1	1.7	1.7	3.0	1
Navicula capitatoradiata Germain	<0.1	0.5	0.5	3.0	1
Navicula cryptocephala Kützing	0.1	0.2	2.0	15.2	1
Navicula cryptotenella Lange-Bertalot	<0.1	0.5	0.6	6.1	1
Navicula cryptotenelloides Lange-Bertalot	<0.1	0.2	0.2	3.0	1
Navicula duerrenbergiana Hustedt	<0.1	0.2	0.2	3.0	1
Navicula oblonga (Kützing) Kützing	0.1	0.2	0.7	21.2	1
Navicula radiosa Kützing	<0.1	0.2	0.2	3.0	1
Navicula salinarum Grunow var. *salinarum*	1.4	0.2	7.9	72.7	1
Navicula veneta Kützing	8.3	0.4	26.3	100.0	1
Navicula wiesneri Lange-Bertalot	23.3	0.8	92.3	93.9	1
Navycimbula pusilla (Grunow) Krammer	0.2	0.2	3.0	18.2	1
Nitzschia acicularis (Kützing) W. Smith	<0.1	0.5	0.5	3.0	1
Nitzschia amphibia Grunow	0.1	0.2	3.3	9.1	1
Nitzschia aurariae Cholnoky	0.3	0.2	3.4	21.2	1
Nitzschia bergi Cleve-Euler	0.1	0.2	1.3	18.2	1
Nitzschia capitellata Hustedt	<0.1	0.5	1.0	6.1	1
Nitzschia communis Rabenhorst	0.2	0.5	4.7	15.2	1
Nitzschia commutata Grunow	0.1	1.0	2.3	9.1	1
Nitzschia dissipata (Kützing) Grunow ssp. *dissipata*	<0.1	0.2	0.2	3.0	1
Nitzschia elegantula Grunow	<0.1	0.3	0.5	6.1	1
Nitzschia fonticola Grunow	<0.1	0.3	0.3	3.0	1
Nitzschia frustulum (Kützing) Grunow	12.2	0.2	38.4	100.0	1
Nitzschia gracilis Hantzsch	0.1	0.2	1.7	21.2	1
Nitzschia inconspicua Grunow	1.6	0.2	9.9	60.6	1
Nitzschia liebetruthii Rabenhorst	<0.1	0.7	0.7	6.1	1
Nitzschia palea var. *debilis* (Kützing) Grunow	0.1	0.2	2.8	9.1	1
Nitzschia palea (Kützing) W. Smith var. *palea*	1.7	0.2	25.8	42.4	1
Nitzschia palea var. *tenuirostris* sensu Lange-Bertalot	1.4	0.2	13.9	33.3	1
Nitzschia paleaceae Grunow	3.4	0.2	77.4	39.4	1
Nitzschia pusilla Grunow	0.2	0.2	1.2	33.3	1
Nitzschia reversa W. Smith	0.3	0.9	5.9	9.1	1
Nitzschia salinarum Grunow	<0.1	0.2	0.2	3.0	1
Nitzschia sigma (Kützing) W. Smith	<0.1	0.5	0.5	3.0	1
Nitzschia solita Hustedt	1.0	0.2	10.3	54.5	1
Nitzschia sp. 1	<0.1	0.3	0.5	6.1	1
Nitzschia sp. 3	0.2	0.2	3.1	30.3	1
Nitzschia supralitorea Lange-Bertalot	1.1	0.5	13.2	48.5	1
Nitzschia thermaloides Hustedt	<0.1	0.5	0.5	6.1	1
Nitzschia valdecostata Lange-Bertalot et Simonsen	0.2	0.3	3.2	12.1	1
Nitzschia vitrea G. Norman var. *vitrea*	0.7	0.2	7.9	30.3	1
Pinnularia brebissonii (Kützing) Rabenhorst	0.3	0.2	1.5	57.6	1
Pinnularia kneuckerii Hustedt	0.2	0.7	3.5	15.2	1
Pinnularia oriunda Krammer	<0.1	0.5	0.5	3.0	1
Pseudostaurosira brevistriata (Grunow) D.M. Williams & Round	0.1	0.7	3.0	6.1	1
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot	0.1	0.2	1.2	9.1	1
Rhoicosphenia adriatica Caput Michalic & Levkov	0.2	0.2	3.3	27.3	1
Rhoicosphenia lacustris Levkov	0.3	0.2	3.8	36.4	1
Rhopalodia gibba (Ehrenberg) Müller	0.5	0.5	6.3	18.2	1
Rhopalodia operculata (Agardh) Håkansson	0.6	0.2	7.9	39.4	1
