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Ecophysiological plasticity of different algal taxa

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"Measure what is measurable, and make measurable what is not so."

Galileo Galilei

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Ph.D. Dissertation

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ECOPHYSIOLOGICAL PLASTICITY OF DIFFERENT ALGAL TAXA

Thesis for obtaining a PhD degree in the Doctoral School of Chemistry and Environmental Sciences of the University of Pannonia

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Abbreviations

P – I curve – Photosynthesis-light intensity curve

PAR – Photosynthetically active radiation (400-800 nm)

P^B_{max} **–** Biomass specific maximal photosynthetic activity

P_s **–** Biomass specific maximal photosynthetic activity in a lack of photoinhibition

R^B **–** Biomass specific respiration

I_k **–** Photoadaptation parameter

I_c **–** Compensation light intensity

α **–** Light utilization parameter

β **–** Photoinhibition

μ **–** Specific growth rate

DO – Dissolved oxygen

Content

Abstract

Inland waters provide diverse habitats. Most of the species of inland waters are sensitive to the changes of environmental factors and also to the most important environmental problem of the 21th century: the global climate change. Previous experiences have shown that the changes of one (or more) environmental factor(s) like temperature, pH or conductivity could result in the changes of entire ecosystems. The present dissertation was aimed at examining ecophysiological effects of three environmental factors under laboratory conditions, namely: temperature, light intensity and conductivity. Specifically:

i. to examine the effect of temperature and light intensity on the photosynthetic activity of different algal and cyanobacterial species to reveal the species specific differences between the photosynthetic response with a special focus on a rapidly spreading group of cyanobacteria;
ii. using the determined photosynthetic parameters to estimate the plasticity of the species along environmental scales with applying literary methods or develop a new one;
iii. to examine the ecophysiology of two East African strains of *Limnospira fusiformis* and *Picocystis salinarum* under wide ranges of temperature, light intensity and conductivity and also to reveal the effect of fast conductivity changes on the coexistence of the species.

For these purposes, monocultures were set up using own isolations (one cell isolation), species from other collections and also natural samples if the sample were highly dominated by one single species. The major conclusions of the examinations are the following:

i. The photosynthetic activity of the selected 16 species showed strong temperature and light intensity dependence, confirming the literary models. However, the reaction norms were species specific with respect to both temperature and light intensity. Though high variability was detected in all examined phyla, cyanobacteria had the highest photosynthetic activity both as a group and also the highest photosynthetic activity was presented by a cyanobacterium: *Limnospira fusiformis*. Also, the highest temperature optima were related to cyanobacterial species.
ii. Plasticity estimating methods in the scientific literature calculate with the ratios of the examined variables, consequently they overestimate the significance of relative changes. Species with low photosynthetic activity (like *Monoraphidium griffithii* in this research) are presented by these methods as highly plastic species due the high relative change in their P^B_{max}. Comparison of the length of reaction norms of species along wide range of

temperature to a reference (CLP - zero plasticity) calculate with both the ratio of change and the absolute values along the temperature scale. However the limitation of this method is that it does not allow the comparison of different units (for which an example is included: comparing data of planktonic and attached algal species).

iii. The photosynthetic characteristics of the two examined African species differed greatly: high level of photosynthetic activity coupled with high temperature and light intensity optima of *Limnospira fusiformis* were determined. In contrast, *Picocystis salinarum* had lower photosynthetic activity by an order of magnitude, with also lower temperature and light intensity optima. Tolerance or even preference of high conductivity of *Picocystis salinarum* was observed, especially if the high conductivity was provided by carbonate forms. Rapid changes of conductivity favoured the picoalga against *Limnospira fusiformis*.

Zusammenfassung

Binnengewässer bieten für die Lebewesen diverse Habitate. Sie reagieren auf Änderungen von Umweltfaktoren und ebenso auf das größte Umweltproblem des 21 Jahrhunderts, dem globalen Klimawandel. Die Erfahrungen zeigen, dass Änderungen eines oder mehrerer Faktoren, z.B. Temperatur, pH-Wert oder Leitfähigkeit zu Änderungen des gesamten Ökosystems und ihrer biotischen Struktur und Funktion führen können. Die vorliegende Dissertation hat zum Ziel, den ökophysiologischen Effekt der Umweltfaktoren Temperatur, Lichtintensität und Leitfähigkeit unter Laboratoriumsbedingungen auf verschiedene Primärproduzenten zu untersuchen. Dabei stehen folgende Aspekte im Mittelpunkt:

I. Analyse des Effektes von Temperatur und Lichtintensität auf die photosynthetische Aktivität verschiedener Cyanobakterien- und Algenarten, um artspezifische Unterschiede im photosynthetischen Verhalten aufzudecken, wobei der Fokus auf die weitverbreiteten Cyanobakterien liegt;
II. Anwendung der ermittelten photosynthetischen Paramenter zur Bewertung der Plastizität der Arten entlang von Umweltindizes aus der Literatur und Entwicklung eines neuen Index‘;
III. Untersuchung der Ökophysiologie von zwei Phytoplanktern aus Ostafrika, Limnospira fusiformis und Picocystis salinarum, unter verschiedenen Temperaturen, Lichtintensitäten und Leitfähigkeiten, um die Koexistenz der beiden Organismen unter sich schnell und dramatisch ändernden Bedingungen zu ergründen.

In die Experimente wurden eigene unialgale Isolate und Stämme aus Kultursammlungen sowie Freilandproben, die von Einzelarten dominiert wurden, einbezogen. Folgende Hauptresultate wurden ermittelt:

I. Die photosynthetische Aktivität von 16 ausgewählten Arten zeigte eine starke Abhängigkeit von Temperatur und Lichtintensität. Die Modelle aus der Literatur konnten bestätigt werden. Starke art- und stammspezifische Reaktionen auf Temperatur und Lichtintensiät wurden beobachtet. Die höchste photosynthetische Aktivität und das höchste Temperaturoptimum wurden bei Cyanobakterien, speziell bei *Limnospira fusiformis* ermittelt.
II. Plastizitätsbewertungsmethoden in der wissenschaftlichen Literatur rechnen mit den Verhältnissen der untersuchten Variablen, folglich überschätzen sie die Bedeutung der relativen Veränderungen. Arten mit geringer photosynthetischer Aktivität (wie

Monoraphidium griffithii in dieser Untersuchung) werden durch diese Methoden aufgrund der hohen relativen Änderung ihrer P^B_{max} als hochplastische Arten dargestellt. Der Vergleich der Länge der Reaktionsnormen der Arten entlang eines breiten Temperaturbereichs mit einer Referenz (CLP - Null-Plastizität), berücksichtigt sowohl das Verhältnis der Änderung als auch die absoluten Werte entlang der Temperaturskala. Die Einschränkung dieser Methode besteht jedoch darin, dass sie den Vergleich verschiedener Einheiten nicht zulässt (hierfür ein Beispiel für den Vergleich von Daten planktonischer und sessiler Algenarten).

III. Die photosynthetische Charakteristik der beiden untersuchten Arten aus einem ostafrikanischen Sodasee unterschied sich stark: Bei *Limnospira fusiformis* wurde eine hohe photosynthetische Aktivität bei gleichzeitig hohen Temperatur- und Lichtintensitätsoptima festgestellt, bei *Picocystis salinarum* dagegen eine um eine Größenordnung niedrigere photosynthetische Aktivität bei niedrigen Temperatur- und Lichtintensitätsoptima. Es wurde eine Toleranz oder sogar Präferenz für eine hohe Leitfähigkeit von *Picocystis salinarum* beobachtet, insbesondere wenn die hohe Leitfähigkeit durch Karbonatformen bereitgestellt wurde. Schnelle Änderungen der Leitfähigkeit begünstigen die Picoalge gegenüber *Limnospira fusiformis*.

Kivonat

A felszíni vizek változatos élővilágnak adnak otthont. Legtöbbjük igen érzékenyek az abiotikus környezeti tényezők változására, így a XXI. század legnagyobb környezeti problémájára, a globális klímaváltozásra is. A tapasztalatok alapján bármely fizikai illetve kémiai paraméterben (pl. hőmérséklet, pH, vezetőképesség) bekövetkező változás biotikus változások sorát indíthatja el, mely gyakran az ökoszisztéma egész rendszerére kihat, azt alapvetően változtatja meg. Jelen kutatás alapvető célja három környezeti változó, a hőmérséklet, a fényintenzitás és a vezetőképesség ökofiziológiai hatásának vizsgálata labororatóriumi körülmények között, az alábbi fő szempontok szerint:

i. a hőmérséklet és fényintenzitás fotoszintézisre gyakorolt hatásának vizsgálata több, különböző törzshöz tartozó faj esetében, a fajspecifikus különbségek feltárása, különös tekintettel a cianobaktériumokra, melyek világszerte tapasztalt terjedésének egyik fő okaként a magasabb hőmérséklet preferenciát jelölték meg;
ii. a meghatározott fotoszintetikus paramétereket felhasználva egy olyan index keresése az irodalomban, vagy egy olyan új index létrehozása mellyel a fajok fotoszintézisének plaszticitása becsülhető környezeti változók széles skálája mentén;
iii. Két Kelet-Afrikából származó törzs (*Limnospira fusiformis* és *Picocystis salinarum*) ökofiziológiai vizsgálata a fény, a hőmérséklet és a vezetőképesség széles tartományában, valamint a gyors vezetőképesség változás hatásának vizsgálata a két faj koegzisztenciájára.

A fenti kérdések megválaszolásának céljából egysejt izolálással létrehozott tiszta tenyészetek mellett más gyűjteményekből kapott fajok illetve természetből vett, egy faj által dominált minták vizsgálatára is sor került. A kísérletek segítségével az alábbi főbb megállapítások tehetők:

i. A vizsgált 16 faj esetében erős összefüggés állapítható meg a hőmérséklet és a fotoszintetikus aktivitás, illetve a fényintenzitás és a fotoszintetikus aktivitás között. A kapott eredmények megfelelnek a korábban leírt modelleknek, de a fajok válaszgörbéinek lefutása között jelentős különbségek vannak, mind hőmérséklet, mind fényintenzitás tekintetében. Bár minden vizsgált törzsön belül nagy változatosság (szórás) tapasztalható, mégis megállapítható, hogy a fotoszintetikus aktivitás tekintetében mind az átlag mind pedig a legnagyobb érték a cianobaktérium fajok esetében volt a legnagyobb, emellett magasabb hőmérséklet optimum is megfigyelhető volt ennél a törzsnél.

ii. A vizsgált irodalmi módszerek mindegyike (PP, CV, heatmap) a környezeti változók arányával dolgozik, így a relatív változások rendkívül hangsúlyosan jelennek meg az eredményekben. Ez okozhatta, hogy az egyik legalacsonyabb fotoszintetikus aktivitást mutató faj (*Monoraphidium griffithii*) esetében mutatták ki az indexek a legnagyobb plaszticitást. Ezzel szemben a válasz görbék vizsgálata, illetve egy referencia állapothoz (amikor nincs plaszticitás) történő hasonlítása a relatív változások mellett a fajok fotoszintézisének abszolút értékeivel is számol. Ez az index a vizsgált fajok közül az első három helyre cianobaktériumot rangsorolt, valamint a nyolc legplasztikusabb fajból öt szintén ebbe a törzsbe tartozott.

iii. A vizsgált két faj fotoszintetikus karakterisztikája nagyban eltért: míg a *Limnospira fusiformis* esetében nagy fotoszintetikus aktivitást, magas hőmérséklet és fényintenzitás optimum került meghatározásra, addig a *Picocystis salinarum* esetében a fotoszintetikus aktivitás jóval alacsonyabb volt csakúgy, mint a hőmérséklet és fényintenzitás optimumok. A *Picocystis salinarum* esetében magas vezetőképesség tűrést, sőt preferencia volt tapasztalható, kiváltképp, ha a magas vezetőképességet karbonátok okozták. A gyors vezetőképesség változás két faj koegzisztenciájára gyakorolt hatásának vizsgálata során bizonyítást nyert, hogy a gyors változások az ezeknek a változásoknak jobban ellenálló pikoalgát részesítik előnyben.

1 General introduction

Living organisms need energy for maintaining their life processes and they can satisfy their need from two sources: chemical energy and/or light. Using light as energy source is the most important process on Earth since photosynthesis has been providing the oxygen to the atmosphere. Photosynthesis is the biological conversion of light energy to chemical energy (Falkowski and Raven 2007). The first step of photosynthesis is the absorption of light, then transfer the energy to reaction centers, where it is used in electrical charge separation (Falkowski and Raven 2007).

Exploring photosynthesis started in the 17th century with the work of J. B. van Helmont, Ingenhousz and Joseph Priestley. In the late 18th century, Jean Senebier identified carbon dioxide as the main nutrients for plants. In the early19th century N.T. de Saussure found that the carbon dioxide reduction could be described analogously with the known process of animals' respiration but in the opposite direction. This is lead to the well-known equation of photosynthesis:

$$6CO_2 + 6H_2O \xrightarrow{light} 6O_2 + 6C_6H_{12}O_6.$$

Later Pelletier and Caventou isolated and named chlorophyll (1817). In the middle 19th century Robert Meyer interpreted photosynthesis as the capture of light energy. In 1905 F.F. Blackman observed light-saturation curve and distinguished light and dark reactions. The conservation of light energy was separated from carbon dioxide fixation when R. Hill showed that isolated chloroplasts could produce oxygen. S. Ruben and M. Kamen proved that the emitted oxygen came from water during photosynthesis. Later on Melvin Calvin, Andrew Benson and James Bassham described the process of carbon assimilation in plants, which called Calvin-cycle (Gregory 1990).

As the groups of oxygenic photosynthetic microorganisms are in the focus of present dissertation, the following chapter is presents briefly some main steps of oxygenic photosynthesis.

1.1 Photosynthetic pigments of cyanobacteria and algae

The major photopigments in oxygenic photosynthetic organisms are chlorophylls (Chl). Chlorophylls are cyclic tetrapyrroles containing a distinctive five-membered ring (Larkum 2016, Wang 2020). There are five described chlorophylls in oxygenic photosynthetic species:

Chl *a*, Chl *b*, Chl *c*, Chl *d* and Chl *f*. The most important is chlorophyll *a*. Chl *a* exists in algae and cyanobacteria and Chl *a* content is responsible for a substantial part of the light harvesting, however there is a huge difference in the accessory pigments of different phyla. Green algae have Chl *b* besides Chl *a* and a structurally similar light-harvesting system as higher plants. (Larkum 2016, Wang 2020).

Carotenoids absorb light mainly in the 400-530 nm spectral range (Hashimoto et al. 2016, Wang 2020). Besides light harvesting, they also have the important role in protection against oxidative stress. In cyanobacteria usually β-carotene and different xanthophylls occur, however there some species with α-carotenes (Takaichi et al. 2012, Wang 2020). The composition and contents of carotenoids may change in response to light intensity: e.g. zeaxanthin concentration increase under high-light. In green algae and plants concentration of carotenoids changes in the so called xanthophyll cycle: rapid epoxidation and de-epoxidation cycle among zeaxanthin, antheraxanthin, and violaxanthin which is driven by the changed light conditions (Demmig-Adams 1990, Goss and Jakob 2010, Wang 2020), although in cyanobacteria this cycle has not been reported, and zeaxanthin may accumulate in high-light conditions through oxidation of β-carotene (Masamoto and Furukawa 1997, Wang 2020).

Cyanobacteria and Rhodophyta (and also some other phyla which have not been studied in present dissertation) species have phycobiliproteins, which play an important role in their light capture. Phycobiliproteins are able to harvest light in the 490–650 nm range, where chlorophylls and carotenoids not, or not efficiently. The evolution of these proteins is pretty unclear, it is said to be possible that these proteins evolved before chlorophylls. However, according to Larkum (2006), it is more likely that some chlorophylls evolved before phycobiliproteins, and phycobiliproteins evolved later to avoid the negative effect of shading (Larkum 2006, 2016).

1.2 Photopigment-binding protein complexes

Chlorophylls, carotenoids and bilins, are carefully arranged inside the pigment-binding protein complexes. The major protein complexes in oxygenic photosynthetic organisms are PSI and PSII (*Figure 1*). These complexes are associated with thylakoid membrane-embedded light-harvesting protein complexes (LHC) and/or extrinsic phycobilisomes (Wang 2020).

Photosystems are made up of a reaction centre core which is surrounding by the inner antenna and there is an associated intrinsic membrane-bound antenna or extrinsic phycobilisomes. In plants and algae, with rare exceptions the intrinsic chlorophyll-binding

antenna is three-helical transmembrane Chl *a*-/*b*-binding light-harvesting complexes (LHCs) (there are some algal species Chl *a*-/*c*-binding LHC). There are two main classes of LHCs: LHC I and LHC II. LHC I is associated with PS I, while LHC II is associated with PS II mainly (Wang 2020).

Red algae also have the extrinsic phycobilisomes as the major antenna system. There are three main components in assembled phycobilisomes: phycoerythrin, phycocyanin and allophycocyanin (Wang 2020).

Most cyanobacteria have two antenna systems, phycobilisomes and Chl-binding antenna systems. The Chl-binding light-harvesting systems is structurally different from the LHCs in eukaryotic photosynthetic organisms(Wang 2020). Cyanobacteria's PS I is a trimer and has extrinsic Chlorophyll *a*-/*b*-binding protein complexes. The core complex of PS I consists of 12 subunits, includes the reaction center core, small transmembrane proteins and 3 stromal subunits. The direct interaction between antenna and PS I is determined after isolation of antenna-PS I supracomplexes. Some cyanobacteria show interaction between phycobilisomes and PS I.

Photosystem II is a multiple protein subunit complex containing RC and intrinsic core antenna and typically arranges as a dimer. PsbA (D1) and PsbD (D2) are the core subunits in RC II and bind six Chls including the special pair of Chl a (P680). CP43 and CP47 are core antenna subunits and bind 13–16 chlorophylls individually. The extra loop of CP43 protein with D1 subunit together forms a binding dock for oxygen evolution center including Mn_4CaO_5 complexes(Wang 2020).

Central features of oxygenic photosynthesis are the sequentially coupled two photosytsems, photosystem II and photosystem I located in the thylakoid membrane and connected by the intersystem electron transport chain. This downhill electron transport chain chain consists of two mobile electron carriers, plastoquinone (PQ) in cyanobacteria and algae the integral membrane cytochrome b_6f (Cyt b6 f) complex.

Beyond being an oxidoreductase, the Cyt b6 f complex operates as a proton pump and couples the downhill, vectorial electron transport with an effective proton translocation.

1.3 Light Absorption and photosynthetic electron transport

The absorption of light causes a change in the energy state of the pigment molecules. A π electron from ground state according to a photon get into excited state (π^*) if the energy of the photon matches the energy gap between the ground and excited state of the π electron. There

are three de-excitation pathways. The first is re-radiation by fluorescence or luminescence, second is to transfer the energy to the environment in a form of heat, the third is the coupling of the excited-state energy dissipation to a chemical reaction (e.g. in the oxidation of a molecule). The energy can be transferred by two basic radiationless methods: the Förster mechanism and the Dexter mechanism. In the Förster mechanism energy transfer is the result of the resonance overlap between the wavefunctions of the singlet excited states of two molecules. In this process a photon is never physically transferred from the donor molecule to the acceptor to give fluorescence, but the excitation energy migrates as anexciton. The excitation migrates from molecule to molecule within the pigment matrix, randomly following overlapping wavefunctions of pigment molecules that alternate between the excited and ground state. This energy transfer is usually from a higher to a lower energy level (Falkowski and Raven 2007).

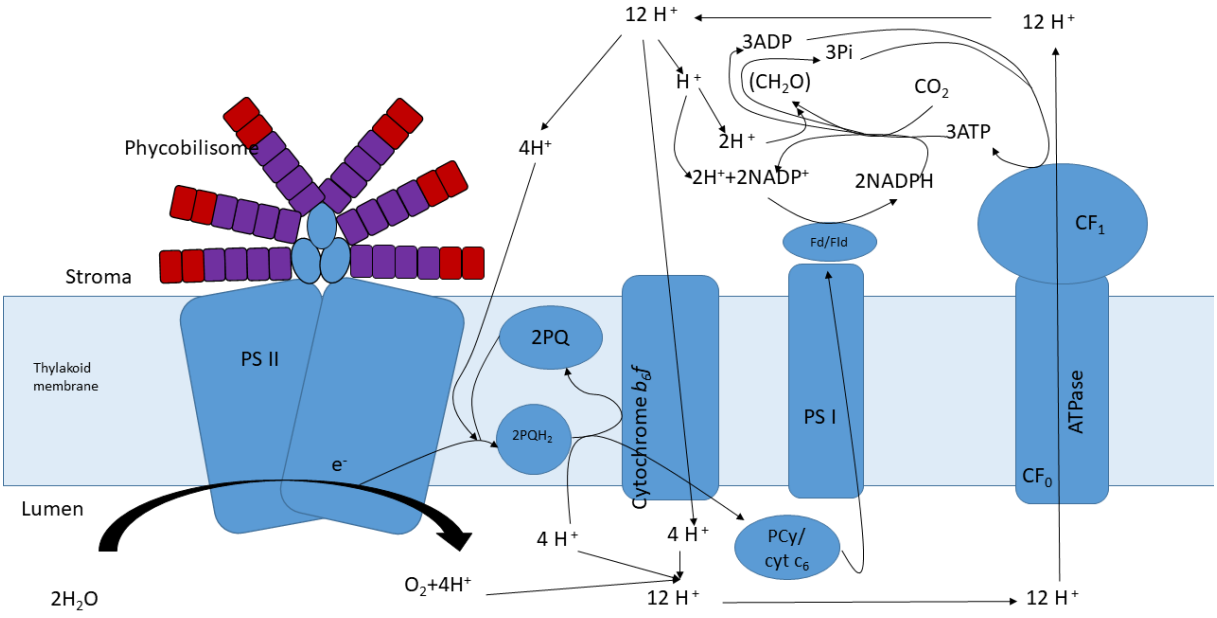

Figure 1 Overall scheme of photosynthetic electron and proton transport (after Falkowski and Raven 2007)

The excited states of the pigment molecules lead to a redistribution of electrons between the pigment molecules. Finally the energy of absorbed photons is used to be physically transferred from a donor via changing the electronic structure of pigment molecules. The lost electron is restored by the Mn containing centrum of PSII. The electrons gained from H_2O are used to reduce molecules in the electron transport chain. The main role of this process is to provide chemical reductants. These reductants used to assimilate inorganic carbon and chemical energy for further metabolic activity. It has a highly organized structure coordinate the electron and proton transfer (Falkowski and Raven 2007).

PSII, cytochrome b_6f and PSI are in a linear electron flow with the aim of generate ATP and NADPH, the ratio of the two product is about 2.7:2. The CO_2 assimilation requires 3:2 ratio, and also there are other processes and environmental factors which increase the ATP demand. Cyclic electron flow of PSI and cytochrome b_6f generate a proton gradient and ATP without reductants as a major ATP supply.

According to the Z-scheme, there are three segments of the electron transport chain: the donor side of PSII, which includes the reactions responsible for the injection of electrons into PSII from water; the intersystem electron transport chain, which includes all the carriers between PSII and PSI; and the acceptor side of PSI, in which the primary reducing agent, NADPH, is formed and exported for carbon fixation (Falkowski and Raven 2007).

1.4 Carbon assimilation

The NADPH and ATP created in the light reactions couple the light reactions to carbon fixation. About 95% of the NADPH and ~60% of the ATP from the light reaction used to assimilate and reduce inorganic carbon. The most important component of the carbon assimilation is an enzyme: ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (Falkowski and Raven 2007). Rubisco catalyses the assimilation of CO_2 into two molecules of 3-phosphoglycerate. The 3-phosphoglycerate in the presence of ATP and NADPD is reduced to glyceraldehyde 3-phosphate. Most of the glyceraldehyde 3-phosphate molecules are used to regenerate Rubisco. The organisms use the three carbon product (3-phosphoglycerate) that has not been regenerated in their life processes.

1.5 Primary affecting environmental factors

1.5.1 Light intensity

Another important environmental factor affecting photosynthesis is light intensity. There are several equations to describe the connection between the photosynthetic activity and light intensity (P-I) (Webb et al. 1974, Jassby and Platt 1976, Platt and Jassby 1976, Platt et al. 1980). According to the equations of these studies, the effect of light intensity on the photosynthetic activity could be divided into three phases. The first is the light limited phase, where the increasing light intensity increases the photosynthetic activity. Higher increasing of photosynthetic activity in this phase is suggest better light utilization, which could be estimated with the light utilization parameter, which is the initial slope of the P-I curve (α). The second is the light saturated phase where the photosynthetic activity reaches its highest value (P^B_{max}) at a well-defined light intensity (I_k). The third is the photoinhibited phase, where further increase of

light intensity results in decrease of photosynthetic activity, the estimator parameter of this negative is effect is the photoinhibition parameter (β), however this phenomenon not necessary occurs in each case and is species specific.

1.5.2 Temperature

Temperature is one of the most important environmental factor that can substantially affect both the community (Adrian et al., 2009, Winder & Sommer, 2012, Winder et al., 2012) and the individuals (Davison 1991). Temperature has major effect on all life processes of a plankton species, including photosynthesis. The temperature dependence or more precisely the positive connection between temperature and the photosynthetic activity is described in several studies (e.g. Collins and Boylen 1982, Padisák 2004, Falkowski and Raven 2007, Lengyel et al. 2015, 2020). Also the warming of aquatic habitats can select species: in general Cyanobacteria species prefer higher temperatures (Robarts and Zohary 1987, Coles and Jones 2000, Vona et al. 2004, Butterwick et al. 2005, Watkinson et al. 2005, Kosten et al. 2012, Üveges et al. 2012, Singh and Singh 2015, Yan et al. 2020) than others. The effect of temperature can usually be described with some kind of a Gaussian-curve, since typically there is a positive connection between temperature and photosynthetic activity, until reaches a maximum, than further increase of temperature has a negative effect, resulting in decreasing photosynthesis.

1.5.3 Conductivity

Conductivity or salinity could play essential role in determining plankton assemblages of saline habitats. Different sensitivity of competing species can be the key factor in often suddenly changing saline waterbodies. Conductivity can control and selectively favour species via ionic stress or by affecting biochemical processes like photosynthesis and also the growth of a species (Kebede 1997, Hasegawa et al. 2000, Munns 2002, Sudhir and Murthy 2004, Lázár et al. 2015, Lengyel et al. 2015, 2020). There are some well-known saline species, e.g. *Dunaliella salina* which can dominate the phytoplankton if the salinity exceed ~70 g L^{-1} (Gómez and González 2005, Liu et al. 2012, Padisák and Naselli-Flores 2021), and diatoms can be prominent in saline-alkaline ponds (Lázár et al. 2015, Lengyel et al. 2015, 2020).

The effect of conductivity, moreover the tolerance for its changes could be a key to understand unexpected changes in phytoplankton assemblages. As the empirical study by Krienitz (2018) suggested and confirmed by experimental studies (Kebede 1997), conductivity seems to be the key factor in determining the phytoplankton in East African alkaline saline lakes, and trough the phytoplankton also the overall ecosystem functions in these lakes.

2 Main objectives

The basic process of photosynthesis is similar in higher plats, algae and cyanobacteria. A further similarity is its very strong dependence on the various environmental factors. General trends of the different factors' effects can be described. Positive correlation between the temperature, light intensity and the photosynthetic activity is well studied, however this effect can be very species specific. Another important environmental factor, especially in saline habitats is conductivity. Also numerous studies has been discussed the effect of salinity and the changes of this factor on the different life processes of algae and cyanobacteria species.

The aim of this dissertation was to study the effect of some selected environmental factors (temperature, light intensity, conductivity) on the growth and photosynthesis of fresh- and saline alkaline water species under laboratory conditions using cross environmental scales. Accordingly, the main objectives were the following:

i. to examine the effect of temperature and light intensity on the photosynthetic activity of different algal and cyanobacterial species to reveal the species specific differences with a special focus on a rapidly spreading group: the cyanobacteria;
ii. using the previously determined photosynthetic parameter to estimate the plasticity of the species along environmental scales with applying literary methods or develop a new one;
iii. to examine the ecophysiology of two East African strains (*Limnospira fusiformis* and *Picocystis salinarum*) under wide ranges of both temperature, light intensity and conductivity and also to reveal the effect of fast conductivity changes on the coexistence of the species.

3 Temperature and light intensity dependent photosynthetic characteristics of some algae and cyanobacteria[1]

3.1 Introduction

Algae, including cyanobacteria, are a very diverse group of photosynthetic microorganisms concerning both their size and morphology. As primary producers, phytoplankton species play an essential role in the aquatic food webs, and are responsible for a great part, about a half, of the primary production of the Earth (Falkowski 1994, Field et al. 1998, Naselli-Flores et al. 2021). Phytoplankton communities are controlled by numerous environmental factors. Glibert (2016) listed twelve of them as most important ones: relative preference for differently oxidized nitrogen forms, availability of inorganic nitrogen and phosphorus, adaptation to different light intensity or being autotrophic/mixotrophic, cell motility, environmental turbulence, pigmentation quality, temperature, cell size, growth rate, production of toxins or reactive oxygen species, and the ecological strategy of the species. Some of these, besides their direct effect, can also affect indirectly the abundance and composition of the phytoplankton through e.g. the modification of the stratification pattern of e.g. dissolved oxygen in lakes (Winder and Sommer 2012, Selmeczy et al. 2018).

