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Biodiversity of phytoplankton in Lake Stechlin (Germany)

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Biodiversity of phytoplankton in Lake Stechlin (Germany)

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“Und nun setzten wir uns an den Rand eines Vorsprungs und horchten in die Stille.

Sie blieb, wie sie war: kein Boot, kein Vogel; auch kein Gewölk.

Nur Grün und Blau und Sonne.”

Theodor Fontane

Wanderung durch die Mark Brandenburg

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Abbreviations

AMT:	aminotransferase
APP:	autotrophic picoplankton
DCM:	Deep Chlorophyll maximum
DHB:	Dihydroxybenzoic acid
DIN:	Dissolved inorganic nitrogen
IV:	Indicator value
NMDS:	Non-metric multidimensional scaling
NPP:	Nuclear Power Plant Rheinsberg
PCR:	polymerase chain reaction
RWCS:	Relative water column stability
SRP:	Soluble reactive phosphorus
SRSi:	Soluble reactive silica
TP:	Total Phosphorus
TN:	Total Nitrogen

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Summary

Terrestrial and aquatic ecosystems are affected by the global climate change, which will accelerate according to most of the climate scenarios. The main goal of the work was to explore some processes related to climate change, which affect the phytoplankton assemblages and biodiversity of Lake Stechlin, such as extreme weather events during summer or changes of stratification pattern.

The main results of the work:

- (1) The possible effects of global climate change on the phytoplankton community were studied in the LakeLab facility in Lake Stechlin. The mixing effect of the wind of an extreme summer storm was simulated, because these events are forecasted to increase both in frequency and intensity in the future. Increased amount of nutrients, decreased amount of phytoplankton biomass and water temperature were observed immediately after the treatment. After that, **X2** and **Y** functional groups, then **H1** codon dominated in the waterbody. In accordance with the results, summer storms can have a major effect on phytoplankton community dynamics and may transfer to higher trophic levels, thus are likely to impact sedimentation rates and further cascade to biogeochemical cycles of a given lake.
- (2) The climate change is likely to result changes in the stratification because of the increasing temperature. Effects of experimentally deepened thermocline on the phytoplankton community were examined in the LakeLab during summer of 2013. Remarkable amount of *Planktothrix rubescens* were observed in the epilimnion of treatment enclosures as the most dominant cyanobacteria during the whole experiment. According to the results, a 2 meter deeper epilimnion than the average epilimnion had a significant effect on the phytoplankton community.
- (3) During the last 15 years incidence and biomass of cyanobacteria increased substantially in Lake Stechlin that raised concern about potential toxicity. Microcystin and microcystin producing genes were detected first by our team in environmental samples from Lake Stechlin by toxicological and molecular analyses. It was proved, that toxins were produced by *Microcystis* cf. *aeruginosa* and *Planktothrix rubescens* present with low biomass, and not by the dominant *Dolichospermum circinale* and *Aphanizomenon flos-aquae*.
- (4) During the analyses of depth distributed samples a rarely occurring deep chlorophyll maximum was observed with contribution of three species (*Cyanobium*, *Planktothrix rubescens* and *Aphanizomenon flos-aquae*), however with spatial segregation, which was very likely resulted by different environmental factors, such as light climate or nutrients availability, limiting them. This study shows a rare phenomenon, when phytoplankton species occur with spatial niche segregation close to equilibrium conditions. These results indicate the necessity of careful calibration using fluorimetric techniques and the usefulness of parallel microscopic analyses during detection of cyanobacterial populations.

Kivonat

A globális klímaváltozás a teresztris és a vízi ökoszisztémákra is hatást gyakorol, mely a legtöbb scenárió szerint a jövőben fokozódni fog. Az értekezés egyik fő célkitűzése volt a specifikusan a Stechlin-tó fitoplankton közösségére ható globális klímaváltozáshoz kötődő folyamatok minél jobb megismerése és részletes vizsgálata, úgymint a nyári extrém időjárási események vagy a rétegződési mintázatok megváltozásának hatása.

A dolgozat főbb, tudományos eredményei:

(1) A Stechlin-tóba telepített mezokozmoszokban vizsgáltam a globális klímaváltozás néhány lehetséges hatását a fitoplankton közösségre. A 2014 nyarán végzett kísérlet során egy extrém időjárási eseményt (erőteljes szél hatása, nyári viharok során) szimuláltunk, mely események a jövőben a klímaváltozás hatására növekvő gyakorisággal és erősséggel prognosztizálhatók. A kísérlet során azonnali tápanyag növekedést tapasztaltunk, a fitoplankton biomassza és a vízhőmérséklet pedig csökkent. Ezt követően először az **X2** és az **Y** funkcionális csoport, majd pedig a **H1** csoport volt domináns. A vizsgálat eredményeivel összhangban megállapítható, hogy a nyári viharok jelentős hatással lehetnek a fitoplankton közösség dinamikájára, mely változás továbbadódhat a magasabb trofitási szintek felé, így befolyásolva az ülepedési rátát, vagy akár a tó biogeokémiai ciklusait is.

(2) A globális klímaváltozás a növekvő hőmérséklet révén a rétegződési mintázatok megváltozását is eredményezheti. Az említett mezokozmoszokban 2013 nyarán az átlagosnál mélyebb epilimnion hatását vizsgáltuk a fitoplankton közösségre. A kezelt mezokozmoszok epilimnionjában jelentős abundanciát ért el a *Planktothrix rubescens*, mely egyben a domináns cianobaktérium faj volt a kísérlet során. Az eredmények azt mutatják, hogy szignifikánsan befolyásolja a közösséget az átlagosnál 2 méterrel mélyebb epilimnion.

(3) Az utóbbi 15 évben a cianobaktériumok fajszáma és biomasszája alapvetően növekedett a Stechlin-tóban, mely növelte a potenciális toxicitást. A Stechlin-tóból származó környezeti minták toxikológiai és genetikai vizsgálata során elsőként detektáltunk microcystint és microcystin termelő géneket, továbbá kimutattuk, hogy a toxinokat nem a domináns *Dolichospermum circinale* és *Aphanizomenon flos-aquae* termeli, hanem az igen kis biomasszával jelenlévő *Microcystis* cf. *aeruginosa* és *Planktothrix rubescens*.

(4) A Stechlin-tóból származó vertikális rétegminták elemzése során egy speciális mélyrétegi maximumot figyeltünk meg, melyet több faj (*Cyanobium*, *Planktothrix rubescens* és *Aphanizomenon flos-aquae*) alakított ki egyidejűleg, viszont térbeli elkülönüléssel, melynek legfőbb oka az őket limitáló különböző környezeti faktorok lehetnek. A vizsgálat során bemutattunk egy ritka esetet, melyben fitoplankton fajok térbeli niche szegregációja történik közel az egyensúlyi állapothoz. Rámotattunk arra, hogy cianobaktérium populációk vizsgálatakor a fluoreszcens módszerek alkalmazásakor elengedhetetlen a megfelelő kalibráció, valamint fontosak lehetnek a párhuzamosan történő mikroszkópos vizsgálatok is.

Zusammenfassung

Terrestrische und aquatische Ökosysteme werden vom weltweiten Klimawandel beeinflusst, der sich gemäß den meisten Klimaszenarien beschleunigen wird. Das Hauptziel der Arbeit war es verschiedene Prozesse zu untersuchen, die mit dem Klimawandel zusammen hängen und die die Phytoplanktongemeinschaften im Stechlinsee beeinflussen, unter anderem Extremwetterereignisse im Sommer oder Veränderungen der Stratifizierung.

Die wichtigsten Ergebnisse der Arbeit:

- (1) Die möglichen Auswirkungen des globalen Klimawandels auf die Phytoplanktongemeinschaft wurden im Seelabor im Stechlinsee untersucht. Der Durchmischungseffekt des Windes während eines extremen Sommersturms wurde simuliert, da prognostiziert wird, dass derartige Ereignisse in der Zukunft an Häufigkeit und Intensität zunehmen werden. Erhöhte Mengen an Nährstoffen und geringere Mengen an Phytoplanktonbiomasse, sowie niedrigere Wassertemperaturen, wurden direkt nach der Simulation beobachtet. Anschließend dominierten die funktionellen Gruppen **X2** und **Y**, gefolgt von Codon **H1**, den Wasserkörper. Aus diesen Ergebnissen geht hervor, dass Sommerstürme einen großen Effekt auf die Dynamik der Phytoplanktongemeinschaft haben und sich weiter auf höhere trophische Ebenen auswirken könnten, und in dessen Folge auch Auswirkungen auf die Kaskade von Sedimentationsraten bis hin zu biogeochemischen Stoffkreisläufen eines Sees wahrscheinlich wären.
- (2) Der Klimawandel resultiert wahrscheinlich in einer Veränderung der Stratifizierung aufgrund der ansteigenden Temperatur. Im Sommer 2013 wurde im Seelabor der Effekt einer experimentell vertieften Thermokline auf die Phytoplanktongemeinschaft untersucht. Beträchtliche Mengen von *Planktothrix rubescens* wurden im Epilimnion der behandelten Mesokosmen beobachtet und stellten die dominanteste Cyanobakterienart während des ganzen Experiments dar. In Anbetracht der Ergebnisse hat ein 2m tieferes Epilimnion im Vergleich zu einem durchschnittlichen Epilimnion einen signifikanten Effekt auf die Phytoplanktongemeinschaft.
- (3) Während der letzten 15 Jahre sind das Vorkommen und die Biomasse von Cyanobakterien im Stechlinsee wesentlich angestiegen und schüren Bedenken über ihre potentielle Toxizität. Mikrozystin und mikrozystinproduzierende Gene wurden von unserem Team durch toxikologische und molekularbiologische Analysen erstmals in Umweltproben des Stechlinsees entdeckt. Es wurde nachgewiesen, dass die Toxine von *Microcystis cf. aeruginosa* und *Planktothrix rubescens*, welche nur in geringer Biomasse vorhanden waren, produziert wurden, und nicht von den dominierenden *Dolichospermum circinale* und *Aphanizomenon flos-aquae*.
- (4) Bei der Analyse tiefenverteilter Proben wurde ein Tiefen-Chlorophyll-Maximum unter Beteiligung dreier Arten (*Cyanobium*, *Planktothrix rubescens* und *Aphanizomenon flos-aquae*) beobachtet, die jedoch räumlich voneinander getrennt vorkamen, höchstwahrscheinlich aufgrund unterschiedlicher limitierender Umweltbedingungen, wie z.B. des Lichtklimas oder der Nährstoffverfügbarkeit. Diese Studie zeigt ein seltenes

Phänomen, in dem Phytoplanktonarten räumlich getrennt nahezu unter Gleichgewichtsbedingungen vorkommen. Die Ergebnisse zeigen die Notwendigkeit einer sorgfältigen Kalibrierung unter Benutzung fluorometrischer Techniken, und den Nutzen paralleler Mikroskopanalysen zur Bestimmung von cyanobakteriellen Populationen.

1. Introduction

1.1. Lake Stechlin

Lake Stechlin is located in North-eastern Germany, roughly 100 km north from Berlin, in the Mecklenburg Lake District (53°10'N, 13°02'E; 59.9 m a.s.l.). The lake was formed by the Weichselian glaciation around 12000 years ago (Casper and Koschel, 1995). The landscape around Lake Stechlin shows ice age erosion: there are thousands of small hills and depressions in this area. The natural surface catchment area of Lake Stechlin amounts 12.4 km² of which 80% are covered by forest. The vegetation in the catchment area is dominated by pine (*Pinus sylvestris*). The majority of the pine forest is manmade replacing the former beech forest. The native beech and beech-oak forests are preserved only in few small plots (Krausch, 1970). Lake Stechlin is located in one of the oldest German's nature reserve (protected since 1938) called "Naturpark Stechlin-Ruppiner Land", which protects 8760 ha.

The climate of this area is at the transition between temperate marine and temperate continental climate zones. The marine influence causes moderately warm summer seasons and relatively mild winters (Fraedrich et al., 2001). Precipitation and groundwater inflow are the two main water-supplies of Lake Stechlin. The yearly average precipitation is around 600 mm (Richter and Koschel, 1985) and the theoretical water retention time is more than 40 years (Holzbecher et al., 1999).

The surface area of Lake Stechlin is 4.25 km². The lake is divided to four basins: north, west, south and central basin. The basins have a relative small surface area (1.3, 1.1, 0.9 and 1.0 km²) and belong to the category deep lakes based on their relative depths (5.3%, 3.5%, 3.3% and 5.2%), which calculated as a ratio of the maximum depth as a percentage of the mean diameter of the lake at the surface (Håkanson, 1981). The maximum depth of the lake (69.5 m) is located in the north basin. In comparison, the maximum depths of other basins are 41, 35 and 59 m (Casper, 1985a). The mean depth of the lake is 23.3 m and the volume is nearly 97*10⁶ m³. The length of the shoreline is 16.1 km. Bathymetric map of Lake Stechlin are given in Fig. 1 (after Casper, 1985a; Padisák et al., 2010) and Table 1 shows the physical and chemical characteristic of the lake.

Lake Stechlin is an oligo-mesotrophic, most of the years dimictic and in some years warm monomictic lake. Thermal stratification develops between April and June and the most stable stratification occurs around late July. In winter, an inverted stratification may form under the ice (Padisák, 2003a).

Anthropogenic influences altered the lake in different ways. During the Middle-Ages the most apparent human impact was reduction of forests (household use, glass industry). The Polzow Canal was constructed during the 18th century in order to connect Lake Stechlin with the River Havel. It resulted in a drastic (approximately 110 cm) decline of groundwater table and the water level of the lake. The most intensively studied anthropogenic influence on Lake Stechlin was the construction of the Nuclear Power Plant Rheinsberg (NPP). The NPP operated from 1966 to 1989 and nearly 300,000 m³ cooling water per day were taken from the mesotrophic Lake Nehmitz, then pumped into Lake

Stechlin as heated cooling water. The canal connection between the two lakes allowed the water flow back to Lake Nehmitz. (Koschel and Adams, 2003). The effect of the cooling water circulation on the lake ecosystem has been complex and contradictory. It is caused an external nutrient loading, which provided an evident reason for eutrophication, however, the thermal pollution changed the stability and position of the thermocline, further decreased the retention time of the water body, and these effects counteracted eutrophication (Koschel and Casper, 1986; Koschel et al., 2002). During the non-stratified period the water retention time decreased to 335 days because of the pumping and during the thermal stratification the retention time was around 124 days, because only the epilimnion was involved in the cooling water circulation (Koschel et al., 1985).

Interestingly, there is an endemic freshwater whitefish in Lake Stechlin (Schulz and Freyhof, 2003), it is called *Coregonus fontanae*, also known as Stechlin cisco.