Scoliopleura peisonis Grunow	0.1	0.2	0.8	15.2	1
Sellaphora capitata D.G.Mann & McDonald, S.M.	0.2	0.2	2.1	21.2	1
Staurophora wislouchii (Poretzsky et Anisimowa) D. G. Mann	2.7	0.2	31.5	42.4	1
Staurosira venter (Ehrenberg) Grunow	<0.1	0.5	0.5	3.0	1
Stephanodiscus minutulus (Kützing) Krieger	0.1	0.2	2.2	12.1	1
Stephanodiscus parvus Stoermer et Håkansson	2.2	0.2	24.4	42.4	1
Surirella brebissoii Krammer et Lange-Bertalot	0.8	0.2	8.5	33.3	1
Surirella brightwelli W.Smith	<0.1	0.3	0.3	6.1	1
Surirella ovalis Brébisson	0.1	0.2	0.8	12.1	1
Surirella peisonis Pantocsek	<0.1	0.3	0.8	6.1	1
Tabularia fasciculata (Agardh) D. W. Williams et Round	3.1	0.5	26.3	54.5	1
Tryblionella apiculata W. Gregory	5.6	0.5	34.0	87.9	1
Tryblionella gracilis W. Smith	0.1	0.2	0.7	15.2	1
Tryblionella hungarica (Grunow) Frenguelli	5.4	0.2	24.8	87.9	1
Ulnaria ulna (Nitzsch) Compère	0.1	0.2	0.7	15.2	1

Appendix 7 *The main environmental parameters measured in the three reconstructed pans and reference sites*

	unit	Legény-tó			Nyéki-szállás			Borsodi-dűlő			Reference		
		mean	SD	range	mean	SD	range	mean	SD	range	mean	SD	range
Oxygen saturation	%	94.5	26.5	22.6 - 136.2	110.1	52.5	35.4 - 192.5	94.5	23.3	22.8 - 129.5	219.3	15.7	193.9 - 227.9
pH		8.9	0.4	7.8 - 9.7	8.9	0.5	7.8 - 9.8	9.0	0.3	8.1 - 9.6	9.3	0.2	9.1 - 9.4
Conductivity	µS cm^{-1}	1967	410	1134 - 2680	2820	1447	754 - 5920	2360	1174	1061 - 4820	6071	4694	3120 - 13650
Temperature	°C	14.3	7.2	2.7 - 24.4	14.8	8.9	2.2 - 25. 6	12.9	7.9	2.2 - 25. 6	-	-	-
Irradiance level	µmol m^{-2}s^{-1}	477	393	15 -1500	457	516	22 - 1700	619.9	717.9	35 - 2150	-	-	-
COD	O$_2$ mg L^{-1}	23.4	13.5	11.1 - 69.7	39.8	30.4	17.9 - 131.1	29.9	16.0	9.7 - 67.2	44.1	17.4	31.8 - 72.0
Cl$^-$	mg L^{-1}	177.6	71.0	66.3 - 290.5	221.4	140.9	61.2 - 550.7	230.2	153.7	66.7 - 729.5	12.6	14.4	4.1 - 35.8
CO$_3^{2-}$	mg L^{-1}	87.1	70.8	0 - 297	97.4	116.3	0 - 381	82.3	69.6	0 - 213	378.4	220	177.0 - 708.0
HCO$_3^-$	mg L^{-1}	443.3	194.0	37.2 - 710.7	478.7	282.7	33.6 - 1024.8	570.1	345.0	42.7 - 1446.3	1009.9	529.2	701.5 - 1866.6
SO$_4^{2-}$	mg L^{-1}	345.3	280.8	73.7 - 1111.9	391.2	305.8	86.5 - 1098.5	297.9	237.8	64.2 - 995.8	657.4	689.0	102.0 - 1734.0
NO$_2$-N$^-$	µg L^{-1}	13.8	20.3	0.3 - 82.7	20.3	24.9	3.4 - 82.2	9.5	16.6	2.1 - 71.8	0.1	0.1	0.01 - 0.2
NO$_3$-N	mg L^{-1}	0.6	0.6	0.1 – 3.1	0.9	1.3	0.1 – 3.4	0.4	0.2	0.1 – 0.7	-	-	-
NH$_4^+$-N	mg L^{-1}	0.2	0.2	0 - 0.7	0.1	0.1	0 - 0.4	0.1	0.1	0 - 0.2	1.5	2.2	0.2 - 5.0
SRSi	mg L^{-1}	10.0	6.5	0.4 - 20.7	11.8	6.8	0.6 - 25.5	6.6	5.5	0.5 - 21.4	1.9	0.8	1.0 - 2.9
SRP	µg L^{-1}	97.9	213.8	2 - 1004.2	301.5	401.8	5.1 - 1216.8	128.6	95.4	5.9 - 351.8	303.8	273.1	25.0 - 682.5