Temperature is one of the most important environmental factors that can affect phytoplankton as well benthic algal communities (Adrian et al., 2009, Winder & Sommer, 2012, Winder et al., 2012). Changes in temperature, especially the warming strongly affects the biological processes both in terrestrial and aquatic ecosystems either directly or via changing the physical and chemical environment (IPCC 2007, Paerl and Paul 2012, Winder and Sommer 2012). Moreover, temperature can selectively favour species: warming of the aquatic ecosystem could be more advantageous for some cyanobacteria species, rather than for members of any other phyla (Robarts and Zohary 1987, Coles and Jones 2000, Vona et al. 2004, Butterwick et al. 2005, Watkinson et al. 2005, Kosten et al. 2012, Üveges et al. 2012, Singh and Singh 2015, 2020, Yan et al. 2020).

[1] Parts of this chapter were published in the following papers:

Pálmai, T., Selmeczy, G.B., Szabó, B., G.-Tóth, L. & Padisák, J. 2016. A *Microcystis flos-aquae* fotoszintetikus aktivitása a Balaton keleti medencéjében 2015 nyarán Photosynthetic activity of *Microcystis flos-aquae* in the eastern basin of Lake Balaton in the summer of 2015. Hidrológiai Közlöny, 96:75–8.

Pálmai, T., Szabó, B., Hubai, K., Padisák, J. (2018). Photosynthetic performance of two freshwater red algal species. Acta Botanica Croatica, 77: 135-140. DOI:10.2478/botcro-2018-0010

Pálmai, T., Szabó, B., Kotut, K., Krienitz, L. & Padisák, J. 2020. Ecophysiology of a successful phytoplankton competitor in the African flamingo lakes: the green alga *Picocystis salinarum* (Picocystophyceae). Journal of Applied Phycology, 32:1813–1825. DOI: 10.1007/s10811-020-02092-6.

Temperature have huge effect on the ecosystem via affecting life processes of the microorganisms. It is already valid in case of short-lived organisms such as phytoplankton. Species with short generation time are able to respond rapidly to the environmental changes. Consequently, any change in the physical and chemical environment (e.g. pollution, drier or wetter seasons) can substantially change not only the flora but also the fauna (Naselli-Flores and Barone 2009). Drastic shifts in phytoplankton composition can crash a food web (especially if it is an extremely short and special "web" e.g. Krienitz et al., 2016). The short lifetime of phytoplankton species makes it easier to examine the effect of the environmental factors on their life processes (Padisák 1998).

Temperature has major impact on photosynthesis. Typically, the rate of photosynthesis increase progressively along a range of temperature (Collins and Boylen 1982, Davison 1991, Padisák 2004, Falkowski and Raven 2007, Lengyel et al. 2015, 2020). Despite general trends of the effect could be described, the response of the species could differ (Coles and Jones 2000, Vona et al. 2004, Butterwick et al. 2005, Staehr and Birkeland 2006, Kosten et al. 2012, Paerl and Paul 2012, Sommer et al. 2012, Üveges et al. 2012, Lengyel et al. 2015, Singh and Singh 2015).

An also very important environmental factor that affects photosynthesis is light intensity. The process of photosynthesis is well studied, and there are several equations to model its light intensity dependence (Jassby and Platt 1976, Platt and Jassby 1976, Platt et al. 1980, Wetzel and Likens 2000). The optimal light intensity for different planktic groups could differ: Bacillariophycae and cyanobacteria usually are able to tolerate low light levels (10-240 μmol m^{-2} s^{-1}) and some of them can grow at 5-10 μmol m^{-2} s^{-1}, in contrast the green algae are able to utilize higher range of light (100-500 μmol m^{-2} s^{-1}), but there are counterexamples too (e.g. *Microcystis* species) (Padisák 2004).

Cyanobacteria are the oldest known oxygen producers, with an age about 2.4 billion years (Shih and Matzke 2013). Nowadays, they have a broad geographical distribution, and can be found from the tropical to the polar regions. Cyanobacterial species not only occur in a wide range of geographical sites, but also dominate various benthic and planktic communities. They can form dense and sometimes also toxic blooms in both marine and freshwater environments (Whitton 2012). The global expansion of toxic (and also non-toxic) cyanobacteria has been a real threat nowadays. Several studies were aimed at describing this threat and also suggested the possible reason of this expansion (Paerl and Paul 2012, Sukenik et al. 2015, Huisman et al. 2018). Though there are several cyanobacteria which have high temperature optima,

unexpected occurrences of highly adaptive representatives of this phylum (Padisák 1997, Üveges et al. 2012) were also described. The so called “Blue-Green Algal Paradox” of Paerl (1988) describes it well: most of the cyanobacteria are sensitive to environmental changes, but cyanobacteria, as a group is adapted to wide range of environmental conditions including of environmental extremes (Paerl 1988, Padisák and Reynolds 1998).

Phytoplankton of inland fresh and saline alkaline waters usually dominated by species of various phyla, but the global expansion of cyanobacteria can affect these ecosystems, trophic cascades and geochemical cycles (Sukenik et al. 2015).

Photosynthetic measurements along wide ranges of both temperature and light intensity were carried out to reveal the differences between the temperature and also the light intensity dependence of the photosynthetic activity of planktic species with a special focus on cyanobacterial species.

3.2 Materials and methods

3.2.1 Isolation and cultivation

For photosynthetic measurements different types of strains were used. Beside own isolates, strains from culture collections were also used as well as natural samples dominated with certain target species. If a bloom was dominated by a single species (more than 90% of the biomass was provided by a single species) the sample was handled as monoculture. Other species were isolated from different habitats with single cell isolation method. Successfully isolated strains were kept in Erlenmeyer-flasks (0.5-5 L) at 19±1°C and 40 µmol photons m^{-2} s^{-1} in the Alga Culturing Laboratory of the Department of Limnology (University of Pannonia, Veszprém). Growth was followed by OD measurements at 750 nm with a Metertech SP-8001 UV-VIS spectrophotometer from a subsample of the homogenised culture for the species which forms homogeneous suspension and/or by microscopic investigation in the case of the filamentous species. Photosynthetic activities of sixteen species with different origin were measured. Their origin, type and the culturing medium is given in *Appendix 1*. The names of the species correspond to those available in the database of algaebase.com on 03.05.2020.

3.2.2 Determination of photosynthetic activities

The photosynthetic characteristics of the species were examined over a wide range of temperature and light intensities in order to determine the optima of the species and also of their temperature and light intensity tolerance ranges.

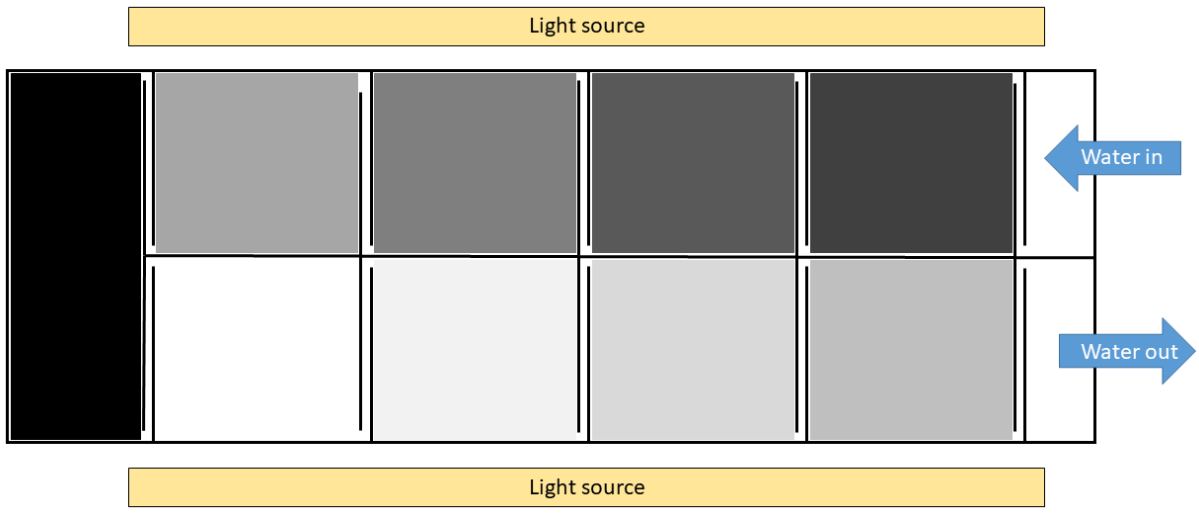

Figure 2 Graphical representation of the photosynthetron (top view): solid lines represent the glass walls and dotted lines represent the mirror walls of the cells of the aquarium system. A circulating water bath (Neslab RTE-211) is responsible for the specific temperature of the instrument via circulating distilled water in the photosynthetron. PAR is provided by daylight tubes (Tungsram F74), different light intensity is set with the number of the used light tubes and the number of used shielding foil.

Measurements were carried out in a special incubation system, the photosynthetron (Üveges et al. 2011). The photosynthetron (*Figure 2*) is an aquarium system with nine measuring cells filled up with distilled water. Specific measuring temperatures were provided by circulating the distilled water in the instrument with a circulating water bath (Neslab RTE-211) in the temperature range of 5 - 45°C. The nine measuring cells (*Figure 2*) provide different light intensities; the available light intensity sets range between 0 and 2200 μmol photons m^{-2} s^{-1}. Light intensity depends on three factors: number of used light tubes, number of used covering foils and the age of the light tubes. Due to the ageing of the tubes, light intensities varied between the measurements, but fitting exponential curves with the measuring data eliminates the effect of these differences. PAR was provided by daylight tubes (Tungsram F74) and light intensities were measured with a LI 1400 DataLogger (LI-COR) equipped with a spherical (4π) quantum sensor (US-SQS/L, Heinz Walz GmbH).

Measurements were performed with mass cultures in their exponential growth phases. Prior to carrying out the photosynthesis measurements, cultures from the culturing Erlenmeyer-flasks and fresh medium were placed in a plastic chamber with an approximate volume of 15 L (*Figure 3*). The sample requirement of the measurement depends on the number of applied light intensities and on the number of replicates. If nine light intensities were applied with three replicate of 250 mL Karlsruhe-flasks in each measuring cells, the net sample requirement of the measurement is 6750 mL. Calculating with the loss during the filling of the flasks and during rehomogenization the real sample need of a measurement is about 10 L.

After the homogenization of the sample in the 15 L plastic chamber, the culture was divided into Karlsruhe-flasks, with an approximate volume of 250 mL, (this type of flasks were used for the measurements in order to avoid gas exchange with the environment) in three replicates at each light intensity (in each measuring cells of the photosynthetron). Photosynthetic measurements were started at the lowest measuring temperature, it was usually 5°C, with a 1-h pre-incubation in dark. Photosynthetic activity of the samples was determined by measuring dissolved oxygen (DO) concentration with an IntelliCAL™ LDO101 sensor (Hach Lange). DO was measured at the beginning of the experiment (t= 0 h), as well as after 1 hour (t=1 h) and if necessary after 2 hours (t= 2 h) (depending on the density of the culture). After the measurement at 5°C, the samples were poured back, mixed and homogenized in the 15 *L* plastic chamber, then divided into the Karlsruhe-flasks again. The temperature of the photosynthetron was raised up to 10°C and after the 1-h pre-incubation at 10°C, the DO concentration was measured again at t= 0 h and t= 1 h (and if it was necessary at t= 2 h). This

process was repeated at different measuring temperatures (15–20–25–30–35–40–45 °C). Followed the photosynthesis measurement at each temperature, chlorophyll *a* concentration was measured in ethanol extracts according to MSZ ISO 10260:1993 from a subsample (~100 mL) of the homogenized culture. Measuring temperature range could differ between species: photosynthetic activity of the species was measured until remarkable decrease was observed, usually measurements were carried out in the temperature range of 5-40°C.

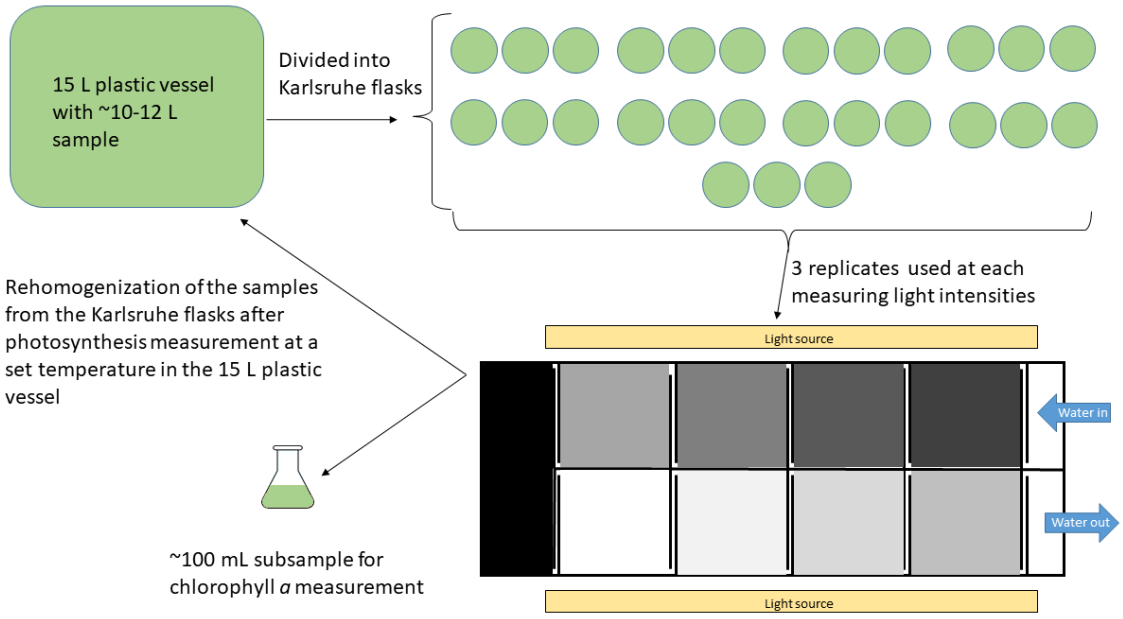

Figure 3 Graphical illustration of the experimental design of the photosynthesis measurements

A different method was used for red algae since they cannot form a homogeneous suspension. Red algal samples were filtered onto 1.2 µm pore size GFC filters, and then their fresh weight was gravimetrically measured with an 0.1 mg accuracy. Samples with known fresh weights were placed into Karlsruhe-flasks, which were then filled with freshly filtered (0.4 µm pore size mixed cellulose-ester membrane filter) stream or lake water before each measurement. Then the same photosynthetic activity measuring procedure was performed as for the other species, except refilling between temperature changes. In case of red algae, the known fresh weight pieces were randomly exchanged between cells with the different light intensity.

Carbon uptake, respiration, gross and net photosynthesis were determined according to Wetzel and Likens (2000) with the following equations:

$$Respiratory\ activity = IB - DB$$

$$Net\ photosynthetic\ activity = LB - IB$$

$$Gross\ photosynthetic\ activity = (LB - IB) + (IB - DB),$$

where *IB* is the initial DO concentration at t= 0 h, *DB* is the DO concentration in the dark bottles at t= 1 h and LB is the DO concentration in the lighted bottles at t= 1 h.

To convert DO to carbon uptake, the DO must be multiplied by the carbon: oxygen mole ratio (12mg C/32mg O_2= 0.375) (Wetzel and Likens 2000), then the following equations were used:

$$Respiration\ (\ mg\ C\ m^{-3}\ h^{-1}) = \frac{(IB - DB) \times RQ \times 1000 \times 0.375}{t}$$

where *t* is the time of incubation, *RQ* is the respiratory quotient (*RQ* = 1.0 according to Wetzel and Likens (2000)),

$$Net\ photosynthetic\ activity\ (\ mg\ C\ m^{-3}\ h^{-1}) = \frac{(LB - IB) \times 1000 \times 0.375}{PQ \times t}$$

where, *t* is the time of incubation, *PQ* is the photosynthetic quotient (*PQ* = 1.2 according to Wetzel and Likens (2000))

$$Gross\ photosynthetic\ activity\ (\ mg\ C\ m^{-3}\ h^{-1}) = \frac{(LB - DB) \times 1000 \times 0.375}{PQ \times t}$$

where, *t* is the time of incubation, *PQ* is the photosynthetic quotient (*PQ* = 1.2 according to Wetzel and Likens (2000)).

To make the results of different species comparable the gross photosynthetic activities were divided by the chlorophyll *a* concentration of the culture, which resulted in the final unit of µgC µgChla^{-1} h^{-1}.

Two equations were used to determine the photosynthetic parameters of the species: in the absence of photoinhibition, photosynthetic parameters were calculated according to Webb et al. (1974):

$$P = P_{max}^{B}\left(1 - e^{\frac{-I}{I_k}}\right)$$

$$\alpha = \frac{P_{max}^{B}}{I_k},$$

Where *P* is the measured photosynthetic activity, P^{B}_{max} is the biomass specific maximal photosynthetic activity, *I* is the used light intensity and I_k is the saturation onset parameter and α is the initial slope of the *P-I* curve which represents the light utilization.

When photoinhibition was observed, β (photoinhibition parameter) and the other parameters were calculated according to Platt et al. (1980):

$$P = P^B_{max}\left(1 - e^{\frac{-I}{I_k}}\right)\left(1 - e^{\frac{-\beta I}{P^B_{max}}}\right)$$

Compensation light intensities were calculated according to:

$$I_c = \frac{P_s * ln\left(1 - \frac{R^B}{P_s}\right)}{-\alpha}$$

where I_c is the light intensity at which photosynthetic production becomes equal to respiration, P_s is the maximal photosynthetic activity obtained in the absence of photoinhibition; without photoinhibition it is equal to P^B_{max}.

To calculate the optimum temperature for the different photosynthetic parameters of the species, Gaussian and exponential curves were fitted. All curves were fitted using GraFit software (Leatherbarrow, 2009).

3.2.3 Statistical analysis

To determine whether the temperature and light intensity treatments had a statistically significant effect on the photosynthetic activity of the selected species, and also to reveal if there are any differences between the photosynthetic activity of the different species and phyla, multiway analysis of variance (ANOVA) was carried out. Tukey's post hoc multiple comparison tests were conducted between each pair of variable. Statistical analyses were carried out using R statistical computing environment (R Core Team 2018).

3.3 Results

As the effect of temperature and light intensity is in the focus of this chapter, the presentation of the results of the photosynthetic measurements also focuses on the parameters which are closely related to these factors: P^B_{max} and I_k values are presented in this chapter but all the calculated variables can be found in *Appendix 3*. The results of the photosynthetic measurements of *Limnospira fusiformis* and *Picocystis salinarum* are presented in *Chapter 5*.

3.3.1 Bacillariophyta

Nitzschia palea (Kützing) W. Smith was the only examined Bacillariophyta. Photosynthetic activity of *N. palea* was examined between 5 and 40°C. In this temperature range the P^B_{max} of the species increased with the increase of temperature (all of the photosynthetic parameters are given in *Appendix 3* for all sixteen species) with a maximum at 35°C and then slight decrease was observed in the P^B_{max} of *N. palea*. P^B_{max} values of the species varied between 0.033 and 1.046 μg C μg Chl a^{-1} h^{-1}. The P_s values of the species followed similar trend than that of P^B_{max}. I_k values of *N. palea* varied between 9.6 and 172.2 μmol photons m^{-2} s^{-1} and reached maximum value at 25°C. Biomass specific respiration of *N. palea* increased with increasing temperature and following a maximum at 35°C, the rate of respiration began to decrease. R^B values ranged between 0.020 and 0.807 μg C μg Chl a^{-1} h^{-1}.

3.3.2 Cyanobacteria

Photosynthetic activities of three cyanobacterial species were examined, these species are namely *Microcystis flosaquae* (Wittrock) Kirchner, *Microcystis* sp. and *Nostoc* sp. The applied temperature range for the two *Microcystis* species was 5-40°C and for *Nostoc* sp. was 5-45°C.

The P^B_{max} values of the species showed high degree of diversity: lowest P^B_{max} values were calculated for *Nostoc* sp., the maximum value was 2.015 μg C μg Chl a^{-1} h^{-1} at 40°C. Also huge differences were found between the two *Microcystis* species: P^B_{max} values *M. flosaquae* ranged between 0.769 μg C μg Chl a^{-1} h^{-1} and 9.513 μg C μg Chl a^{-1} h^{-1} in contrast those of *Microcystis* sp. which had P^B_{max} values between 0.117 μg C μg Chl a^{-1} h^{-1} and 3.218 μg C μg Chl a^{-1} h^{-1}. Also huge differences were found between the temperature optima of the species: *Microcystis* sp. and *Nostoc* sp. had temperature optimum about 37-38°C in contrast, the theoretical temperature optimum of the P^B_{max} values of *M. flosaquae* is over 50°C.

The differences between the photoadaptation parameters of the examined species were similar to that was observed in the case of P^B_{max}. *Microcystis* sp. and *Nostoc* sp. had similar I_k

values, their highest values were 127.2 μmol photons m^{-2} s^{-1} and 121.7 μmol photons m^{-2} s^{-1} in contrast the highest I_k value of *M. flosaquae* was 619.6 μmol photons m^{-2} s^{-1}.

3.3.3 Chlorophyta

The photosynthetic activity of seven Chlorophyta were examined usually in the 5-40°C temperature range. There were two exceptions: the applied method was unable to detect photosynthetic activity of *Monoraphidium griffithii* (Berkeley) Komárková-Legnerová at 5°C, therefore the applied temperature range was 10-40°C. The other species with different temperature treatment is *Scenedesmus* sp., the used temperature range was 5-45°C.

The examined species can be divided into three groups depending on their P^B_{max}: there species with low P^B_{max}, namely *Monoraphidium griffithii* and *Raphidocelis subcapitata* (Korshikov) Nygaard, Komárek, J. Kristiansen & O.M. Skulberg. The highest P^B_{max} of these species is 0.565 μg C μg Chl a^{-1} h^{-1} and 0.566 μg C μg Chl a^{-1} h^{-1}. The second group contains species with medium level of P^B_{max}, these are *Mucidosphaerium pulchellum* (H.C. Wood) C. Bock, Proschold & Krienitz, *Tetradesmus obliquus* (Turpin) M.J. Wynne and *Scenedesmus* sp. The P^B_{max} of these species can be found in the 2-4 μg C μg Chl a^{-1} h^{-1} range. The third group contains *Coelastrum* sp. and *Dunaliella salina* (Dunal) Teodoresco which have the highest P^B_{max} among the examined Chlorophyta species (5.353 μg C μg Chl a^{-1} h^{-1} and 5.404 μg C μg Chl a^{-1} h^{-1}). The temperature optima of the species' P^B_{max} was in the 30±2°C temperature range with two exceptions, the temperature optimum of *D. salina* was 37.2±5.4 and of *Scenedesmus* sp. was 36.0±1.3.

The photoadaptation parameters of the Chlorophyta species increased with increasing temperature until reaching a maximum in the 30-40°C range, then decrease was observed in all cases. Remarkable differences were found in the I_k values of the chlorophyta species: lowest values were calculated for *R. subcapitata* and *M. griffithii* (159.0 μmol photons m^{-2} s^{-1} and 100.8 μmol photons m^{-2} s^{-1}). Examined Chlorophyta species with highest I_k values in the 200-300 μmol photons m^{-2} s^{-1} range are *Coelastrum* sp., *D. salina* and *T. obliquus*. Highest I_k maxima were calculated for *M. pulchellum* (434.8 μmol photons m^{-2} s^{-1}) and *Scenedesmus* sp. (327.2 μmol photons m^{-2} s^{-1}).

3.3.4 Charophyta

The photosynthetic activity of the only examined Charophyta species, *Cosmarium majae* Ström, was examined at 8 different temperatures between 5 and 40°C. Highest P^B_{max} was observed at 30°C and the calculated temperature optimum is 27.8°C. According to the observed high level of photoinhibition, remarkable differences were found between the P_s and P^B_{max}

values of the species. The biggest difference was higher than 20% at 35°C. High and increasing I_k values were found according to the increasing temperature, remarkable decrease in the photoadaptation parameter was observed only at the highest (40°C) measuring temperature. Biomass specific dark respiration of the species increased with increasing temperature and reached a plateau above 30°C.

3.3.5 Rhodophyta

Photosynthetic activities of two red algae were examined. The biomass specific maximal production (P^B_{max}) of the species increased parallel with the temperature. The increase of the P^B_{max} was about 75-80% of both species and both had highest values at 25 °C. A remarkable difference was found between the levels of the species' P^B_{max}. The highest P^B_{max} of *Batrachospermum* was 0.683 μg C μg FW^{-1} h^{-1} in contrast to *Bangia*, that exhibited a photosynthetic production higher by an order of magnitude (P^B_{max} = 8.171 μg C μg FW^{-1} h^{-1}). At 35 °C, the highest experimental temperature, both species' photosynthetic activity dropped remarkably.

Photoadaptation parameters (I_k) of *Bangia* varied between 61.6 and 275.1 μmol m^{-2} s^{-1}. It increased with the increasing temperature till 25 °C. At higher temperatures a slow decrease was observed in the I_k values. I_k values of *Batrachospermum* were lower and ranged from 32 to 165.8 μmol m^{-2} s^{-1}. The highest value was found at 30 °C.

Table 1 Effect of temperature, light intensity treatments phyla and species on the photosynthetic activity of the examined 16 species based on the results of multiway ANOVA (Df = degrees of freedom, F = F-value, P = P-value)

	Df	F	P
Temperature	8	174.56	<0.001
Light intensity	8	148.01	<0.001
Phylum	3	391.53	<0.001
Species	10	185.17	<0.001
Residuals	880		

3.3.6 Statistical analysis

Multiway ANOVA revealed that both temperature and light intensity have significant effect on the photosynthetic activity of the species. The statistical analysis showed that there are significant differences between the photosynthetic activity of the species, and also between the four examined phyla (*Table 1*). Tukey's post hoc multiple comparison tests revealed significant differences between almost all phyla. No significant differences were found among phyla

except between the photosynthetic activity of the Cyanobacteria and the Chlorophyta species. Results of the comparison are summarized in *Appendix 2*.

3.4 Discussion

The photosynthetic activity of algae and cyanobacterial species is affected by several environmental factors. Temperature and light intensity are two of the major factors (Padisák 2004, Winder and Sommer 2012, Glibert 2016); these were examined in this research.

There is a positive relationship between temperature and the life process of algae and cyanobacterial species, and more specifically between temperature and photosynthesis. Several experimental studies confirmed this relationship, both theoretically and experimentally, however, there are less physiological studies that were carried out on a wide range of an environmental factor, like temperature or light intensity or on a number of species (cf. Dauta 1982, Coles and Jones 2000).

The previously described positive relationship between temperature, light intensity and the examined species' photosynthetic activity is confirmed (Collins and Boylen 1982, Dauta 1982, Coles and Jones 2000, Padisák 2004, Vona et al. 2004, Üveges et al. 2012, Lázár et al. 2015, Lengyel et al. 2015, 2020). However, the extension of the measuring range provides additional information about tolerance ranges of the species as well as about the run of the reaction norms along a wide range of the environmental variable. Unfortunately, studies carried out on a wide range of a variable are rare (Collins and Boylen 1982, Üveges et al. 2012, Lengyel et al. 2015, 2019), because often there is a reason for a special focus which reduces this range. From biotechnological point of view finding of optima are the main target of such measurements that narrows the variable ranges. In the contrary, geographic or environmental distribution ranges of a species are determined by the tolerance of sub- or supraoptimal values and therefore extension of the variable ranges are essential from ecological point of view.

Significant differences were found between the different phyla's photosynthetic activity, however the strength of statistical comparison is reduced by the different number of the examined species and also by the different units used. Comparison fully acceptable only in the case of the Cyanobacteria and Chlorophyta species, the Rhodophyta species been excluded from the analysis because of the different unit, and since there is only one diatom and also one Charophyta species, the comparison of their phyla is inappropriate.

The statistical analysis did not reveal significant differences between Cyanobacteria and Chlorophyta species, but less number of examined cyanobacterial species exhibited higher mean and maximum P^B_{max} values cumulatively than the examined Chlorophyta species (*Figure 4*). Statistical analysis also weakened by the overlapping of the different species' data according

to the wide range of the environmental variables. Photosynthetic activity of species in both phyla performed well in a wide range of temperature and light intensity supporting that within phylum variability of species is high in this respect. However, the photosynthesis measurements confirmed the high photosynthetic productivity as one of the possible reason of the increasing dominance of the cyanobacterial species (Coles and Jones 2000, Sukenik et al. 2015, Huisman et al. 2018). Highest photosynthetic activity to dark respiration ratio (P^B_{max}/R^B) was found for the cyanobacterial species, confirming the previous observation on other cyanobacteria species (Van Liere and Mur 1979, Vonshak 2002). The green algae species' P^B_{max}/R^B values are similar to those were recorded by Humphrey (1975) for several algal species.