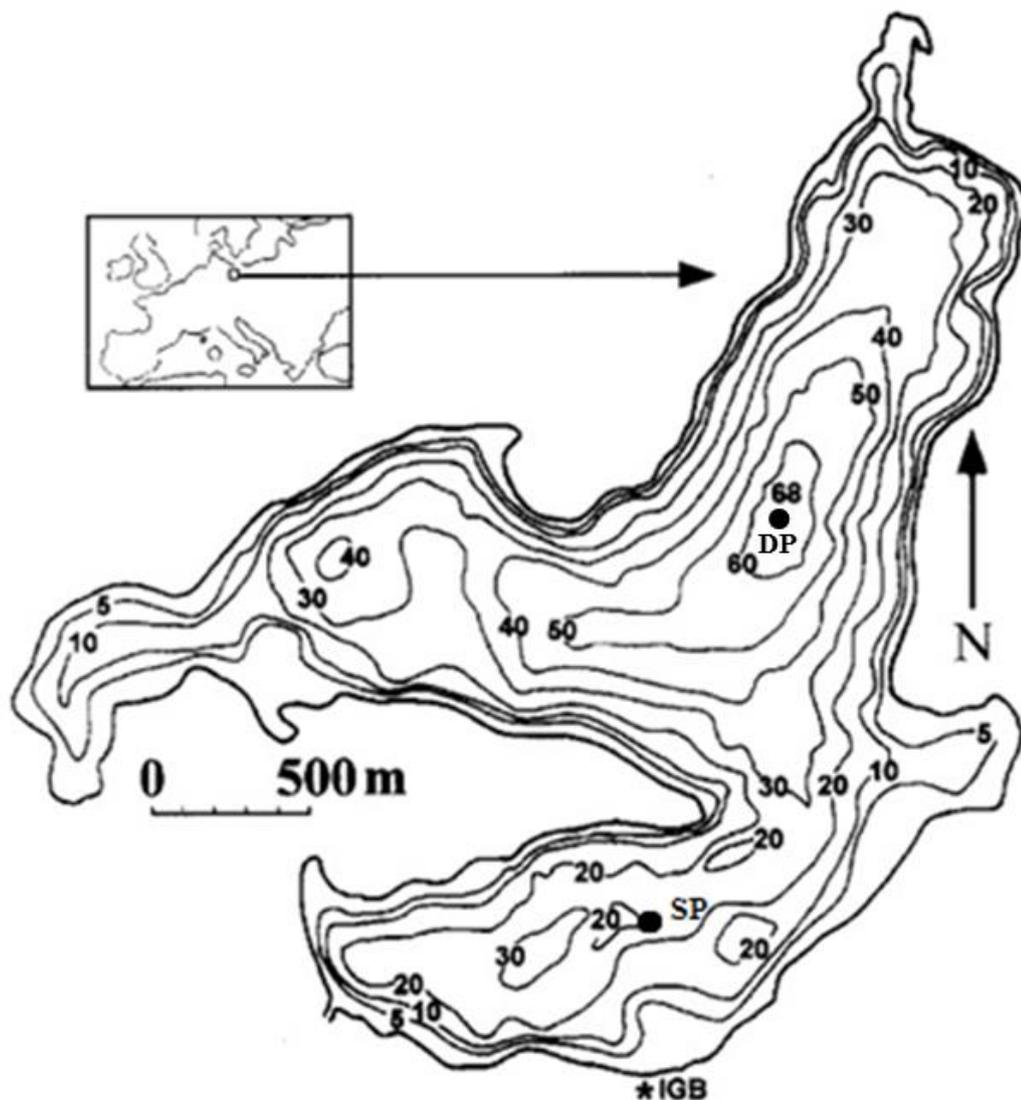


Fig. 1 Bathymetric map of Lake Stechlin with the place of mesocosms (SP) and the deepest point (DP) (after Casper, 1985a)

Table 1 Some physical and chemical variables in Lake Stechlin (average of 2014 in the euphotic zone)

Parameter	unit	value
Secchi transparency	m	6.8
Oxygen concentration	mgL ⁻¹	10.5
Oxygen saturation	%	93.5
pH		8.2
Chl-a	µgL ⁻¹	1.7
TP	mgL ⁻¹	0.016
SRP	mgL ⁻¹	0.004
TN	mgL ⁻¹	0.462
NO ₃ -N	mgL ⁻¹	0.032
NH ₄ -N	mgL ⁻¹	0.018

1.2. Phytoplankton succession in Lake Stechlin

Investigation of phytoplankton started in 1959, when the Limnological Laboratory was founded on the shore of Lake Stechlin. Since then, numerous investigations on different issues of phytoplankton were performed such as species composition, temporal and spatial distribution of dominant species, cell number or biomass calculation, however these studies were carried out with different sampling frequencies. The first quantitative phytoplankton results were published by Büsse (1972) and KÜchler (1981, 1982). Later, Casper (1985b) synthesised the periods of 1959-1962, 1963-1964, 1969-1972 and 1976-1978. Continuous phytoplankton dataset is available from the mid of '90s. One of the recent study (Padisák et al., 2010) about the phytoplankton of Lake Stechlin encompasses the results from 1994 to 2008.

From 1994 until end of the last millennium monomodal phytoplankton succession was characteristic with a spring maximum, then a bimodal pattern more characteristic. The spring assemblages between 1994 and 1997 were dominated by members of Codon **A**. Small centric diatoms such as *Cyclotella tripartita* and *C. pseudocomensis* are typical within this group (Padisák et al., 2010). After this period, species of codon **B** appeared in increasing amounts (Fig. 2). The dominant members were *Stephanodiscus neoastraea*, *S. alpinus* and *Aulacoseira islandica*. During the summer, an epilimnetic and a meta- and/or upper hypolimnetic phytoplankton assemblage can develop because of the proper stratification pattern and light regime of Lake Stechlin. Phytoplankton community of the summer epilimnion was very diverse and until 2005 it was dominated by the members of Codon **L**₀, such as *Ceratium hirundinella* or *Peridinium umbonatum*, further several species from the genera of *Chroococcus*, *Radiocystis* and *Coelosphaerium*. Additionally numerous chlorococcalean species, mainly from Codon **F**, appeared in the summer epilimnetic assemblages. In the twenty-first century, a rapid invasion by nostocalean cyanobacteria occurred in the lake (Fig. 3): a number of *Aphanizomenon* and

Dolichospermum species belonging to **H1** group appeared and from 2008 became dominant over the members of **L₀** group. *Rhodomonas lacustris* and *R. lens* are two frequently occurring species during the whole year and they belong to codon **X2**. *R. lens* reaches the highest biomass during autumn in most of the years, however in 2016 both species were quite dominant in the spring assemblages (Judit Padisák, personal communication). Codon **X3** is a stable part of the phytoplankton community and can be found at least one representative of the functional group in nearly every sample. *Gymnodinium helveticum* and *Katablepharis ovalis* are the most important species in this group.

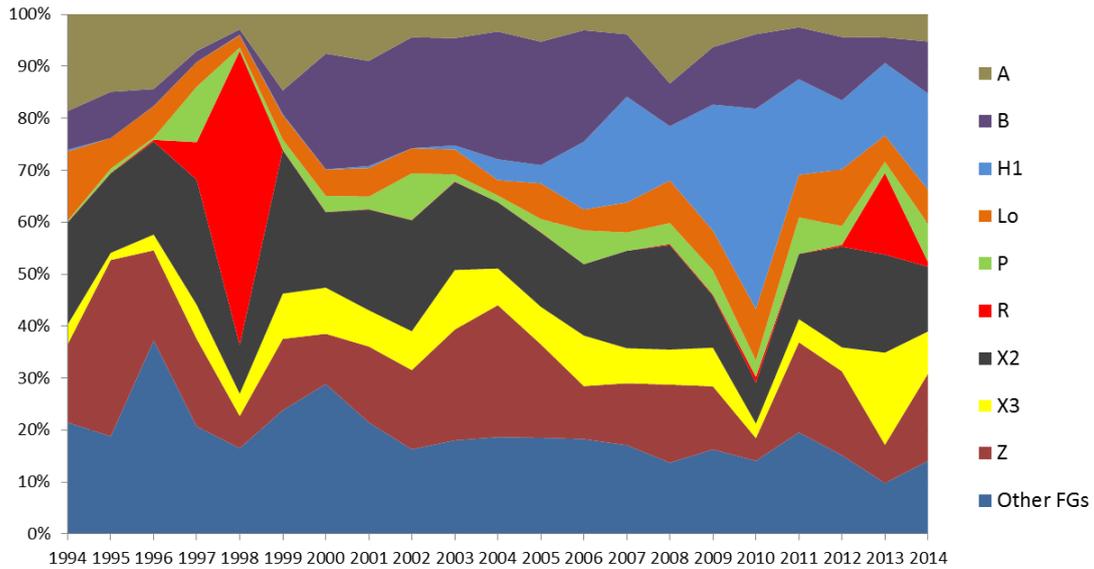


Fig. 2 The most frequently occurring functional groups in Lake Stechlin between 1994 and 2014

A deep-layer maximum by cyanobacteria occurs regularly in the meta- or in the upper hypolimnion, mainly by the picocyanobacterium, *Cyanobium* sp. as the main representative of Codon **Z** (Padisák et al., 1997) or occasionally by *Planktothrix rubescens* (Padisák et al., 2003b). Surprisingly, in 2013, *Aphanizomenon flos-aquae* was observed in the metalimnion (Tapolczai et al., 2013) with parallel presence of *Cyanobium* sp. and *Planktothrix rubescens* (Selmeczy et al., 2016).

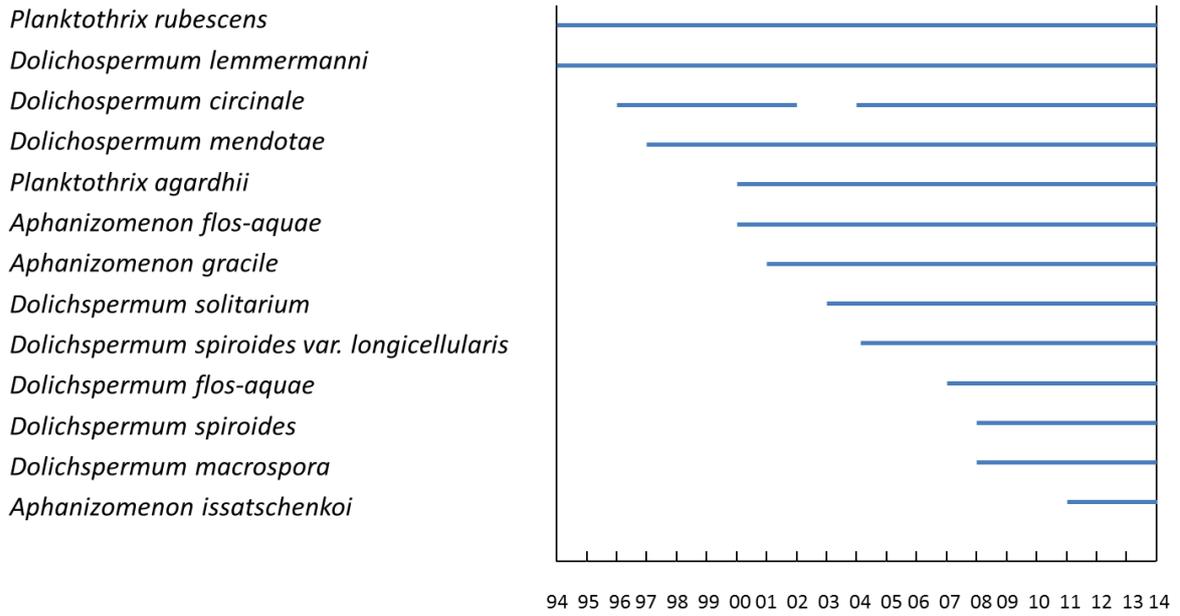


Fig. 3 Accumulating cyanobacteria records in Lake Stechlin between 1994 and 2014

2. Significance of the study

Importance of the phytoplankton in aquatic ecosystems is unquestionable because of several reasons. Phytoplankton generates nearly half of the primary production of the biosphere (Field et al., 1998). This community affects the abundance and diversity of other aquatic organisms, moreover drives aquatic ecosystem functioning. Phytoplankton is very important in the biogeochemical cycle as well, because of the crucial role in the carbon fixation (Falkowski, 1994; Sabine et al., 2004) and oxygen production. Further, phytoplankton forms the base of the food-web structure. Most of the phytoplankton species are autotrophic, thus they provide the energy-flux to the higher trophic levels.

Phytoplankton is a very diverse group of biota. There are several thousands of species in both the marine and freshwater environments (Reynolds, 1996). Since the biodiversity strongly contributes to ecosystem functioning (Juhász-Nagy, 1993; Hooper et al., 2005; Balvanera et al., 2006), the biodiversity of phytoplankton is necessary to the resilience and proper functioning of the previously mentioned complex and important functions.

In spite of the long history of phytoplankton studies, our knowledge has been fragmented on the ecology of numerous species or special communities. Extending this knowledge is very important to understand and evaluate better the results of monitoring assessments, which is strongly related to the conservation of the biodiversity of phytoplankton and to sustaining or restoring the good ecological conditions of aquatic ecosystems.

Climate change has significant effects on the aquatic ecosystems, thus phytoplankton community dynamics will very likely be altered mediated through direct and indirect effects (Winder and Sommer, 2012).

Lake Stechlin originally is a deep, oligotrophic lake, and the phytoplankton community shows sensitivity to the effects of global climate change (Padisák et al., 2010), thus this lake provides exceptional opportunities to study the previously mentioned issues.

3. Thesis objectives

Objective 1: Study the possible effects of global climate change, specifically the effect of an extreme weather event, on the phytoplankton community of Lake Stechlin in mesocosm experiments

The main consequences of the global climate change are the temperature increase in the lower atmosphere and the more frequently occurring extreme weather events (eg. IPCC, 2007). The possible effects of temperature increase are much more studied compared to the effects of extreme events, because of several reasons. One of the most important reasons is that studies of the impact of these events have started only recently (Jentsch et al., 2007). Further, it is rather hard to predict these meteorological events and taking samples short after, and nearly impossible taking samples before them. Thus experiments in mesocosm facilities may provide a deeper insight to understanding short-term impact of such events. Accordingly, the 1st thesis objective is to study (i) how the hydrological parameters (T, RWCS, SRP, DIN) of the lake will be affected by a simulated summer storm in large mesocosm facilities (ii) what will be the impact of these changes on the phytoplankton community, more precisely how will change the ratio of the species with different CSR life-strategies, and (iii) how will change the ratio of phytoplankton functional groups?

Objective 2: Study the possible effects of global climate change, specifically the altered summer stratification depth, on the phytoplankton community of Lake Stechlin in mesocosm experiments

As mentioned afore, according to IPCC (2007) the two main consequences of the global climate change are the temperature increase and the more frequently occurring extreme weather events. One, but probably the most important selective factor of phytoplankton species selection is the water column stability relative to other environmental factors such as light climate (Reynolds et al., 1983). According to forecasts, climate change is very likely have an impact on the stratification patterns, thus it may cause changes in the phytoplankton community composition as well. The depth of the thermocline was deepened by 2 m in a mesocosm experiment and the aim of the research was to study the effects of this hydrological change on the phytoplankton community.

Objective 3: Establishment algal, mainly cyanobacterial, cultures to detect cyanobacterial strains with genetic potential to produce microcystin or other cyanotoxins

Apart that Lake Stechlin is a distinguished site for ecological research, it is a well-known touristic place in northeastern Germany and during the summer a popular bathing-site. Hence, it is crucial to supplement our knowledge on cyanobacterial mass developments and potential toxin production in the lake. Thus, in this research I intended to answer the following questions: (i) is there any toxin producing gene related to cyanobacteria in environmental samples from Lake Stechlin and (ii) can we confirm the result of environmental samples with isolated strains?

Objective 4: Study the vertical distribution of the phytoplankton community of the lake during summer stratification

A continuous dataset of biomass and abundance of phytoplankton of Lake Stechlin is available from the beginning of 1990s (Padisák et al., 2010). Lake Stechlin is a deep, meso-oligotrophic lake, and metalimnetic or upper hypolimnetic phytoplankton populations were observed during most of the summers dominated mainly by the picocyanobacterium *Cyanobium* sp. or occasionally by the filamentous *Planktothrix rubescens* (Padisák et al., 2003a). Although the first reports of deep living populations of phytoplankton species appeared long time ago (ie. Juday, 1934), our knowledge about these populations is incomplete. Since the metalimnetic or upper hypolimnetic layers during stratification are relatively long-lasting and the limiting factors are few, summer stratification in lakes where extension of the euphotic region exceeds that of the mixed layer offer good opportunities to study the relation of environmental factors and the given population/s. Further because of the very limited number of species it could help to understand the competition between phytoplankton populations.

4. Materials and Methods

4.1. Phytoplankton analyses

Phytoplankton samples were taken and biomass was determined with the classical methodology by Utermöhl (1958) and Lund et al. (1958). Samples were collected from the deepest point of the lake and from the mesocosms according to the research question of the given project. The details of the sampling campaigns are shown in the specific materials and methods. Samples were preserved in Lugol's solution and were stored in a dark place and at room temperature. Altogether 400 settling units (cells, filaments and colonies) were counted at minimum in each sample using an inverted microscope (Zeiss Axiovert 100, Oberkochen, Germany) microscope. Volume of the cells was calculated by the most similar geometric form according to Hillebrand et al. (1999), then biovolume was converted to biomass using the $1 \text{ mm}^3\text{L}^{-1} = 1 \text{ mgL}^{-1}$ conversion factor. Opticount cell counting software (Opticount, 2008) was used to estimate the biomass.