TP	µg L^{-1}	246.1	331.6	2.9 - 1535.7	919.2	989.9	172.9 - 3519.5	526.4	385.3	147.6 - 1670.9	766.4	399.9	414.6 - 1374.6
Colour	mg Pt^{-1}	87.1	46.3	28.3 - 196.1	211.2	172.8	70.3 - 787.6	145.3	75.4	53.5 - 334.6	116.7	51.9	54.3 - 159.2

Appendix 8 *Canonical correspondence analysis (CCA) based on the main environmental variables (C) and diatom assemblages (B) in the studied sites including references and reconstructed pans (A) (plus and yellow ellipse: Legény-tó; open diamond and red ellipse: Borsodi-dűlő; open triangle and green ellipse: Nyéki-szállás; times and blue ellipse: reference pans; Cond: conductivity and Pt: water colour*



Appendix 9 *The indicator values of indicator species for the pans based on the IndVal analysis (constancy: the percentage of the samples where the each taxon was presented; B: Borsodi-dűlő, L: Legény-tó, N: Nyéki-szállás, R: reference site)*

Code	Species	IndVal	Comp A	Comp B	Mean abundance (%)	Constancy (%)	Site
CBUD	*Craticula buderii* (Hustedt) Lange-Bertalot	0.70	0.77	0.63	0.62	87.8	R
HDOM	*Halamphora dominici* Ács & Levkov	0.67	0.89	0.50	0.16	84.7	R
HSUO	*Halamphora subcapitata* (Kisselew) Levkov	0.61	0.99	0.38	0.48	83.7	R
ADMI	*Achnanthidium minutissimum* (Kützing) Czarnecki var. *minutissimum*	0.92	0.86	0.97	5.31	90.8	L
ACOP	*Amphora copulata* (Kützing) Schoeman and Archibald	0.80	0.95	0.67	0.83	90.8	L
CSIL	*Caloneis silicula* (Ehrenberg) Cleve	0.52	0.87	0.31	0.06	84.7	L
CNCI	*Cymbella neocistula* Krammer	0.77	0.89	0.67	0.48	90.8	L
ESOR	*Epithemia sorex* Kützing	0.56	0.76	0.41	0.17	87.8	L
FUAT	*Ulnaria acus* (Kützing) Aboal	0.69	0.93	0.51	0.52	88.8	L
FFAM	*Fragilaria famelica* (Kützing) Lange-Bertalot	0.46	0.93	0.23	0.18	79.6	L
GOLI	*Gomphonema olivaceum* (Hornemann) Brébisson	0.76	0.99	0.59	1.27	85.7	L
HHUN	*Hippodonta hungarica* (Grunow) Lange-Bertalot, Metzeltin and Witkowski	0.75	0.92	0.59	0.29	89.8	L
MSMI	*Mastogloia sp.*	0.49	0.84	0.28	0.15	85.7	L
NCTO	*Navicula cryptotenelloides* Lange- Bertalot	0.56	1	0.31	0.14	80.6	L
RGIB	*Rhopalodia gibba* (Ehrenberg) Müller	0.66	0.94	0.46	0.71	91.8	L
FULN	*Ulnaria ulna* (Nitzsch) Compère	0.60	0.87	0.41	0.15	92.9	L
GYOB	*Gyrosigma obtusatum* (Sullivant & Wormley) C.S.Boyer	0.62	0.95	0.41	0.37	80.6	B
HAMP	*Hantzschia abundans* Lange-Bertalot	0.68	0.96	0.48	1.19	80.6	B
NACI	*Nitzschia acicularis* (Kützing) W.Smith	0.37	1	0.14	0.03	79.6	B
NIGR	*Nitzschia gracilis* Hantzsch	0.54	0.64	0.45	0.26	82.7	B
SHAN	*Stephanodiscus hantzschii* Grunow	0.49	1	0.24	0.25	91.8	B
SHTE	*Stephanodiscus hantzschii* f. *tenuis* (Hustedt) H.Håkansson & E.F.Stoermer	0.62	1	0.38	0.66	91.8	B