Highest P^B_{max} values were observed for bloom forming species: in case of two cyanobacterial and two green algal species. The absolutely highest P^B_{max} value out of the 16 examined species in all of temperature vs light intensity combination was measured for *Limnospira fusiformis*. It is a common bloom forming species in the East African soda lakes, serving as food source for huge populations of Lesser Flamingo, so the high level of photosynthetic activity did not seem like a surprise, rather it was expected (Jenkin 1957, Vareschi 1978, Krienitz and Kotut 2010). Very huge difference was found between the P^B_{max} values of *L. fusiformis* and other 15 species: the second highest P^B_{max} was provided by another bloom forming cyanobacterium species. *Microcystis flosaquae* reached only about the half of *Limnospira fusformis*' values. These high photosynthetic rates coupled with high temperature optima, for these summer (warm water) bloom forming species was also expected (van der Westhuizen and Eloff 1985, Kebede and Ahlgren 1996, Coles and Jones 2000, Nalewajko and Murphy 2001). Besides these, the two bloom forming green algae had high photosynthetic activity, the Chlorophyta *Mucidosphaerium pulchellum* and the Charophyta *Cosmarium majae*. *Mucidosphaerium pulchellum* is a cosmopolitan species, which sometimes dominates the plankton assemblages, and has high light optimum (Ragsdale and Clebsch 1970, Irfanullah and Moss 2006). In contrast, even if *Cosmarium* species are globally distributed (Epstein and López-García 2009, Ramos et al. 2018, Ramos and do Nascimento Moura 2019), in Hungary they are not so common and specifically *C. majae* marked as an endangered species (Németh 2005). Another two Chlorophyta had remarkable photosynthetic activity: *Dunaliella salina* and *Coelastrum* sp. Their preference of high light intensity and/or temperature were already known as well as their ability of fast growing and high level of photosynthesis. (Dauta 1982, Comín and Northcote 1990, Jiménez et al. 1990, Bouterfas et al. 2002, Padisák 2004, Gómez and González 2005, Wu et al. 2016). Although the different chlorophyll *a* content/cell of the species

(which was neglected in present study) may complicate the comparison of the chlorophyll *a* specific photosynthetic activities of the species, but not the main trends or temperature optima.

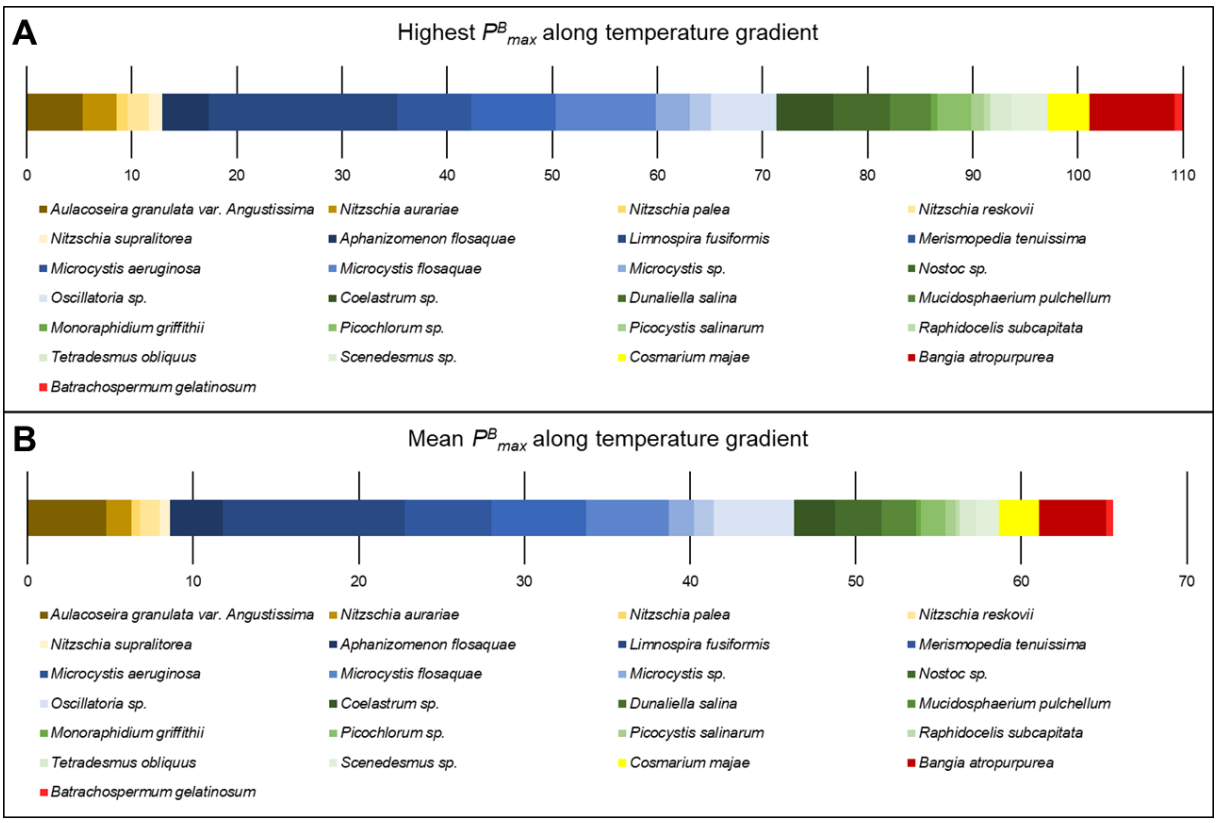

Figure 4 A: Highest P^B_{max} values along the temperature scales of the species. B: Mean P^B_{max} values along the temperature scales of the species. The units of the P^B_{max} values of the species are the followings: µg C µg Chl a^{-1} h^{-1} for microscopic species and µg C µg FW^{-1} h^{-1} for the macroscopic Rhodophyta species *Bangia atropurpurea* and *Batrachospermum gelatinosum*. The shades of brown represents the Bacillariophyta species, the shades of blue represents the Cyanobacteria species, the shades of green represents Chlorophyta species, yellow represents the Charophyta species and the shades of red represents the Rhodophyta species. Beside own measurement for some species the following literary data were used: *Aulacoseira granulata* var. *granulata*, *Merismopedia tenuissima*, *Microcystis aeruginosa* and *Oscillatoria* sp. from Coles and Jones (2000), *Nitzschia aurariae*, *Nitzschia reskovii* and *Nitzschia supralitorea* from Lengyel et al. (2020), *Aphanizomenon flosaquae* from Üveges et al. (2012) and *Picochlorum* sp. from Mucko et al. (2020).

The green algae (including both Chlorophyta and Charophyta species) form a very diverse group in the plankton, they are able reach dominance, usually high light intensity optimum is associated with them (Padisák 2004, Naselli-Flores and Barone 2009). The present study also confirmed this, since there are result of two bloom forming (in small garden ponds) green algae species, and their P^B_{max} values close to or exceed those of some examined Cyanobacteria. High light intensity optimum also proven by present photosynthesis measurements.

Lower level of photosynthetic activity was determined for diatoms, especially for *Nitzschia* species, with a strongly temperature dependent light optimum in the 100-300 µmol photons m^{-2} s^{-1} range (Lázár et al. 2015, Lengyel et al. 2015, 2020), however the light optimum of *N. palea* could be strain specific (Vitug and Baldia 2014).

The direct comparison of the examined Rhodophyta species with the other is difficult because of the different unit. Adaptation to low light intensity and temperature has been reported both for *Batrachospermum gelatinosum* and *Bangia. atropurpurea* (Geesink 1973, Sommerfeld and Nichols 1973, Necchi and Zucchi 2001, Necchi Júnior and Alves 2005). Because Rhodophyta species were commonly found at low temperatures and light intensities, most previous experiments were limited to low temperature and light intensity ranges. In most cases, these values varied between 9-20 °C and 4-200 μmol m^{-2} s^{-1} (Belcher 1960, Geesink 1973, Sommerfeld and Nichols 1973, Sheath and Cole 1980, Charnofsky et al. 1982). Graham and Graham (1987) found that *Bangia* has temperature optimum at 20 °C and light intensity optimum at 750 μmol m^{-2} s^{-1} which differs from previous findings as well as from present observations. The extremely high light optimum should be a result of the different data analysis. *B. gelatinosum,* like red algae in general, occurs in cold (7-14 °C), clean running waters (Kremer 1983, Vis et al. 1996, Vis and Sheath 1997, Drerup and Vis 2014). Several experiments were carried out on the photosynthesis of different *Batrachospermum* species. In accordance with present results, Kremer (1983) found temperature optimum at 20-25 °C for the photosynthetic production of *Batrachospermum* sp. when short temperature adaptation time was used before measurement, however Kremer (1983) found lower temperature optimum (15 °C) if the adaptation time was longer, and suggested the use of longer adaptation time is needed. Temperature optimum of the species was determined about 20°C by various authors (Necchi and Zucchi 2001, Zucchi and Necchi O. 2001, Necchi Júnior and Alves 2005, Drerup et al. 2015)

The photosynthesis measurements of the above listed 16 species experimentally confirmed that temperature has an essential role in determining the abundance and composition of phytoplankton as empirical studies described it (Adrian et al. 2009, Winder and Sommer 2012, Winder et al. 2012). The results of present study also confirmed that warming favours cyanobacterial species: in general Cyanobacteria had higher temperature optimum, however their determined light intensity optimum is higher than previous works suggested (Collins and Boylen 1982, Padisák 2004). Even the positive effect of temperature was detectable for all examined species, the common bloom forming ones (e.g. *Limnospira. fusiformis, Microcystis* species) had the highest photosynthetic activity (Krienitz et al. 2016, Steffen et al. 2017).

4 Quantitative estimation of photosynthetic plasticity: effect of temperature on various algal species

4.1 Introduction

Phenotypic plasticity is described by Pigliucci (2001) as the property of a given genotype to produce different phenotypes in response to distinct environmental conditions. Whitman and Agrawal (2009) also collected several definitions of phenotypic plasticity (*Table 2*). These definitions suggested that plasticity, including phenotypic, morphological and also physiological, is a reaction of the individual to changes in the environment. DeWitt and Scheiner (2004) described it as "an environment-dependent phenotype expression or the environmentally sensitive production of alternative phenotypes by given genotypes". Another definition by Agrawal (2001): "The ability of an organism to express different phenotypes depending on the environment", or "any change in an organism's characteristics in response to an environmental signal" as explained by Schlichting and Smith (2002). Previously, plasticity and acclimation were distinguished: plasticity was used for morphological and acclimation was used for physiological response of the individuals/species/populations to a treatment. However, this distinction is nowadays not typical.

In the present study, the physiological responses of algae and cyanobacteria were examined along a wide temperature scale, which makes it impossible (but at least very inaccurate) to apply the fundamental method of describing plasticity (slope of the reaction norm). Plasticity can be described with the difference between the reaction of a phenotype - or in present study an algal species - and the mean of average reaction (*Figure 5A, B*) to the selected treatment(s). However ,models like described by Pigliucci (2001) are applicable only in cases when there are two, or only very few treatments. Use of cross-environmental scales excludes the application of a linear model, since in most of the cases the reaction norm of a species along a wide range of temperature could be described by e.g. a Gaussian curve instead of linear trends (e.g. Coles and Jones 2000, Üveges et al. 2012, Lengyel et al. 2020). The term of plasticity here is used similarly to the above mentioned definition of Schlichting and Smith (2002), as the ability of a species to giving different reactions according to the environmental changes, more precociously, it means to give different photosynthetic reaction at different temperatures.

To examine the species' specific response, or the plasticity of the species several studies were carried out. The determination of plasticity of the algal species in previous studies is based

on experiences, trends or comparing the measured variable(s) (Ensminger et al. 2005, Rothäusler et al. 2011, Üveges et al. 2012, Sordet et al. 2014, Aguilera et al. 2020, Ji et al. 2020), but the quantitative determination or rankings regarding to any kind of any plasticity indices or methods are missing. The term of plasticity in previous phycological studies was used mainly to describe the effect of some factor on the selected organism without exact definition in contrast to studies on higher plats (Valladares et al. 2000, 2006, Balaguer et al. 2001, Gratani et al. 2003, Nicotra et al. 2010) or insects (Whitman and Agrawal 2009). Any kind of indices to compare was not used by even Ji et al. (2020) who examined phenotypic plasticity of *Microcystis* strain, plasticity meant in this study the comparison of the different phenotypes of the species, however without a quantitative form.

Table 2 Some selected definitions of plasticity from Whitman and Agrawal (2009)

Definition	**Reference**
"Plasticity is shown by a genotype when its expression is able to be altered by environmental influence… it does not have any implications concerning the adaptation value of the change occurring…"	Bradshaw (1965)
"A change in the expressed phenotype of a genotype as a function of the environment or when an individual's phenotype is influenced by its environment."	Scheiner (1993)
"The ability of an organism to express different phenotypes depending on the environment."	Agrawal (2001)
"The property of a given genotype to produce different phenotypes in response to distinct environmental conditions."	Pigliucci (2001)
"Any change in an organism's characteristics in response to an environmental signal."	Schlichting and Smith (2002)
"Environment-dependent phenotype expression or the environmentally sensitive production of alternative phenotypes by given genotypes."	DeWitt and Scheiner (2004)
"Variation, under environmental influence, in the phenotype associated with genotype."	Freeman and Herron (2007)
Environmental sensitivity for a trait.	Various authors

The above mentioned tendency of the cyanobacterial expansion around the word keep in focus this group of oxyphotogenic organisms (Paerl and Paul 2012, Sukenik et al. 2015, Huisman et al. 2018) and makes it important to study their physiology. They evolved a diversity of physiological and ecological abilities, which are highly competitive and make them able to

form high density blooms and be distributed across wide geographical scales. Preference and/or tolerance of higher temperatures, besides the field observations, is confirmed by several experimental studies as by the previous chapter of present dissertation (Nicklisch et al. 1981, Collins and Boylen 1982, Nicklisch and Kohl 1983, Mastala et al. 1996, Padisák 2004, Üveges et al. 2012). The ability to use very low light intensity makes them potentially good competitors within the phytoplankton as well as the tolerance of even direct illumination by the sun (Padisák 2004).

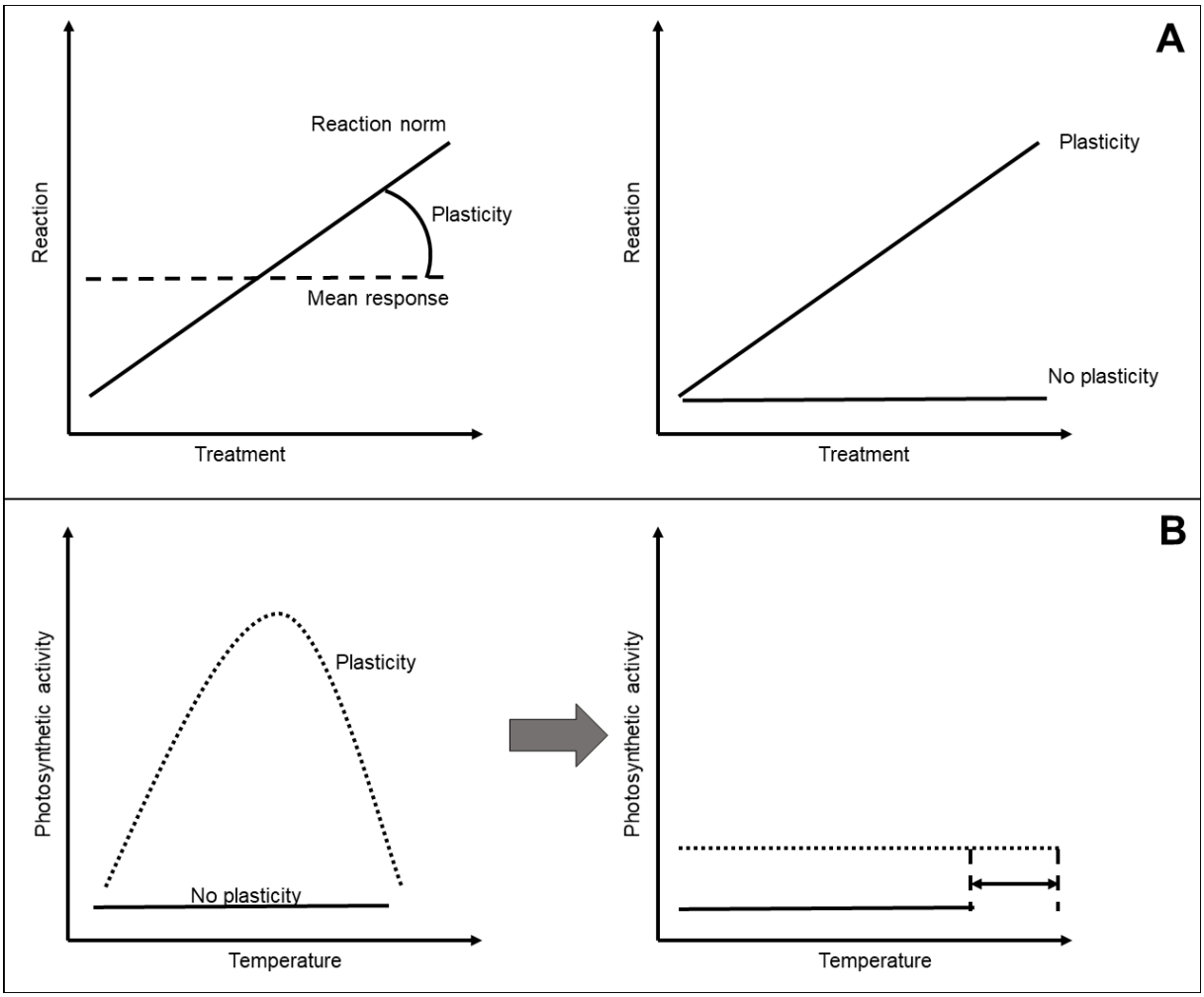

Figure 5 A: Conceptional diagram of the relationship between plasticity and the reaction after (Pigliucci 2001). B: Estimating the plasticity of the species P^{B}_{max} along a wide range of temperature: solid line represent when no plasticity in the temperature range, dotted line when plasticity was observed. The ratio of the length of the two curves estimate the plasticity. Value of plasticity increase with the increasing difference (black arrow) between the solid and dotted line.

Using empirical data (e.g. phytoplankton composition data vs. environmental variables) makes possible to use these organisms e.g. for the estimation of the water quality, and also according to these kind of data it is possible to determine their indicator roles and values (Padisák et al. 2006, Lugoli et al. 2012). However, these indices provide information rather on

species' optimum ranges then their tolerance limits since these based on occurrences in field samples and, additionally, carry less (or no) information about the potentials of the species.

Effect of temperature is in the focus of this chapter, because of its major role in the controlling of not only infra-, but also supraindividual processes (Davison 1991, Adrian et al. 2009, Sommer et al. 2012, Winder and Sommer 2012). The well-known general relationship between photosynthesis and temperature is confirmed by the previous chapter of present dissertation as well as the high temperature preference of several bloom forming cyanobacteria. The increasing temperature of the habitats selectively favours certain cyanobacteria species (Collins and Boylen 1982, Robarts and Zohary 1987, Davison 1991, Coles and Jones 2000, Vona et al. 2004, Padisák 2004, Butterwick et al. 2005, Watkinson et al. 2005, Staehr and Birkeland 2006, Falkowski and Raven 2007, Sommer et al. 2012, Üveges et al. 2012, Kosten et al. 2012, Paerl and Paul 2012, Singh and Singh 2015, Lengyel et al. 2015, Yan et al. 2020).

The aim of this chapter was to compare plasticity estimating methods by use of previously described and own methods. Since the method would be responsible for the estimation of a species' plasticity along an environmental scale, with the aim of finding the potentially best competitor, there are some requirements against the method:

i. it should calculate with the changes in the examined variable along the scale;
ii. it should calculate with the absolute values of the variable;
iii. it has to take into account what part of the scale is involved by a species;

and it is advantageous if it allows the comparison of different units.

4.2 Materials and methods

4.2.1 Examined strains and photosynthetic variables

Biomass specific maximal photosynthesis (P^B_{max}) of 25 algal and cyanobacterial species were examined, including 5 Bacillariophyta, 8 Cyanobacteria, 9 Chlorophyta, 1 Charophyta and 2 Rhodophyta strains both from own measurements and from the literature. *Table 3* contains the list of the examined species. For the estimation of plasticity beside the results of *Chapter 3*, some data from the literature were also used. Though there are a number of physiological papers focusing on the photosynthetic activity of algal species, there are also several different measuring methods which applied different units and in some cases some very different scales.

Table 3 List of the examined species from different phyla

Phylum	Species	Type	Reference
Bacillariophyta	*Aulacoseira granulata* var. *angustissima* (O.Müller) Simonsen	culture	Coles and Jones (2000)
	Nitzschia aurariae Cholnoky	culture	Lengyel et al. (2020)
	Nitzschia palea (Kützing) W.Smith	culture	Present study
	Nitzschia reskovii Ács, Duleba, C.E. Wetzel & Ector	culture	Lengyel et al. (2020)
	Nitzschia supralitorea Lange-Bertalot	culture	Lengyel et al. (2020)
Cyanobacteria	*Aphanizomenon flosaquae* Ralfs ex Bornet & Flahault	sample	Üveges et al. (2012)
	Limnospira fusiformis (Voronichin) Nowicka-Krawczyk, Mühlsteinová & Hauer	culture	Present study
	Merismopedia tenuissima Lemmermann	culture	Coles and Jones (2000)
	Microcystis aeruginosa (Kützing) Kützing	culture	Coles and Jones (2000)
	Microcystis flosaquae (Wittrock) Kirchner	sample	Present study
	Microcystis sp.	culture	Present study
	Nostoc sp.	culture	Present study
	Oscillatoria sp.	culture	Coles and Jones (2000)
Chlorophyta	*Coelastrum* sp.	culture	Present study
	Dunaliella salina (Dunal) Teodoresco	culture	Present study
	Mucidosphaerium pulchellum (H.C.Wood) C.Bock, Proschold & Krienitz	sample	Present study
	Monoraphidium griffithii (Berkeley) Komárková-Legnerová	culture	Present study
	Picochlorum sp.	culture	Mucko et al. (2020)
	Picocystis salinarum Lewin	culture	Present study
	Raphidocelis subcapitata (Korshikov) Nygaard, Komárek, J.Kristiansen & O.M.Skulberg	culture	Present study
	Tetradesmus obliquus (Turpin) M.J.Wynne	culture	Present study
	Scenedesmus sp.	culture	Present study
	Cosmarium majae Ström	sample	Present study
Rhodophyta	*Bangia atropurpurea* (Mertens ex Roth) C.Agardh	sample	Present study
	Batrachospermum gelatinosum (Linnaeus) De Candolle	sample	Present study

4.2.2 Statistical and other data analysis

Multiway ANOVA was used to test if there any effect of temperature on the P^B_{max} of species. Differences among species and among phyla were also revealed with this test, comparisons were made by Tukey HSD post-hoc test. Statistical analyses were performed in R statistical computing environment (R.3.2.3, R Development Core Team, 2013).

The biomass specific maximal photosynthetic activity (P^B_{max}) was used to estimate the plasticity of the species (see the values in *Appendix 3*). To calculate temperature optima of the species photosynthesis, Gaussian curves were fitted onto the P^B_{max} values measured along the temperature scale. All curves were fitted using GraFit7.0 software (Leatherbarrow 2009).

4.2.3 Estimating the plasticity of different species in a wide range of temperature

Four different methods, three literary (PP, CV, HM) and one newly applied (CLP), were used for the estimation and/or visualisation of the plasticity of the species' photosynthesis (*Table 3*) along temperature scale, and then the species were ranking due to these indices.

I. Phenotypic plasticity index (PP)

Phenotypic plasticity index of Valladares et al. (2000) with the following equation was used:

$$PI = \left(1 - \frac{PV_{min}}{PV_{max}}\right),$$

where PI is the plasticity of a species photosynthesis, PV_{min} is the minimum value and PV_{max} is the maximum value of P^B_{max} along the examined temperature range. This formula results in a dimensionless number which ranges between 0 and 1, and the level of plasticity is increasing with the increasing value (Valladares et al. 2000).

II. Coefficient of variation (*CV*):

Coefficient of variation is a wildly used method, with a simple calculation:

$$CV = \frac{\sigma}{\mu},$$

where CV is the coefficient of variation, μ is the mean and σ is the standard deviation of the P^B_{max} values along the examined temperature range. This formula also resulted in a dimensionless number, where higher values represents higher level of plasticity.

III. Heatmap visualization (HM):

Heatmap visualization of the P^B_{max} of the examined species along the temperature range means the graphical representation of the $\log_2$ transformed relative P^B_{max}. For all species the P^B_{max} at the lowest temperature, which is usually 5°C, is the reference so at this temperature values for all species represent 0. Higher values mean higher difference compared to the P^B_{max} at reference temperature. Results are presented in a scale between 0 and 5, higher values shown with darker colour.

IV. Curve length plasticity index (CLP):

Gauss-curves were fitted with the P^B_{max} values along the examined temperature range. The length of these curves was calculated between 0 and 50°C (*Figure 5B*) and it was used to estimate the plasticity according to the following equation:

$$CLP = 1 - \frac{S_G}{S_0},$$

where S_G is the arc length of the fitted Gaussian-curves, S_0 is length of the curve when there is no plasticity (straight line, parallel with x axis). This formula results in a dimensionless number. When P=0, there is no plasticity, plasticity increasing with the increasing value of P *(Figure 5B).*

4.3 Results

4.3.1 Statistical analysis

The statistical analysis revealed a significant differences between the P^B_{max} values of the species, and also differences were found between some of the phyla. The analysis showed the significant effect of the temperature treatments on the photosynthetic activity of the species. Significant difference was found between the phyla Cyanobacteria and Bacillariophyta ($p<0.05$), between the Cyanobacteria and Chlorophyta ($p<0.0001$) and between the Cyanobacteria and Rhodophyta ($p<0.05$). The results of the comparisons between the species' and temperatures P^B_{max} are quantified in *Appendix 4*.

4.3.2 Quantitative estimation of the species' plasticity

Four different methods were used to estimate the plasticity of the species P^B_{max} along the examined temperature range. The plasticity of the different phyla also was estimated by the average plasticity values of the examined species.

I. Phenotypic plasticity index (PP):

This index gave the highest value for the diatom species *Nitzschia palea* with a value of 0.972 (*Table 4*). Second highest value was observed in the case of *Microcystis* sp. (0.964). It was followed by five Chlorophyta species: *Coelastrum* sp., *Raphidocelis subcapitata*, *Scenedesmus* sp., *Monoraphidium griffithii* and *Mucidosphaerium pulchellum* (0.959, 0.959, 0.956, 0.947 and 0.936). Plasticity values of further seven species were higher than 0.9 (three Chlorophyta species and two-two diatom and Cyanobacteria). Five more species had plasticity value in the 0.8-0.9 range, lowest value was calculated for *Microcystis aeruginosa*, *Oscillatoria* sp. *and Aulacoseira granulata* var. *granulata* (0.652, 0.478 and 0.386).

The PP index did show the highest average plasticity of the Chlorophyta species with a value of 0.926±0.037 (*Table 4*). The only examined Charophyta species reached 0.840, close to value that was calculated for the two Rhodophyta species (0.833±0.058). With 0.808±0.240, the average value of the diatoms was just over 0.8, lowest average value was calculated for the cyanobacteria species as 0.772±0.170.

II. Coefficient of variation (CV):

CV index: highest value was calculated in the case of *Scenedesmus* sp. (0.852) (*Table 4*). The second highest was also a Chlorophyta, *Monoraphidium griffithii* with a 0.843 value. Two more species had higher value than 0.8: *Nitzschia aurariae* and *Microcystis* sp., both with 0.829. Six species had values in the 0.7-0.8 range: two Bacillariophyta and four Chlorophyta. Lowest

values were under 0.5: six species had that low CV, four of them is cyanobacteria and there is one diatom and one Charophyta. Lowest value was calculated for *Aulacoseira granulata* var. *granulata* (0.210).

Similarly to the PP index, the highest average value was determined for the Chlorophyta species with CV index, too (*Table 4*). The highest value is 0.727±0.101. According to this index, the second highest is the phylum Bacillariophyta (0.606±0.247), followed by the Rhodophyta (0.538±0.020). Cyanobacteria species with 0.506±0.170 and the only Charophyta (0.496) had the lowest CV index values.

III. Heatmap visualization (HM):

The heatmap representation indicated highest change (6.0) for *Monoraphidium griffithii*, (*Table 4*). It was followed by *Nitzschia palea* and *Microcystis* sp. with values of 5.2 and 4.8, respectively. Four Chlorophyta and one Cyanobacterium had values between 4.0 and 4.8, these are the following: *Raphidocelis subcapitata*, *Coelastrum* sp., *Scenedesmus* sp., *Limnospira fusiformis* and *Mucidosphaerium pulchellum*. Species with the lowest changes for the temperature treatments are *B. gelatinosum* (1.7), *Merismopedia tenuissima* (1.6), *Microcystis aeruginosa* (1.5) and there were two species below 1.0: *Oscillatoria* sp. and A*ulacoseira granulata* var. *granulata* (0.9 and 0.7, respectively).