Phytoplankton taxa were identified according to Fott (1968), Ettl et al. (1978), Ettl et al. (1985), Tikkanen (1986), Popovský and Pfiester (1990), Komárek and Anagnostidis (1998), Nagy-Tóth and Barna (1998), Komárek and Anagnostidis (2005), Komárek (2013).

4.2. Mesocosms

Within the TemBi (Climate changes impact on biodiversity of microbiota and matter- and energy-fluxes in lakes) project, an experimental setup consisting of 24 large-sized enclosures and a central reservoir was built in the south basin of Lake Stechlin (Bauchrowitz, 2012) (Fig. 4). This facility is called "LakeLab". Diameters of the enclosures are around 9 m and their plastic walls are anchored to the bottom of the lake. Since the bottom of the lake is not flat under the LakeLab, the depths of the enclosures varies between 17 and 20 m. Physical and chemical parameters (temperature, conductivity, pH, redox potential, oxygen concentration, oxygen saturation, and the photosynthetically available radiation—PAR), pigment concentrations of different algal groups (chlorophytes, cyanobacteria, diatoms, cryptophytes) and yellow substances are measured with a BBE (biological, biophysical, engineering) fluoroprobes and Yellow Springs Instruments (YSI) sensors. These instruments were installed in all enclosures and in the central reservoir too, additionally 4 instruments were placed in the lake around the LakeLab.

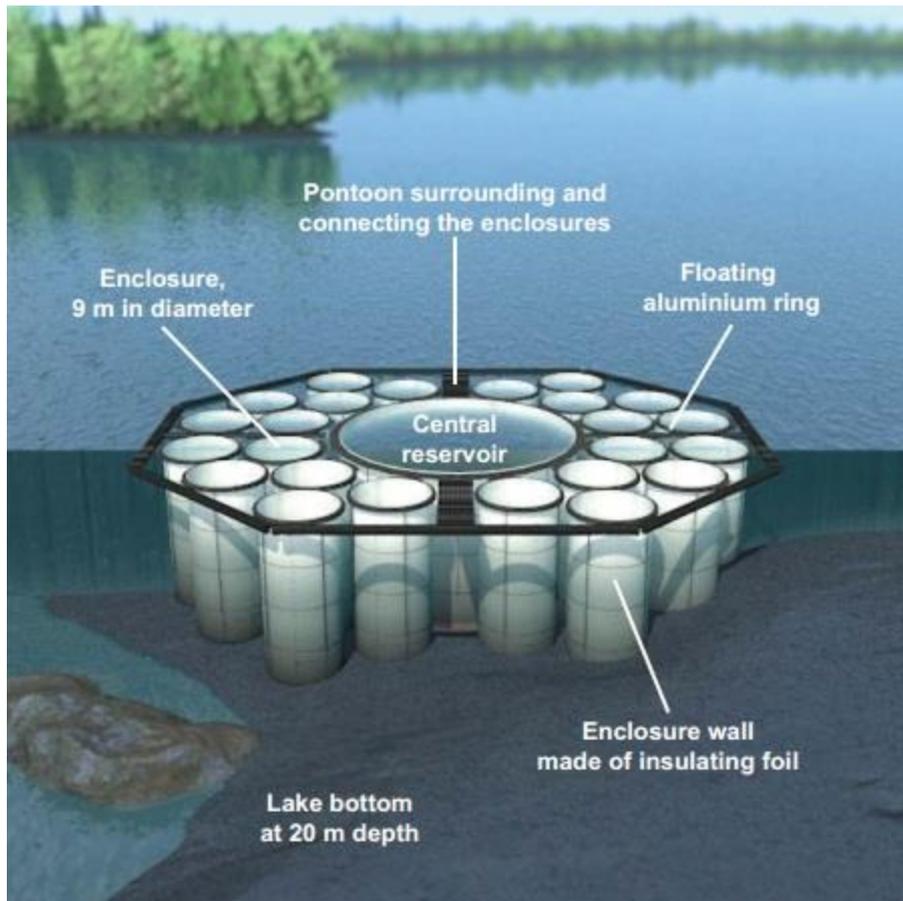


Fig. 4 Design of the LakeLab in Lake Stechlin (after Bauchrowitz, 2012)

4.3. Statistical analyses

For the statistical analyses, I used program R (R Core Team, 2013) with vegan package (Oksanen et al., 2015).

In Chapter 5.1: Community analyses were performed with non-metric multidimensional scaling (NMDS) method with Bray-Curtis dissimilarity index, and influence of factors on the community, such as depth or treatment, were analysed with a code in vegan package called envfit.

In Chapter 5.2: Analysis of variance using distance matrices, function ADONIS in R, was used to test how depth (epilimnion or hypolimnion), month of the sampling (June, July, August) and treatment (control, treatment) influence the community composition. Bray-Curtis dissimilarity was used for the distance matrix. Indicator species analysis according to Dufrene and Legendre (1997) was run to identify characteristic taxa of depths, months and treatments. INDVAL function was used by the *labdsv* package (Roberts, 2012) in R environment.

In Chapter 5.4: Community analyses were performed with NMDS method with Bray-Curtis dissimilarity index, and the relationships of environmental variables and the phytoplankton community were assessed with envfit. Seven environmental variables (SRP, TP, DIN, TN, ratio of DIN/SRP, Depth, and T) were screened and those were accepted,

which had P-values of at least 0.01 (p values based on 999 permutation). For the analyses, biomasses were used without any preliminary transformation.

5. Results

5.1. Effect of a simulated extreme weather event on the summer phytoplankton assemblage of Lake Stechlin¹



¹ This chapter is based on the following paper:

Selmeczy GB; Berger SA; Nejstgaard JC; Giling DP; Grossart HP; Kasprzak P; Casper P; Gessner MO; Padišák J (in prep): Simulating an extreme weather event in large mesocosms: changes phytoplankton community dynamics and an example of the memory effect

5.1.1. Specific introduction

Potential effects of global climate change on aquatic ecosystems belong to the most frequently studied topics. Basically, there are two main consequences of global climate change: temperature increase in the lower atmosphere and increasing probability of extreme weather events (IPCC, 2007). According to some model projections (eg. Beniston et al., 2007), extreme events such as heat waves, heavy rainfalls, wind storms are expected to occur more frequently in the future as a characteristic feature of global warming. However, most of the studies focus on the effect of temperature increase such as bias in spring bloom timing (Lassen et al., 2010) or mismatch between trophic levels and functional groups such as primary producers, copepods or meroplankton including fish larvae (Keller et al., 1999; Edward and Richardson, 2004). Temperature increase may affect phytoplankton directly through physiological processes while extreme weather events act mainly indirectly through terrigenous inputs or modifying mixing patterns with consequences on stratification pattern, nutrient availability or light conditions. Several mesocosm studies tested the effect of these factors on the phytoplankton community separately (e.g. Berger et al., 2007), and only a few experiments combined some of them (Graham and Vinebrooke, 2009; Nicolle et al., 2012).

Vertical mixing processes of a lake is defined mainly by climate and some morphological data (depth, fetch length, location, e.g.) of the lake (Borics et al., 2015). The composition of the phytoplankton assemblages of a given lake is significantly influenced by the mixing processes as they strongly influence the resource availability and entrainment strategies in the epilimnion. These processes can be altered by extreme weather events, thus these meteorological situations may strongly impact the hydrodynamics and the plankton assemblages (Anneville et al., 2010; Straile et al., 2010). It has been widely accepted that changes in trophic levels have a great impact on standing crop of phytoplankton: with increasing P loadings mostly cyanobacteria become predominant. Proliferation of cyanobacteria has been a worldwide issue in many aquatic environments (Sukenik et al., 2015), and the ability of cyanobacteria to form blooms (Reynolds, 2006) and produce toxins (Carmichael, 2001) raise scientific and social interest. The involved organisms belong to about 40 genera. In case of blooms of these species, the given environment can be negatively affected (Codd et al., 2005). However, proliferation of cyanobacteria is not an obligatory response to increasing P loadings: in many cases species belonging to other large phytoplankton groups may dominate (Medeiros et al., 2015). In contrast, composition of the phytoplankton assemblages of a given lake is largely determined by the physical environment selecting for functional traits adapted to the offered conditions (Zohary et al., 2010). There are several field observations showing that extreme weather events such as hurricanes (Havens et al., 2011; Beaver et al., 2013a), summer heat waves (Anneville et al., 2010; Gallina et al., 2011) droughts (Flanagan et al., 2009; García-Jurado et al., 2012) floods (Gong et al., 2011) alone or in combination (Beaver et al., 2013b) have strong impact on aquatic ecosystems. Observations in many cases are strongly related to monitoring systems with protocols prescribing frequent sampling. There is little information about the short-term effects, because study of the

impact of extreme weather events has started only recently (Jentsch et al., 2007). Additionally, it is rather hard to predict these meteorological events and taking samples short after. Thus, experiments in mesocosm facilities may provide a deeper insight to study short-term impact of such events.

During late summer, the typical phytoplankton community is diverse and the total phytoplankton biomass could reach a second, lower peak after the clear water phase (Sommer et al., 2012) in deep, oligo-mesotrophic lakes such as Lake Stechlin. This summer community is consisted of numerous K-selected, S-strategist species, which are primarily acquisitive such as *Ceratium hirundinella* or larger species of *Peridinium* (Reynolds, 1997). Our hypothesis is that, if the stratification is broken or eroded by an extreme summer storm, several consequences can occur: (i) nutrient addition to the epilimnion from the deeper waters, (ii) decrease the number of S-strategist species, and (iii) increase the number of invasive C-strategist species in the short-term.

5.1.2. Specific materials and methods

Eight enclosures were randomly selected for the experiments excluding 6 mesocosms, which contained submerged macrophytes on the sediment (Fig. 5). Prior to the experiment, water exchange was performed in all mesocosm to reach similar initial conditions. First, the hypolimnetic water was changed, than the epi- and metalimnion. The mixing effect of a summer storm was experimentally simulated in 4 of the 8 mesocosms; the other four mesocosms served as controls. The mixing was performed by Flygt pumps during 4 hours. The pumping capacity was $90 \text{ m}^3\text{h}^{-1}$. Epilimnetic and metalimnetic samples were taken two days before the experiment, immediately after the mixing, then 5, 13, 27, 41 days later to follow the short- and medium time-scale effects of the mixing.

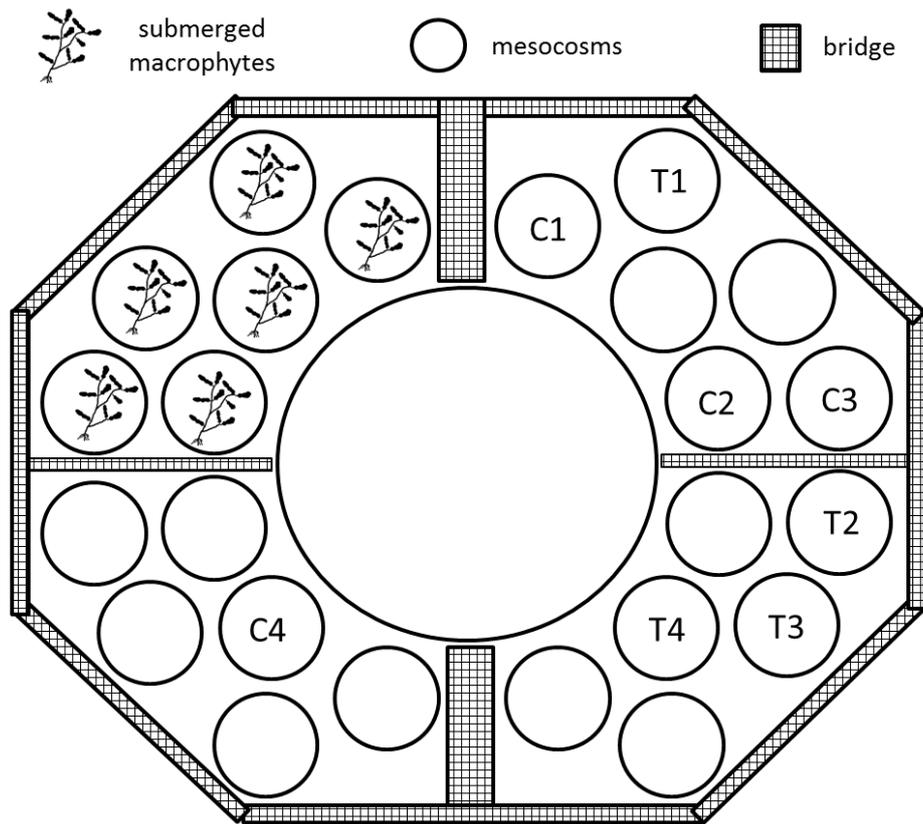


Fig. 5 Lake Lab platform during the experiment of extreme weather simulation, C1, C2, C3, C4 indicate control mesocosms and T1, T2, T3, T4 indicate treated mesocosms

Physical and chemical parameters (temperature, conductivity, pH, redox potential, oxygen concentration, oxygen saturation and the photosynthetically available radiation - PAR) were measured with YSI (Yellow Springs Instruments) sensor. These data were recorded in half a meter intervals from the surface (0.5 m) to the bottom. Concentrations of TP, SRP, TN, NO_2^- , NO_3^- , NH_4^+ and SRSi were measured according to (APHA, 1998). All inorganic N fractions (NO_2^- -N, NO_3^- -N and NH_4^+ -N) were added for estimating dissolved inorganic nitrogen (DIN), and nutrient ratio (DIN/SRP).

Relative water column stability (RWCS) (Welch, 1992) was calculated using the formula:

$$RWCS = \frac{D_b - D_s}{D_4 - D_5}$$

where D_b is the density of the bottom water, D_s is the density of surface water and D_4 - D_5 is the density difference between 4 and 5 °C water.

C-, S-, R- primary strategies of the 30 most frequently occurring species were determined according to the general morphological features of the species during the experiment. The classification based on a size and a shape descriptor of the species which were plotted on an X-Y graph. Shape descriptor was calculated as the maximal linear dimension and the surface-volume ratio along X axis, additionally size descriptor was

determined as the surface-volume ratio along Y axis. This method was adopted from Reynolds (1997).

5.1.3. Results

Two days prior to the experiment RWCS values of the mesocosms were rather similar: 312 ± 7 . The mixing nearly homogenised the top 14 m water column and the RWCS values strongly decreased in the treated enclosures (162 ± 8), however similar values (310 ± 3) were calculated in the control mesocosms than two days before. The temperature profiles of the control and treatment mesocosms during the beginning of the experiment are given on Figure 6.

Two days prior to the study, SRP values were strongly limiting both in the control and the treatment mesocosms (0.001 mgL^{-1}). The amounts of SRP were near to detection limit in the control enclosures almost during the whole experiment, except the last sampling event (day 41) when 0.025 mgL^{-1} was measured in the metalimnion, however the epilimnetic concentration remained at 0.001 mgL^{-1} . In the treatment mesocosms, SRP doubled both in the meta- and epilimnion (0.002 mgL^{-1}), immediately after the mixing; 5 days later SRP values dropped to 0.001 mgL^{-1} again. The amounts of DIN varied between 0.009 mgL^{-1} and 0.029 mgL^{-1} in the epilimnion and between 0.016 mgL^{-1} and 0.043 mgL^{-1} in the metalimnion before to the study, then continuously decreased in the epilimnion of the control mesocosms. The lowest value of DIN (0.001 mgL^{-1}) was measured 13 days after the mixing. The highest values were recorded immediately after the mixing in the epilimnion (0.074 mgL^{-1}) and in the metalimnion (0.053 mgL^{-1}) of the treatment enclosures. The DIN/SRP ratios varied between 1 and 44 during the experiment (Fig. 7).