STIN	*Cyclostephanos invisitatus* (Hohn & Hellermann) Theriot, Stoermer & Håkasson	0.45	0.96	0.21	0.08	79.6	B
SPAV	*Stephanodiscus parvus* Stoermer and Håkansson	0.64	0.99	0.41	4.03	91.8	B
GPAS	*Gomphonema parvulum* f. *saprophilum* Lange-Bertalot & Reichardt	0.37	1	0.14	0.04	79.6	N
NWIE	*Navicula wiesneri* Lange-Bertalot	0.92	0.85	1	9.63	92.9	N
NICO	*Nitzschia commutata* Grunow	0.36	0.95	0.14	0.07	79.6	N
NINC	*Nitzschia inconspicua* Grunow	0.63	0.72	0.55	0.76	87.8	N
ROPE	*Rhopalodia operculata* (Agardh) Håkansson	0.58	0.91	0.36	0.20	91.8	N
DITE	*Diatoma tenuis* Agardh	0.65	0.90	0.47	1.83	87.8	R + L
NAVY	*Navicymbula pusilla* Grunow	0.80	0.94	0.68	1.13	90.8	R + L
ACOS	*Anomoeoneis costata* (Kützing) Hustedt	0.47	1	0.22	0.06	81.6	R + B
CMEN	*Cyclotella meneghiniana* Kützing	0.84	0.9	0.79	2.67	88.8	L + B
EPSU	*Entomoneis paludosa* var. *subsalina* (W. Smith) Reimer	0.83	1	0.69	4.88	86.7	L + B
SBRE	*Surirella brebissonii* Krammer & Lange-Bertalot	0.80	0.88	0.74	2.85	92.9	L + B
NTEN	*Nitzschia palea* var. *tenuirostris* Grunow	0.67	0.95	0.47	1.21	86.7	L + B
NTHE	*Nitzschia thermaloides* Hustedt	0.64	1	0.41	0.36	86.7	L + B
NAUR	*Nitzschia aurariae* Cholnoky	0.59	0.99	0.35	2.18	79.6	L + B
FBRE	*Pseudostaurosira brevistriata* (Grunow) D.M.Williams & Round	0.51	1	0.26	0.25	91.8	L + B
NSAL	*Navicula salinarum* var. *salinarum* Grunow	0.72	0.87	0.59	1.05	87.8	L + N
NHUN	*Tryblionella hungarica* (Grunow) D.G. Mann in Round, Crawford and Mann	0.79	0.93	0.67	2.51	91.8	B + N
CAMB	*Craticula ambigua* (Ehrenberg) D.G. Mann	0.78	0.97	0.63	1.10	81.6	B + N
ABIN	*Achnanthes brevieps* var. *intermedia* Agardh	0.66	1	0.43	0.40	52.0	B + N
NPAL	*Nitzschia palea* var. *palea* (Kützing) W.Smith	0.84	0.95	0.74	5.45	89.8	R + L + B
SSOL	*Scoliopleura peisonis* Grunow	0.69	0.74	0.51	0.05	91.8	R + L + N
AVEN	*Halamphora veneta* Kützing	0.8	0.97	0.66	0.51	82.7	R + B + N
NCON	*Tryblionella apiculatus* W. Gregory	0.92	0.92	0.92	3.94	100.0	L + B + N
FSUB	*Fallacia pygmaea* ssp. *subpygmaea* Lange-Bertalot, Cavicini, Tagliaventi and Alfinito	0.75	1	0.57	0.75	83.7	L + B + N
FPYG	*Fallacia pygmaea* (Kützing) A.J. Stickle and D.G. Mann	0.75	1	0.56	0.65	86.7	L + B + N

Appendix 10 *The main environmental parameters determined generally the benthic diatom communities*

	Study site	Species number	Sample number	Main environmental variables	Statistical methods	Reference
1	Mid-altitude streams in Italy	174	72	N–NO$_3$, TP, Cl$^-$, conductivity, pH	CCA (Canonical Correspondence Analyses)	Bona et al., 2007
2	Boreal streams in Finland	448	223	Catchment area, colour, altitude, TP, TN, pH	RDA (Redundancy Analysis)	Heino et al., 2010
3	Mid-Appalachian stream in USA	522	199	Conductivity, pH, TP, TN, Cl$^-$	CCA	Hill et al., 2001