A. granulata	*N. aurariae*	*N. reskovii*	*N. palea*	*N. supralitorea*	*A. flos-aquae*	*L. fusiformis*	*M. tenuissima*	*M. aeruginosa*	*M. flos-aquae*	*Microcystis* sp.	*Nostoc* sp.	*Oscillatoria* sp.	*Coelastrum* sp.	*D. salina*	*M. pulchellum*	*M. griffithii*	*Picochlorum* sp.	*P. salinarum*	*R. subcapitata*	*T. obliquus*	*Sceneesmus* sp.	*C. majae*	*B. atropurpurea*	*B. gelatinosum*
	0.0	0.0	0.0	0.0	0.0	0.0			0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0
	0.6	-0.3	1.8	0.6	1.4	1.8			1.5	1.3	1.3		2.1	0.7	1.5	1.8	1.0	0.0	1.2	0.8	0.8	1.0	0.5	0.6
0.0	1.0	1.5	2.2	1.7	2.2	2.7	0.0	0.0	2.4	2.1	1.6	0.0	2.2	1.2	2.5	2.6	1.4	0.3	1.9	1.3	1.7	1.7	1.2	1.2
0.7	2.0	1.8	4.2	2.0	2.7	3.3	1.0	0.8	2.8	3.0	2.8	0.3	3.1	1.6	3.1	4.9	2.6	1.5	3.4	2.7	2.3	2.1	1.1	1.6
0.7	3.4	2.2	4.8	3.3	2.7	3.9	1.6	1.3	2.8	3.7	3.2	0.8	3.8	1.9	3.6	5.7	3.0	2.3	4.2	2.9	3.2	2.4	2.3	1.7
0.7	3.3	2.3	4.4	3.4	3.1	4.3	1.6	1.5	3.0	4.5	3.5	0.9	4.4	2.1	4.0	6.0	3.4	3.0	4.6	3.1	3.6	2.6	1.7	1.4
	3.5	2.5	5.2	3.7	3.2	4.4			3.1	4.8	3.7		4.6	2.7	3.9	5.0	2.8	3.6	4.4	3.4	4.3	2.5	0.7	-1.3
	1.2	1.5	4.8	2.9	3.6	4.5			3.5	4.7	3.8		3.7	2.2	2.5	3.2	0.6	3.7	3.2	1.9	4.5	1.3		
											3.6							2.8			2.8			

Figure 6 Heatmap visualization of the plastic response of the examined species along the examined temperature range. All P^B_{max} values are compared to P^B_{max} at the lowest measuring temperature (reference). Higher values, which is marked with darker colour, represents the higher difference compared to the reference.

Heatmap visualisation revealed the highest plasticity for the Chlorophyta species (4.1±0.96) (*Table 4, Figure 6*). Similar values were calculated for the Bacillariophyta and Cyanobacterium species: 3.120±1.662 and 3.025±1.481, respectively. The Charophyta species had a value of 2.6, and the same value for the Rhodophyta species was 2.000±0.424.

Table 4 The result of the quantitative estimation of the species plasticity. Indices were calculated, all resulted in a dimensionless number. The results of the four different calculation method represents the mean of the plasticity values of the species belong to the phyla and the standard deviaton.

Species	**PP index**	**CV index**	**Heat map visualisation**	**CLP index**
A. granulata var. a*ngustissima*	0.386	0.210	0.7	0.0239
N. aurariae	0.910	0.829	3.5	0.0145
N. reskovii	0.852	0.533	2.5	0.0027
N. palea	0.972	0.754	5.2	0.0005
N. supralitorea	0.921	0.704	3.7	0.0012
Bacillariophyta	**0.808±0.240**	**0.606±0.247**	**3.1±1.7**	**0.0086±0.0103**
A. flosaquae[*]	0.722	0.374	3.6	0.0102
L. fusiformis	0.849	0.540	4.5	0.1061
M. tenuissima	0.667	0.424	1.6	0.0524
M. aeruginosa	0.652	0.406	1.5	0.0483
M. flosaquae	0.919	0.571	3.5	0.0193
Microcystis sp.	0.964	0.829	4.8	0.0060
Nostoc sp.	0.928	0.610	3.8	0.0015
Oscillatoria sp.	0.478	0.290	0.9	0.0152
Cyanobacterium	**0.772±0.170**	**0.506±0.170**	**3.0±1.5**	**0.0324±0.0352**
Coelastrum sp.	0.959	0.735	4.6	0.0240
D. salina	0.848	0.527	2.7	0.0060
M. pulchellum	0.936	0.659	4.0	0.0139
M. griffithii	0.947	0.843	6.0	0.0004
Picochlorum sp.	0.906	0.728	3.4	0.0105
P. salinarum	0.921	0.736	3.7	0.0013
R. subcapitata	0.959	0.799	4.6	0.0004
T. obliquus	0.906	0.667	3.4	0.0029
Scenedesmus sp.	0.956	0.852	4.5	0.0094
Chlorophyta	**0.926±0.036**	**0.727±0.102**	**4.1±1.0**	**0.0076±0.0078**
C. majae	0.840	0.496	2.6	0.0105
Charophyta	**0.840**	**0.496**	**2.6**	**0.011**
B. atropurpurea	0.792	0.553	2.3	0.0404
B. gelatinosum	0.874	0.524	1.7	0.0005
Rhodophyta	**0.833±0.058**	**0.539±0.021**	**2.0±0.4**	**0.0205±0.0282**

[*] P_{max} values were converted to P^B_{max} with the biomass concentration given in (Üveges et al. 2012), then CLP index was calculated.

IV. Curve length plasticity index (CLP):

According to the *Curve length plasticity index (CLP)*, the three highest values were calculated for Cyanobacteria species (*Table 4*) of which the absolute highest was for *Limnospira fusiformis* (0.1061). The subsequent species reached only about the half of the previous' values: *Merismopedia tenuissima* with 0.0524 and *Microcystis aeruginosa* with 0.0483. Fourth in the rank was the red alga *Bangia atropurpurea* with 0.0404. Nine species had

values between 0.01 and 0.04 (three Chlorophyta and Cyanobacteria, two Bacillariophyta and the only Charophyta species). Species with the lowest values are *Nitzschia palea* and *Batrachospermum gelatinosum*, both with 0.0005, moreover *Monoraphidium griffithii* and *Raphidocelis subcapitata* (both with 0.0004).

The CLP calculations showed that the Cyanobacteria species have the highest plasticity (0.032±0.035) (*Table 4*). The second highest value was calculated for the Rhodophyta species (0.020±0.028), than the Charophyta (0.0105). The lowest values was calculated for the diatoms (0.009±0.010) and for the Chlorophyta species (0.008±0.008). Very remarkable differences were found between the species of all phyla.

4.4 Discussion

Photosynthetic activity of algae is strongly affected by environmental factors. Physiological studies revealed that temperature is one of the most important of these factors (Davison 1991). Temperature was found to be strongly influencing the photosynthetic activity of species from different phyla (Konopka and Brock 1978, Nicklisch et al. 1981, Collins and Boylen 1982, Nicklisch and Kohl 1983, Torzillo and Vonshak 1994, Coles and Jones 2000, Zucchi and Necchi O. 2001, Padisák 2004, Vona et al. 2004, Necchi 2004, Üveges et al. 2012, Shafik et al. 2014, Kokubu et al. 2015, Lázár et al. 2015, Lengyel et al. 2015, 2020).

The photosynthetic activity of a species along a wide range of temperature, with rare exceptions, could not be described as a linear function, but even more could be described with a kind of Gaussian curve as shown by the previous chapter and also by previous studies (Üveges et al. 2012, Anderson et al. 2020, Lengyel et al. 2020). However, the shape of the reaction norm is highly dependent upon the range of the examined temperatures. Using a wide range of temperature (e.g. 5-40°C, like in the present study) excludes the use of linear equation, however there are exceptions, mainly associated to tropical or summer bloom forming species (*Appendix 3, Chapter 3.3.2*).

P^B_{max} values of the examined species also showed this kind of tendencies: with the exception of two cyanobacteria (*Limnospira fusiformis* and *Microcystis flosaquae*) Gaussian curves described the temperature dependences of the species within the applied measuring range. Remarkable differences were found between the species: highest photosynthetic activity was observed in *Limnospira fusiformis*, which is a common bloom forming cyanobacteria species in East African and Indian saline alkaline waters (Dadheech et al. 2013, Krienitz et al. 2016). The second highest P^B_{max} was observed for *Microcystis flosaquae*, which may also form high biomass summer blooms, like in the shallow Lake Balaton in 2014 and 2015. This research confirmed the general view that cyanobacterial species have high chlorophyll *a* specific photosynthetic activity/growth rate in general, even if there are high variability between the species (*Figure 4A, B*) that makes them potential dominants in the phytoplankton (Sukenik et al. 2015, Huisman et al. 2018, Budzyńska et al. 2019).

Papers mentioning the term “plasticity” in their titles commonly compare some kind of ability of two or only a few species, or focus on a single species but examining it in a wide range of a variable (e.g. Üveges et al. 2012, Ji et al. 2020). Dealing with only two, three or at least not too many species allows for simple cross-comparisons even confirmed with statistical analyses. However, to compare a variable of numerous species in a wide range of the target

variable makes the use of empirical methods impossible. Further difficulty is set by diversity of the applied methods sometimes with hardly convertible or even with unconvertible units (Geesink 1973, Collins and Boylen 1982, Coles and Jones 2000, Necchi and Zucchi 2001, Necchi 2004, Vona et al. 2004, Ceschin et al. 2013). Therefore, in such cases only trends and optima of the different examined variables can be compared (e.g. it was hard to find measurements on the examined Rhodophyta species with the same, similar, or at least a convertable unit).

There are traditional methods to estimate plasticity, such as the slope of the reaction norm. Though the slope provides correct results only if the reaction norm is quasi-linear and only a few treatments are involved. If a reaction is examined along a wide range of an environmental variable (e.g. temperature), due to the non-linear trend of the data (see *Chapter 2* and *Appendix 3*) the slope will provide false result, since it underestimates the plasticity.

To solve this problem Valladares et al. (2000) offered a method for the quantitative estimation of the species plasticity for higher plants. This index provides a dimensionless number, which makes comparable the measurements with different units. For the phytoplankton data of the present study highest value was calculated with this index for the cosmopolitan *Nitzschia palea,* even the species has a low P^B_{max} absolute values along the examined temperature range. The second was *Microcystis* sp. with a medium level of P^B_{max}. This clearly demonstrates that the PP index disregards the absolute values, but, in turn, very sensitive to the differences. The application of the PP index on a wide variable range results very high plasticity regardless the value, since it calculates only with the rates. The lowest plasticity values were calculated for the species from Coles and Jones (2000), who used only four temperature treatments in the 15-30°C range. Using low number of treatments, without extremes, e.g. if the temperature range is reduced for the same 15-30°C for *N. palea,* the calculated plasticity would decrease to 0.836, which drops the species into the lower part of the plasticity list. This means that the PP index is only slightly applicable for studies carried out along a wide range of temperature and, additionally, disregards the level of the photosynthetic activity. Since it calculates with ratios, the increase of photosynthetic activity of *N. palea* from 0.029 to 1.046 μg C μg Ch a^{-1} h^{-1} (means 1.017 μg C μg Ch a^{-1} h^{-1} increase) is resulted in 0.972 plasticity, in contrast the increase of *Limnospira fusiformis*' P^B_{max} from 2.708 to 17.927 μg C μg Ch a^{-1} h^{-1} (it is 15.219 μg C μg Ch a^{-1} h^{-1} increase) resulted only in 0.849 plasticity. Since this index calculates with the minimum and maximum values, using a wide range of treatment causes high plasticity values (Valladares et al. 2000). The index also ignores that what part of the range is

involved by a species: Rhodophyta are in the middle of the list of phyla, however their photosynthetic activity was measureable only in a narrow range of temperature (5-35°C). Besides the lot of advantages, this method have some very important weaknesses: not, or just slightly applicable on a wide range of an examined variable and does not calculate with the absolute values, only with the relative changes.

Coefficient of variation is another commonly used method to describe plasticity (Schlichting and Levin 1984). It is also results in a dimensionless number, which allows the comparison between different units. With this method, the highest values were calculated for *Scenedesmus* sp. and, surprisingly, for *Monoraphidium griffithii*. While P^B_{max} of *Scenedesmus* sp. showed increasing tendency along the examined temperature range, and reached ~3.5 µg C µg Ch a^{-1} h^{-1} in contrast *M. griffithii*'s maximum is 0.565 µg C µ Ch a^{-1} h^{-1}. This leads to similar problems as the previous method: mean and standard deviation ignores the absolute values of the photosynthetic activity, just as the covered temperature range.

The heatmap visualizes very well the changes of the P^B_{max} along the examined temperature range. This method allows for empirical comparisons of a number of species (*Figure 6*), and also suitable for the comparison of measurements with different units. However, this method shares some weaknesses of the previous two: the dimensionless number represents the changes of the reaction of a species compared to a reference value. Since each species has own references, the method ignores the differences between the level of the species' P^B_{max}. Designate a common reference for all species would make enable the method to compare data with different units.

The common features of the three above-described methods is the ignorance of the absolute values of the photosynthetic activities, and the calculation only with their ratios. Though species with rapidly increasing photosynthetic activity along a temperature scale could be successful, but the level of P^B_{max} also very important.

Since plasticity could be shown graphically very well (*Figure 5A;* Pigliucci 2001), it makes possible to estimate quantitatively the performance of a species. If there are several treatments, which fit to any known function, the calculation the slope of the reaction norms (one of the most commonly applied method), cannot be used. If a species shows plasticity along a scale (in this case along a temperature scale) it means that the reaction norm of the species would differ from the reference, where there is no plasticity (*Figure 5A,B*, Pigliucci 2001). This difference is increasing with increasing level of plasticity, and for a non a linear reaction norm, could be described with ratio of the reference curves length and the reaction norms length of

the species: CLP method (*Figure 5*). This newly applied method eliminates the shortcomings of the previously described methods: it calculates with the absolute values, therefore it can distinguish between e.g. an order of a magnitude difference in the P^B_{max} and does not rely only on the relative changes.

The CLP method ranked *Limnospira fusiformis* to the first place with the highest plasticity, regarding its well-known high level of photosynthesis and rapid growth, and their positive correlation with the temperature (Kebede and Ahlgren 1996, Kebede 1997). There are five other examined cyanobacterial species out of the first eight, which supports the field observations about the expansion of cyanobacterial species (Paerl and Paul 2012, Whitton 2012, Sukenik et al. 2015, Huisman et al. 2018). The two Rhodophyta species had the lowest temperature optima ranges. Presence of *Bangia* in the top four reveals one of the weakness of this method: it does not allow for comparison between different units. Since P^B_{max} values of *B. atropurpurea* and the other species have different units, but have values in the same magnitude there is the possibility of the comparison, however it provides false information. It is obvious that *Bangia* have a small tolerance range, so it is possibly not such plastic.

5 Growth and photosynthetic response to changing environmental conditions of *Picocystis salinarum* and *Limnospira* (*Arthrospira*) *fusiformis* strains from saline-alkaline Flamingo lakes of East Africa with special focus on the poorly studied picoalga[2]

5.1 Introduction

Inland saline lakes occur worldwide with a total volume almost equal to that of freshwater lakes (Shiklomanov 1990, Williams 1993). These lakes are very diverse in size, morphology, hydrology, water level and ionic composition. Alkaline saline lakes have a low biodiversity (Vareschi 1982, Oduor and Schagerl 2007a). Soda lakes of East Africa are characterized by sodium, carbonate and bicarbonate ionic dominance (Jirsa et al. 2013). The core soda lakes in the Kenyan part of the African Rift Valley are Nakuru, Bogoria, and Elmentaita. These lakes provide extreme habitats with high pH (9-11), conductivity (20-120 mS cm^{-1}), water temperature (20-40°C) and high grazing pressure of the primary producer (Vareschi 1982, Ballot et al. 2004, Oduor and Schagerl 2007a, Schagerl and Burian 2016). The Kenyan soda lakes are endorheic and are recharged mainly by rainfall, temporary streams and (mostly hot) springs (Oduor and Schagerl 2007a, Renaut et al. 2017). As a result of their highly stochastic environmental dynamics, temporal fluctuations in ionic composition are characterized by sudden changes and fluctuations (Vareschi 1982, Melack 1988, Oduor and Schagerl 2007a, Krienitz and Kotut 2010, Schagerl 2016).

The East African soda lakes are well known for supporting huge populations of Lesser Flamingos (*Phoeniconaias minor* Saint Hilaire 1798). Lake Nakuru being the most famous (Vareschi 1978). These lakes are among the most productive ecosystems in the world owing to their high primary productivity provided by phytoplankton (Melack 1981, Oduor and Schagerl 2007b, Schagerl et al. 2015). During most of the time, phytoplankton is dominated by a spirally twisted, filamentous cyanobacterium *Limnospira fusiformis* (Voronichin) Nowicka-Krawczyk, Mühlsteinová & Hauer (syn. *Arthrospira fusiformis* (Voronichin) Komárek & J.W.G. Lund) (Cyanobacteria, Oscillatoriales) (Vareschi 1978, Krienitz and Kotut 2010, Mary N. Kaggwa et al. 2013, Mary Nakabungo Kaggwa et al. 2013, Krienitz 2018). The key to the survival, success

[2] A part of this chapter was published in the following paper:
Pálmai, T., Szabó, B., Kotut, K., Krienitz, L. & Padisák, J. 2020. Ecophysiology of a successful phytoplankton competitor in the African flamingo lakes: the green alga *Picocystis salinarum* (Picocystophyceae). Journal of Applied Phycology. 32:1813–25, DOI: 10.1007/s10811-020-02092-6.

and dominance of *L. fusiformis* is its fast growth and high photosynthetic rate (Talling et al. 1973, Melack and Kilham 1974, Oduor and Schagerl 2007b). This cyanobacterium serves as the main food source for Lesser Flamingos. These birds are on a special diet and the spirally twisted cyanobacterium is the best food that the birds are able to filter with their special bill lamellae (Jenkin 1957, Vareschi 1978, Vareschi and Vareschi 1984, Dadheech et al. 2010, Krienitz and Kotut 2010). Though there are other phytoplankton species within the optimal size range, only *L. fusiformis* is available in the required quantity. In the absence of their main food source, Lesser Flamingos survive by grazing on diatoms, other cyanobacteria and algae of suitable size or they migrate to other soda lakes (Tuite 2000, Krienitz et al. 2016). Tuite (2000) described two distinct types of Lesser Flamingos' distributions: the "clumped" distribution pattern, in which the majority of the total Lesser Flamingo population is concentrated at one or two lakes, and the dispersed distribution pattern, in which the population is spread across all available habitats. These patterns are strongly related to the availability of *L. fusiformis*: a clumped distribution was observed when the preferred cyanobacterium formed high density blooms, whereas a dispersed distribution pattern was recorded in the absence of *L. fusiformis* bloom (Tuite 2000).

An abrupt change in phytoplankton composition was recently observed by Krienitz and Kotut (2010): following the collapse of *L. fusiformis*' population, a picoplanktic green alga, *Picocystis salinarum* R.A. Lewin (Picocystophyceae) became dominant. Although *P. salinarum* was characterized by high abundance, their picoplanktic cells were too small to be grazed by the flamingos. *Picocystis salinarum* is a member of the class Picocystophyceae (Lopes dos Santos et al. 2017). *P. salinarum* was first described from a saline pond at the San Francisco Salt Works, California, as green spherical cells with a diameter of 2-3µm, without flagella, basal bodies and superficial body scales, living in saline waters. The major pigments present in the species are chlorophylls *a* and *b* and the carotenoids alloxanthin, diatoxanthin and monadoxanthin (Lewin et al. 2000; Lopes dos Santos et al. 2016). Identification of the species is difficult; only the trilobite cell morphology (described by Roesler et al. (2002) as "being reminiscent of Mickey Mouse") in older cultures or sometimes field samples can be helpful for visual identification (Lewin et al. 2000, Krienitz et al. 2012).

P. salinarum has been recorded in alkaline saline waters of four continents (*Appendix 5*). Owing to its tiny cell size, information on the general ecology of this species, especially the Kenyan strain, is scarce. Available information on the ecological role and habitat preferences of *P. salinarum* report that it usually occurs in temperate alkaline saline waters (*Appendix 5*),

is a potentially good food source for invertebrates (Roesler et al. 2002), tolerates heavy metal stress, and has the ability to remove bisphenol forms (Ben Ali et al. 2017, Ben Ouada et al. 2018b, 2018a).

Both *L. fusiformis* and *P. salinarum* prefer temperate alkaline saline habitats, however, the number of documented co-occurrences is minor (*Appendix 5*). The comparison of the two species is fairly difficult, because of limited information about *P. salinarum* as it was described only in 2000 by Lewin et al. (2000). In contrast, *L. fusiformis*, formerly known as *Arthrospira fusiformis* and earlier as *Spirulina fusiformis* (*platensis*), is a well-studied species. *L. fusiformis* was described and renamed from time to time in the last more than 130 years (Sili et al. 2012). Many aspects of photosynthesis and growth of *L. fusiformis* were studied commonly agreeing in the high productivity and/or growth of *L. fusiformis*. However, much less is known about the relationship between the effects of different environmental factors and the growth and/or photosynthesis of *L. fusiformis*, since the aim of the previous studies was to maximize the biomass production of the species in bioreactors or in open-air cultures (e.g. Chen, 2011; Xue et al., 2011).

Since the late identification of *P. salinarum* in 2000, only few experiments (Roesler et al. 2002, Fanjing et al. 2009, Ben Ali et al. 2017, Ben Ouada et al. 2018b, 2018a) have been carried out with this eukaryote. In the case of the Kenyan *P. salinarum* strain there has not been any previous study. Similarly, there is no documented laboratory study on the coexistence of the two species.

Picocystis strains have also been recorded in several other saline waterbodies: in North Africa (Ben Ali et al. 2017), in the North American region in Mono Lake, USA (Roesler et al. 2002), in the South American region in Peru (Tarazona Delgado et al. 2017), in an Asian soda lake in Inner Mongolia (Hollibaugh et al. 2001, Fanjing et al. 2009), in Lake Sambhar, India (Krienitz 2018) and in Lake Dziani Dzaha, Mayotte Island (Indian Ocean; Cellamare et al. 2018; Bernard et al. 2019). Phylogenetic analysis of strains from Africa and India revealed that both strains belong to one and the same species, *Picocystis salinarum*.

The co-occurrence of *Picocystis* and *Limnospira* was first observed in Lakes Nakuru and Bogoria in 2010 (Krienitz and Kotut 2010, Krienitz et al. 2012) and later in Lake Dziani Dzaha (Cellamare et al. 2018, Bernard et al. 2019). There are similarities and also differences between these co-occurrences. Common to the two observations is the huge dominance of *L. fusiformis* in the phytoplankton biomass. In the East-African soda lakes, this dominance was followed by a collapse of *L. fusiformis* populations and subsequently, *P. salinarum* became dominant

(Krienitz and Kotut 2010). However, in Lake Dziani Dzaha *P. salinarum* did not replace the cyanobacterium, but remained subdominant species. Hence, both species were dominant within their taxonomic and ecological groups in Lake Dziani Dzaha: *L. fusiformis* was responsible for 99.99% (8,249,182 sequences) of the cyanobacteria abundance, while *P. salinarum* accounted for also 99.99% (1,480,251 sequences) of eukaryotic phytoplankton species (Bernard et al. 2019).

Although *L. fusiformis* is a well-known species and has been the target of many ecological and biotechnological studies (e.g. Ciferri 1983, Affan et al. 2015, Castro et al. 2015, Shao et al. 2019), there has been no laboratory study on the coexistence of *L. fusiformis* and *P. salinarum.*

The main aim of the current study was to establish the reason for the dominance of *P. salinarum* via laboratory experiments. It was investigated whether it might be due to the different photosynthetic characteristics of the two species or their co-occurrence is affected by the rapid environmental changes (rapid increase and decrease of conductivity) as suggested by Schagerl et al. (2015) and Krienitz (2018).

5.2 Materials and methods

5.2.1 Strains and cultivation

Photosynthesis, growth and competition experiments were carried out with *Limnospira fusiformis* (KR 2005/117) and *Picocystis salinarum* (KR 2010/2) strains from the collection of Leibniz-Institute of Freshwater Ecology and Inland Fisheries (Stechlin, Germany). Both strains were collected from Lake Nakuru, Kenya. Their taxonomic identity was confirmed by molecular phylogenetic analyses (Dadheech et al. 2010, Krienitz et al. 2012). The sequences of 16S-23S ITS and *cpc* BA IGS of the *Limnospira fusiformis* strain were stored at the National Center for Biotechnology Information (NCBI) under the accession numbers FJ001900 and FJ001933. The sequence of the small-subunit (SSU) rRNA gene of the *Picocystis salinarum* strain was stored at NCBI under the accession number HM990668.

Monoalgal stock cultures of the two species were held in M_0 medium with the following ingredients (see ingredients also in *Appendix 6*): 15 g $NaHCO_3$, 4 g Na_2CO_3, 0.1 g NaCl, 0.08 g Na_2-EDTA, 0.01 g $FeSO_4 \cdot 7H_2O$, 0.2 g $MgSO_4 \cdot 7H_2O$, 0.5 g K_2HPO_4, 2.5 g $NaNO_3$, 0.04 g $CaCl_2$ and 1 ml L^{-1} of A_5-micronutrients (Shafik et al. 2014) at 19±1°C and 50 µmol photons m^{-2} s^{-1} in the Alga Culturing Laboratory of Department of Limnology (University of Pannonia, Veszprém).

5.2.2 Photosynthesis measurements

The photosynthetic characteristic of *L. fusiformis* and *P. salinarum* were examined in the above described medium during exponential growth phase of both species' monoalgal cultures. Photosynthetic activity of both species was examined in 63 combinations of temperature and light intensity within the ranges of their natural habitats. The above described photosynthesis measurement protocol was used in cases of *L. fusiformis* and *P. salinarum*. The measurements were carried out between 10 and 40°C with 5°C increments. The following nine light intensities were applied: 0; 15; 55; 130; 250; 360, 680; 1480 and 1900 µmol m^{-2} s^{-1}.

5.2.3 Chemostat measurements: Growth and competition experiments

Growth characteristics of P. salinarum in different media

To determine the effects of conductivity on the growth rate of *P. salinarum*, experiments were carried out in a continuous algal culturing system (chemostat) described by Shafik et al. (2001) (*Figure 7*). The experiment was carried out at 29±1°C, a Thermo Scientific AC150-A25 circulating bath was responsible to keep the distilled water at the specific temperature in the aquarium and also indirectly in the culturing vessel. Light intensity of 200 µmol m^{-2} s^{-1} with

12:12 light:dark cycle was provided by daylight tubes of Tungsram (F74). Light intensity was measured before the experiments in distilled water. The aquarium was illuminated from one side and the wall of the other three part of the aquarium was covered by mirrors to provide homogenous illumination. During the experiment the light intensity inside the culturing vessel probably decreased according to the self-shading of *P. salinarum* cells. The cultures were aerated with sterilized air (obtained by passing air through a Millipore membrane with 0.2 μm pore size). The air supply was not only responsible for the supply of CO_2 but also for the continuous mixing of the culture.

Subsamples from the main culture at an exponential phase were transferred into the culturing vessels. The cultures were first grown in the initial medium (M_0) before carrying out tests on the performance of the species under different salt concentrations. Fourteen different culture media were used (*Appendix 6*) to test the effect of the different concentrations of chloride (NaCl) and carbonate forms (both Na_2CO_3 and $NaHCO_3$) on the growth of *P. salinarum*. Shifts between media of different concentrations were done when the cultures reached steady state, therefore, sample numbers from different media slightly differed. Effects of increasing the concentration of chloride and carbonate forms were examined separately in two different culture vessels with an approximate volume of 1000 mL. The growth medium was continuously added with a Masterflex L/S Variable-Speed Drive, at a flow rate of 160±15 mL d^{-1}. The flow rate was determined based on pilot studies, which were carried out both on *P. salinarum* and *L. fusiformis*. The chosen experimental conditions were found to be optimal for the photosynthesis of *P. salinarum* in the present study and are similar to conditions in the species' natural habitat.

Changes in biomass were monitored by measuring the optical density of the samples at 750 nm with spectrophotometer (Metertech SP-8001) and/or by checking the samples under microscopy if it was necessary. Samples were taken three times a week. Growth rate (μ) were calculated using the formula of Shafik et al. (1997) as previously described by Novick and Szilard (1950) and Monod (1978):

$$\mu = \frac{ln(A_1 - A_0)}{t_1 - t_0} + D,$$

Where A_1 is the absorbance of the culture at time t_1, A_0 is the absorbance of the culture at time t_0 and D is the dilution rate.

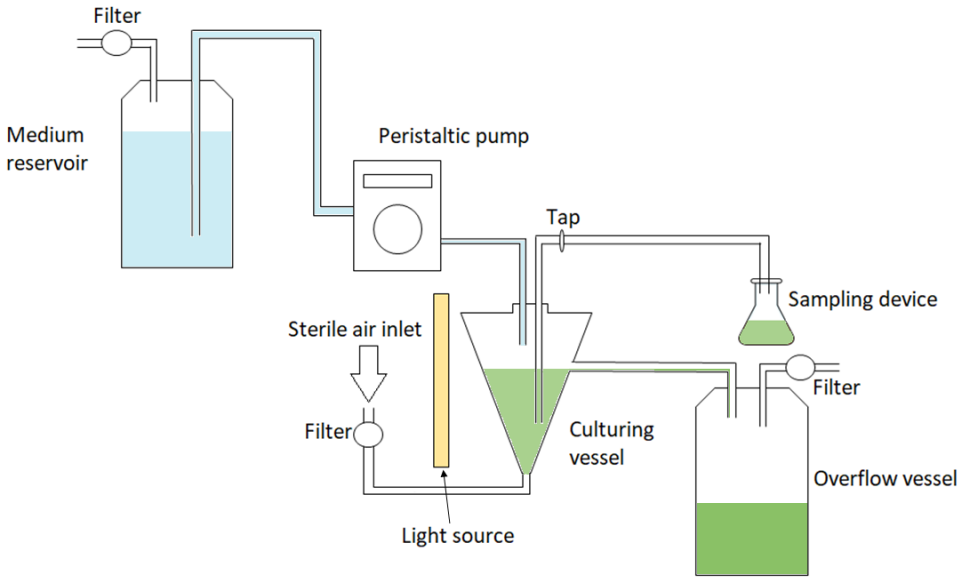

Figure 7 Graphical illustration of the continuous culturing system (chemostat), after Shafik et al. (2001)

Competition experiment

Growth and competition of the two species were examined in the above described chemostat (*Figure 7*). Same experimental setup was used in the case of the mixed culture as previously described in the case of *P. salinarum*. The only difference was the flow rate, which was increased to 285±18 mL d^{-1}. Higher flow rate was applied because of the huge differences between the growth rate of *L. fusiformis* and *P. salinarum* (in pilot studies *L. fusiformis* was found to grow very fast even under ~500 mL d^{-1} dilution rate but and *P. salinarum* disappeared from the cultivating vessel at such high rates).