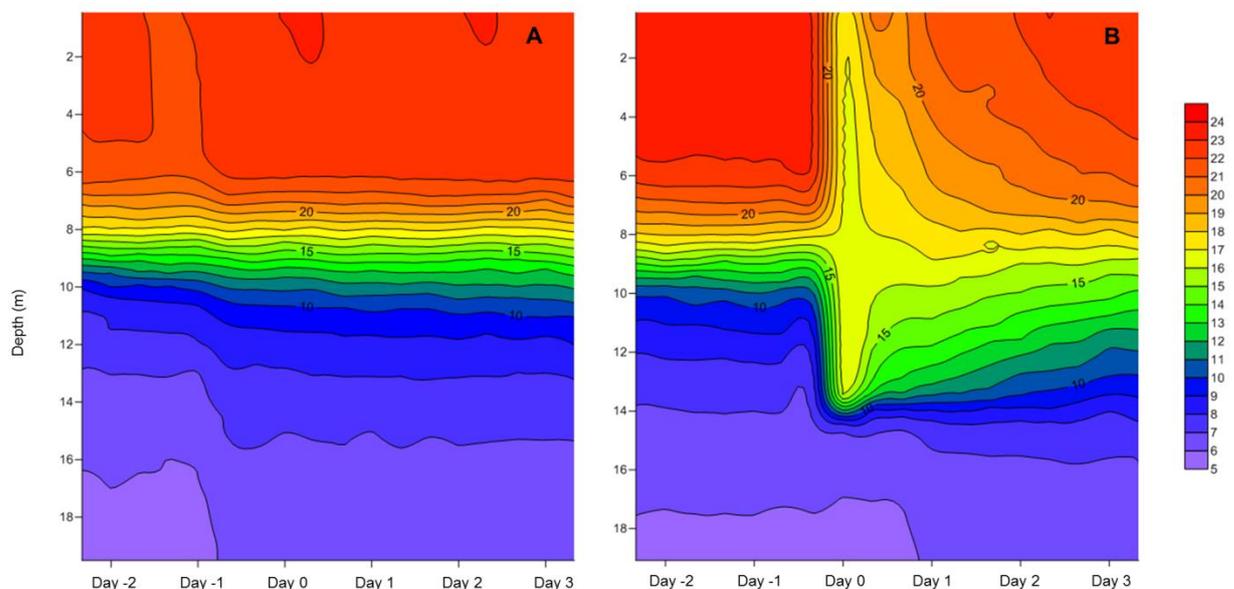


Fig. 6 Depth profiles of temperature in ($^{\circ}\text{C}$) A: a control enclosure (E1) and B: a mixed enclosure (E16)

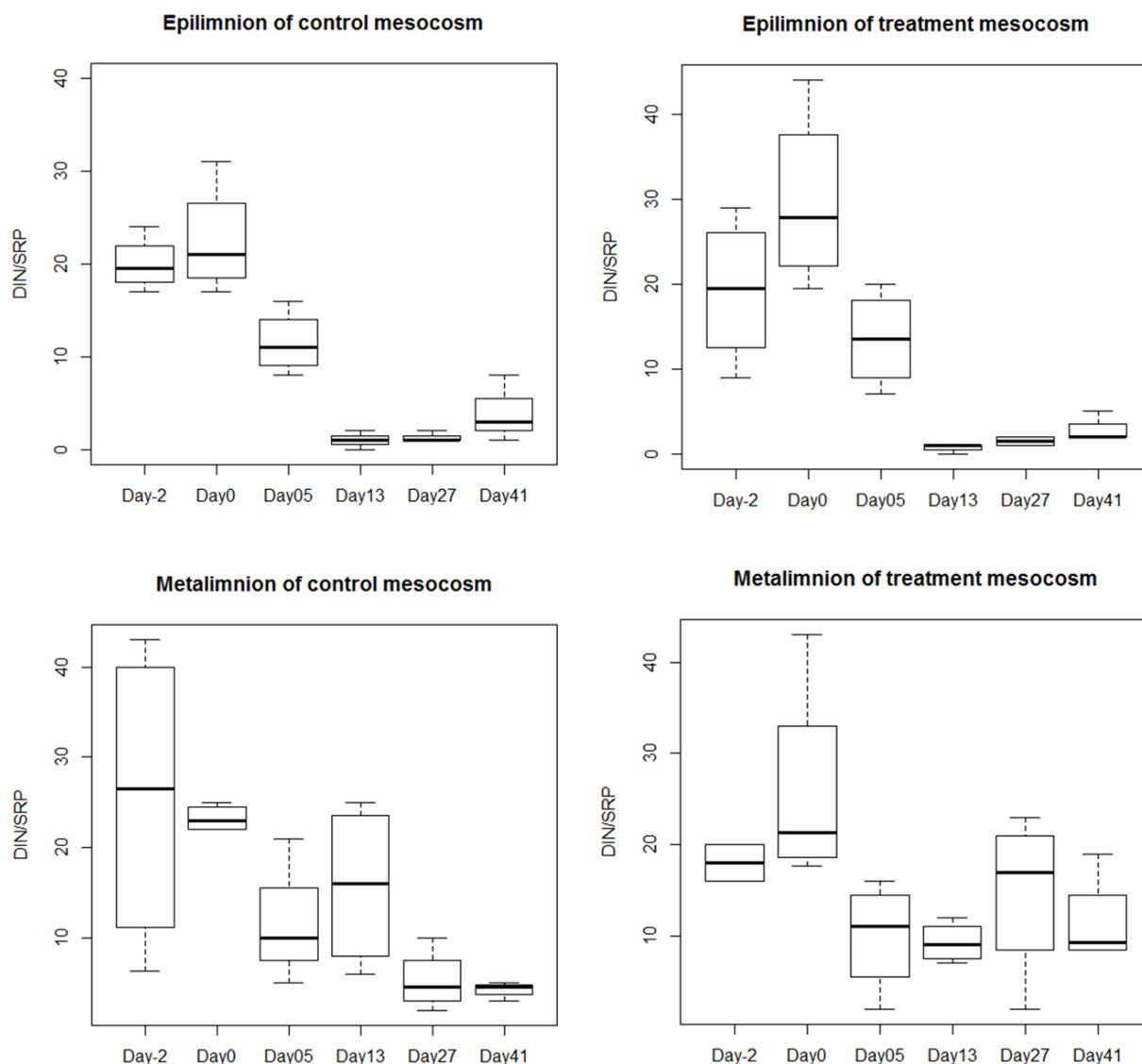


Fig. 7 DIN/SRP ratios in the mesocosms

Cyanophytes, Cryptophytes and Chlorophytes were the most prominent taxonomic groups during the experiment. Altogether 128 taxa were found belonging to 21 functional groups. **H1**, **Y** and **X2** were the most abundant coda. *Dolichospermum flos-aquae* (Brébisson ex Bornet & Flahault) Wacklin, *D. circinale* (Raberhorst ex Bornet & Flahault) Wacklin, *D. solitarium* (Klebahn) Wacklin and *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault were the most dominant members of codon **H1**, *Cryptomonas erosa* Ehrenberg and *C. ovata* Ehrenberg were present in significant amounts in **Y** codon and *Rhodomonas lacustris* Pascher & Ruttner, *R. lens* Pascher & Ruttner and *Chrysochromulina parva* Lackey were the main representatives of **X2**.

Two days prior to the experiment codon **X2** was dominant in the epilimnion of control mesocosms, however **Y** and **H1** were significant as well (Fig. 8A). Codon **H1** was the most abundant functional group in the epilimnion of treatment enclosures (Fig. 8C), but **X2**, **Y** and **F** group were remarkable too. In spite of the slightly distinct proportions of

functional groups, there were no statistically significant differences between the experimental and control mesocosms before the experiment; however, the communities of epilimnion and metalimnion significantly differed (Table 2).

Table 2 Summary of analyses of dissimilarities by categories. Significantly different categories are highlighted in bold

Day -2	R ²	P
Depth	0.3989	0.001
Treatment	0.1179	0.171
Day 0		
Depth	0.1157	0.188
Treatment	0.5293	0.001
Day 5		
Depth	0.1600	0.091
Treatment	0.2760	0.014
Day 13		
Depth	0.0299	0.610
Treatment	0.0917	0.235
Day 27		
Depth	0.0304	0.525
Treatment	0.2058	0.070
Day 41		
Depth	0.3401	0.006
Treatment	0.1266	0.155

Prior to the experiment, **H1** codon contributed nearly 50% of the total biomass in the metalimnion of each enclosure, thus it was the most dominant functional group (Fig. 8 B, D). Other groups were present in low abundance, which caused the significant difference from the epilimnetic community.

Within a few hours after the mixing event, the total biomass decreased by 12-42% in the epi- and metalimnion of the stirred enclosures. Further, the **H1** dominance significantly decreased in the metalimnion, thus the epi and metalimnetic assemblages became fairly similar and consequently the phytoplankton community composition of treatment mesocosms differed significantly from the control mesocosms (Table 2). Control and treated mesocosms are separated on the NMDS ordination (Fig. 9), moreover, the epi- and metalimnion samples are mixed in case of treated mesocosms, however in the control enclosures the epi and metalimnion samples still appeared as two distinct groups.

On the 5th day after the mixing, the biomass started to increase and **Y** and **X2** coda became the most frequently occurring members of the phytoplankton assemblages in the epilimnion and **Y** and **H1** coda were prominent in the metalimnion of the treatment enclosures (Fig. 9). In the epilimnion of control mesocosms *Dolichospermum* species increased their biomass share in the community (14 - 44%).

On the 13th day after the mixing event the total biomass reached its maximum level in the epilimnion ($718\mu\text{gL}^{-1}$ - $325\mu\text{gL}^{-1}$) paralleled with a sharp decrease in the metalimnion in the treatment mesocosms. During this sampling event, *Dolichospermum*

species dominated in the epilimnion, then continuously decreased in the treatment enclosures. In the epilimnion of control mesocosms **H1** codon decreased and coda **Y** and **X2** increased until the end of the experiment.

Surprisingly, two weeks later (day 27), the meta and epilimnion of enclosure T2 and T3 was dominated (between 20 and 41% of the total biomass) by *Asterionella formosa* Hassall, however, the biomass of this species was nearly negligible in the other two treated mesocosms (less, than 9% in Enclosure 5 and less, than 1% in Enclosure 13). During the last sampling event (day 41) the biomass reached minimum levels ($148\mu\text{gL}^{-1}$ - $291\mu\text{gL}^{-1}$) and it was quite evenly distributed among **H1**, **Y** and **X2** coda in the epilimnion and *A. formosa* became rather rare again in the samples.

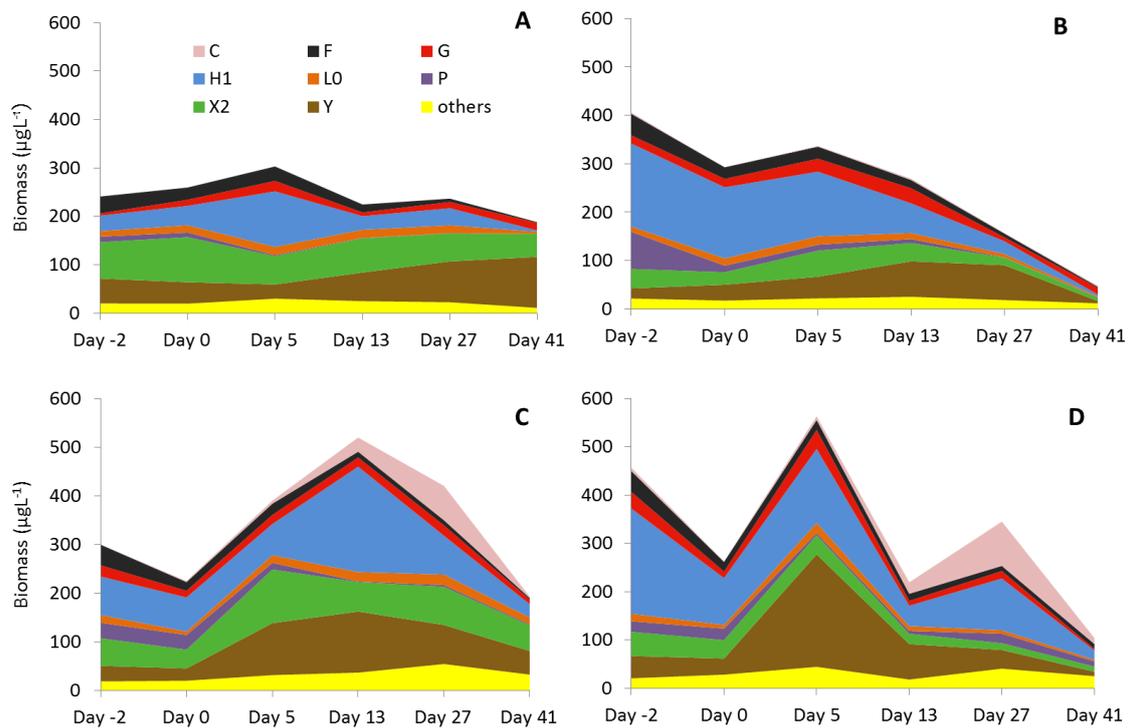


Fig. 8 Average biomass of the most dominant functional groups during the experiment (A: Epilimnion of control mesocosms, B: Metalimnion of control mesocosms, C: Epilimnion of treatment mesocosms, D: Metalimnion of treatment mesocosms)

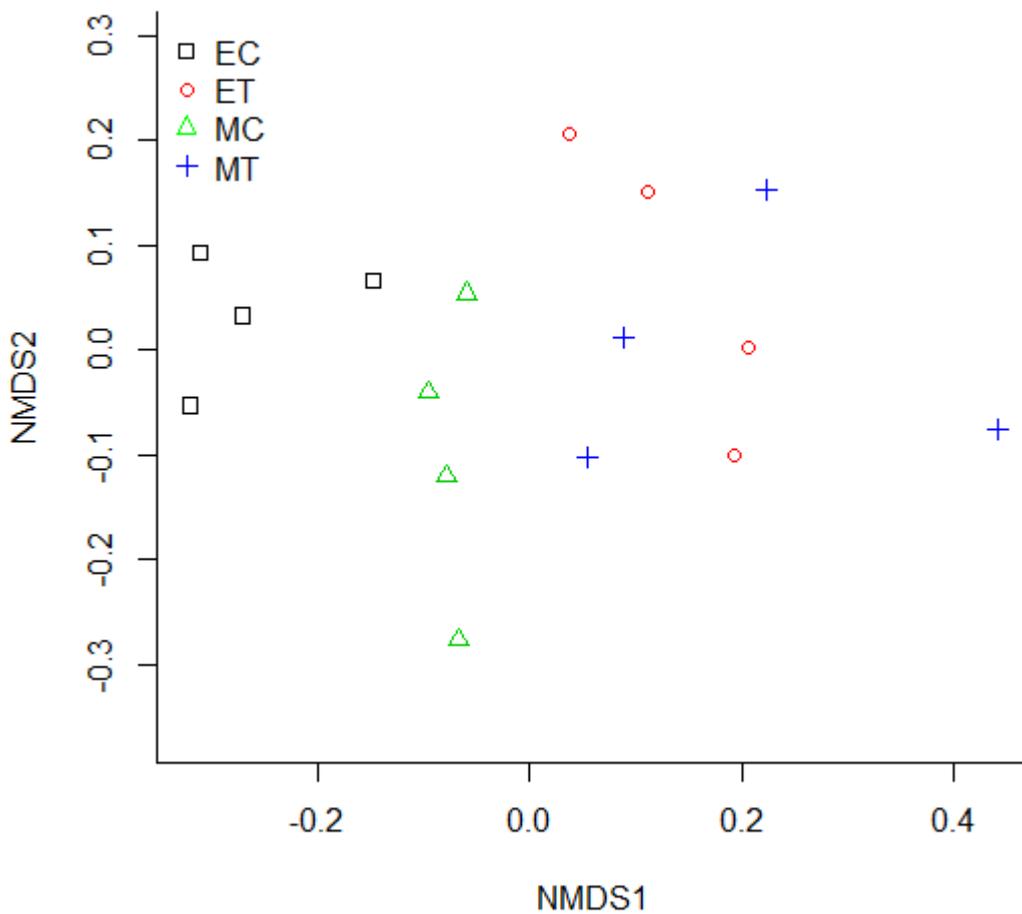


Fig. 9 Ordination of the phytoplankton community during the first sampling event (day 0). EC: Epilimnion of control mesocosms, ET: Epilimnion of treatment mesocosms, MC: metalimnion of control mesocosms, MT: metalimnion of treatment mesocosms

The 30 most frequently occurring phytoplankton species were divided to C-, S-, R-primary strategies according to the morphological features of the species. The C – S axis was divided into three categories: C, SC and S group (Fig. 10). Two days prior to the experiment C-, and S- species were dominant in the epilimnion both in the control and treatment mesocosms (Fig. 11 A, B). The clearly C-strategist species show a decreasing tendency in the control mesocosms and a fluctuating trend in the treatment ones. Immediately after the treatment the total phytoplankton biomass decreased significantly, but the ratio of the different groups did not show notable changes. After 5 days C-, SC-, and S-strategists increased and C-strategist reach their maximum biomass. During the next sampling event (day 13) S group became dominant and reached a maximum level, after that it continuously decreased. The presence of R-strategist species were the most significant differences between the phytoplankton community of control and treatment mesocosms. This group reached their maximum biomass during day 27.