4	Schwaartzbaach, Consdorferbaach, Sauerbaach and Hemeschbaach streams in Luxemburg	65	20	Conductivity, SO$_4^{2-}$, NH$_4^+$, potassium, TOC, pH, temperature, Mg^{2+}, slope	PCA (Principal Component Analysis), CCA	Hlúbiková et al., 2014
5	Streams in Hungary and Sweden	246	102	Ca^{2+}, alkalinity, Mg^{2+}, pH, conductivity, NH$_4^+$	CCA	Kovács et al., 2006
6	Muga, Fluvia, Ter, Tordera, Besos, Llobregat, Segre, Foix, Gaia, Francoli sterams in Spain	195	57	Temperature, conductivity, altitude, NO$_3^-$, BOD, stream order	CCA	Leira, Sabater, 2005
7	Rodríguez Stream in Argentína	66	24	Temperature, conductivity, BOD, COD, NH$_4^+$, NO$_3^-$, NO$_2^-$, SRP	PCA , t-test	Licursi, Gómez, 2009
8	Corona stream in Portugal	133	28	Conductivity, pH, HCO$_3^-$, SO$_4^{2-}$, Ca^{2+}, Cl$^-$, Cu^{2+}, Li$^+$, Mg^{2+}, Na$^+$, B, Mn, Ni, Zn, Co, Fe	CCA	Luís et al., 2011
9	Nairobi River in Kenya	190	50	Altitude, DO, pH, NO$_3^-$, NO$_2^-$, Conductivity, PO$_4^{3-}$, COD, alkalinity	CCA	Ndiritu et al., 2006
10	Cozine creek in Oregon	159	25	SiO$_2$, NH$_4^+$, ANC, pH, TN	CCA	Pan et al., 2004
11	Buck Creek in the Adirondacks, USA	27	69	Water level, Cl$^-$, SO$_4^{2-}$, Mg^{2+}, organic and inorganic monomeric Al, DOC, pH, NO$_3^-$	RDA, MANOVA (Multivariate Analysis of Variance)	Passy, 2006
12	Mesta River in Bulgaria	47	99	Current velocity, phosphates, nitrates	ANOVA (Analysis of Variance)	Passy, 2007
13	Streams in Ontario	231	41	Watershed area, wetland and urban area, conductivity, TP, Cl$^-$, DOC, TDN, TSS	RDA	Porter-Goff et al., 2013
14	USA rivers and streams	1548	2735	Temperature, pH, water mineral content	CCA	Potapova and Charles, 2002
15	Headwater streams in Luxembourg	411	289	NO$_2^-$, DO, TP, Carbonate hardness, NO$_3^-$, pH	CCA, forward selection	Rimet et al., 2004
16	Boreal stream in Finland	212	141	Conductivity, TP, pH, latitude, colour, turbidity	CCA, PCA	Soininen et al., 2004
17	Felent creek in Turkey	117	41	Temperature, conductivity, pH	CCA	Solak et al., 2012
18	Torna strearm, Hungary			Temperature, irradiance level, DO, TN, COD, conductivity, DO%, Cl$^-$, discharge	PCA, CCA	Stenger-Kovács et al., 2013
19	46 rivers, brooks, and ditches in the islands of Hiiumaa and Saaremaa and in West Estonia	205	75	Temperature, BOD, SRP, NO$_2^-$, NO$_3^-$, pH, NH$_4^+$, N:P	RDA	Vilbaste & Truu, 2003
20	Clear Creek, Deep Creek, Johnson Creek in Oregon, USA	84	45	Conductivity, SRP, NO$_3^-$, NO$_2^-$, temperature, turbidity	CCA	Walker & Pan, 2006
21	Grand River, Ontario, in Canada	148	186	Alkalinity, BOD, TP, conductivity, suspended solids, NO$_3^-$	CCA	Winter and Duthie, 2000