In the competition experiment, the mixture of the above described monoalgal cultures was applied. The initial biomass concentration ratio in the mixed culture of the two species was 90:10 *L. fusiformis: P. salinarum* µg chlorophyll *a* L^{-1} in a cultivating chamber with an approximate volume of 1 L. Samples were taken three times a week to estimate population sizes by counting individual number according to Utermöhl (1958).

To examine the effect of the rapidly changing environment (increase and decrease of conductivity) on the species' growth and co-occurrence, the concentration of $NaHCO_3$ was increased to 60 g L^{-1} and Na_2CO_3 to 16 g L^{-1} in M_0 medium. Mixed cultures were grown for the first 30 days in M_0 medium, then for 30 days in the medium with increased conductivity, and after that for further 30 days in M_0 medium again. The changes were monitored in the concentration of carbonate forms by measuring the conductivity at each sampling time.

The growth of both species was separated into sections according to the experimental setup and growth rates were calculated for each section separately. The growth curve of *L. fusiformis* and *P. salinarum* was divided into three phases: phase I was the initial growth in the initial M_0 medium, in phase II the level of conductivity was increased and in phase III biomass was recorded after the return to the initial medium. Growth rates were calculated according to the formula provided by Sprouffske and Wagner (2016) with the addition of dilution, since continuous culture was used:

$$N_t = \frac{K}{1 + \left(\frac{K - N_0}{N_0}\right) e^{-rt}} + D,$$

where N_t is the number of cells at time t, N_0 gives the population size at the beginning, K is the maximum possible population size in a particular environment, or the carrying capacity, r is the growth rate if there were no restrictions imposed on total population size and D is the dilution rate.

5.2.4 Statistical analysis

To determine whether temperature and/or light intensity treatments had a statistically significant effect on the photosynthetic activity of *L. fusiformis* and *P. salinarum*, two-way analysis of variance (ANOVA) was conducted.

Because of the unequal variances and sample sizes, Welch's t-test was applied to determine whether the difference in average growth rates under carbonate dominated and chloride dominated media were significant. Spearman rank correlation coefficient was used to assess the relationship between growth rate and conductivity in carbonate and chloride dominated media. In case of both main media types, a one-way analysis of variance (ANOVA) was performed to test whether the modification of carbonate and chloride content (indicated by the different medium subtypes, *Appendix 6*) affects significantly the growth rates of *P. salinarum*. Subsequently, Tukey's post hoc multiple comparison tests were conducted between each pair of carbonate and chloride dominated media.

To determine whether temperature and/or light intensity treatments had a statistically significant effect on the photosynthetic activity of *L. fusiformis* and *P. salinarum*, a two-way analysis of variance (ANOVA) was carried out. Statistical analyses were carried out using R statistical computing environment (R Core Team 2018).

5.3 Results

5.3.1 Photosynthesis-light characteristics

Increasing photosynthetic activity of both species was recorded in wide range of temperature between 10 and 40°C. However, the steepness of this increase and the level of photosynthetic activity was quite different. Biomass specific maximal photosynthetic activity (P^B_{max}) of *L. fusiformis* was found to be higher by an order of magnitude at all measuring temperature that of *P. salinarum*s values (*Appendix 3*). The highest P^B_{max} was obtained for both species at 40°C, for *L. fusiformis* it was 17.927 µg C µg Chl a^{-1} h^{-1} and for the green alga, it was 1.33 µg C µg Chl a^{-1} h^{-1}. The highest P^B_{max} for *P. salinarum* was nearly a half of *L. fusiformis'* lowest P^B_{max} (obtained at 10°C).

The difference between the P^B_{max} values of the two species was higher at the lower temperature range (10-15°C) and decreased with increasing temperature, even though there was an order of magnitude difference. Similarly, temperature positively influenced the photoadaptation parameters (I_k) of the two species, with also remarkable differences between the species. *L. fusiformis* had higher optimum light intensity at all measuring temperatures, its highest I_k was 336.6 µmol m^{-2} s^{-1}, whereas *P. salinarum* had a maximum at 40°C with a value of 89.3 µmol m^{-2} s^{-1}. Good light utilization (α) of both species was observed along the applied temperature scale: α values of the two species varied between 0.0061 and 0.1 (µg C µg Chl a^{-1} h^{-1}) (µmol m^{-2} s^{-1})$^{-1}$. Photoinhibition in *L. fusiformis* culture occurred at the temperature range of 10-25°C while in the case of *P. salinarum*, higher values of photoinhibition occurred along the whole temperature range. The biomass specific respiration of the two species did not differ remarkably: their values increased with increasing temperature and peaked at 40°C. Due to the similar levels of respiration of the two species, the photosynthesis to respiration ratio differed greatly. P^B_{max}/R^B values of *P. salinarum* varied between 1.349 and 6.385 in contrast to *L. fusiformis*' whose ratios ranged from 25.00 to 82.47.

5.3.2 Photosynthesis-temperature characteristics

Photosynthesis-temperature characteristics of the two species confirmed the huge difference between the photosynthetic activities of the species. At low light intensities (15-250 µmol m^{-2} s^{-1}), the photosynthetic activity of both species could fit with a bell curve with a maximum at about 30°C. The lowest, but still considerable photosynthetic activity for *L. fusiformis* in the 15-130 µmol m^{-2} s^{-1} and for *P. salinarum* in the 15-45 µmol m^{-2} s^{-1} light intensity ranges was recorded. The rapid increase in photosynthesis with increasing light intensity confirms the good

light utilization of both species. Alongside an increase in photosynthetic activity at higher light intensity range, a slight increase in temperature optima was observed. At high light intensities, photosynthetic activity of the species increased with the increasing temperature, with the highest photosynthetic activity being recorded at the highest temperature. As in the case of the temperature scale, the photosynthetic activity of *L. fusiformis* was also higher by an order of magnitude along the light intensity scale.

Table 5 Effect of temperature and light intensity treatments on the photosynthetic activity of *Limnospira fusiformis* and *Picocystis salinarum* based on the results of two-way ANOVA (Df = degrees of freedom, F = F-value, P = P-value).

	Df	F	P
Limnospira fusiformis			
Temperature	6	655.496	<0.001
Light intensity	7	792.894	<0.001
Temperature × Light intensity	42	66.237	<0.001
Residuals	112		
Picocystis salinarum			
Temperature	6	2471.493	<0.001
Light intensity	7	429.854	<0.001
Temperature × Light intensity	42	80.864	<0.001
Residuals	110		

The two-way ANOVA indicated that the temperature and light intensity treatments alone as well as the interaction of the two factors affected significantly the photosynthetic activity of both species (*Table 5*).

5.3.3 Chemostat measurements: Growth and competition experiments

Growth characteristics of P. salinarum in different media

Fourteen different media in increasing concentration of carbonate or chloride forms were used to examine the effect of conductivity changes on the growth rate of *P. salinarum*. Welch's t-test indicated that mean growth rate in the carbonate dominated media was significantly higher ($t=13.96$, $df=329.05$, $p<0.001$) than the chloride dominated media (*Figure 8*).

In the carbonate dominated medium, Spearman's rank correlation revealed a strong positive correlation between conductivity and the growth rate of *P. salinarum* ($r=0.64$, $p<0.001$). A one-way ANOVA revealed the existence of a significant difference in the growth rates of the different media subtypes ($df=5$, $F=53.614$, $p<0.001$). The mean growth rate of *P. salinarum* in the initial medium (M_0) was 0.131 ± 0.035 d^{-1}. In M_1 medium, the mean growth

rate was significantly higher (0.160±0.019 d^{-1}). From M_1 to M_2 (mean growth rate: 0.16±0.027d^{-1}), a slight, non-significant increase was observed (*Figure 8A, Appendix 7*). The difference in mean growth rates in media M_3-M_5 was not significant (*Appendix 7*). Mean growth rates recorded in M_3, M_4 and M_5 were 0.220±0.024 d^{-1}, 0.214±0.043 d^{-1} and 0.243±0.027 d^{-1} respectively.

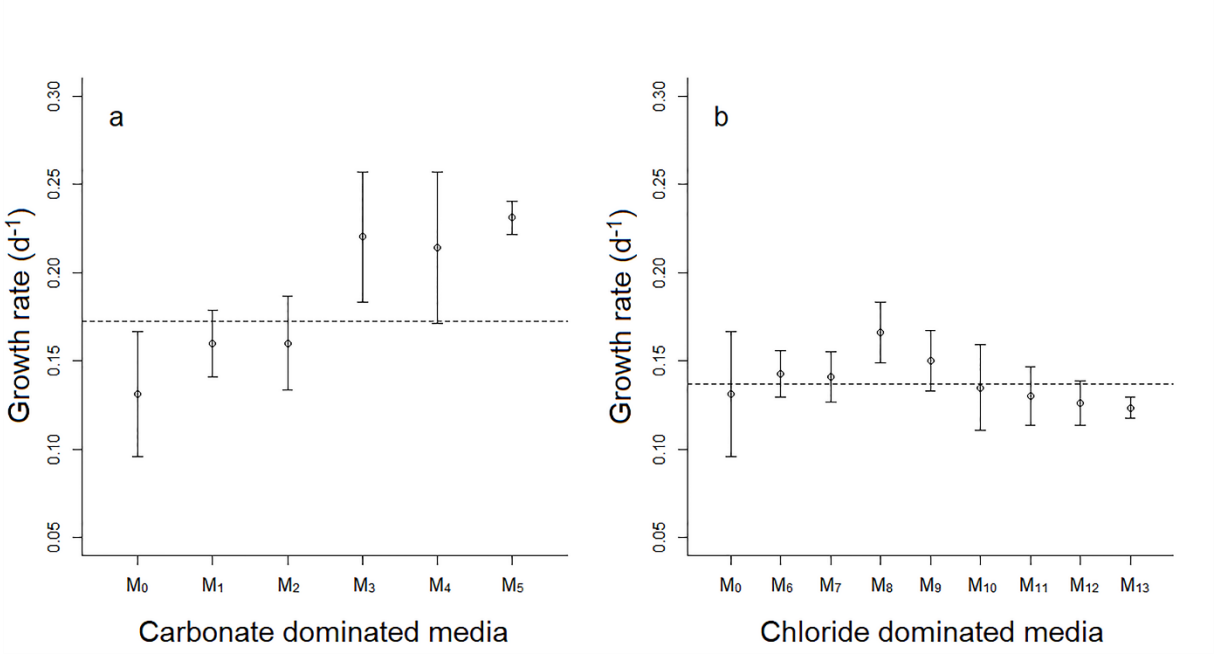

Figure 8 Growth rate of *P. salinarum* as a function of carbonate (a) and chloride (b) dominated culture media (M_0 indicates the initial medium, M_1-M_5 the carbon dominated media and M_6-M_{13} the chloride dominated media).

For the chloride dominated media, a weak negative correlation between conductivity and the growth rate (r=-0.26, p<0.001) was recorded. A one-way ANOVA test revealed that the growth rate of *P. salinarum* differed significantly in culture media containing different chloride concentrations (df=8, F=8.473, p<0.001). An initial increase in the mean growth rate (M_6: 0.143±0.013 d^{-1}, M_7: 0.141±0.014 $d^{-1}$and M_8: 0.166±0.017 d^{-1}) was observed (*Figure 8B*). However, whereas the difference between M_6 and M_7 was not significant, the difference between M_7 and M_8 was significant (*Appendix 7*). A further increase in sodium chloride concentration resulted in a decline in growth rate (*Figure 8B*). However, the difference in the growth rate of the species in the subsequent growth media was not significant (*Appendix 7*). The mean growth rates registered in the remaining media concentrations were 0.150±0.017 d^{-1}, 0.135±0.024 d^{-1}, 0.130±0.017 d^{-1}, 0.126±0.012 d^{-1} and 0.123±0.006 d^{-1} in M_9, M_{10}, M_{11}, M_{12} and M_{13} respectively.

The effect of rapid shifts in conductivity on the growth of *L. fusiformis* and *P. salinarum* was examined in two culturing media characterised by different conductivity achieved by the alteration of $NaHCO_3$ and Na_2CO_3 concentration.

Table 6 Growth rate of *Limnospira fusiformis* and *Picocystis salinarum* during the salinity stress experiment

Species	***Limnospira fusiformis***	***Picocystis salinarum***
r in phase I. (d^{-1})	0.5348±0.0341	0.7161±0.1137
r in phase II. enhanced salt content (d^{-1})	0.2596±0.0091	0.2975±0.0025
r in phase III. (d^{-1})	0.4334±0.0036	0.4339±0.0128

Competition experiment

In phase I the increasing individual number of both species was observed in the initial medium: *L. fusiformis* reached a growth rate of 0.5348 d^{-1} and *P. salinarum* had 0.7161 d^{-1} (*Figure 9*). This increase of the individual number was continuous and straight for *L. fusiformis* until the shift to high conductivity medium in contrast to *P. salinarum*, which reached almost steady state at the end of phase I.

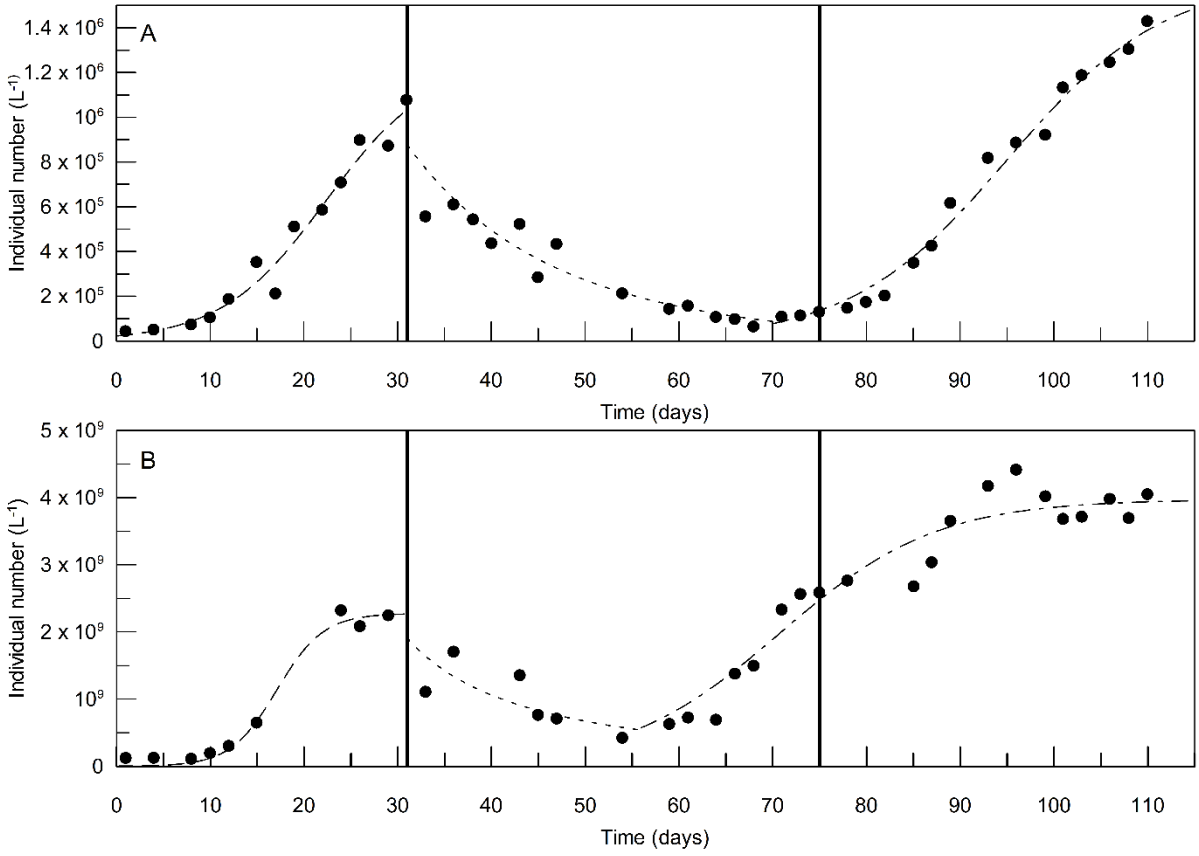

Figure 9 Growth curves of *Limnospira fusiformis* (A) and *Picocystis salinarum* (B) in continuous culture in phase I (dash line), phase II - elevated salt content (dot line), phase III (dash-dot line). Dots represent the counted cell numbers, vertical lines represent the change of the medium on day 31 and 75.

Following the shift in medium, the individual number of both species began to decrease. In phase II the individual number of *L. fusiformis* decreased, and this was a typical for the blue-green alga during the entire high conductivity phase. In the individual number of *P. salinarum* also a remarkable decrease was found, however the green alga was able to adapt to the changes in the conductivity and from the middle of phase II (~ 2 weeks after the medium change) the individual number began to grow. At the end of phase II. *P salinarum* reached the steady state again between day 72 and 82. After the return to the initial medium, in phase III both species' individual number began to increase following an initial stationary state. In phase III *L. fusiformis* was in a rapidly growing phase even at the end of the experiment in contrast to *P. salinarum* that reached steady state again. Growth rates of the two species did not reach the level of the initial section, their lowest growth rate (where the individual number decreased) was observed in phase II (*Table 6*).

5.4 Discussion

Soda lakes of East Africa are amongst the most productive ecosystems in the world (Melack 1979, 1981, Oduor and Schagerl 2007b, Schagerl et al. 2015). This very high primary production is usually brought about by one single phytoplankton species, *Limnospira fusiformis.* Phytoplankton productivity in lakes plays an important role in biogeochemical cycles and supply food to heterotrophs. This is especially true for soda lakes of the semi-arid regions because phytoplankton primary production is almost the only carbon supply in these aquatic ecosystems. Poor macrophyte growth is due to both limited rainfall and discharge from inflows as well as to poor light climate of the water column and littoral areas caused by high primary production of phytoplankton (Vareschi 1978, 1982; Cloern 1996; Oduor and Schagerl 2007). The main consumers of these lakes, the Lesser Flamingos, are on a special diet as they feed preferably on *L. fusiformis* (Jenkin 1957, Vareschi 1978, Krienitz and Kotut 2010, Krienitz 2018). Hence this species is a critical food resource in soda lakes. In these extreme habitats, phytoplankton composition is affected by several factors that include inter- and intraspecific competition and variation in a number of physical and chemical environmental factors such as nutrient availability, temperature, light intensity, conductivity as well as predation pressure (Vareschi 1979, 1982, Vareschi and Vareschi 1984, Jirsa et al. 2013, Krienitz et al. 2016).

A number of factors have created perfect habitats in the soda lakes of East Africa for phytoplankton species to form blooms with high biomass. This include an abundant supply of phosphorus and nitrogen forms of nutrients owing to a high population of birds and a unique geochemistry that ensures a virtually unlimited availability of dissolved carbon dioxide (Vareschi 1982, Oduor and Schagerl 2007a, Jirsa et al. 2013). High temperature could also favour high primary production since at higher temperature biological processes are faster (Davison 1991). *L. fusiformis* is considered to prefer high temperature: the positive correlation between temperature and photosynthetic activity of the species is well known and has been confirmed by several experiments (Vonshak 2002). However, considerable photosynthetic activity was observed along a wide range of temperature, whereas photoinhibition occurred only at low temperatures. The photosynthetic activity of *P. salinarum* was found to be at about the same level as reported in previous study by Roesler et al. (2002) with values that were lower by an order of magnitude or more than that of *L. fusiformis*. The photosynthetic activity of the green alga showed a strong temperature dependence with photoinhibition occurring over a wide range of temperature. The differences in the photosynthetic activity of the two species clearly demonstrate the differences in growth requirements and attributes of the two species: *L.*

fusiformis prefers warm habitats with good light supply in contrast to *P. salinarum*, which has a lower temperature and much lower light optimum (Kebede and Ahlgren 1996, Roesler et al. 2002, Vonshak 2002, Fanjing et al. 2009).

The adaptation of *P. salinarum* to low light intensity was described by Roesler et al. (2002). This adaptation explains its occurrence in the turbid waters of East Africa (Krienitz et al. 2012) and is consistent with its bloom formation under snowy ice (Fanjing et al. 2009). The preference of low light levels along wide range of temperature values (10-45°C) was confirmed. Adaptation to low light with good light utilization along the wide range of temperature allows the species to be successful in light limited habitats. *L. fusiformis*, the most important competitor of *P. salinarum* in the East African soda lakes in terms of its mass production provides shaded, low light habitat for *P. salinarum*, thus allowing the picoeukaryote species to survive and in this case to become dominant.

Since there is a lack of data on the respiration of *P. salinarum*, its dark respiration (R^B) and its photosynthetic activity to dark respiration ratio (P^B_{max}/R^B) can be compared with those of its competitor *L. fusiformis*. P^B_{max}/R^B was found to be very different between the two species. The cyanobacterium *L. fusiformis* had high P^B_{max} along the temperature scale investigated with low dark respiration. This observation has also been described for other cyanobacteria species (Van Liere and Mur 1979, Vonshak 2002). The huge difference results in an extremely high P^B_{max}/R^B ratio. In contrast, *P. salinarum* had a moderate ratio along the temperature scale resulting in a remarkable difference between the P^B_{max}/R^B of the two species. P/R values similar to those of *P. salinarum* were recorded by Humphrey (1975) for several algal species.

Light availability in the East African region is quite good: high light intensity coupled with many hours of sunshine provides perfect conditions for phototrophs (Vareschi 1982). Despite the high amount of incident light received in soda lakes, the high turbidity caused by both wind and bioturbation by a huge population of birds and shading by high phytoplankton crop results in a sharp reduction in light intensity with the depth (Vareschi 1982, Oduor and Schagerl 2007b). These environmental conditions create perfect habitat for both species: high light intensity satisfies the light requirements of *L. fusiformis* while the turbid and light limited water column creates perfect conditions for *P. salinarum*, which is able to utilize low light intensity (Roesler et al. 2002). The description of the pigment composition of the species by Bernard et al. (2019) also supports findings of present study on the difference in the light requirements of the two species. The effective light utilization by both species is advantageous in turbid habitats. Although, photoinhibition in *P. salinarum* was recorded over a wide range

of temperature, in its natural environment, the species can avoid the negative effect of high light intensity of the surface layer by occurring in the deeper parts of the water column characterized by lower light availability (this sometimes means only 20-30 cm below the surface), hence avoiding the surface layer (Vareschi 1982, Oduor and Schagerl 2007b).

The photosynthesis measurements did not support one of the hypotheses: the differences in the photosynthetic activity of the two species alone cannot be the reason for the replacement of *L. fusiformis* by *P. salinarum* in the Kenyan soda lakes. Additionally, none of the photosynthetic parameters was responsible for this phenomenon. Since the experimental setting of present study covered each possible temperature – light intensity combination in Lake Nakuru, neither temperature, light intensity nor any combination of the two can drive the increasing dominance of *P. salinarum* over *L. fusiformis*.

Significant differences in the effect of carbonates and chlorides on the growth rate of *P. salinarum* were confirmed in the present study. *L. fusiformis* has also been reported to have a higher growth rate in carbonate dominated media as compared to chloride dominated ones. However, the mean growth rate of the species showed a negative correlation with salinity increase (Kebede 1997). Tolerance, or even a preference for a high conductivity by *P. salinarum* seems to be one of the most important features of the species: Fanjing et al. (2009) recorded the highest growth at a sodium chloride range from 29.2 to 58.4 g L^{-1}, and no growth at higher concentration range (from 230 to 300 g L^{-1}). The effect of salinity on the growth of the species has also been investigated for a strain from Mono Lake over a wide range, with a peak in the growth rate at 40 ppt (~60 mS cm^{-1}) (Roesler et al. 2002). The highest growth rate recorded in the present study in the M_5 medium is close to the salinity level of the Mono Lake strain. However, present dissertations finding was ~1 d^{-1} lower than that determined by Roesler et al. (2002). Comparing the findings of Kebede and Ahlgren (1996) and Kebede (1997) on the maximum specific growth rate (1.78 and 2.14 d^{-1}) of the outcompeted *L. fusiformis* to that of the Kenyan strain of *P. salinarum* (0.243 d^{-1}), it is evident that specific growth rate of *L. fusiformis* is higher by an order of magnitude than that of *P. salinarum*. However, the growth rate values were strongly dependent on temperature and salinity. Although the present study confirmed that the concentration of both carbonate forms and chloride significantly affected the growth of *P. salinarum*, this effect was less pronounced than was recorded in previous studies (Roesler et al. 2002, Fanjing et al. 2009). This difference can be explained by a difference in experimental conditions and culture methods. In the present study, an African strain of *P. salinarum* and different media with a different culture method was used. Chemostat was applied

instead of batch cultures, which provided continuous transition between different media thus eliminating drastic shifts in conductivity, which favours the acclimation of the species to the new medium. Although an increase in conductivity has a significant effect on the growth of *P. salinarum*, the impact of light intensity and temperature appear to be much more important.

Previous studies of various authors as well as present study show that both photosynthetic activity and growth of *P. salinarum* are far below the values of *L. fusiformis*' (Kebede and Ahlgren 1996, Roesler et al. 2002, Fanjing et al. 2009), another environmental factor or changes in this factor could be the reason for the dominance change between the two species in the Kenyan soda lakes. Krienitz and Kotut (2010), Schagerl et al. (2015) and Krienitz (2018) attributed the dominance of *P. salinarum* in the soda lakes of East Africa to the rapid changes in salinity/conductivity. Hence, according to these authors, the dominance change between the two species resulted from salinity/conductivity changes.

Furthermore, the role of the dominant ion might be also important. It has been shown that a medium with a high chloride concentration is not favourable for both species: lower photosynthetic activity and also lower growth rate was observed in a chloride dominated medium as compared to the carbonate forms (CO_3^{2-} and HCO_3^-) dominated one (Roesler et al. 2002, Fanjing et al. 2009, Shafik et al. 2014).

Although there are no past experiments on the growth of the Kenyan strains of the two species in mixed cultures, some studies have revealed that the two species differ greatly in salt tolerance. Even when they occur in alkaline saline waters, increasing sodium salt (Na_2SO_4, NaCl, $NaHCO_3$) concentrations has a negative effect on the growth of *L. fusiformis* and also alter the morphology of the cyanobacterium (Kebede 1997). Kebede (1997) recorded a negative correlation between the concentration of three sodium salts and the growth rate of *L. fusiformis*, with the highest growth occurring at a salinity of 13.2 g L^{-1}. A salinity range 10-25 g L^{-1} was found to be optimal for the growth of *L. fusiformis* in different media (Chen 2011), whose preference was also confirmed by the observations of present study. The negative effect of a high salinity (high NaCl concentration) was also recorded for *P. salinarum*, however, the eukaryote species tolerates a higher salinity range than *L. fusiformis* (Roesler et al. 2002, Fanjing et al. 2009). Nevertheless, the dominant ion also plays an important role. Krienitz et al. (2012) observed that *P. salinarum* became dominant in Lake Nakuru following a drastic decrease in water level, which was accompanied by rapid and drastic changes in conductivity/salinity.

Past studies have confirmed that the population of *L. fusiformis* collapse from time to time. The population collapse has been associated with a high turbidity and/or conductivity periods of the lake (Melack 1988, Schagerl et al. 2015). In the light of the periodic collapse, some of the previous studies on the cyanobacterium species have suggested that the possibility of the replacement of *L. fusiformis* by *P. salinarum* is a real threat (e.g., Kebede and Ahlgren (1996), Kebede (1997), Roesler et al. (2002), Fanjing et al. (2009)). Empirical studies by Krienitz and Kotut (2010), Schagerl et al. (2015) and Krienitz (2018) established a close relation between *L. fusiformis* biomass and conductivity. Similar finding was also recorded in current experimental study under laboratory conditions. Consequently, the fast increase or decrease in conductivity appears to have a greater impact on the population of *L. fusiformis* than on that of *P. salinarum*.

Observations in Lake Dziani Dzaha, however, showed that the two species can co-dominate the phytoplankton (Bernard et al. 2019). Due to a lack of nutrient limitation in the East African lakes and that the Kenyan strains occupied different light niches (see I_k values in *Appendix 3*), resource competition between the two species can be excluded. This co-occurrence implies that *P. salinarum* and *L. fusiformis* can exist in the same habitat and dominate the phytoplankton together, however, the green alga cannot outgrow *L. fusiformis* under stable environment conditions. Whereas the biomass of *L. fusiformis* in the soda lakes of East Africa is usually measured in tens to hundreds of mg L^{-1}, the highest biomass of *P. salinarum* in Lake Nakuru ranges from 7100 to 7400 µg L^{-1} (Vareschi 1982, Krienitz et al. 2012, 2016). These data suggest that *P. salinarum* benefits more from the environmental changes, hence becoming an active competitor for *L. fusiformis*.