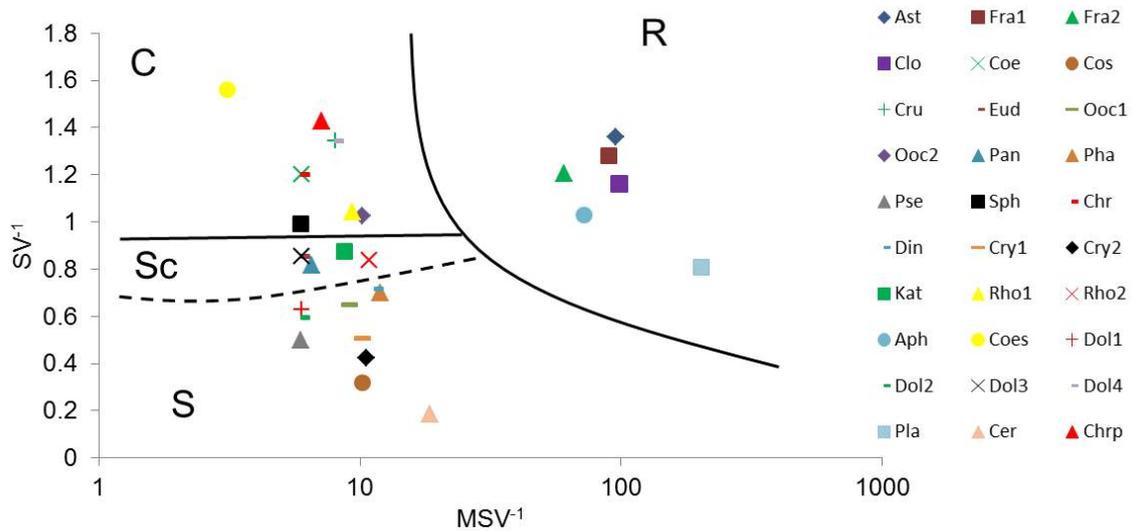


Fig. 10 Morphological ordination of the most frequently occurring species, with the C-, S-, R- strategic tendencies. M: maximal linear dimension, S: surface area and V: volume of the cells. Ast: *Asterionella formosa*, Fra1: *Fragilaria crotonensis*, Fra2: *Fragilaria* sp. Clo: *Closterium acutum* var. *variable*, Coe: *Coenocystis polycocca*, Cos: *Cosmarium phaseolus*, Cru: *Crucigenia rectangularis*, Eud: *Eudorina* sp. Ooc1: *Oocystis borgei*, Ooc2: *Oocystis lacustris*, Pan: *Pandorina morum*, Pha: *Phacotus lenticularis*, Pse: *Pseudosphaerocystis* sp. Sph: *Sphaerocystis* sp. Chr: *Chrysoflagellate* Din: *Dinobryon divergens*, Cry1: *Cryptomonas erosa/ovata* small, Cry2: *Cryptomonas erosa/ovata* big, Kat: *Katablepharis ovalis*, Rho1: *Rhodomonas lacustris*, Rho2: *Rhodomonas lens*, Aph: *Aphanizomenon flos-aquae*, Coes: *Coelosphaerium kuetzingianum*, Dol1: *Dolichospermum circinale*, Dol2: *Dolichospermum flos-aquae*, Dol3: *Dolichospermum solitaria*, Dol4: *Dolichospermum mendotae*, Pla: *Planktothrix rubescens*, Cer: *Ceratium hirundinella*, Chrp: *Chrysocromulina parva*

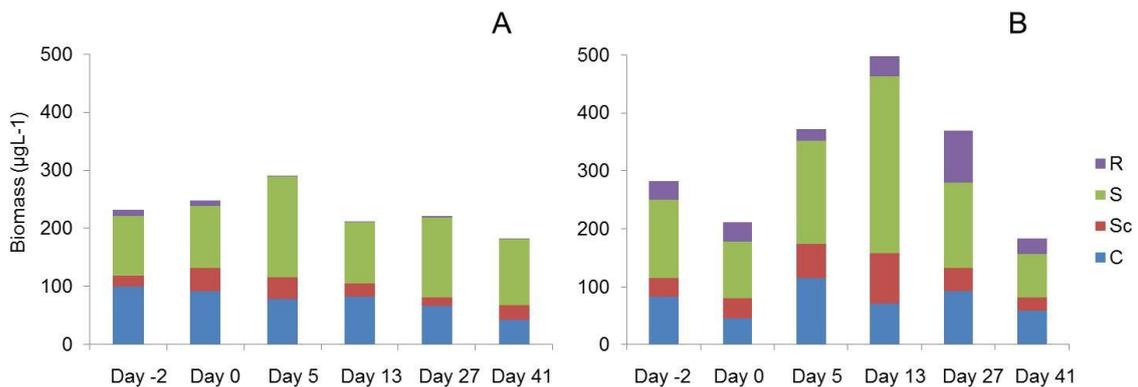


Fig. 11 Average biomass of C-, S-, R-, primary strategies of phytoplankton during the experiment (A: Epilimnion of control mesocosms, B: Epilimnion of treatment mesocosms)

5.1.4. Discussion

Changes of the phytoplankton community largely depend on the water column stability relative to other environmental factors such as light climate. Isothermal mixing processes, during autumn and early spring, have a major role on conditioning the starting condition of the annual succession. Additionally, during the stratified period micro-stratification (for example, by convective mixing) is very important to set the ratio between the motile or buoyant self-regulating organisms and non-motile phytoplankton species. Thus, the mixing processes belong to the most important environmental factors driving the characteristic periodic cycles of the phytoplankton community in temperate lakes (Reynolds et al., 1983).

Mixing processes are affected by climate change, even in case of huge lakes such as Lake Baikal (Moore et al., 2009). Stronger stratification is very likely occur in the future, because of the higher air temperatures (Winder and Sommer, 2012), which is advantageous for motile species such as cyanobacteria or flagellates, because these species are able to stay in the epilimnion and avoid to sediment. Moreover, the higher water temperatures favour bloom-forming cyanobacteria, because many species exhibit higher maximum growth rates at higher temperatures compared to diatoms and green algae (Jöhnk et al., 2008). Water bodies in some cases can offer opportunities to development of deep living communities (Camacho, 2006), which can be made up of wide range of phytoplankton taxa (Selmeczy et al., 2016).

Extreme strong summer storms however may alter or break the stratification, and even if they are ephemeral events can have serious and spectacular consequences on the phytoplankton community, which was observed on Lake Stechlin during the summer of 2011 (Müller et al., 2016): during this summer *Dolichospermum* bloom was observed in Lake Stechlin, which led to a strong decrease of Secchi-depth because of a calcite precipitation.

During our experiment we wanted to mimic an extreme weather event and analyse the effect of the modified stratification pattern on the phytoplankton community structure. The most important short term, within a few hours, consequence of the mixing was a sharp decrease of the biomass and the homogenization of the epilimnetic and metalimnetic community similarly to wind-induced stir-up in shallow lakes (Padisák et al., 1990). The most probably reason of the biomass drop is that the mixing reached the upper hypolimnion with lower biomass, which diluted the epi and the metalimnion.

Extreme summer storms can increase the available nutrients in the epilimnion as was observed in case of Lake Okeechobee (Beaver et al., 2013a), where the amount of SRP more than doubled during a post hurricane period. The increased level of nutrients may favour C-strategist species, which prefer the disturbed environments and appear after the onset of new hydrologic conditions (Reynolds, 1997). These species are characterised by relatively small cell size, fast replication and by rapid nutrient absorption. Typical representatives belong to **X** and **Z** associations such as *Ankyra*, *Chlamydomonas* or *Rhodomonas* (Reynolds, 1997). In our experiment C-strategist species were present both in the control and treatment mesocosms during the whole experiment, however they reached their maximum level 5 days after the mixing event, which support the expectation based on the conception of C-S-R life strategies. That time, *Rhodomonas lacustris* was the main

representative of the group. Although the different biomasses of R-strategist species, represented mainly by *Asterionella formosa*, *Fragilaria crotonensis* and *Aphanizomenon flos-aquae*, were the most visible difference between the control and treatment mesocosms

Several studies show that the mixing has a positive effect on diatom population (eg. Diehl et al., 2002), however in our case it was not observable during in the first days of this experiment. Rather, Coda **Y** and **X2** became more abundant in the epi- and metalimnion after 5 days of the mixing. Members of genus *Cryptomonas* comprise all the three primary strategies, thus can be found in a wide range of habitats. Cells are sufficiently motile and because of fast growth rate sometimes dominate in the spring assemblages in small lakes (Barone and Naselli-Flores, 2003) similar to R-like species. Moreover, cryptomonads contain numerous pigments such as carotene, xanthophylls, phycocyanin or even phycoerythrin, thus they can utilize low light levels. Gervais (1997 a,b) showed that *Cryptomonas phaseolus* and *C. undulata* had optimal growth under limiting light conditions ($5-7 \mu\text{mol m}^{-2}\text{s}^{-1}$) suggesting photoadaptation to low light environments. Thus, in some cases monospecific metalimnetic maxima are formed by *Cryptomonas* species (Gasol et al., 1992), which is a decisive feature of S-strategies. Additionally, these species can be prominent in post-stratification community or the population can peak following disturbances caused by precipitation periods or wind actions (Reynolds and Reynolds, 1985; Bicudo et al., 2009).

Two weeks after the mixing *Dolichospermum* species became the most abundant members of the phytoplankton community. Dominance of **H1** codon most probably is largely attributable to two phenomena. First, the water column re-stratified and these species are favoured in stable water bodies because, as buoyant species, they can regulate their position unlike non-motile species, which can experience increased loss rate in stable water bodies. Secondly, the DIN/SRP ratio became extremely low (1), which obviously favours nitrogen-fixing species like *Dolichospermum*.

On the day 27 *Asterionella formosa* appeared in some mesocosms in different amounts. As this species is as heavy diatom, its presence in the epilimnion strongly depends on the turbulence, which is the major condition against sedimentation loss. The sinking velocity of *A. formosa* colonies to be typically between $2 - 4.2 \mu\text{m s}^{-1}$ (Reynolds, 2006; Fraisse et al., 2015), comes to $0.17-0.36 \text{ m d}^{-1}$. Thus, without any further turbulence, the colonies after 27 days had to sink at least until 4.6m depth, however, because the metalimnion laid around on 7.5 m and most probably the epilimnion turbulences several times allowing the population of *A. formosa* to develop. Accordingly, *A. formosa* and/or other diatoms, which mostly appear at the beginning of autumn overturn (Sommer et al., 1986) can become dominant during shorter or longer period in the community of summer assemblages because of destabilization of the thermocline, which can be a result of an extreme weather event.

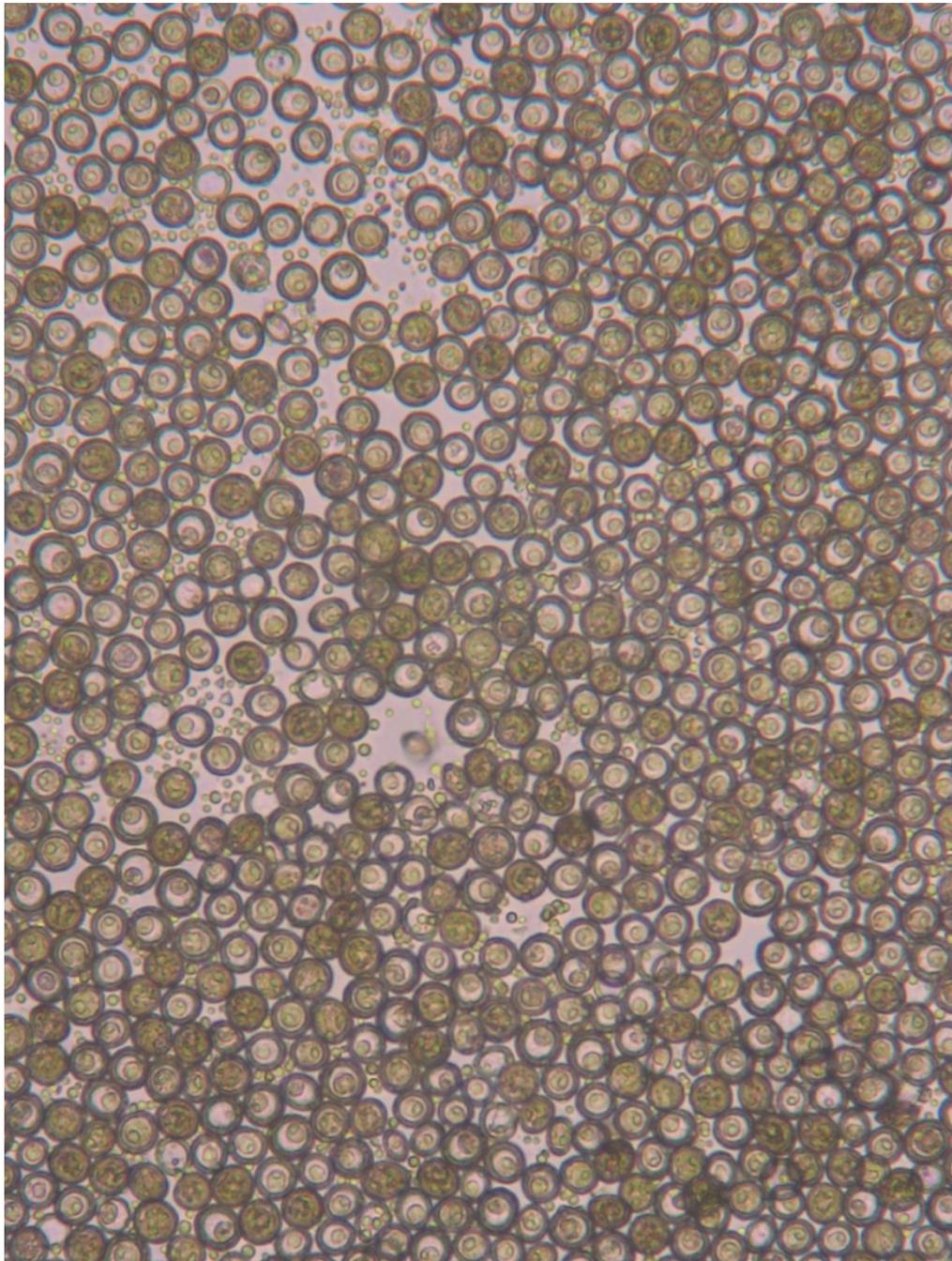
Appearance of *A. formosa* in the given mesocosms serves as an example of the ecological memory concept, which is considered as the capacity of past states or experiences to influence present or future responses of the community (Padisák, 1992). Biomass of *A. formosa* in the hypolimnion was very similar ($5-8 \mu\text{g L}^{-1}$) and it was quite comparable in the epilimnion as well ($0-7.5 \mu\text{g L}^{-1}$) in all treated mesocosms two days before the experiment. However, on day 27 remarkable differences were recorded: the

biomass of *A. formosa* in T1 and T4 remained low (1 and 30 μgL^{-1}), but increased significantly in T2 (106 μgL^{-1}) and T3 (143 μgL^{-1}). Additionally, we should notice, that integrated samples were taken during the previous year (in the same month) and T1 and T4 did not contain any *A. formosa*, but in T2 and T3 2 μgL^{-1} and 5 μgL^{-1} was recorded. According to these observations, small initial differences may magnify if some management or environmental event takes place, which may produce favourable environment for a species ready to emerge from a seed population.