Another important factor during the collapse and the recovery of *L. fusiformis* population is the high grazing pressure. Vareschi (1978) estimated the food requirements for an adult flamingo to be 70 g d^{-1} of dry mass. This means that there is a strong pressure on *L. fusiformis* population even under favourable environmental conditions. A drastic change in the lake level of the observed cases was followed by a crash in the population of *L. fusiformis*. A lack of tolerance for this kind of change coupled with a high grazing can easily lead to the disappearance of the *L. fusiformis* populations. Following the collapse of the cyanobacterium, the Lesser Flamingos migrate to other lakes resulting in a dispersed distribution pattern (Tuite 2000) and a reduction in grazing pressure. This allows the recovery of *L. fusiformis* population.

Lesser Flamingos are specialized feeders equipped with bill lamellae that enable them to filter food in the size range of 15–800 µm from the water (Jenkin 1957, Krienitz 2018). This

bill structure makes them unable to filter *P. salinarum*, even if it is the dominant species of the phytoplankton. The small size, which makes *P. salinarum* a good food source for invertebrates, as shown by the grazing experiments of Roesler et al. (2002), also serves as a perfect defence against grazing by flamingos in the East African soda lakes.

The periodic collapse of *L. fusiformis* is therefore strongly associated with rapid environmental changes (Vareschi 1982, Melack 1988, Kebede 1997, Schagerl et al. 2015, Oduor and Kotut 2016) and biotic factors, such as cyanophage attack or interspecific competition (Peduzzi et al. 2014, Schagerl et al. 2015). The high sensitivity of *L. fusiformis* to rapid changes in the physical environment (e.g., conductivity) predicts the possibility of systematic collapses of the cyanobacterium population in future as a result of the rapid changes in water level in between the dry and flood periods in the East African soda lakes (Oduor and Kotut 2016, Bett et al. 2018), especially under the increasing frequency of extreme events driven by the ongoing climate change (Jentsch et al. 2007, Coumou and Rahmstorf 2012, Reichstein et al. 2013). Such an incident was experienced in the early 2010's when *L. fusiformis* was replaced by *P. salinarum* (Krienitz and Kotut 2010, Oduor and Kotut 2016). After taking into account all the factors cited above as being responsible for the dominance changes, present experiments demonstrated that the rapid conductivity changes are most likely the driver of this process. To a certain extent, the metaphor of David and Goliath is applicable here - a small, supposedly weak organism (*Picocystis*) gains prevalence over a large, supposedly strong one (*Limnospira*).

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7 Contribution to the research

The sample collection and isolation of *L. fusiformis* and *P. salinarum* from Lake Nakuru, Kenya was made by Dr Lothar Krienitz and Dr Kiplagat Kotut.

The sample collection of some species was carried out with some assistance of Prof Dr László G-Tóth, Dr Katalin Eszter Hubai, Dávid Németh, and Dr Beáta Szabó.

The identification of some phytoplankton species was done by Zsuzsanna Zámbóné Doma and Dr Géza Balázs Selmeczy.

Statistical analysis were carried out with the essential help and guidance of Dr Beáta Szabó.

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Results in thesis points

1 Temperature and light intensity dependent photosynthetic characteristics of some algal and Cyanobacteria species

1.1 Photosynthetic activity of 16 species collected from very different kinds of ecosystems was measured in wide ranges of both temperature and light intensity. This research found a significant effect of these major environmental variables on the photosynthetic activity of the species. Though temperature and light intensity affected positively the photosynthesis for all studies species, the general outcome is that the response is quite species specific.

1.2 P^B_{max} results revealed a possible cause of the global expansion of Cyanobacteria species: highest level of biomass specific photosynthetic activity was recorded for the two bloom forming Cyanobacteria species: *Limnospira fusiformis* and *Microcystis flosaquae*. Also, higher temperature optima (over 30°C) was revealed for Cyanobacteria species, in contrast to species belonging to other phyla with not or just reaching the 30°C. I_k values of the species varied much within and across the examined four phyla. In general higher I_k values of green algae was observed, however summer bloom forming Cyanobacteria also reached that level.

1.3 P-T characteristics of the species confirmed the differences between the temperature optima of the examined four phyla. In accordance with the previous findings of various authors, higher temperature optima of the examined Cyanobacteria species were recorded in general, however high variance of values was recorded in all examined phyla.

2 Quantitative estimation of photosynthetic plasticity: effect of temperature on various algal species

2.1 Plasticity measures available in the scientific literature calculate with the ratios of the examined variable, consequently they overestimate the significance of relative changes. Species with one of the lowest photosynthetic activity (like *Monoraphidium griffithii* in this research) are presented by these methods as highly plastic due the high relative change in their P^B_{max}. Methods like PP index, coefficient of variations are applicable if there are two or only a few treatments (best is the linear relationship), but not applicable when cross environmental ranges of variables are used.

2.2 A newly applied method, the comparison of the length of reaction norms of species along the temperature scale compared to a reference (CLP - zero plasticity) calculate with both the ratio of change and the absolute values along the temperature scale. However, this method

does not allows the comparison of different units (for which is an example of comparing data of planktonic and attached algal species).

2.3 The CLP method confirmed the global expansion of cyanobacterial species, since this method calculated the three highest values for cyanobacteria. There are five cyanobacterial species out of the first eight, which support the field observations about the expansion of cyanobacterial species.

3 Growth and photosynthetic response to changing environmental conditions of *Picocystis salinarum* and *Limnospira* (*Arthrospira*) *fusiformis* strains from saline-alkaline Flamingo lakes of East Africa with a special focus on the little known picoalga

3.1 The photosynthetic characteristic of the two focused species showed different patterns: *L fusiformis* had high P^B_{max} along wide range of temperature, while *P. salinarum* had a P^B_{max} lower by and order of a magnitude. This remarkable difference could be found also in the I_k values: the cyanobacterial species had much higher light intensity optimum that of the green alga. No environmentally relevant combination of temperature and light intensity was found at which the photosynthetic activity of the green alga could reach or exceed that of the examined cyanobacterium.

3.2 The effect of salinity stress on *P. salinarum* was examined in fourteen different media. These experiments revealed the difference between the effects of chloride and carbonate-forms dominated media: the green alga grew significantly better in carbonate-forms dominated medium than in chloride dominated ones. The examination in chemostat confirmed the high salinity/conductivity preference of the species.

3.3 The examination of the co-existence of *L. fusiformis* and *P. salinarum* in a chemostat confirmed the previously suggested and most likely cause of the replacement of the two species. *P. salinarum* showed a higher level of tolerance of the rapid change in conductivity, which could cause the collapse of *L. fusiformis'* population and make possible *P. salinarum* to become dominant.

9 List of publications

9.1 Papers related to the dissertation

Pálmai T., Selmeczy G. B., Szabó B., G.-Tóth L., Padisák J., 2016. A *Microcystis flos-aquae* fotoszintetikus aktivitása a Balaton keleti medencéjében 2015 nyarán, HIDROLÓGIAI KÖZLÖNY 96(5-6), 75-78.

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9.2 Other papers and book chapter

Pálmai T., Üveges V., Krienitz L., Padisák J., 2013. Az *Arthrospira fusiformis* és a *Picocystis salinarum* fotoszintézisének karakterisztikái különböző fényintenzitásokon és hőmérsékleten, HIDROLÓGIAI KÖZLÖNY 93: (5-6), 64-66.

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biológusai: avagy szemelvények a magyarországi felsőoktatási intézményekben végzett tudományos munka eredményeiből. Válogatás a XXXI. Országos Tudományos Diákköri Konferencia Biológia szekciójának dolgozataiból. 124 p. JATEPress Kiadó, 2014. pp. 45-58. (ISBN:978-963-315-212-6)

9.3 Congress attendances related to the dissertation

Pálmai, T., Szabó B., Padisák J.: Különböző divízióba tartozó algafajok ökofiziológiai plaszticitásának jellemzése, 10. Magyar ökológus Kongresszus, 12-14 August 2015. ***oral presentation***

Pálmai, T., Selmeczy, G. B., Szabó, B., G.-Tóth, L., Padisák, J.: A *Microcystis flos-aquae* fotoszintetikus aktivitása a Balaton keleti medencéjében 2015 nyarán, LVII. Hidrobiológus Napok, 7-9 October 2005. ***oral presentation***

Pálmai, T., Szabó, B., Padisák, J.: Kerti tavak szerepe az algakutatásban és az ökofiziológiai vizsgálatokban, Aktuális eredmények a kriptogám növények kutatásában konferencia, Eger, 17-18 November 2015. ***oral presentation***

Pálmai, T., Szabó, B., Padisák, J.: Comparison of the photosynthesis of a stream and a lake red alga, 5th Interdisciplinary Doctoral Conference, Pécs, 27-29 May 2016. ***oral presentation***

Pálmai, T., Szabó, B., Lengyel, E., Stenger-Kovács, Cs., Padisák, J.: Photosynthetic characteristics of four *Nitzschia* species, 11th Central European Diatom Meeting, Czech Republic, Prague, 22-25 March 2017. ***oral presentation***

Pálmai, T., Szabó, B., Hubai, K. E., Selmeczy, G. B., Padisák, J.: Temperature- and light intensity preference of four freshwater green algae from different habitats, 5th meeting of Fresh Blood for FreshWater, Czech Republic, České Budějovice, 9-13 April 2017. ***oral presentation***

Pálmai, T., Szabó, B., Padisák, J.: Plaszticitás, X. Algológiai Találkozó és Továbbképzés, Budapest, 3 May 2017. ***oral presentation***

Pálmai, T., Szabó, B., Padisák, J.: A *Picocystis salinarum* ökofiziológiai vizsgálata folyamatos algatenyésztőben, X. Algológiai Találkozó és Továbbképzés, Budapest, 3 May 2017. ***oral presentation***

Pálmai, T., Szabó, B., Padisák, J.: A *Picocystis salinarum* ökofiziológiai vizsgálata. LX. Hidrobiológus Napok, Tihany, 3-5 October 2018. ***oral presentation***

Pálmai, T.: Az *Arthrospira fusiformis* és a *Picocystis salinarum* fiziológiai vizsgálata, I. Régiós Környezettoxikológiai PhD Konferencia, Veszprém, 12 December 2018. ***oral presentation***

Pálmai, T.: Az *Arthrospira fusiformis* és a *Picocystis salinarum* közötti kompetíció laboratóriumi vizsgálata, Műszaki Kémiai Napok 2019, Veszprém, 16-18 April 2019. ***oral presentation***

Pálmai, T., Szabó, B., Padisák, J.: A sókoncentráció változás hatása az *Arthrospira fusiformis* és a *Picocystis salinarum* koegzisztenciájára, XII. Algológiai találkozó és továbbképzés, Budapest, 9 May 2019. ***oral presentation***

9.4 Other congress attendances

Pálmai, T., Üveges, V.: Az *Arthrospira fusiformis* és a *Picocystis salinarum* fotoszintézisének karakterisztikái különböző fényintenzitásokon és hőmérsékleten, Mérnöki Kari Tudományos Diákköri Konferencia, Veszprém, 26. April 2012. ***oral presentation***

Pálmai, T., Üveges, V.: Az *Arthrospira fusiformis* és a *Picocystis salinarum* fotoszintézisének karakterisztikái különböző fényintenzitásokon és hőmérsékleten, II. Pannon Tehetségnap, 14 May 2012. ***oral presentation***

Pálmai, T., Üveges, V., Krienitz, L., Padisák, J.: Az *Arthrospira fusiformis* és a *Picocystis salinarum* fotoszintézisének karakterisztikái különböző fényintenzitásokon és hőmérsékleten, LIV. Hidrobiológus Napok, Tihany, 3-5 October 2012. ***poster presentation***

Pálmai, T., Üveges, V., Krienitz, L., Padisák, J.: Az *Arthrospira fusiformis* és a *Picocystis salinarum* fotoszintézisének karakterisztikái különböző fényintenzitásokon és hőmérsékleten, Magyar Hidrológiai Társaság - XX. Ifjúsági Napok, Szeged, 19-20 September 2013. ***oral presentation***

Shafik, H. M., **Pálmai, T.**, Leitold, H., Padisák, J.: Módosított tápoldat egy trópusi sóstóból izolált *Arthrospira fusiformis* és *Picocystis salinarum* algafajok számára, LV. Hidrobiológus Napok, Tihany, 2-4 October 2013. ***oral presentation***

Pálmai, T., Shafik, H. M, Padisák, J.: Trópusi fitoplankton fajok ökofiziológiai vizsgálata, Tavaszi Szél 2014., Debrecen, 21-23 March 2014. ***oral presentation***

Appendix

Appendix 1 Origin, type and culturing medium of the examined species

Species	Origin	Type	Culturing medium
Nitzschia palea	Own isolation from Öreg-tó, Tata	Culture	DIAT medium
Limnospira fusiformis	Collection of Leibniz-Institute of Freshwater Ecology and Inland Fisheries	Culture	M_0 medium
Microcystis flosaquae	Lake Balaton	Natural sample (>95% of the biomass)	Filtered lake water
Microcystis sp.	Own isolation from Öreg-tó, Tata	Culture	ALLEN's medium
Nostoc sp.	Collection of Department of Botany (University of Debrecen)	Culture	ALLEN's medium $-NO_3^-$
Coelastrum sp.	Own isolation from Öreg-tó, Tata	Culture	BG11 medium
Dunaliella salina	Collection of Department of Botany (University of Debrecen)	Culture	Johnsons medium
Mucidosphaerium pulchellum	Garden pond	Natural sample (>95% of the biomass)	Filtered pond water
Monoraphidium griffithii	Department of Hydrobiology (University of Debrecen)	Culture	ALLEN's medium
Picocystis salinarum	Collection of Leibniz-Institute of Freshwater Ecology and Inland Fisheries	Culture	M_0 medium
Raphidocelis subcapitata	Own isolation	Culture	ALLEN's medium
Tetradesmus obliquus	Department of Hydrobiology (University of Debrecen)	Culture	ALLEN's medium
Scenedesmus sp.	Own isolation	Culture	BG11 medium
Cosmarium majae	Garden pond	Natural sample (>90% of the biomass)	Filtered pond water
Bangia atropurpurea	Lake Balaton	Natural sample	Filtered lake water
Batrachospermum gelatinosum	Tapolca-stream	Natural sample	Filtered stream water

Appendix 2 Result of the Tukey's post hoc multiple comparison test between the photosynthetic activity of different species, temperatures and light intensities. At the light intensity comparisons letters represent the different light intensities: A always the highest light intensity and H is lowest. Diff the difference in the observed means, lwr the lower end point of the interval, upr the upper end point of the interval, p.adj adjusted P value.

Species comparison	**diff**	**lwr**	**upr**	**p adj**
Coelastrum sp.-*C. majae*	0.094771	0.060769	0.128774	0
M. pulchellum-C. majae	0.03954	0.005538	0.073543	0.00748
D. salina-C. majae	0.132814	0.098811	0.166816	0
L. fusiformis-C. majae	0.121548	0.087545	0.15555	0
M. flosaquae-C. majae	0.039422	0.00542	0.073425	0.007819
M. griffithii-C. majae	-0.14911	-0.18311	-0.11511	0
Microcystis sp.-*C. majae*	-0.07155	-0.10555	-0.03755	0
Nostoc sp.-*C. majae*	-0.07949	-0.11252	-0.04645	0
N. palea-C. majae	0	-0.03442	0.034421	1
P. salinarum-C. majae	-0.04077	-0.07477	-0.00676	0.00467
R. subcapitata-C. majae	-0.11619	-0.15019	-0.08219	0
Scenedesmus sp.-*C. majae*	0.023722	-0.00931	0.05676	0.470075
T. obliquus-C. majae	0.012252	-0.02175	0.046255	0.995199
M. pulchellum-Coelastrum sp.	-0.05523	-0.08937	-0.0211	6.1×10^{-6}
D. salina-Coelastrum sp.	0.038042	0.003908	0.072176	0.013691
L. fusiformis-Coelastrum sp.	0.026776	-0.00736	0.060911	0.31759
M. flosaquae-Coelastrum sp.	-0.05535	-0.08948	-0.02121	5.7×10^{-6}
M. griffithii-Coelastrum sp.	-0.24388	-0.27802	-0.20975	0
Microcystis sp.-*Coelastrum* sp.	-0.16632	-0.20045	-0.13219	0
Nostoc sp.-*Coelastrum* sp.	-0.17426	-0.20743	-0.14108	0
N. palea-Coelastrum sp.	-0.09477	-0.12932	-0.06022	0
P. salinarum-Coelastrum sp.	-0.13554	-0.16967	-0.1014	0
R. subcapitata-Coelastrum sp.	-0.21096	-0.24509	-0.17683	0
Scenedesmus sp.-*Coelastrum* sp.	-0.07105	-0.10422	-0.03788	0
T. obliquus-Coelastrum sp.	-0.08252	-0.11665	-0.04839	0
D. salina-M. pulchellum	0.093273	0.059139	0.127407	0
L. fusiformis-M. pulchellum	0.082008	0.047874	0.116142	0
M. flosaquae-M. pulchellum	-0.00012	-0.03425	0.034016	1
M. griffithii-M. pulchellum	-0.18865	-0.22278	-0.15452	0
Microcystis sp.-*M. pulchellum*	-0.11109	-0.14522	-0.07695	0
Nostoc sp.-*M. pulchellum*	-0.11903	-0.1522	-0.08585	0
N. palea-M. pulchellum	-0.03954	-0.07409	-0.00499	0.009458
P. salinarum-M. pulchellum	-0.08031	-0.11444	-0.04617	0
R. subcapitata-M. pulchellum	-0.15573	-0.18986	-0.12159	0
Scenedesmus sp.-*M. pulchellum*	-0.01582	-0.04899	0.017355	0.94514
T. obliquus-M. pulchellum	-0.02729	-0.06142	0.006846	0.287139
L. fusiformis-D. salina	-0.01127	-0.0454	0.022868	0.997989
M. flosaquae-D. salina	-0.09339	-0.12753	-0.05926	0
M. griffithii-D. salina	-0.28192	-0.31606	-0.24779	0
Microcystis sp.-*D. salina*	-0.20436	-0.2385	-0.17023	0
Nostoc sp.-*D. salina*	-0.2123	-0.24547	-0.17913	0
N. palea-D. salina	-0.13281	-0.16736	-0.09826	0

P. salinarum-D. salina	-0.17358	-0.20771	-0.13945	0
R. subcapitata-D. salina	-0.249	-0.28314	-0.21487	0
Scenedesmus sp.-*D. salina*	-0.10909	-0.14226	-0.07592	0
T. obliquus-D. salina	-0.12056	-0.1547	-0.08643	0
M. flosaquae-L. fusiformis	-0.08213	-0.11626	-0.04799	0
M. griffithii-L. fusiformis	-0.27066	-0.30479	-0.23652	0
Microcystis sp.-*L. fusiformis*	-0.1931	-0.22723	-0.15896	0
Nostoc sp.-*L. fusiformis*	-0.20103	-0.23421	-0.16786	0
N. palea-L. fusiformis	-0.12155	-0.1561	-0.087	0
P. salinarum-L. fusiformis	-0.16231	-0.19645	-0.12818	0
R. subcapitata-L. fusiformis	-0.23774	-0.27187	-0.2036	0
Scenedesmus sp.-*L. fusiformis*	-0.09783	-0.131	-0.06465	0
T. obliquus-L. fusiformis	-0.1093	-0.14343	-0.07516	0
M. griffithii-M. flosaquae	-0.18853	-0.22267	-0.1544	0
Microcystis sp.-*M. flosaquae*	-0.11097	-0.14511	-0.07684	0
Nostoc sp.-*M. flosaquae*	-0.11891	-0.15208	-0.08574	0
N. palea-M. flosaquae	-0.03942	-0.07397	-0.00487	0.009871
P. salinarum-M. flosaquae	-0.08019	-0.11432	-0.04605	0
R. subcapitata-M. flosaquae	-0.15561	-0.18975	-0.12148	0
Scenedesmus sp.-*M. flosaquae*	-0.0157	-0.04887	0.017472	0.948176
T. obliquus-M. flosaquae	-0.02717	-0.0613	0.006964	0.293987
Microcystis sp.-*M. griffithii*	0.077562	0.043428	0.111696	0
Nostoc sp.-*M. griffithii*	0.069625	0.036452	0.102797	0
N. palea-M. griffithii	0.14911	0.114559	0.183662	0
P. salinarum-M. griffithii	0.108345	0.074211	0.142479	0
R. subcapitata-M. griffithii	0.032922	-0.00121	0.067056	0.071703
Scenedesmus sp.-*M. griffithii*	0.172833	0.139661	0.206005	0
T. obliquus-M. griffithii	0.161362	0.127228	0.195497	0
Nostoc sp.-*Microcystis* sp.	-0.00794	-0.04111	0.025235	0.999939
N. palea-Microcystis sp.	0.071549	0.036998	0.1061	0
P. salinarum-Microcystis sp.	0.030783	-0.00335	0.064917	0.128626
R. subcapitata-Microcystis sp.	-0.04464	-0.07877	-0.01051	0.001016
Scenedesmus sp.-*Microcystis* sp.	0.095271	0.062099	0.128444	0
T. obliquus-Microcystis sp.	0.083801	0.049667	0.117935	0
N. palea-Nostoc sp.	0.079486	0.045884	0.113087	0
P. salinarum-Nostoc sp.	0.03872	0.005548	0.071893	0.00707
R. subcapitata-Nostoc sp.	-0.0367	-0.06988	-0.00353	0.015093
Scenedesmus sp.-*Nostoc* sp.	0.103208	0.071026	0.13539	0
T. obliquus-Nostoc sp.	0.091738	0.058565	0.12491	0
P. salinarum-N. palea	-0.04077	-0.07532	-0.00621	0.006002
R. subcapitata-N. palea	-0.11619	-0.15074	-0.08164	0
Scenedesmus sp.-*N. palea*	0.023722	-0.00988	0.057324	0.499945
T. obliquus-N. palea	0.012252	-0.0223	0.046803	0.99589
R. subcapitata-P. salinarum	-0.07542	-0.10956	-0.04129	0
Scenedesmus sp.-*P. salinarum*	0.064488	0.031316	0.097661	0
T. obliquus-P. salinarum	0.053018	0.018884	0.087152	1.94×10^{-5}
Scenedesmus sp.-*R. subcapitata*	0.139911	0.106739	0.173084	0
T. obliquus-R. subcapitata	0.128441	0.094307	0.162575	0

T. obliquus-Scenedesmus sp.	-0.01147	-0.04464	0.021702	0.996791
Temperatures comparisons	**diff**	**lwr**	**upr**	**p adj**
10-5	0.06467	0.040235	0.089105	0
15-5	0.103796	0.079361	0.128231	0
20-5	0.162766	0.138331	0.1872	0
25-5	0.19687	0.172435	0.221305	0
30-5	0.21206	0.187625	0.236495	0
35-5	0.213141	0.188706	0.237576	0
40-5	0.185343	0.160908	0.209778	0
45-5	0.130385	0.089881	0.170888	0
15-10	0.039126	0.015269	0.062983	1.47×10^{-5}
20-10	0.098096	0.074239	0.121953	0
25-10	0.1322	0.108343	0.156057	0
30-10	0.147391	0.123533	0.171248	0
35-10	0.148471	0.124614	0.172328	0
40-10	0.120674	0.096816	0.144531	0
45-10	0.065715	0.025557	0.105873	1.56×10^{-5}
20-15	0.05897	0.035113	0.082827	0
25-15	0.093074	0.069217	0.116932	0
30-15	0.108265	0.084408	0.132122	0
35-15	0.109345	0.085488	0.133202	0
40-15	0.081548	0.05769	0.105405	0
45-15	0.026589	-0.01357	0.066747	0.50246
25-20	0.034105	0.010247	0.057962	0.000338
30-20	0.049295	0.025438	0.073152	0
35-20	0.050375	0.026518	0.074232	0
40-20	0.022578	-0.00128	0.046435	0.080244
45-20	-0.03238	-0.07254	0.007777	0.229712
30-25	0.01519	-0.00867	0.039048	0.557907
35-25	0.016271	-0.00759	0.040128	0.4597
40-25	-0.01153	-0.03538	0.012331	0.854554
45-25	-0.06649	-0.10664	-0.02633	1.15×10^{-5}
35-30	0.00108	-0.02278	0.024938	1
40-30	-0.02672	-0.05057	-0.00286	0.015254
45-30	-0.08168	-0.12183	-0.04152	0
40-35	-0.0278	-0.05165	-0.00394	0.00932
45-35	-0.08276	-0.12291	-0.0426	0
45-40	-0.05496	-0.09512	-0.0148	0.000774
Light intensity comparisons	**diff**	**lwr**	**upr**	**p adj**
B-A	-0.00201	-0.02576	0.021744	0.999999
C-A	0.006942	-0.01681	0.030693	0.992493
D-A	-0.00285	-0.02655	0.02085	0.999989
E-A	-0.00021	-0.02391	0.023486	1
F-A	-0.03015	-0.05385	-0.00645	0.002659
G-A	-0.09796	-0.12166	-0.07426	0
H-A	-0.19024	-0.21394	-0.16654	0
I-A	-0.10948	-0.2888	0.069835	0.614969
C-B	0.008949	-0.0148	0.0327	0.96225

D-B	-0.00084	-0.02454	0.022857	1
E-B	0.001794	-0.02191	0.025493	1
F-B	-0.02814	-0.05184	-0.00444	0.007253
G-B	-0.09595	-0.11965	-0.07225	0
H-B	-0.18823	-0.21193	-0.16454	0
I-B	-0.10748	-0.2868	0.071842	0.639071
D-C	-0.00979	-0.03349	0.013908	0.935755
E-C	-0.00716	-0.03085	0.016544	0.990676
F-C	-0.03709	-0.06079	-0.01339	4.71×10^{-5}
G-C	-0.1049	-0.1286	-0.0812	0
H-C	-0.19718	-0.22088	-0.17348	0
I-C	-0.11643	-0.29574	0.062893	0.530458
E-D	0.002636	-0.02101	0.026283	0.999994
F-D	-0.0273	-0.05095	-0.00365	0.010497
G-D	-0.09511	-0.11876	-0.07146	0
H-D	-0.18739	-0.21104	-0.16375	0
I-D	-0.10663	-0.28595	0.072678	0.649049
F-E	-0.02993	-0.05358	-0.00629	0.00287
G-E	-0.09774	-0.12139	-0.0741	0
H-E	-0.19003	-0.21368	-0.16638	0
I-E	-0.10927	-0.28858	0.070042	0.617491
G-F	-0.06781	-0.09146	-0.04416	0
H-F	-0.16009	-0.18374	-0.13645	0
I-F	-0.07934	-0.25865	0.099977	0.906818
H-G	-0.09228	-0.11593	-0.06864	0
I-G	-0.01153	-0.19084	0.167786	1
I-H	0.080758	-0.09855	0.26007	0.897739

Appendix 3 Photosynthetic parameters of the examined 16 species at different temperatures. P^B_{max}: Biomass specific maximal photosynthetic production (µg C µg Chl a^{-1} h^{-1}), P_s: Maximal production obtained in the absence of photoinhibition; without photoinhibition it is equal to P^B_{max} (µg C µg Chl a^{-1} h^{-1}), I_k: photoadaptation parameter (µmol m^{-2} s^{-1}), I_c: compensation light intensity (µmol m^{-2} s^{-1}), α: light utilization parameter ((µg C µg Chl a^{-1} h^{-1}) (µmol m^{-2} s^{-1})$^{-1}$), β: photoinhibition parameter ((µg C µg Chl a^{-1} h^{-1}) (µmol m^{-2} s^{-1})$^{-1}$), R^B: biomass specific respiration (µg C µg Chl a^{-1} h^{-1}). In the case of the red algae species instead of Chl a concentration fresh weight (FW) was measured, the unit of the red algae are the following: P^B_{max}: µg C µg FW^{-1} h^{-1}, P_s: µg C µg FW^{-1} h^{-1}, α: (µg C µg FW^{-1} h^{-1}) (µmol m^{-2} s^{-1})$^{-1}$, β: (µg C µg FW^{-1} h^{-1}) (µmol m^{-2} s^{-1})$^{-1}$, R^B: µg C µg FW^{-1} h^{-1}.

Nitzschia palea												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	0.033	0.106	0.146	0.542	0.863	0.603	1.046	0.917	-	0.033	1.046	36.1±4.2
P^B_{max}	0.029	0.099	0.136	0.514	0.830	0.603	1.046	0.813	-	0.029	1.046	24.7±3.1
I_k	9.6	26.1	36.6	70.5	101.2	172.2	168.7	104.2	-	9.6	172.2	32.1±0.9
I_c	3.0	17.1	18.3	35.7	47.3	84.8	64.8	20.6	-	3.0	84.8	29.9±1.0
α	0.003	0.0038	0.0037	0.0073	0.0082	0.0035	0.0062	0.0078	-	0.003	0.0082	
β	9.022×10^{-5}	4.551×10^{-5}	5.062×10^{-5}	6.636×10^{-5}	5.261×10^{-5}	2.341×10^{-5}	-	0.0002	-	2.341×10^{-5}	0.0002	
R^B	0.020	0.122	0.137	0.457	0.690	0.567	0.807	0.430	-	0.020	0.807	30.8±1.4
P^B_{max}/R^B	1.445	0.811	0.992	1.126	1.203	1.064	1.296	1.891	-	0.811	1.891	
Limnospira fusiformis												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	-	3.000	6.168	9.685	13.760	15.748	16.219	17.927	-	3.000	17.927	37.0±1.8
P^B_{max}	-	2.708	5.225	7.553	11.653	15.748	16.219	17.927	-	2.708	17.927	38.7±1.6
I_k	-	51.7	96.8	135.6	189.2	237.5	299.2	336.3	-	51.7	336.3	47.4±2.2
I_c	-	3.5	2.2	3.2	7.2	6.9	6.0	8.4	-	2.2	8.4	46.0±25.4
α	-	0.0524	0.054	0.0557	0.0616	0.0663	0.0542	0.0533	-	0.0524	0.0663	
β	-	0.0011	0.0021	0.0037	0.0024	-	-	-	-	0.0011	0.0037	
R^B	-	0.108	0.073	0.085	0.210	0.217	0.197	0.237	-	0.073	0.237	41.2±15.5

P^B_{max}/R^B	-	25.00	71.25	88.86	55.49	72.68	82.47	75.75	-	25.00	88.86	
Microcystis flosaquae												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	0.827	2.348	4.274	5.838	5.569	7.806	7.187	9.513	-	0.827	9.513	42.9±9.6
P^B_{max}	0.769	2.091	3.517	5.092	5.008	6.714	7.187	9.513	-	0.769	9.513	54.3±18.3
I_k	26.1	73.1	140.7	192.9	183.4	256.2	619.6	511.4	-	26.1	619.6	50.8±27.0
I_c	11.9	17.6	30.9	45.1	100.2	168.1	338.9	355.5	-	11.9	338.9	40.2±2.3
α	0.0295	0.0286	0.025	0.0264	0.0273	0.0262	0.0116	0.0186	-	0.0116	0.0295	
β	0.0004	0.0007	0.0012	0.0008	0.0006	0.0009	-	-	-	0.0004	0.0012	
R^B	0.068	0.108	0.217	0.330	0.662	0.852	0.847	0.825	-	0.068	0.852	34.8±0.9
P^B_{max}/R^B	11.259	19.304	16.231	15.430	7.569	7.883	8.489	11.530	-	7.569	19.304	
***Microcystis* sp.**												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	0.117	0.298	0.509	0.939	1.497	2.553	3.218	3.367	-	0.117	3.367	39.8±1.2
P^B_{max}	0.117	0.294	0.500	0.939	1.497	2.553	3.218	3.040	-	0.117	3.218	37.6±1.0
I_k	0.2	17.5	20.7	40.1	65.7	96.0	109.4	127.2	-	0.2	127.2	41.5±2.1
I_c	0.0	1.2	1.3	2.4	3.4	3.8	5.4	7.7	-	0.0	7.7	81.3±17.0
α	0.5854	0.0168	0.0242	0.0234	0.0228	0.0266	0.0294	0.0239	-	0.0168	0.5854	
β	-	3.749×10^{-5}	5.903×10^{-5}	-	-	-	-	0.0005	-	3.749×10^{-5}	0.0005	
R^B	0.007	0.040	0.060	0.110	0.150	0.157	0.243	0.280	-	0.007	0.280	52.4±11.9
P^B_{max}/R^B	17.475	7.338	8.338	8.532	9.982	16.298	13.223	10.857	-	7.338	17.475	
***Nostoc* sp.**												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	0.148	0.358	0.461	1.090	1.386	1.692	1.925	2.015	1.989	0.148	2.015	39.7±1.2
P^B_{max}	0.145	0.346	0.453	1.028	1.344	1.692	1.925	2.015	1.801	0.145	2.015	38.2±0.7
I_k	10.4	21.2	20.0	53.8	64.9	85.0	97.7	121.4	121.7	10.4	121.7	45.9±3.0

I_c	0.9	1.1	1.7	1.9	5.2	8.0	9.3	10.6	19.2	0.9	19.2	100.8±21.7
α	0.014	0.0163	0.0226	0.0191	0.0207	0.0199	0.0197	0.0166	0.0148	0.0148	0.0226	
β	2.978×10^{-5}	9.171×10^{-5}	5.750×10^{-5}	0.0002	0.0001	-	-	-	0.0003	2.978×10^{-5}	0.0003	
R^B	0.023	0.033	0.070	0.080	0.157	0.230	0.300	0.290	0.457	0.023	0.457	68.3±27.8
P^B_{max}/R^B	6.226	10.379	6.468	12.854	8.578	7.354	6.415	6.948	3.943	3.943	12.854	
***Coelastrum* sp.**												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	0.220	1.010	1.130	2.113	3.137	5.358	5.353	2.985	-	0.220	5.358	31.9±1.0
P^B_{max}	0.217	0.937	1.011	1.923	3.064	4.716	5.353	2.794	-	0.217	5.353	32.1±1.0
I_k	5.0	16.8	39.2	72.8	109.4	145.6	277.3	113.6	-	5.0	277.3	33.5±1.7
I_c	1.0	0.2	1.4	3.8	5.4	4.2	16.0	12.5	-	0.2	16.0	40.1±7.7
α	0.0437	0.0559	0.0258	0.0264	0.028	0.0324	0.0193	0.0246	-	0.0193	0.0559	
β	0.0001	0.0008	0.0006	0.0005	0.0001	0.0009	-	0.0003	-	0.0001	0.0009	
R^B	0.032	0.005	0.032	0.087	0.132	0.090	0.240	0.233	-	0.032	0.240	52.3±24.2
P^B_{max}/R^B	6.673	28.395	31.941	22.183	23.267	52.398	22.303	11.974	-	6.673	52.398	
Dunaliella salina												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	0.841	1.408	2.017	2.492	3.441	3.884	5.404	3.781	-	0.841	5.404	35.5±3.5
P^B_{max}	0.824	1.337	1.960	2.418	3.180	3.509	5.404	3.781	-	0.824	5.404	37.2±5.4
I_k	38.7	60.2	87.5	114.6	160.6	182.7	278.6	243.9	-	38.7	278.6	43.6±8.0
I_c	1.5	1.3	1.3	2.9	7.6	13.1	12.3	29.2	-	1.3	29.2	69.9±7.8
α	0.0213	0.0222	0.0224	0.0211	0.0198	0.0192	0.0194	0.0155	-	0.0155	0.0224	
β	6.284×10^{-5}	0.0002	0.0001	0.0001	0.0003	0.0004	-	-	-	6.284×10^{-5}	0.0004	
R^B	0.207	0.195	0.190	0.333	0.820	1.207	1.093	2.007	-	0.190	2.007	95.0±75.6
P^B_{max}/R^B	3.989	6.858	10.318	7.255	3.878	2.908	4.943	1.884	-	1.884	10.318	
Mucidosphaerium pulchellum												

T (°C)	5	10	15	20	25	30	35	40	45	Min.	Max.	T_{opt}
P_s	0.266	0.759	1.521	2.116	3.106	3.941	3.826	1.474	-	0.266	3.941	29.4±1.0
P^B_{max}	0.253	0.718	1.443	2.116	3.106	3.941	3.826	1.474	-	0.252	3.941	29.5±0.9
I_k	60.1	102.6	134.8	220.4	237.1	358.2	434.8	163.8	-	60.1	434.8	30.7±2.2
I_c	3.8	12.7	2.9	11.3	12.2	19.8	29.7	20.7	-	2.9	29.7	42.4±20.5
α	0.0042	0.007	0.0107	0.0096	0.0131	0.011	0.0088	0.009	-	0.0042	0.0131	
β	3.849×10^{-5}	6.743×10^{-5}	0.0001	-	-	-	-	-	-	3.849×10^{-50}	0.0001	
R^B	0.040	0.217	0.087	0.302	0.332	0.377	0.448	0.330	-	0.040	0.448	33.1±3.4
P^B_{max}/R^B	6.312	3.315	16.647	7.013	9.366	10.462	8.534	4.467	-	3.315	16.647	

Monoraphidium griffithii

T (°C)	5	10	15	20	25	30	35	40	45	Min.	Max.	T_{opt}
P_s	-	0.031	0.056	0.258	0.433	0.565	0.283	0.088	-	0.031	0.565	28.2±0.4
P^B_{max}	-	0.030	0.054	0.249	0.433	0.565	0.283	0.079	-	0.030	0.565	28.3±0.3
I_k	-	8.0	16.2	50.9	71.0	100.8	58.9	26.3	-	8.0	100.8	28.6±0.5
I_c	-	3.6	3.5	1.6	2.9	3.4	3.8	18.7	-	1.6	18.7	
α	-	0.0037	0.0033	0.0049	0.0061	0.0056	0.0048	0.003	-	0.0037	0.0061	
β	-	1.760×10^{-5}	2.182×10^{-5}	2.631×10^{-5}				6.489×10^{-5}	-	1.760×10^{-5}	6.489×10^{-5}	
R^B	-	0.110	0.107	0.073	0.167	0.183	0.137	0.320	-	0.073	0.320	88.5±24.8
P^B_{max}/R^B	-	0.271	0.503	3.401	2.600	3.080	2.068	0.246	-	0.246	3.401	

Picocystis salinarum

T (°C)	5	10	15	20	25	30	35	40	45	Min.	Max.	T_{opt}
P_s	-	0.097	0.122	0.272	0.486	0.807	1.223	1.330	0.712	0.097	1.330	36.9±0.8
P^B_{max}	-	0.097	0.119	0.268	0.474	0.788	1.180	1.233	0.682	0.097	1.233	36.8±0.7
I_k	-	1.0	19.5	15.4	29.4	41.9	78.7	89.3	49.8	1.0	89.3	37.8±1.3
I_c	-	0.3	3.0	1.2	2.3	2.8	5.2	7.7	14.2	0.3	14.2	45.0±0.2

α	-	0.1	0.0061	0.0174	0.0161	0.0188	0.015	0.0138	0.0137	0.0061	0.1	
β	-	3.288×10^{-5}	2.427×10^{-5}	3.496×10^{-5}	6.305×10^{-5}	6.742×10^{-5}	8.649×10^{-5}	0.0002	0.0001	2.427×10^{-5}	0.0002	
R^B	-	0.072	0.050	0.050	0.087	0.123	0.197	0.263	0.440	0.050	0.440	85.2±6.4
P^B_{max}/R^B	-	1.349	2.375	5.354	5.466	6.385	6.001	4.680	1.549	1.349	6.385	
Raphidocelis subcapitata												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	0.023	0.052	0.084	0.249	0.421	0.566	0.493	0.219	-	0.023	0.566	30.2±0.4
P^B_{max}	0.023	0.052	0.084	0.249	0.421	0.566	0.493	0.208	-	0.023	0.566	30.1±0.4
I_k	12.1	14.7	32.2	67.2	82.5	111.0	159.0	76.9	-	12.1	159.0	32.5±1.7
I_c	0.1	1.9	2.5	3.0	3.2	5.2	18.5	20.4	-	0.1	20.4	38.2±1.1
α	0.0019	0.0035	0.0026	0.0037	0.0051	0.0051	0.0031	0.0027	-	0.0019	0.0051	
β	-	-	-	-	-	-	-	2.555×10^{-5}	-	2.555×10^{-5}	2.555×10^{-5}	
R^B	0.000	0.070	0.070	0.103	0.153	0.243	0.433	0.390	-	0.000	0.433	41.9±7.4
P^B_{max}/R^B	-	0.737	1.197	2.408	2.742	2.326	1.137	0.532	-	0.532	2.742	
Tetradesmus obliquus												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	0.204	0.363	0.480	1.283	1.630	1.608	2.044	0.866		0.204	2.044	29.8±1.3
P^B_{max}	0.193	0.346	0.463	1.211	1.475	1.608	2.044	0.728		0.193	2.044	29.8±1.4
I_k	26.0	38.0	50.3	124.8	150.5	160.8	224.6	99.7		26.0	224.6	30.9±1.8
I_c	0.7	1.1	1.9	2.9	5.4	6.5	8.6	17.9		0.7	17.9	83.3±6.3
α	0.0074	0.0091	0.0092	0.0097	0.0098	0.01	0.0091	0.0073		0.0073	0.01	
β	7.216×10^{-5}	7.434×10^{-5}	5.353×10^{-5}	0.0001	0.0002	-	-	0.0003		$5.353\times10^{-5}5$	0.0003	
R^B	0.030	0.060	0.100	0.147	0.273	0.323	0.350	0.553		0.030	0.553	74.1±48.6
P^B_{max}/R^B	6.424	5.765	4.629	8.257	5.395	4.972	5.839	1.316		1.316	8.257	
Scenedesmus sp.												

T (°C)	5	10	15	20	25	30	35	40	45	Min.	Max.	T_{opt}
P_s	0.155	0.269	0.515	0.765	1.406	1.835	2.926	3.468	1.961	0.155	3.468	37.7±1.3
P^B_{max}	0.153	0.267	0.507	0.765	1.406	1.835	2.926	3.468	1.042	0.153	3.468	36.0±1.3
I_k	25.9	22.6	41.2	72.1	130.2	173.2	252.2	327.2	165.4	22.6	327.2	37.5±1.5
I_c	3.0	0.5	0.7	0.6	4.0	4.6	11.4	19.8	25.0	0.5	25.0	48.9±4.4
α	0.0059	0.0118	0.0123	0.0106	0.0108	0.0106	0.0116	0.0106	0.0063	0.0059	0.0123	
β	1.271×10^{-5}	8.700×10^{-6}	2.679×10^{-5}						0.0016	8.700×10^{-6}	0.0016	
R^B	0.060	0.020	0.030	0.033	0.213	0.230	0.537	0.847	0.677	0.020	0.847	41.2±1.1
P^B_{max}/R^B	2.544	13.344	16.896	22.938	6.591	7.980	5.452	4.096	1.540	1.540	22.938	

Cosmarium majae

T (°C)	5	10	15	20	25	30	35	40	45	Min.	Max.	T_{opt}
P_s	0.682	1.357	2.196	2.945	3.558	4.710	4.637	1.565	-	0.682	4.710	28.6±1.4
P^B_{max}	0.629	1.289	2.078	2.784	3.283	3.932	3.600	1.565	-	0.629	3.932	27.8±1.0
I_k	48.4	57.8	101.4	138.5	170.1	213.7	244.9	87.5	-	48.4	244.9	29.4±1.8
I_c	2.8	2.8	5.5	7.9	14.2	11.6	27.5	27.8	-	-4.8	27.8	47.2±16.9
α	0.013	0.0223	0.0205	0.0201	0.0193	0.0184	0.0147	0.0179	-	0.013	0.0223	
β	0.0002	0.0002	0.0002	0.0002	0.0003	0.0008	0.001		-	0.0002	0.001	
R^B	0.035	0.070	0.127	0.178	0.305	0.233	0.433	0.427	-	0.035	0.433	46.4±13.5
P^B_{max}/R^B	17.982	18.419	16.409	15.614	10.764	16.850	8.307	3.669	-	3.669	18.419	

Bangia atropurpurea

T (°C)	5	10	15	20	25	30	35	40	45	Min.	Max.	T_{opt}
P_s	1.889	2.849	3.920	3.756	8.171	5.686	2.704	-	-	1.889	8.171	24.4±2.1
P^B_{max}	1.700	2.359	3.920	3.756	8.171	5.686	2.704	-	-	1.700	8.171	24.7±1.9
I_k	61.6	72.4	130.7	116.6	275.1	262.0	194.5	-	-	61.6	275.1	28.9±3.0
I_c	5.8	4.1	20.1	15.8	29.8	35.0	76.6	-	-	4.1	76.6	74.2±8.8
α	0.0276	0.0326	0.03	0.0322	0.0297	0.0217	0.0139	-	-	0.0139	0.0326	

β	0.0006	0.0015	-	-	-	-	-	-	-	0.0006	0.0015	
R^B	0.155	0.132	0.558	0.476	0.839	0.711	0.880	-	-	0.132	0.880	33.0±6.1
P^B_{max}/R^B	10.987	17.869	7.025	7.884	9.739	8.002	3.072	-	-	3.072	17.869	
Batrachospermum gelatinosum												
T (°C)	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	**45**	**Min.**	**Max.**	**T_{opt}**
P_s	0.229	0.336	0.512	0.725	0.860	1.195	0.106	-	-	0.106	1.195	24.6±2.2
P^B_{max}	0.218	0.336	0.512	0.661	0.683	0.580	0.086	-	-	0.086	0.683	21.5±1.2
I_k	32.0	57.0	83.9	122.5	136.6	165.8	95.9	-	-	32.0	165.8	26.4±1.3
I_c	2.1	3.1	7.5	10.4	10.6	16.3	56.2	-	-	2.1	56.2	49.6±10.6
α	0.0068	0.0059	0.0061	0.0054	0.005	0.0035	0.0009	-	-	0.0009	0.0068	
β	5.846×10^{-5}	-	-	1.00×10^{-4}	3.00×10^{-4}	1.10×10^{-3}	4.60×10^{-5}	-	-	4.6×10^{-5}	0.0011	
R^B	0.014	0.018	0.044	0.054	0.051	0.056	0.040	-	-	0.014	0.056	25.3±1
P^B_{max}/R^B	16.006	18.707	11.690	12.260	13.316	10.391	2.145	-	-	2.145	18.707	

Appendix 4 Result of the Tukey's post hoc multiple comparison test between the P^{B}_{max} values of different phyla, species and temperatures (diff the difference in the observed means, lwr the lower end point of the interval, upr the upper end point of the interval, p.adj adjusted P value).

Phyla's comparisons	**diff**	**lwr**	**upr**	**p adj**
Charophyta-Bacillariophyta	0.110234	0.059842	0.160625	1×10^{-7}
Chlorophyta-Bacillariophyta	-0.00231	-0.02863	0.024003	0.999224
Cyanobacteria-Bacillariophyta	0.164772	0.136708	0.192836	0
Rhodophyta-Bacillariophyta	0.05063	0.010023	0.091237	0.006611
Chlorophyta-Charophyta	-0.11255	-0.16059	-0.0645	0
Cyanobacteria-Charophyta	0.054538	0.005513	0.103564	0.021011
Rhodophyta-Charophyta	-0.0596	-0.11674	-0.00246	0.036261
Cyanobacteria-Chlorophyta	0.167086	0.14349	0.190681	0
Rhodophyta-Chlorophyta	0.052944	0.015287	0.090601	0.001442
Rhodophyta-Cyanobacteria	-0.11414	-0.15304	-0.07524	0
Species comparisons	**diff**	**lwr**	**upr**	**p adj**
A. granulata var. *angustissima-A. flosaquae*	-0.00745	-0.11656	0.101657	1
B. atropurpurea-A. flosaquae	-0.05068	-0.14373	0.042365	0.940466
B. gelatinosum-A. flosaquae	-0.30799	-0.40104	-0.21494	0
C. majae-A. flosaquae	-0.17934	-0.26943	-0.08924	0
Coelastrum sp.*-A. flosaquae*	-0.08363	-0.17372	0.006467	0.108825
D. salinarum-A. flosaquae	-0.04802	-0.13811	0.042077	0.952173
L. fusiformis-A. flosaquae	-0.06085	-0.1539	0.032194	0.73669
M. aeruginosa-A. flosaquae	-0.15517	-0.26428	-0.04606	0.000113
M. flosaquae-A. flosaquae	-0.15177	-0.24187	-0.06168	0.000001
M. griffithii-A. flosaquae	-0.35668	-0.44973	-0.26363	0
Microcystis sp.*-A. flosaquae*	-0.32184	-0.41193	-0.23175	0
M. pulchellum-A. flosaquae	-0.09679	-0.18689	-0.0067	0.020312
M. tenuissima-A. flosaquae	-0.16789	-0.277	-0.05878	0.000015
N. aurariae-A. flosaquae	-0.14256	-0.23265	-0.05246	6.8×10^{-6}
Nostoc sp.*-A. flosaquae*	-0.3278	-0.41552	-0.24007	0
N. palea-A. flosaquae	-0.27087	-0.36096	-0.18077	0
N. reskovii-A. flosaquae	-0.15413	-0.24423	-0.06404	6×10^{-7}
N. supralitorea-A. flosaquae	-0.23573	-0.32582	-0.14564	0
Oscillatoria sp.*-A. flosaquae*	-0.17222	-0.28133	-0.06311	7.3×10^{-6}
Picochlorum sp.*-A. flosaquae*	-0.13776	-0.22786	-0.04767	1.78×10^{-5}
P. salinarum-A. flosaquae	-0.25508	-0.34517	-0.16498	0
R. subcapitata-A. flosaquae	-0.32792	-0.41801	-0.23783	0
Scenedesmus sp.*-A. flosaquae*	-0.15564	-0.24337	-0.06792	2×10^{-7}
T. obliquus-A. flosaquae	-0.17764	-0.26773	-0.08754	0
B. atropurpurea-A. granulata var. *angustissima*	-0.04323	-0.15234	0.065876	0.998925
B. gelatinosum-A. granulata var. *angustissima*	-0.30054	-0.40965	-0.19143	0
C. majae-A. granulata var. *angustissima*	-0.17189	-0.27849	-0.06529	0.000004
Coelastrum sp.*-A. granulata* var. *angustissima*	-0.07618	-0.18277	0.030424	0.568258
D. salinarum-A. granulata var. *angustissima*	-0.04057	-0.14717	0.066034	0.999423
L. fusiformis-A. granulata var. *angustissima*	-0.0534	-0.16251	0.055706	0.981301
M. aeruginosa-A. granulata var. *angustissima*	-0.14772	-0.27081	-0.02463	0.00367
M. flosaquae-A. granulata var. *angustissima*	-0.14432	-0.25092	-0.03772	0.000347
M. griffithii-A. granulata var. *angustissima*	-0.34923	-0.45834	-0.24012	0

Microcystis sp.-*A. granulata* var. *angustissima*	-0.31439	-0.42099	-0.20779	0
M. pulchellum-A. granulata var. *angustissima*	-0.08934	-0.19594	0.017258	0.249286
M. tenuissima-A. granulata var. *angustissima*	-0.16044	-0.28353	-0.03735	0.000774
N. aurariae-A. granulata var. *angustissima*	-0.13511	-0.24171	-0.02851	0.00135
Nostoc sp.-*A. granulata* var. *angustissima*	-0.32034	-0.42495	-0.21574	0
N. palea-A. granulata var. *angustissima*	-0.26342	-0.37002	-0.15682	0
N. reskovii-A. granulata var. *angustissima*	-0.14668	-0.25328	-0.04008	0.000242
N. supralitorea-A. granulata var. *angustissima*	-0.22828	-0.33488	-0.12168	0
Oscillatoria sp.-*A. granulata* var. *angustissima*	-0.16477	-0.28786	-0.04168	0.000444
Picochlorum sp.-*A. granulata* var. *angustissima*	-0.13031	-0.23691	-0.02371	0.002648
P. salinarum-A. granulata var. *angustissima*	-0.24763	-0.35423	-0.14103	0
R. subcapitata-A. granulata var. *angustissima*	-0.32047	-0.42707	-0.21387	0
Scenedesmus sp.-*A. granulata* var. *angustissima*	-0.14819	-0.2528	-0.04358	0.000124
T. obliquus-A. granulata var. *angustissima*	-0.17019	-0.27679	-0.06359	5.3×10^{-6}
B. gelatinosum-B. atropurpurea	-0.25731	-0.35035	-0.16426	0
C. majae-B. atropurpurea	-0.12865	-0.21875	-0.03856	0.000102
Coelastrum sp.-*B. atropurpurea*	-0.03294	-0.12304	0.05715	0.999695
D. salinarum-B. atropurpurea	0.002666	-0.08743	0.09276	1
L. fusiformis-B. atropurpurea	-0.01017	-0.10322	0.082877	1
M. aeruginosa-B. atropurpurea	-0.10449	-0.21359	0.004623	0.080059
M. flosaquae-B. atropurpurea	-0.10109	-0.19118	-0.011	0.010888
M. griffithii-B. atropurpurea	-0.306	-0.39905	-0.21295	0
Microcystis sp.-*B. atropurpurea*	-0.27116	-0.36125	-0.18106	0
M. pulchellum-B. atropurpurea	-0.04611	-0.1362	0.043984	0.968908
M. tenuissima-B. atropurpurea	-0.11721	-0.22632	-0.0081	0.020339
N. aurariae-B. atropurpurea	-0.09187	-0.18197	-0.00178	0.039702
Nostoc sp.-*B. atropurpurea*	-0.27711	-0.36484	-0.18939	0
N. palea-B. atropurpurea	-0.22019	-0.31028	-0.13009	0
N. reskovii-B. atropurpurea	-0.10345	-0.19354	-0.01336	0.007625
N. supralitorea-B. atropurpurea	-0.18505	-0.27514	-0.09495	0
Oscillatoria sp.-*B. atropurpurea*	-0.12153	-0.23064	-0.01243	0.012146
Picochlorum sp.-*B. atropurpurea*	-0.08708	-0.17717	0.003012	0.072688
P. salinarum-B. atropurpurea	-0.20439	-0.29449	-0.1143	0
R. subcapitata-B. atropurpurea	-0.27724	-0.36733	-0.18714	0
Scenedesmus sp.-*B. atropurpurea*	-0.10496	-0.19269	-0.01723	0.003868
T. obliquus-B. atropurpurea	-0.12695	-0.21705	-0.03686	0.00014
C. majae-B. gelatinosum	0.128654	0.03856	0.218747	0.000102
Coelastrum sp.-*B. gelatinosum*	0.224364	0.134271	0.314457	0
D. salinarum-B. gelatinosum	0.259974	0.169881	0.350067	0
L. fusiformis-B. gelatinosum	0.247137	0.154089	0.340184	0
M. aeruginosa-B. gelatinosum	0.152822	0.043713	0.26193	0.000161
M. flosaquae-B. gelatinosum	0.156216	0.066123	0.246309	4×10^{-7}
M. griffithii-B. gelatinosum	-0.04869	-0.14174	0.044356	0.960479
Microcystis sp.-*B. gelatinosum*	-0.01385	-0.10394	0.076243	1
M. pulchellum-B. gelatinosum	0.211198	0.121105	0.301291	0
M. tenuissima-B. gelatinosum	0.140098	0.03099	0.249206	0.001046
N. aurariae-B. gelatinosum	0.165433	0.07534	0.255526	1×10^{-7}
Nostoc sp.-*B. gelatinosum*	-0.01981	-0.10753	0.067921	1

N. palea-B. gelatinosum	0.037122	-0.05297	0.127215	0.998077
N. reskovii-B. gelatinosum	0.153856	0.063762	0.243949	7×10^{-7}
N. supralitorea-B. gelatinosum	0.072261	-0.01783	0.162355	0.329782
Oscillatoria sp.-*B. gelatinosum*	0.135773	0.026665	0.244881	0.001912
Picochlorum sp.-*B. gelatinosum*	0.170226	0.080132	0.260319	0
P. salinarum-B. gelatinosum	0.052912	-0.03718	0.143005	0.881423
R. subcapitata-B. gelatinosum	-0.01993	-0.11002	0.070163	1
Scenedesmus sp.-*B. gelatinosum*	0.152348	0.064622	0.240074	4×10^{-7}
T. obliquus-B. gelatinosum	0.130353	0.04026	0.220446	7.41×10^{-5}
Coelastrum sp.-*C. majae*	0.09571	0.008672	0.182748	0.014659
D. salinarum-C. majae	0.13132	0.044282	0.218358	2.54×10^{-5}
L. fusiformis-C. majae	0.118483	0.02839	0.208576	0.000644
M. aeruginosa-C. majae	0.024168	-0.08243	0.130768	1
M. flosaquae-C. majae	0.027562	-0.05948	0.114601	0.999974
M. griffithii-C. majae	-0.17735	-0.26744	-0.08725	0
Microcystis sp.-*C. majae*	-0.1425	-0.22954	-0.05547	2.5×10^{-6}
M. pulchellum-C. majae	0.082544	-0.00449	0.169583	0.088345
M. tenuissima-C. majae	0.011444	-0.09516	0.118044	1
N. aurariae-C. majae	0.036779	-0.05026	0.123817	0.997236
Nostoc sp.-*C. majae*	-0.14846	-0.23305	-0.06387	3×10^{-7}
N. palea-C. majae	-0.09153	-0.17857	-0.00449	0.027008
N. reskovii-C. majae	0.025202	-0.06184	0.11224	0.999995
N. supralitorea-C. majae	-0.05639	-0.14343	0.030646	0.752221
Oscillatoria sp.-*C. majae*	0.007119	-0.09948	0.113719	1
Picochlorum sp.-*C. majae*	0.041572	-0.04547	0.12861	0.986052
P. salinarum-C. majae	-0.07574	-0.16278	0.011297	0.189354
R. subcapitata-C. majae	-0.14858	-0.23562	-0.06155	7×10^{-7}
Scenedesmus sp.-*C. majae*	0.023695	-0.06089	0.108281	0.999997
T. obliquus-C. majae	0.0017	-0.08534	0.088738	1
D. salinarum-Coelastrum sp.	0.03561	-0.05143	0.122648	0.998266
L. fusiformis-Coelastrum sp.	0.022773	-0.06732	0.112866	1
M. aeruginosa-Coelastrum sp.	-0.07154	-0.17814	0.035057	0.691251
M. flosaquae-Coelastrum sp.	-0.06815	-0.15519	0.01889	0.377668
M. griffithii-Coelastrum sp.	-0.27306	-0.36315	-0.18296	0
Microcystis sp.-*Coelastrum* sp.	-0.23821	-0.32525	-0.15118	0
M. pulchellum-Coelastrum sp.	-0.01317	-0.1002	0.073872	1
M. tenuissima-Coelastrum sp.	-0.08427	-0.19087	0.022334	0.358417
N. aurariae-Coelastrum sp.	-0.05893	-0.14597	0.028107	0.674954
Nostoc sp.-*Coelastrum* sp.	-0.24417	-0.32876	-0.15958	0
N. palea-Coelastrum sp.	-0.18724	-0.27428	-0.1002	0
N. reskovii-Coelastrum sp.	-0.07051	-0.15755	0.01653	0.310729
N. supralitorea-Coelastrum sp.	-0.1521	-0.23914	-0.06506	3×10^{-7}
Oscillatoria sp.-*Coelastrum* sp.	-0.08859	-0.19519	0.018009	0.263934
Picochlorum sp.-*Coelastrum* sp.	-0.05414	-0.14118	0.0329	0.813466
P. salinarum-Coelastrum sp.	-0.17145	-0.25849	-0.08441	0
R. subcapitata-Coelastrum sp.	-0.24429	-0.33133	-0.15726	0
Scenedesmus sp.-*Coelastrum* sp.	-0.07202	-0.1566	0.01257	0.223101
T. obliquus-Coelastrum sp.	-0.09401	-0.18105	-0.00697	0.018875