On the last sampling event (day41) the lowest value of biomass was recorded and the differences among the phytoplankton assemblages in the epi- and in the metalimnetic samples were higher, than the differences among the treatment and control mesocosms, like two days before the experiment. This recover its former structure is explainable as the resilience of the system (Reynolds, 2002).

As a conclusion, our study highlights, that extreme weather events can strongly alter phytoplankton dynamics in the short term during summer stratification, however after several shifts the phytoplankton community may return to its common successional sequence, which driven by seasonality. Additionally, successional events during such periods are sensitive to the system memory in the sense that seed populations might get an opportunity to emerge.

5.2. Effect of the deepened summer stratification on the summer phytoplankton assemblage of Lake Stechlin²



² This chapter is based on the following manuscript:

Selmeczy GB; Krienitz L; Grossart HP; Casper P; Gessner MO; Padisák J (in prep.): Deepened summer stratification changes phytoplankton community dynamics: a mesocosm experiment

5.2.1. Specific introduction

The global climate change has a significant effect on the terrestrial and aquatic ecosystems as well and it will increase in the future according to numerous scenarios (IPCC, 2007). Because of the climate warming some polymictic lakes are expected to become dimictic, dimictic lakes may become warm monomictic and numerous monomictic lakes may turn into oligomictic (Gerten and Adrian, 2002). One of the most significant effect of climate change on phytoplankton communities in stratifying lakes will be presumably the effects related to the changes of stratification pattern, because several key variables, which are driving the phytoplankton community depend on the stratification processes (Winder and Sommer, 2012). The duration and intensity of thermal stratification strongly affect the nutrient input from the hypolimnion to the upper layers (Behrenfeld et al., 2006). Stratification results in complex physical and chemical gradients, which increase the heterogeneity of the water column, thus increases habitat heterogeneity (Selmeczy et al., 2016). Stratification suppresses the turbulence (Turner, 1979), thus favours the species, which are motile (Gervais, 1997a) or possess good buoyancy such as *Microcystis* sp. (Huisman et al., 2004) and negatively affect most of the planktonic diatoms with high sinking rates (Reynolds, 2006) and some green algal species as well (Huisman et al., 2004). Thus, it is expected that because of the climate change diatoms and other non-motile species will be replaced by other groups, which are able to tolerate the reduced mixing (Findlay et al., 2001). Though, in a few other cases diatoms may dominate over other taxonomic groups (Winder et al., 2009; Medeiros et al., 2015) in stratifying lakes, according to most of the scenarios increase of cyanobacteria will occur.

Cyanobacteria have several unique abilities to surpass other taxonomic groups in different environments affected by climate change. The most important eco-physiological traits, which help them to the adaptation in the changing environment are: (i) the ability to grow at warmer temperatures, (ii) the buoyancy regulation by gas vesicles, (iii) potential nitrogen-fixation with heterocytes, (iv) high affinity for, and ability to store phosphorus, (v) potential akinete production, (vi) very good light harvesting in a wide range of wavelengths with chromatic adaptation, (vii) good UV resistance (Ehling-Schulz and Scherer, 1999; Carey et al., 2012) and different antipredator properties. Obviously, not all cyanobacteria species possess these abilities because of the great diversity of this taxonomic group, however these features could help a given species to become the dominant member of the phytoplankton assemblages in different kinds of water bodies.

The main goal of the experiment described in this chapter was to mimic a deepened thermocline during the summer stratification in large size mesocosms and answer the following questions: (i) are there any changes in the phytoplankton community because of the altered stratification, if yes, (ii) can we confirm the proliferation of cyanobacteria, if not, (iii) what kind of species, taxonomic groups or functional groups will get advantages from the changed environment?

5.2.2. Specific materials and methods

Twelve enclosures were randomly selected for the experiments excluding 6 mesocosms that contained submerged macrophytes on the sediment (Fig. 12). Prior to the experiment, water exchange occurred in all mesocosms to ensure the possible highest similarity. First the hypolimnion water was exchanged, than the epi- and metalimnion. The thermocline was deepened by 2 m experimentally in 6 of 12 mesocosms; the other six mesocosms served as controls. The water exchanged and the alteration of the stratification was performed by underwater pumps (SUPS 4-12-5, SPECK Pumpen Verkaufsgesellschaft GmbH, Neunkirchen am Sand, Germany) transporting nearly $6 \text{ m}^3 \text{ h}^{-1}$ of water via aluminium release rings. During alteration of the stratification, the warmest period of the day, surface water was pumped down to a given depth. In the control mesocosms, aluminium rings were placed in the thermocline in order to affect equally all systems by pumping activities.

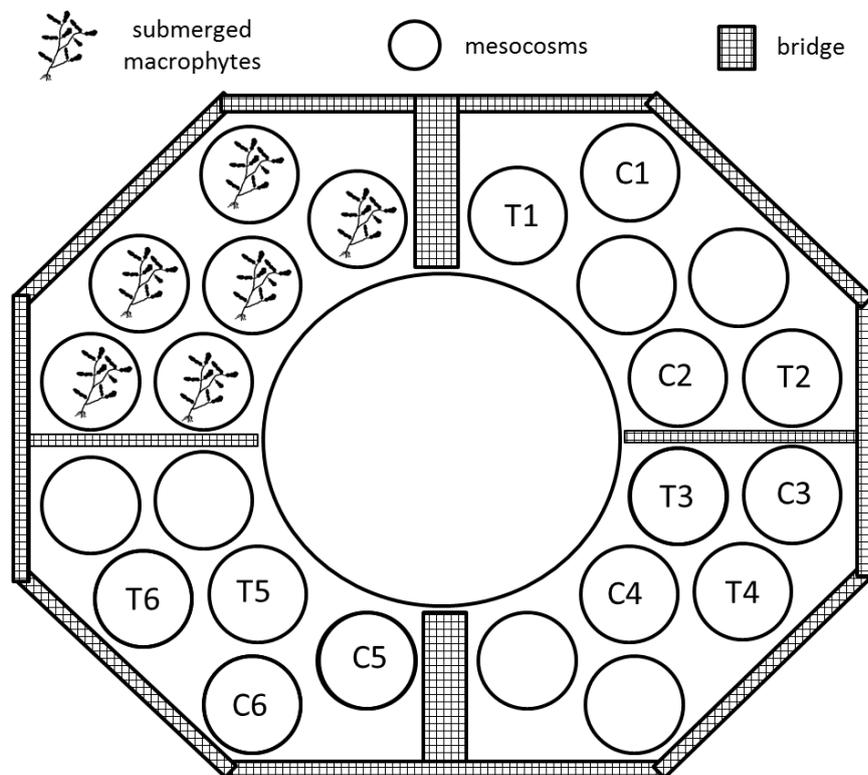


Fig. 12 Lake Lab platform during the experiment of deepened summer stratification, C1, C2, C3, C4, C5, C6 indicate control mesocosms and T1, T2, T3, T4, T5, T6 indicate treated mesocosms

Phytoplankton samples were taken on 25 June 2013, 23 July 2013 and 20 August 2013 from the epi- and hypolimnion as well. Physical and chemical parameters (temperature, conductivity, pH, redox potential, oxygen concentration, oxygen saturation and the photosynthetically available radiation - PAR) were measured with YSI (Yellow Springs Instruments) sensor. These data were recorded in half a meter intervals from the surface (0.5 m) to the bottom. Concentrations of TP, SRP, TN, NO_2^- , NO_3^- , NH_4^+ and SRSi were

measured according to (APHA, 1998). All inorganic N fractions (NO_2^- -N, NO_3^- -N and NH_4^+ -N) were added for estimating dissolved inorganic nitrogen (DIN), and nutrient ratio (DIN/SRP).

5.2.3. Results

The alteration of stratification caused multiple changes in the stratification pattern: the border of the hypolimnion and metalimnion sank, and in the epilimnion a weak, secondary thermocline developed. The typical temperature profile of the treatment and control mesocosms are shown on Fig. 13. Similar patterns were observed in the control and treatment mesocosms related to SRP values: at the beginning, the amounts of SRP were near to the detection limit in the epilimnion and hypolimnion as well, later in the epilimnion remained low during the whole experiment, however it increased in the hypolimnion after mid-July. In spite of the similar pattern, the average values of SRP were higher in the hypolimnion of treatment mesocosms compared to the controls (Fig. 14). The DIN values were close to 0.05 mgL^{-1} at beginning of the experiment in the hypolimnion and epilimnion as well in both types of mesocosms (Fig. 15). After that it decreased in the epilimnion and increased in the hypolimnion both in the treatment and control mesocosms. The maximum level of DIN/SRP (92) was calculated in a hypolimnetic sample at the beginning of September and the lowest value (4) was calculated at the end of the experiment in several epilimnetic samples. In general, the DIN/SRP values showed a decreasing pattern in the epilimnion and an alternating pattern in the hypolimnion.

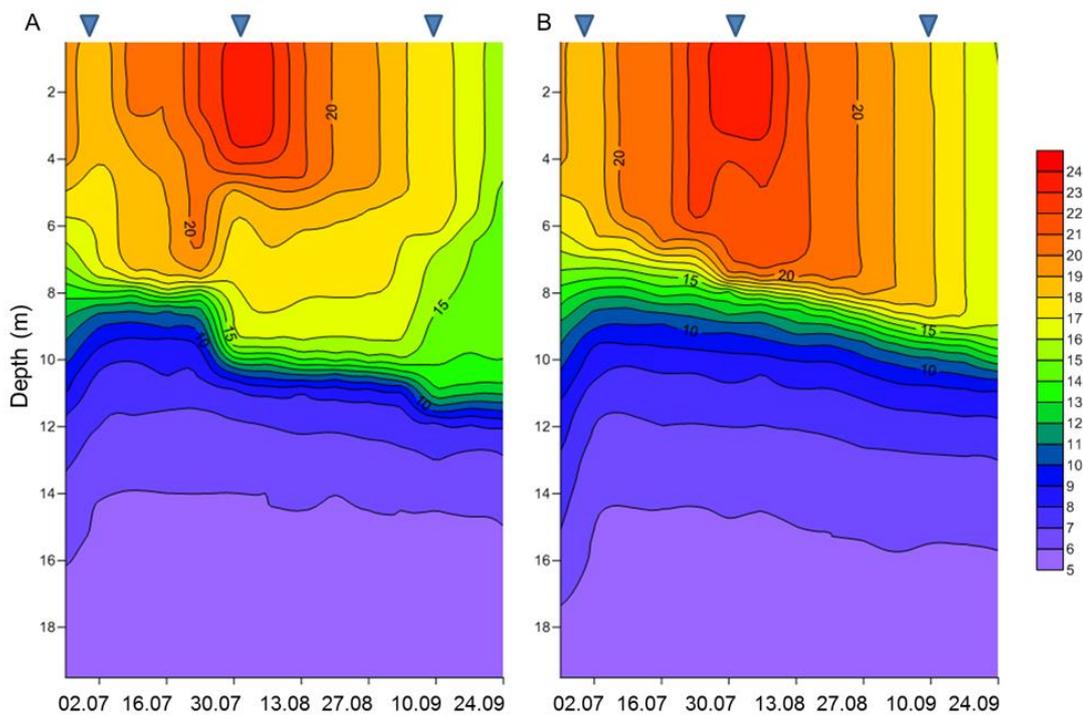


Fig. 13 Typical temperature profiles of treatment (A) and control (B) mesocosms. The blue triangles indicate the pumping activity

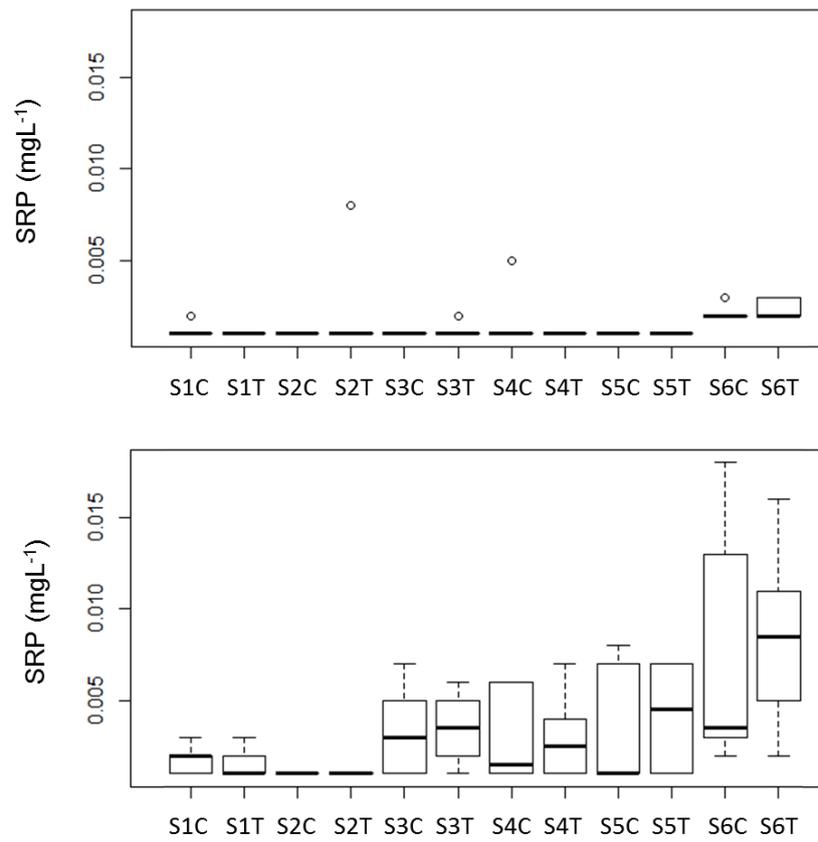


Fig. 14 Average SRP values during the experiment in the epilimnion (upper panel) and in the hypolimnion (lower panel), S1: 29.05, S2: 25.06, S3: 10.07, S4: 23.07, S5: 06.08, S6: 20.08; C indicates control, T indicates treatment mesocosms

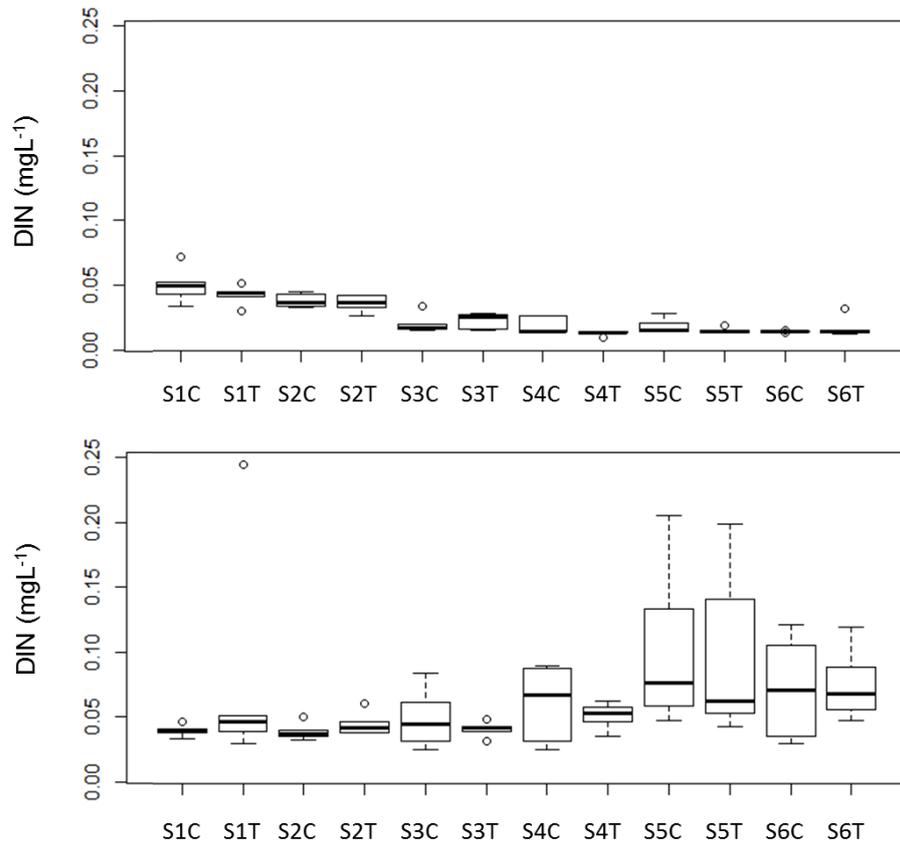


Fig. 15 Average DIN values during the experiment in the epilimnion (upper panel) and in the hypolimnion (lower panel), S1: 29.05, S2: 25.06, S3: 10.07, S4: 23.07, S5: 06.08, S6: 20.08; C indicates control, T indicates treatment mesocosms

Altogether 78 samples were analysed and 130 taxa were found in these samples, which can be categorised in 21 functional groups. **F**, **H1**, **X2**, **X3**, and **Y** were the most frequently occurring FGs, which showed up more than 90 % of the samples and **R**, **H1** and **Y** were the most dominant ones. The main representatives of the FG's are shown in Table 3 and the whole species list is provided in Table 9 (Appendix).