L. fusiformis-D. salinarum	-0.01284	-0.10293	0.077256	1
M. aeruginosa-D. salinarum	-0.10715	-0.21375	-0.00055	0.047098
M. flosaquae-D. salinarum	-0.10376	-0.1908	-0.01672	0.004117
M. griffithii-D. salinarum	-0.30867	-0.39876	-0.21857	0
Microcystis sp.*-D. salinarum*	-0.27382	-0.36086	-0.18679	0
M. pulchellum-D. salinarum	-0.04878	-0.13581	0.038263	0.921824
M. tenuissima-D. salinarum	-0.11988	-0.22648	-0.01328	0.010533
N. aurariae-D. salinarum	-0.09454	-0.18158	-0.0075	0.017454
Nostoc sp.*-D. salinarum*	-0.27978	-0.36437	-0.19519	0
N. palea-D. salinarum	-0.22285	-0.30989	-0.13581	0
N. reskovii-D. salinarum	-0.10612	-0.19316	-0.01908	0.002777
N. supralitorea-D. salinarum	-0.18771	-0.27475	-0.10067	0
Oscillatoria sp.*-D. salinarum*	-0.1242	-0.2308	-0.0176	0.006035
Picochlorum sp.*-D. salinarum*	-0.08975	-0.17679	-0.00271	0.034671
P. salinarum-D. salinarum	-0.20706	-0.2941	-0.12002	0
R. subcapitata-D. salinarum	-0.2799	-0.36694	-0.19287	0
Scenedesmus sp.*-D. salinarum*	-0.10763	-0.19221	-0.02304	0.001251
T. obliquus-D. salinarum	-0.12962	-0.21666	-0.04258	3.58×10^{-5}
M. aeruginosa-L. fusiformis	-0.09432	-0.20342	0.014793	0.199325
M. flosaquae-L. fusiformis	-0.09092	-0.18101	-0.00083	0.044959
M. griffithii-L. fusiformis	-0.29583	-0.38888	-0.20278	0
Microcystis sp.*-L. fusiformis*	-0.26099	-0.35108	-0.17089	0
M. pulchellum-L. fusiformis	-0.03594	-0.12603	0.054155	0.99881
M. tenuissima-L. fusiformis	-0.10704	-0.21615	0.002069	0.061979
N. aurariae-L. fusiformis	-0.0817	-0.1718	0.008389	0.134512
Nostoc sp.*-L. fusiformis*	-0.26694	-0.35467	-0.17922	0
N. palea-L. fusiformis	-0.21001	-0.30011	-0.11992	0
N. reskovii-L. fusiformis	-0.09328	-0.18337	-0.00319	0.032939
N. supralitorea-L. fusiformis	-0.17488	-0.26497	-0.08478	0
Oscillatoria sp.*-L. fusiformis*	-0.11136	-0.22047	-0.00226	0.039282
Picochlorum sp.*-L. fusiformis*	-0.07691	-0.167	0.013182	0.218781
P. salinarum-L. fusiformis	-0.19422	-0.28432	-0.10413	0
R. subcapitata-L. fusiformis	-0.26707	-0.35716	-0.17697	0
Scenedesmus sp.*-L. fusiformis*	-0.09479	-0.18251	-0.00706	0.01878
T. obliquus-L. fusiformis	-0.11678	-0.20688	-0.02669	0.000866
M. flosaquae-M. aeruginosa	0.003394	-0.10321	0.109994	1
M. griffithii-M. aeruginosa	-0.20151	-0.31062	-0.09241	0
Microcystis sp.*-M. aeruginosa*	-0.16667	-0.27327	-0.06007	9.6×10^{-6}
M. pulchellum-M. aeruginosa	0.058376	-0.04822	0.164976	0.937256
M. tenuissima-M. aeruginosa	-0.01272	-0.13581	0.110367	1
N. aurariae-M. aeruginosa	0.012611	-0.09399	0.119211	1
Nostoc sp.*-M. aeruginosa*	-0.17263	-0.27723	-0.06802	0.000002
N. palea-M. aeruginosa	-0.1157	-0.2223	-0.0091	0.017643
N. reskovii-M. aeruginosa	0.001034	-0.10557	0.107634	1
N. supralitorea-M. aeruginosa	-0.08056	-0.18716	0.026039	0.45093
Oscillatoria sp.*-M. aeruginosa*	-0.01705	-0.14014	0.106042	1
Picochlorum sp.*-M. aeruginosa*	0.017404	-0.0892	0.124004	1
P. salinarum-M. aeruginosa	-0.09991	-0.20651	0.00669	0.099226

R. subcapitata-M. aeruginosa	-0.17275	-0.27935	-0.06615	3.4×10^{-6}
Scenedesmus sp.-*M. aeruginosa*	-0.00047	-0.10508	0.104134	1
T. obliquus-M. aeruginosa	-0.02247	-0.12907	0.084131	1
M. griffithii-M. flosaquae	-0.20491	-0.295	-0.11481	0
Microcystis sp.-*M. flosaquae*	-0.17007	-0.2571	-0.08303	0
M. pulchellum-M. flosaquae	0.054982	-0.03206	0.14202	0.791495
M. tenuissima-M. flosaquae	-0.01612	-0.12272	0.090481	1
N. aurariae-M. flosaquae	0.009217	-0.07782	0.096255	1
Nostoc sp.-*M. flosaquae*	-0.17602	-0.26061	-0.09144	0
N. palea-M. flosaquae	-0.11909	-0.20613	-0.03206	0.000275
N. reskovii-M. flosaquae	-0.00236	-0.0894	0.084678	1
N. supralitorea-M. flosaquae	-0.08395	-0.17099	0.003084	0.074286
Oscillatoria sp.-*M. flosaquae*	-0.02044	-0.12704	0.086156	1
Picochlorum sp.-*M. flosaquae*	0.01401	-0.07303	0.101048	1
P. salinarum-M. flosaquae	-0.1033	-0.19034	-0.01627	0.004436
R. subcapitata-M. flosaquae	-0.17615	-0.26318	-0.08911	0
Scenedesmus sp.-*M. flosaquae*	-0.00387	-0.08845	0.080718	1
T. obliquus-M. flosaquae	-0.02586	-0.1129	0.061175	0.999992
Microcystis sp.-*M. griffithii*	0.034842	-0.05525	0.124935	0.999258
M. pulchellum-M. griffithii	0.25989	0.169797	0.349983	0
M. tenuissima-M. griffithii	0.18879	0.079681	0.297898	4×10^{-7}
N. aurariae-M. griffithii	0.214124	0.124031	0.304218	0
Nostoc sp.-*M. griffithii*	0.028886	-0.05884	0.116612	0.999948
N. palea-M. griffithii	0.085814	-0.00428	0.175907	0.084566
N. reskovii-M. griffithii	0.202547	0.112454	0.29264	0
N. supralitorea-M. griffithii	0.120953	0.03086	0.211046	0.000417
Oscillatoria sp.-*M. griffithii*	0.184465	0.075356	0.293573	9×10^{-7}
Picochlorum sp.-*M. griffithii*	0.218917	0.128824	0.30901	0
P. salinarum-M. griffithii	0.101604	0.011511	0.191697	0.010085
R. subcapitata-M. griffithii	0.028761	-0.06133	0.118854	0.99997
Scenedesmus sp.-*M. griffithii*	0.20104	0.113314	0.288766	0
T. obliquus-M. griffithii	0.179045	0.088952	0.269138	0
M. pulchellum-Microcystis sp.	0.225048	0.138009	0.312086	0
M. tenuissima-Microcystis sp.	0.153947	0.047348	0.260547	7.76×10^{-5}
N. aurariae-Microcystis sp.	0.179282	0.092244	0.266321	0
Nostoc sp.-*Microcystis* sp.	-0.00596	-0.09054	0.07863	1
N. palea-Microcystis sp.	0.050972	-0.03607	0.13801	0.884267
N. reskovii-Microcystis sp.	0.167705	0.080667	0.254743	0
N. supralitorea-Microcystis sp.	0.086111	-0.00093	0.173149	0.056454
Oscillatoria sp.-*Microcystis* sp.	0.149623	0.043023	0.256222	0.000154
Picochlorum sp.-*Microcystis* sp.	0.184075	0.097037	0.271114	0
P. salinarum-Microcystis sp.	0.066762	-0.02028	0.1538	0.419877
R. subcapitata-Microcystis sp.	-0.00608	-0.09312	0.080958	1
Scenedesmus sp.-*Microcystis* sp.	0.166198	0.081612	0.250784	0
T. obliquus-Microcystis sp.	0.144203	0.057165	0.231241	1.7×10^{-6}
M. tenuissima-M. pulchellum	-0.0711	-0.1777	0.035499	0.702474
N. aurariae-M. pulchellum	-0.04577	-0.1328	0.041273	0.958434
Nostoc sp.-*M. pulchellum*	-0.231	-0.31559	-0.14642	0

N. palea-M. pulchellum	-0.17408	-0.26111	-0.08704	0
N. reskovii-M. pulchellum	-0.05734	-0.14438	0.029696	0.724168
N. supralitorea-M. pulchellum	-0.13894	-0.22597	-0.0519	5.3×10^{-6}
Oscillatoria sp.-*M. pulchellum*	-0.07543	-0.18202	0.031175	0.588561
Picochlorum sp.-*M. pulchellum*	-0.04097	-0.12801	0.046066	0.988339
P. salinarum-M. pulchellum	-0.15829	-0.24532	-0.07125	1×10^{-7}
R. subcapitata-M. pulchellum	-0.23113	-0.31817	-0.14409	0
Scenedesmus sp.-*M. pulchellum*	-0.05885	-0.14344	0.025736	0.622457
T. obliquus-M. pulchellum	-0.08084	-0.16788	0.006193	0.108138
N. aurariae-M. tenuissima	0.025335	-0.08126	0.131935	1
Nostoc sp.-*M. tenuissima*	-0.1599	-0.26451	-0.0553	1.79×10^{-5}
N. palea-M. tenuissima	-0.10298	-0.20958	0.003624	0.073139
N. reskovii-M. tenuissima	0.013758	-0.09284	0.120357	1
N. supralitorea-M. tenuissima	-0.06784	-0.17444	0.038763	0.780497
Oscillatoria sp.-*M. tenuissima*	-0.00432	-0.12742	0.118766	1
Picochlorum sp.-*M. tenuissima*	0.030128	-0.07647	0.136727	0.999997
P. salinarum-M. tenuissima	-0.08719	-0.19379	0.019414	0.292808
R. subcapitata-M. tenuissima	-0.16003	-0.26663	-0.05343	0.000029
Scenedesmus sp.-*M. tenuissima*	0.01225	-0.09236	0.116857	1
T. obliquus-M. tenuissima	-0.00974	-0.11634	0.096855	1
Nostoc sp.-*N. aurariae*	-0.18524	-0.26982	-0.10065	0
N. palea-N. aurariae	-0.12831	-0.21535	-0.04127	4.64E-05
N. reskovii-N. aurariae	-0.01158	-0.09862	0.075461	1
N. supralitorea-N. aurariae	-0.09317	-0.18021	-0.00613	0.02134
Oscillatoria sp.-*N. aurariae*	-0.02966	-0.13626	0.07694	0.999998
Picochlorum sp.-*N. aurariae*	0.004793	-0.08225	0.091831	1
P. salinarum-N. aurariae	-0.11252	-0.19956	-0.02548	0.000914
R. subcapitata-N. aurariae	-0.18536	-0.2724	-0.09832	0
Scenedesmus sp.-*N. aurariae*	-0.01308	-0.09767	0.071501	1
T. obliquus-N. aurariae	-0.03508	-0.12212	0.051959	0.998611
N. palea-Nostoc sp.	0.056928	-0.02766	0.141514	0.686104
N. reskovii-Nostoc sp.	0.173661	0.089075	0.258247	0
N. supralitorea-Nostoc sp.	0.092067	0.007481	0.176653	0.016956
Oscillatoria sp.-*Nostoc* sp.	0.155579	0.050972	0.260186	0.000037
Picochlorum sp.-*Nostoc* sp.	0.190031	0.105445	0.274617	0
P. salinarum-Nostoc sp.	0.072718	-0.01187	0.157304	0.207731
R. subcapitata-Nostoc sp.	-0.00012	-0.08471	0.084461	1
Scenedesmus sp.-*Nostoc* sp.	0.172154	0.090093	0.254214	0
T. obliquus-Nostoc sp.	0.150159	0.065573	0.234745	2×10^{-7}
N. reskovii-N. palea	0.116734	0.029695	0.203772	0.000426
N. supralitorea-N. palea	0.035139	-0.0519	0.122178	0.998575
Oscillatoria sp.-*N. palea*	0.098651	-0.00795	0.20525	0.111937
Picochlorum sp.-*N. palea*	0.133104	0.046065	0.220142	1.77×10^{-5}
P. salinarum-N. palea	0.01579	-0.07125	0.102828	1
R. subcapitata-N. palea	-0.05705	-0.14409	0.029986	0.732853
Scenedesmus sp.-*N. palea*	0.115226	0.03064	0.199812	0.000303
T. obliquus-N. palea	0.093231	0.006193	0.180269	0.021155
N. supralitorea-N. reskovii	-0.08159	-0.16863	0.005444	0.099009

Oscillatoria sp.-*N. reskovii*	-0.01808	-0.12468	0.088517	1
Picochlorum sp.-*N. reskovii*	0.01637	-0.07067	0.103408	1
P. salinarum-N. reskovii	-0.10094	-0.18798	-0.01391	0.006504
R. subcapitata-N. reskovii	-0.17379	-0.26082	-0.08675	0
Scenedesmus sp.-*N. reskovii*	-0.00151	-0.08609	0.083079	1
T. obliquus-N. reskovii	-0.0235	-0.11054	0.063536	0.999999
Oscillatoria sp.-*N. supralitorea*	0.063511	-0.04309	0.170111	0.866422
Picochlorum sp.-*N. supralitorea*	0.097964	0.010926	0.185002	0.010394
P. salinarum-N. supralitorea	-0.01935	-0.10639	0.067689	1
R. subcapitata-N. supralitorea	-0.09219	-0.17923	-0.00515	0.02458
Scenedesmus sp.-*N. supralitorea*	0.080087	-0.0045	0.164673	0.089809
T. obliquus-N. supralitorea	0.058092	-0.02895	0.14513	0.70128
Picochlorum sp.-*Oscillatoria* sp.	0.034453	-0.07215	0.141052	0.999963
P. salinarum-Oscillatoria sp.	-0.08286	-0.18946	0.023739	0.392444
R. subcapitata-Oscillatoria sp.	-0.1557	-0.2623	-0.0491	5.86×10^{-5}
Scenedesmus sp.-*Oscillatoria* sp.	0.016575	-0.08803	0.121182	1
T. obliquus-Oscillatoria sp.	-0.00542	-0.11202	0.10118	1
P. salinarum-Picochlorum sp.	-0.11731	-0.20435	-0.03028	0.000383
R. subcapitata-Picochlorum sp.	-0.19016	-0.27719	-0.10312	0
Scenedesmus sp.-*Picochlorum* sp.	-0.01788	-0.10246	0.066709	1
T. obliquus-Picochlorum sp.	-0.03987	-0.12691	0.047166	0.991742
R. subcapitata-P. salinarum	-0.07284	-0.15988	0.014196	0.251737
Scenedesmus sp.-*P. salinarum*	0.099436	0.01485	0.184022	0.00521
T. obliquus-P. salinarum	0.077441	-0.0096	0.164479	0.158403
Scenedesmus sp.-*R. subcapitata*	0.172279	0.087693	0.256865	0
T. obliquus-R. subcapitata	0.150284	0.063245	0.237322	5×10^{-7}
T. obliquus-Scenedesmus sp.	-0.022	-0.10658	0.062591	0.999999

Temperature comparisons	**diff**	**lwr**	**upr**	**p adj**
10-5	0.056528	0.009321	0.103735	0.007084
15-5	0.128551	0.08312	0.173981	0
20-5	0.189737	0.144306	0.235168	0
25-5	0.236489	0.191058	0.28192	0
30-5	0.254015	0.208585	0.299446	0
35-5	0.226628	0.179421	0.273835	0
40-5	0.171869	0.12288	0.220858	0
45-5	0.137453	0.045803	0.229103	0.000183
15-10	0.072022	0.028519	0.115526	2.15×10^{-5}
20-10	0.133209	0.089706	0.176712	0
25-10	0.179961	0.136458	0.223464	0
30-10	0.197487	0.153984	0.24099	0
35-10	0.170099	0.124744	0.215454	0
40-10	0.115341	0.068134	0.162548	0
45-10	0.080925	-0.00979	0.171635	0.121651
20-15	0.061186	0.019618	0.102755	0.000263
25-15	0.107938	0.06637	0.149507	0
30-15	0.125464	0.083896	0.167033	0
35-15	0.098077	0.054574	0.14158	0
40-15	0.043318	-0.00211	0.088749	0.074596

45-15	0.008902	-0.0809	0.098701	0.999997
25-20	0.046752	0.005183	0.088321	0.015227
30-20	0.064278	0.02271	0.105847	0.000098
35-20	0.036891	-0.00661	0.080394	0.167958
40-20	-0.01787	-0.0633	0.027563	0.946597
45-20	-0.05228	-0.14208	0.037515	0.660234
30-25	0.017526	-0.02404	0.059095	0.921575
35-25	-0.00986	-0.05336	0.033642	0.998538
40-25	-0.06462	-0.11005	-0.01919	0.000498
45-25	-0.09904	-0.18883	-0.00924	0.018969
35-30	-0.02739	-0.07089	0.016116	0.558328
40-30	-0.08215	-0.12758	-0.03672	2.3×10^{-6}
45-30	-0.11656	-0.20636	-0.02676	0.002274
40-35	-0.05476	-0.10197	-0.00755	0.010574
45-35	-0.08917	-0.17988	0.001536	0.058007
45-40	-0.03442	-0.12607	0.057234	0.959102

Appendix 5 Selected occurrences of *Limnospira fusiformis* and *Picocystis salinarum* in alkaline saline lakes worldwide (Schagerl et al. 2015, Krienitz et al. 2016, Tarazona Delgado et al. 2017)

Species	Continent	Country	Lake	GPS	References
L. fusiformis	Africa	Kenya	Bogoria	0.252955; 36.101129	(Schagerl and Oduor 2008, Krienitz and Kotut 2010, Krienitz et al. 2016)
			Nakuru	-0.360927; 36.090687	(Melack and Kilham 1974, Vareschi 1982, Schagerl and Oduor 2008, Krienitz and Kotut 2010, Krienitz et al. 2016)
			Sonachi	-0.78262; 36.261692	(Ballot et al. 2005, Krienitz et al. 2016)
			Simbi	-0.367341; 34.629801	(Ballot et al. 2005, Krienitz et al. 2016)
			Oloidien	-0.813959; 36.277494	(Krienitz and Kotut 2010, Krienitz et al. 2016)
			Elmenteita	-0.444375; 36.24069	(Melack and Kilham 1974, Schagerl and Oduor 2008, Krienitz et al. 2016)
			Magadi	-1.9124; 36.269837	(Tuite 1981, Krienitz et al. 2016)
		Ethiopia	Abijata	7.625062; 38.611943	(Talling et al. 1973)
			Arenguade	8.695547; 38.975971	(Talling et al. 1973)
			Chitu	7.405367; 38.42133	(Kebede and Ahlgren 1996, Kebede 1997)
			Kilotes	8.804113; 39.084535	(Talling et al. 1973)
		Tanzania	Big Momella	-3.222658; 36.908526	(Melack and Kilham 1974, Tuite 1981, Krienitz et al. 2016)
			Magad	-3.189168; 35.534479	(Melack and Kilham 1974)
			Manyara	-3.627707; 35.823856	(Melack and Kilham 1974, Tuite 1981, Kihwele et al. 2014, Krienitz et al. 2016)
			Reshitani	-3.231451; 36.908277	(Melack and Kilham 1974)
			Tulusia	-3.211139; 36.906988	(Tuite 1981, Krienitz et al. 2016)
		Mayotte Island, France	Lake Dziani Dzaha	-12.771; 45.288667	(Cellamare et al. 2018, Bernard et al. 2019)
		Namibia	Walvis Bay Bird Paradise	-22.964366, 14.533817	(Krienitz et al. 2016)
		South Africa	Kamfers Dam	-28.672288, 24.763816	(Krienitz et al. 2016)
		Uganda	Katwe	-0.128273; 29.867407	(Mungoma 1990, Krienitz et al. 2016)
			Masehe	-0.100676; 30.177943	(Mungoma 1990)
		Chad	Chad	13.102705; 14.510394	(Sili et al. 2012)
			Rombou	14.091489; 15.216202	(Iltis 1969)
			Mombolo	14.029776; 14.497099	(Iltis 1971)

		Sudan	Dariba	12.951702; 24.256724	(Fott and Karim 1973)
			Jebel Marra	12.95182; 24.259121	(Fott and Karim 1973)
	Asia	Turkey	Van	38.619062; 42.948814	(Hammer 1986)
		India	Shambhar	26.933713; 75.089209	(Dadheech et al. 2010)
			Mansagar	26.956082; 75.848905	(Dadheech et al. 2010)
		Israel	River Yarqon	32.097258; 34.791249	(Barinova and Tavassi 2009)
			Kishon River	32.588693; 35.264852	(Barinova et al. 2004)
	Central America	Mexico	Texoco	19.465917; -98.9699	(Dadheech et al. 2010)
	South America	Brazil	Salina da Reserva	-18.960278, -56.623611	(Costa et al. 2016)
			Salina do Meio	-18.974167, -56.6475	(Costa et al. 2016)
	Europe	Serbia	salty puddles (Baranda)	45.080955; 20.476929	(Fužinato et al. 2010)
		Greece	Lake Koroneia	40.686704; 23.141598	(Moustaka-Gouni et al. 2007)
P. salinarum	Africa	Kenya	Bogoria	0.252955; 36.101129	(Krienitz et al. 2012)
			Nakuru	-0.360927; 36.090687	(Krienitz et al. 2012)
			Magadi	-1.9124; 36.269837	(Krienitz et al. 2012)
			Hot Springs Magadi	-1.977585; 36.23848	(Krienitz et al. 2012)
		Mayotte Island, France	Lake Dziani Dzaha	-12.771; 45.288667	(Cellamare et al. 2018, Bernard et al. 2019)
		Tunisia	Essed valley, sewage	35.989757; 10.502778	(Ben Ali et al. 2017, Ben Ouada et al. 2018b, 2018a)
		Uganda	Katwe	-0.128273; 29.867407	(Krienitz et al. 2012, 2016)
			Bagusa	-0.102778, 30.173333	(Krienitz et al. 2016)
	Asia	P.R. China	Lake Dagenoer	42.683485; 115.84986	(Fanjing et al. 2009)
		Russia	Lake Tanatar VI	51.620276; 79.816436	(Samylina et al. 2010)
		India	Lake Sambhar	26.941672, 75.086469	(Krienitz et al. 2016, Krienitz 2018)
	North America	USA	San Francisco Salt Works	37.688579; -122.3176	(Lewin et al. 2000)
		USA	Lake Mono	38.006943; -118.9864	(Roesler et al. 2002)
		USA	San Elijo Lagoon	33.014362; -117.2532	(Wang et al. 2014)
	South America	Peru	Laguna La Milagrosa	-12.54471; -76.72312	(Tarazona Delgado et al. 2017)
		Peru	Laguna La Mellicera	-12.54287; -76.72521	(Tarazona Delgado et al. 2017)

Appendix 6 Composition of the media used in the experiments.

	M_0 *g L^{-1}*	**M_1** *g L^{-1}*	**M_2** *g L^{-1}*	**M_3** *g L^{-1}*	**M_4** *g L^{-1}*	**M_5** *g L^{-1}*	**M_6** *g L^{-1}*	**M_7** *g L^{-1}*	**M_8** *g L^{-1}*	**M_9** *g L^{-1}*	**M_{10}** *g L^{-1}*	**M_{11}** *g L^{-1}*	**M_{12}** *g L^{-1}*	**M_{13}** *g L^{-1}*
$NaHCO_3$	15	22,5	30	45	60	75	15							
Na_2CO_3	4	6	8	12	16	20	4							
NaCl	0,1						5	10	20	25	30	35	40	45
Na_2-EDTA	0,08													
$FeSO_4 \cdot 7H_2O$	0,01													
$MgSO_4 \cdot 7H_2O$	0,2													
K_2HPO_4	0,5													
$NaNO_3$	2,5													
$CaCl_2$	0,04													
A_5 microelements	1 *ml L^{-1}*													

Appendix 7 Results of the Tukey post hoc multiple comparisons between each pair of carbonate and chloride dominated media (diff the difference in the observed means, lwr the lower end point of the interval, upr the upper end point of the interval, p.adj adjusted P value).

culturing medium comparisons	diff	lwr	upr	p adj
M_1-M_0	0.029	0.010	0.048	<0.001
M_2-M_0	0.029	0.012	0.046	<0.001
M_3-M_0	0.089	0.070	0.109	<0.001
M_4-M_0	0.083	0.063	0.103	<0.001
M_5-M_0	0.010	0.060	0.140	<0.001
M_2-M_1	0.000	-0.019	0.019	1.000
M_3-M_1	0.061	0.040	0.081	<0.001
M_4-M_1	0.054	0.032	0.076	<0.001
M_5-M_1	0.071	0.031	0.112	<0.001
M_3-M_2	0.060	0.041	0.079	<0.001
M_4-M_2	0.054	0.034	0.074	<0.001
M_5-M_2	0.071	0.031	0.111	<0.001
M_4-M_3	-0.006	-0.028	0.016	0.963
M_5-M_3	0.011	-0.030	0.051	0.974
M_5-M_4	0.017	-0.024	0.058	0.844
M_{10}-M_0	0.004	-0.011	0.019	0.997
M_{11}-M_0	-0.001	-0.019	0.017	1.000
M_{12}-M_0	-0.005	-0.022	0.011	0.987
M_{13}-M_0	-0.008	-0.024	0.009	0.894
M_6-M_0	0.012	-0.006	0.029	0.473
M_7-M_0	0.010	-0.005	0.025	0.486
M_8-M_0	0.035	0.018	0.053	<0.001
M_9-M_0	0.019	0.000	0.038	<0.05
M_{11}-M_{10}	-0.005	-0.024	0.014	0.997
M_{12}-M_{10}	-0.009	-0.027	0.009	0.828
M_{13}-M_{10}	-0.011	-0.030	0.007	0.591
M_6-M_{10}	0.008	-0.011	0.027	0.924
M_7-M_{10}	0.006	-0.010	0.023	0.962
M_8-M_{10}	0.031	0.012	0.050	<0.001
M_9-M_{10}	0.015	-0.005	0.036	0.303
M_{12}-M_{11}	-0.004	-0.024	0.016	0.999
M_{13}-M_{11}	-0.007	-0.027	0.014	0.986
M_6-M_{11}	0.013	-0.008	0.034	0.626
M_7-M_{11}	0.011	-0.008	0.030	0.687
M_8-M_{11}	0.036	0.015	0.057	<0.001
M_9-M_{11}	0.020	-0.002	0.043	0.118
M_{13}-M_{12}	-0.002	-0.022	0.017	0.100
M_6-M_{12}	0.017	-0.003	0.037	0.179

M_7-M_{12}	0.015	-0.003	0.033	0.177
M_8-M_{12}	0.040	0.020	0.061	<0.001
M_9-M_{12}	0.024	0.003	0.046	<0.05
M_6-M_{13}	0.019	-0.001	0.040	0.081
M_7-M_{13}	0.017	-0.001	0.036	0.074
M_8-M_{13}	0.043	0.022	0.063	<0.001
M_9-M_{13}	0.027	0.005	0.049	<0.01
M_7-M_6	-0.002	-0.021	0.017	0.100
M_8-M_6	0.024	0.002	0.045	<0.05
M_9-M_6	0.008	-0.015	0.030	0.979
M_8-M_7	0.025	0.006	0.044	<0.01
M_9-M_7	0.009	-0.011	0.030	0.886
M_9-M_8	-0.016	-0.038	0.007	0.395