Table 3 Most important representatives of the main functional groups

Functional group	Dominant species
F	<i>Oocystis lacustris</i> <i>Sphaerocystis</i> sp.
H1	<i>Aphanizomenon flos-aquae</i> <i>Dolichospermum circinale</i> <i>Dolichospermum solitaria</i>
X2	<i>Rhodomonas lacustris</i> <i>Rhodomonas lens</i> <i>Chrysocromulina parva</i>
X3	<i>Katablepharis ovalis</i> <i>Gymnodinium helveticum</i>
Y	<i>Cryptomonas</i> sp.
R	<i>Planktothrix rubescens</i>

Cryptophytes were the most dominant phytoplankton group in the epilimnetic samples at the beginning of the experiment (Fig. 16 A, C). After that, this group strongly decreased in the control mesocosms until the end of the experiment. Chlorophytes showed maximum abundance during July in the epilimnetic samples of the treatment mesocosm, but reached maximum level during August in the control enclosures. Prominent difference was observed related to the biomass of cyanobacteria species in the epilimnion of the treatment and control mesocosms.

Maximum abundance of cryptophytes were registered during July in the hypolimnion of both type of mesocosms (Fig. 16 B, D). Biomass of dinoflagellates and chlorophytes were slightly increased in the hypolimnion. Furthermore, cyanobacteria was the most dominant taxonomic group reaching 59% contribution to total biomass in the treatment mesocosms and 75% in the control enclosures. Species belonging to the chrysophyceae group were observed in negligible amounts. Diatoms occurred rarely in our experiment, although higher amounts were registered in the hypolimnetic samples still not reaching 12% of the total biomass.

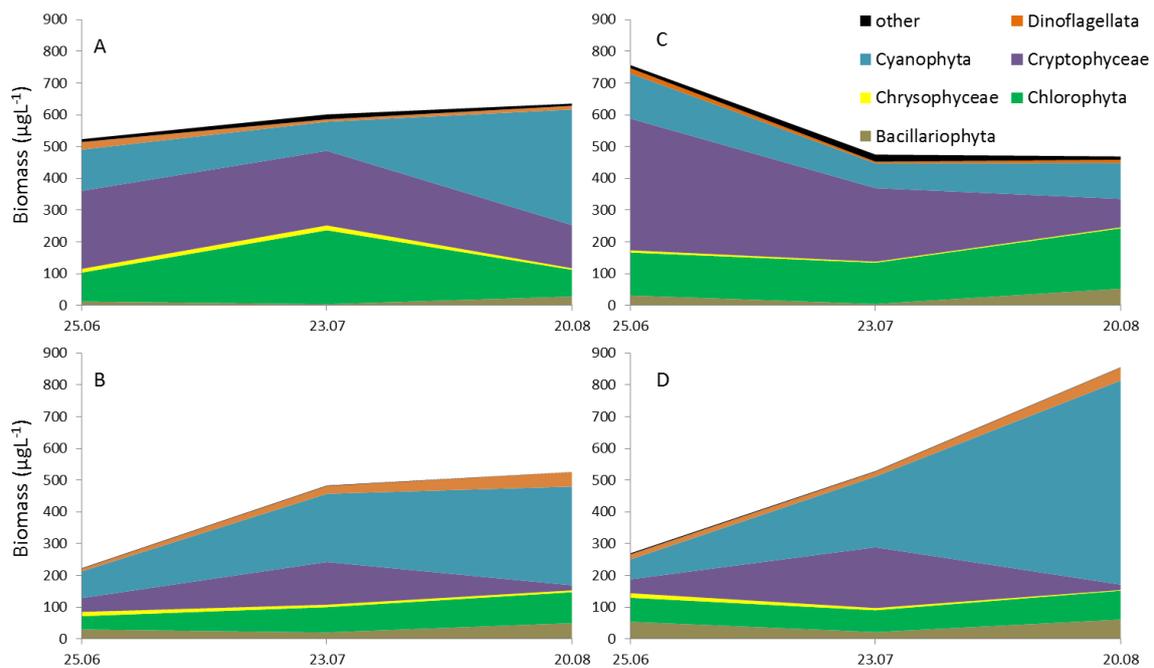


Fig. 16 Average biomass of the different taxonomical groups during the experiment (A: Epilimnion of treatment mesocosms, B: Hypolimnion of treatment mesocosms, C: Epilimnion of control mesocosms, D: Hypolimnion of control mesocosms)

The changes of the seven most dominant functional groups are shown on Figure 17. At the beginning, **H1**, **X2** and **Y** coda dominated in the epilimnetic samples. Notice, that the abundance of latter one was higher in the epilimnion of control mesocosms, than in the treatment enclosures (Fig. 17 A, C). At the end of the experiment, decrease of the total biomass was observed in the control mesocosms, but a slight increase was registered in the

treatment enclosures. This difference was caused by the high amount of *Planktothrix rubescens* (the only member of codon **R**), which started to increase after July in the treatment enclosures. This species dominated in the hypolimnetic samples. It started to increase already from the beginning of the experiment and became the most dominant in August. That time nearly 70% of the total biomass belonged to this species (functional group) in the control mesocosms and reached 51% in the treatment enclosures.

X_{ph} coda with only a species, *Phacotus lenticularis* (Ehrenberg) Deising was not belonging to the frequently occurring functional groups, but we should notice, because during July in a mesocosm (T6) became the dominant member of the phytoplankton community, but remain low in other mesocosms (not showing on graphs) and nearly disappeared from T6 during August. Thus this coda caused the highest uncertainty during the experiment.

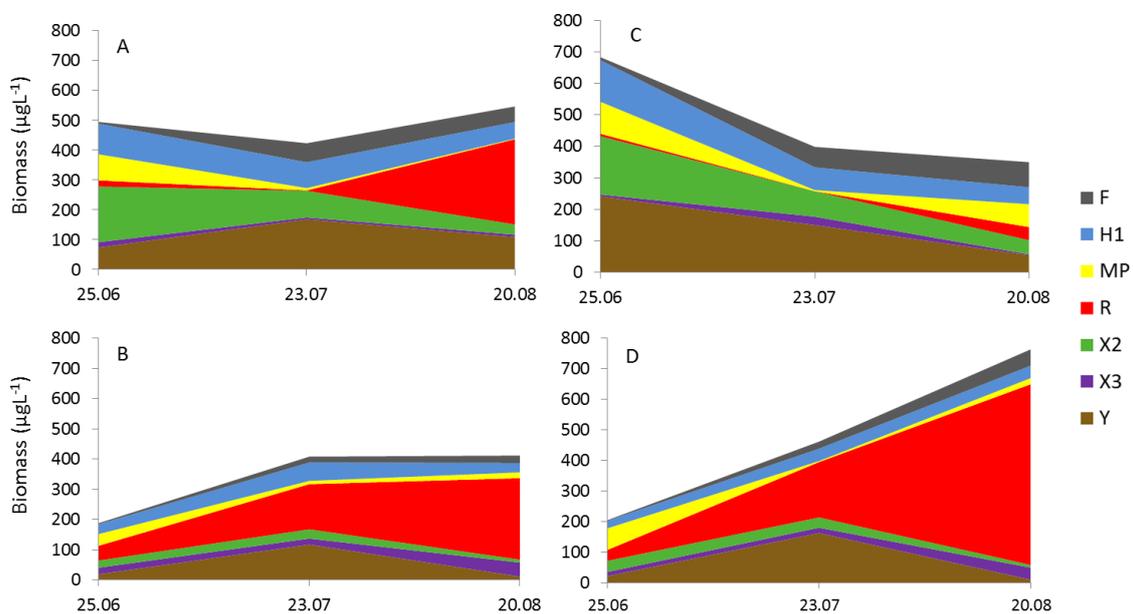


Fig. 17 Average biomass of the most dominant functional groups during the experiment (A: Epilimnion of treatment mesocosms, B: Hypolimnion of treatment mesocosms, C: Epilimnion of control mesocosms, D: Hypolimnion of control mesocosms)

ADONIS revealed that the depths (epi-, or hypolimnion), months and treatment individually, further the interaction of months and depths affect significantly the phytoplankton community composition of mesocosms (Table 4). According to INDVAL analyses **X2** (Indicator value [IV]=0.81, P=0.001), **L₀** (IV=0.81, P=0.001), **X1** (IV=0.71, P=0.004), **Y** (IV=0.70, P=0.004), **F** (IV=0.67, P=0.041) and **H1** (IV=0.63, P=0.039) functional groups are indicators of epilimnetic samples. Moreover, **R** (IV=0.76, P=0.001), **X3** (IV=0.70, P=0.002), and **C** (IV=0.69, P=0.001) groups are indicators of hypolimnetic samples (Fig. 18). Additionally, there are functional groups, which are indicators of different months (Table 5). Interestingly, INDVAL did not find any indicator codon of treatment or control mesocosms.

NMDS analyses (Fig. 19) were carried out to visualize differences between samples belong to different months, treatment and depths suggested by ADONIS analyses. Epilimnetic and hypolimnetic samples are separated according mainly to the vertical axis, other samples from different months differentiated based mainly on the horizontal axis.

Table 4 Summary of analyses of variance using distance matrices (ADONIS) testing the individual and joint effects of month, treatment and depth on community composition.

Factors	Df	SS	MS	F	R ²	P
Month	2	3.8095	1.9047	14.0068	0.2307	0.001
Treatment	1	0.2225	0.2225	1.6361	0.0135	0.001
Depth	1	2.7321	2.7321	20.0906	0.1654	0.001
Month: treatment	2	0.2306	0.1153	0.8478	0.0140	0.590
Month: depth	2	0.8788	0.4394	3.2312	0.0532	0.002
Treatment: depth	1	0.1351	0.1351	0.9931	0.0082	0.412
Month: treatment: depth	2	0.3467	0.1734	1.2748	0.0210	0.238
Residuals	60	8.1593	0.1360		0.4941	
Total	71	16.5146			1.0000	

Significant factors are highlighted in bold.

Table 5 Summary of indicators coda of given months

Codon	Month	Indicator value	P
MP	June	0.6244	0.001
X2	June	0.5654	0.001
C	June	0.3911	0.009
Y	July	0.5254	0.001
X_{ph}	July	0.5240	0.007
A	August	0.7661	0.001
R	August	0.7278	0.001
J	August	0.6252	0.009
P	August	0.5687	0.001
L₀	August	0.5237	0.020
F	August	0.5224	0.031

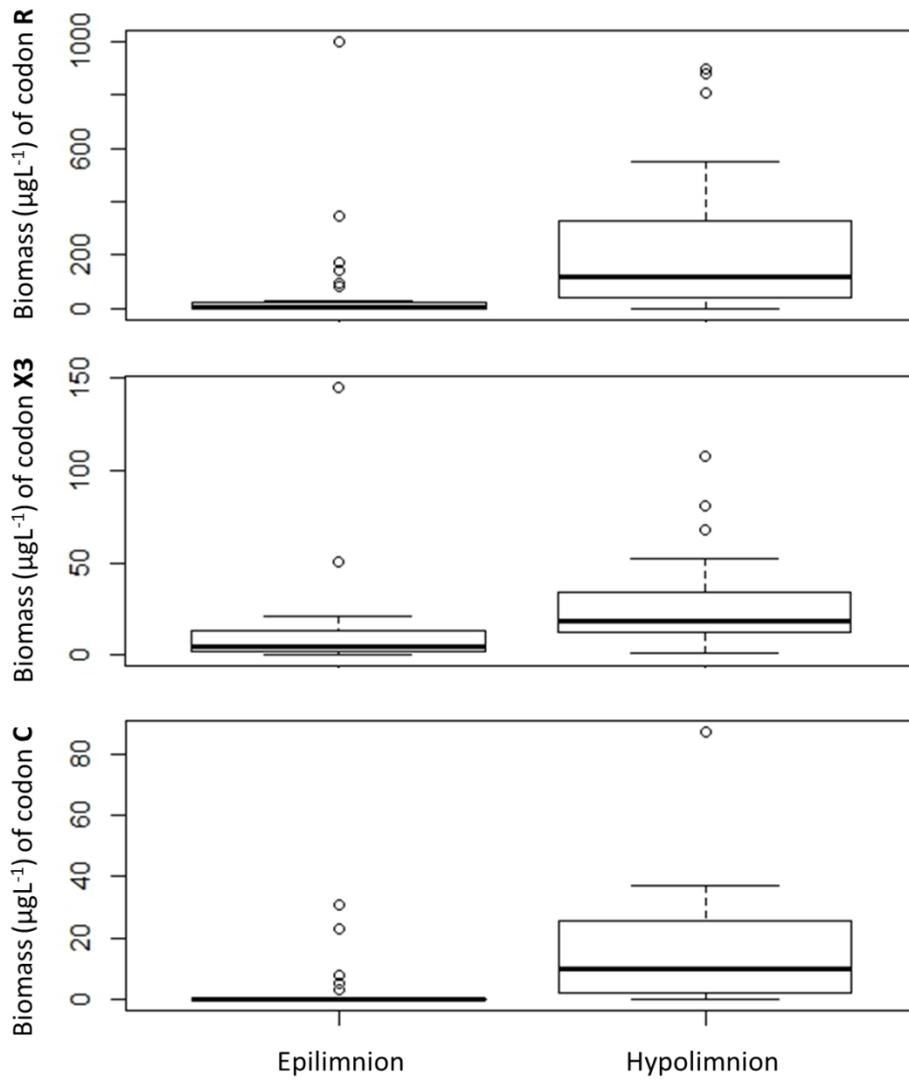


Fig. 18 Boxplot of biomass of coda **C**, **X3** and **R** in epilimnetic and hypolimnetic samples

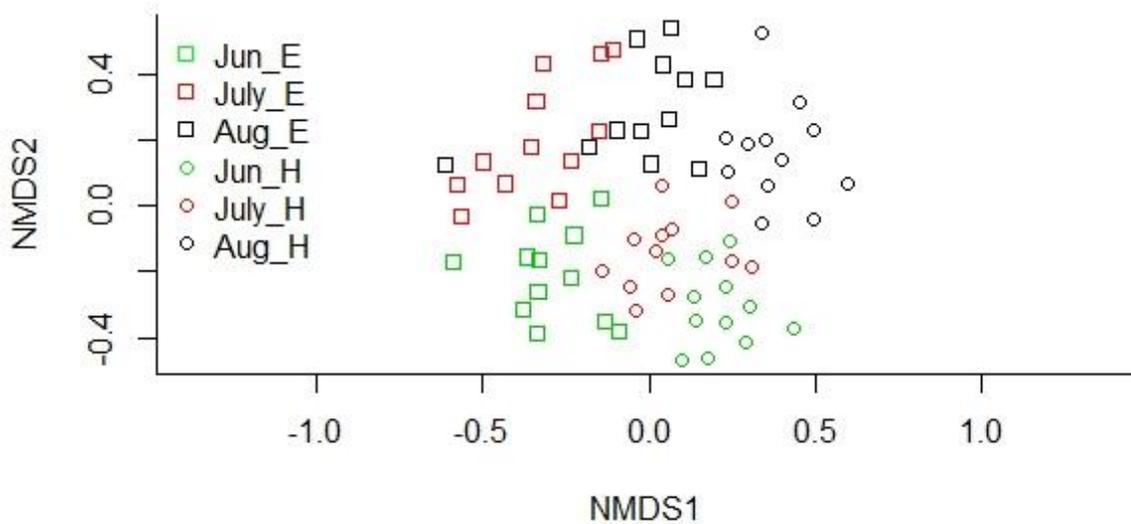


Fig. 19 NMDS ordination diagram based on the functional group composition of the samples. E= Epilimnetic samples, H=Hypolimnetic samples

5.2.4. Discussion

The heat-balance of lakes is determined substantially by meteorological forcing at the air-water interface, that is why it's possible to take some general predictions concerning changes of the thermal characteristics of lakes in relation to climate change. However, other features such as morphometry, residence time of water, optical properties and landscape setting can have a major effect on the thermal characteristic of lakes (Arvola et al., 2010). For this reason, lakes respond individually to the effect of climate change concerning changes of stratification pattern and very likely to numerous other hydrological changes as well. For example, both shallower and deeper thermoclines were predicted and observed in numerous studies. Modell predictions for four Finish lakes suggested deeper thermocline in three cases and a shallower thermocline in one case according to Elo et al. (1998). Another study on North-temperate lakes in Wisconsin (USA) based on 10 year's thermal records predicted changes in thermocline depth ranging from 3.5 m deeper to 4.0 m shallower compared to the average depth (DeStasio et al., 1996). Thermocline deepening was observed during long term studies (1970-1990) in boreal lakes in Canada by Schindler et al. (1996) and it was explained by three reasons: (i) increasing wind velocities, (ii) increasing effects of wind, because of decreasing number of trees in the area, however, the most important reason was (iii) the rising temperature in sub-thermocline water layers caused by increasing transparency of epilimnetic water. Fee et al. (1996) got similar outcome and the authors emphasised that the increasing transparency is an important factor especially in case of small lakes (<500 ha). The deeper Secchi-depth

was the consequence of decreasing DOC level in the water because of the less precipitation runoff caused by longer periods of droughts.

The general findings of numerous studies is that warmer air temperatures cause warmer surface temperature and this layer of warmer and lighter water weakens wind induced mixing, thus a shallower and warmer epilimnia predicted in the future (Robertson and Ragotzkie, 1990; King et al., 1997; Vincent, 2009). Coats et al. (2006) analysed the thermal structure of Lake Tahoe (USA) from 1970 to 2002 and observed a strong decrease of depth of the October thermocline, but reasons remained unrevealed. Straile et al. (2003) and Livingstone (2003) analysed long dataset from deep European lakes (Lake Constance and Lake Zurich) and they found increasing epilimnetic temperatures like in most of the studied lakes around the globe, although these two studies did not observe clear changes related to thermocline depth.

Thus it is possible to draw an important lesson from these examples, namely that we must be cautious with general statements related to lake responses to climate change, because even similar lakes can react at different ways to changing climatic conditions. Either the thermocline depth of Lake Stechlin will decrease or increase in the future, it is likely to result in changes in overall phytoplankton biomass and taxonomic composition, because mixing depth is a key factor determining light availability and sedimentation losses (Reynolds, 1984; Visser et al., 1996).

In our experiment, the thermocline of treated mesocosms was deeper by 2 meter compared to the control mesocosms and small, but strongly significant ($P < 0.001$) differences were observed between the phytoplankton community composition of the treated and control enclosures. The observed differences confirm the prominent importance of the position of mixing depth. The most obvious difference between the control and treatment mesocosms is the high abundance of *Planktothrix rubescens* in the epilimnion of treatment and in the hypolimnion of control enclosures. Further, the amounts of Chlorophytes were higher in the epilimnion of control mesocosms, as a consequence of the considerable abundance of **F** and **MP** coda.

Cantin et al. (2011) got similar, but more spectacular results, in an experiment of thermocline deepening, however at a whole-basin scale not in mesocosms. The authors could demonstrate an important shift in the structure of the phytoplankton community: chlorophytes increased in the epilimnion in response to thermocline deepening. In our experiment we did not observe this phenomenon, although green algae belong to codon **F**, such as *Oocystis lacustris*, frequently occurred in epilimnetic samples, though reached higher biomass in the control mesocosm.

Ptacnik et al. (2003) analysed the phytoplankton community changes in a gradient of mixing depths in a mesocosm experiment. High biomass of diatoms was observed in this experiment even at low mixing depth and it was explained by the fast growth rates of diatoms under sufficient supply of available silica. Our experiment cannot support this result, because the diatoms never exceeded the 12% contribution to the total biomass, though in more than 80% of the samples the SRSi concentration was higher than 0.1 mgL^{-1} , however none of them were higher than 0.5 mgL^{-1} . According to Reynolds (2006) silica concentration below 0.5 mgL^{-1} begin to interfere the growth of diatoms, but the growth-limiting concentration is below 0.1 mgL^{-1} in most lacustrine environment. Sommer (1988)

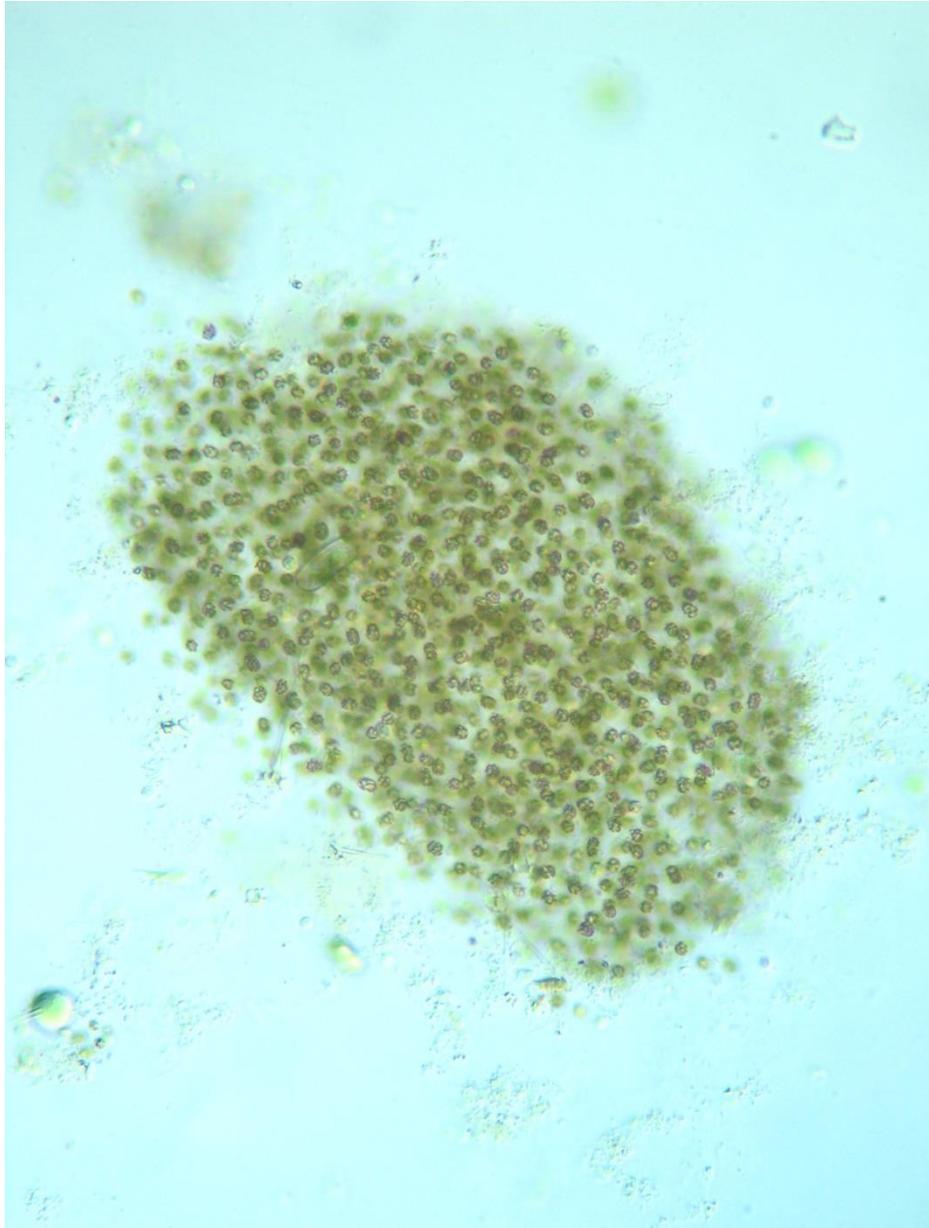
reviewed a number of experiment and field observations and conclude, that the limitation strongly depends on the given species, which between 0.9 μM Si ($\sim 0.023 \text{ mgL}^{-1}$) and 20 μM Si ($\sim 0.5 \text{ mgL}^{-1}$). Others indicate 0.5 mgL^{-1} as limitation threshold for *Asterionella formosa*, (Lund, 1950; Vaccari et al., 2006), which was the most dominant diatom species during our experiment.

Planktothrix rubescens is an important member of the phytoplankton community of Lake Stechlin for a long time (Krieger, 1927). Although the abundance of this species is generally low, if the circumstances are appropriate can be the dominant taxon in the lake, such as in 1997-1998 (Padisák et al., 2003a) or 2012-2013 (this year) (Selmeczy et al., 2016). During these periods, this species can be classified as an “ecosystem engineer”, because it can strongly modify the annual phytoplankton succession of the lake (Padisák et al., 2010). *Planktothrix rubescens* is typical a DCM forming cyanobacterium in the metalimnion or in the upper hypolimnion in deep lakes (Micheletti et al., 1998; Camacho, 2006), thus the depth of the thermocline is very likely crucial for this species. The euphotic depth of Lake Stechlin extends to the upper 20-25 meter and the thermocline develops around 8 meter below the surface during the stratified period, thus there is more or less 10-15 meter water depth available to form DCM. If the thermocline will be lower because of the climate change by two or even more meters, still there is “enough space” for DCM forming phytoplankton species. Thus we can conclude that the thermocline deepening is not likely to affect the development of DCM by *Planktothrix rubescens*. However, other species such as *Aphanizomenon flos-aquae*, or more frequently *Cyanobium* sp. can form DCM in Lake Stechlin as well. According to our experience these species are forming DCM in the middle of the thermocline (Padisák, 2003a; Selmeczy et al., 2016) mainly spatially separated from that of *Planktothrix rubescens*. However, if the thermocline depth will decrease, the amount of available light will decrease as well, which basically influences the community of DCM forming species. Consequently, *P. rubescens* may outcompete the above mentioned species, if the thermocline depth decrease until a certain point, because *P. rubescens*, can utilize low light levels much more effectively, than either *Aphanizomenon flos-aquae* or *Cyanobium* sp.

IndVal analyses did not find functional groups which indicate the phytoplankton assemblage of treatment or control mesocosms, however statistically significant differences were registered between them. Thus, the differences between the two communities related to numerous smaller or bigger differences of the proportion of functional groups, instead of one or few groups which are present in just one type of mesocosm.

As a conclusion, we documented small, but significant changes in the epilimnetic phytoplankton community: higher level of biomass of *Planktothrix rubescens* (codon **R**) and Cryptophytes, further lower amount of codon **F** and **MP** were registered after the treatment. Additionally, *P. rubescens* was the dominant member of the phytoplankton community in the treatment mesocosms, however it is not a clear confirmation about the proliferation of cyanobacteria related to deepened thermocline, because this year (2013) *P. rubescens* were present with high biomass during the whole vegetation period, similarly to 1998 (Padisák et al., 2010).

5.3. Toxin production in Lake Stechlin³



³ This chapter is based on the following paper:
Daadhech PK; Selmechzy GB; Vasas G; Padišák J; Arp W; Tapolczai K; Casper P; Krienitz L (2014)
Presence of potentially toxin producing cyanobacteria in an oligo-mesotrophic lake in Baltic Lake District,
Germany: An ecological, genetic and toxicological survey. TOXINS 6: 2912-2931.

5.3.1. Specific introduction

Toxin production by cyanobacteria is a common and worldwide prevalent phenomenon in many aquatic environments. The responsible organisms belong to about 40 genera, but the main ones according to Carmichael (2001) are *Dolichospermum* (former *Anabaena*), *Aphanizomenon*, *Cylindrospermopsis*, *Lyngbya*, *Microcystis*, *Nostoc* and *Planktothrix*. Blooms of these cyanobacteria can negatively affect the given environment and can seriously endanger human and animal health (eg. Codd et al., 1999; Codd et al., 2005; Funari and Testai, 2008). Additionally, toxic blooms may restrict the water's multipurpose use such as fishing, recreation or as drinking water supply. Cyanotoxins, which are secondary metabolites of cyanophytes can be classified into categories that reflect their biological effect, such as hepatotoxins, neurotoxins cytotoxins, irritants, gastrointestinal toxins and other cyanotoxins (Codd et al., 2005). Among all cyanotoxins, microcystins, cylindrospermopsins and nodularins are the most common hepatotoxins that are produced by a wide range of cyanobacteria (Carmichael, 2001).

In a recent study in the north-eastern lakes of Germany, Ballot et al. (2010a) confirmed the occurrence of cyanotoxins (saxitoxin, anatoxin-a and cylindrospermopsin) and genotypes of putative saxitoxin-producing *Aphanizomenon flos-aquae* and *Anabaena planktonica* in Lake Stechlin. Earlier, microcystin and a putative microcystin-producing species (*Planktothrix rubescens* HUB151) were detected in Lake Stechlin (Mbedi et al., 2005). Apart from these studies, no additional sources of microcystin production have been identified in Lake Stechlin. Increasing frequency and intensity of cyanobacterial blooms have been reported in numerous temperate lakes, which is a strong potential for elevated toxin production, however the number of reports on toxin production in lakes of the Baltic Lake District is much lower. Thus, the aim of the study was to detect genetic potential to produce microcystin and other cyanotoxins in Lake Stechlin, not only related to mass-developing cyanobacteria, but also those, which constitute a minor part of the cyanobacterial community of the lake.

5.3.2. Specific materials and methods

Pelagic phytoplankton samples from the deepest point of the lake were collected biweekly during stratification and monthly during mixed periods. Additionally, during mass developments of cyanobacteria with scum-development at the shoreline, scum samples were collected in July 2011 and November 2012. These samples were pooled and filtered onto glass fibre filters (GF/C, Whatman, Maidstone, UK). Physical parameters (temperature, conductivity, pH, oxygen concentration, oxygen saturation and Secchi transparency) were measured and concentrations of total and dissolved phosphorous and nitrogen (TP, TN, SRP and DIN) were analysed as described in Padisák et al. (2003b).

The clonal culture of the strains of *Dolichospermum* (A1, A5 and A7), *Aphanizomenon* (AP1), *Planktothrix* (P1, P2) and *Microcystis* (M1, M2) were established by isolating filaments and cells using a micropipettes method. The strains were maintained at the algal culture collection of the Leibniz-Institute of Freshwater Ecology and Inland

Fisheries in a suspension using a Z8 medium (Kotai, 1972) for *Microcystis* and *Dolichospermum* and a modified Bourrelly medium (Krienitz and Wirth, 2006) for *Aphanizomenon* and *Planktothrix*. The cultures were stored at 20 °C and under a 14h:10h light-dark cycle. Strains were identified based on morphological traits according to Komárek and Anagnostidis (1998), Komárek and Anagnostidis (2005), and Komárek (2013). We consequently used the revised designations of genera according to the latest studies: *Planktothrix* (syn. planktonic *Oscillatoria*, Komárek and Komárková (2004)), *Dolichospermum* (syn. planktonic *Anabaena*, Wacklin et al. (2009)).

The genomic DNA was extracted from pooled phytoplankton field samples from July 2011 and November 2012, as well as from cyanobacterial strains of the IGB algal collection using the Dynabead DNA Direct System I (Invitrogen/Dynal Biotech, Oslo, Norway), following the steps outlined in the manufacturer's manual. The polymerase chain reactions (PCR) were performed in a Peltier Thermal Cycler PTC 200 (MJ Research Inc., San Francisco, CA, USA). The volume and concentrations of the PCR cocktail used were as described by Dadheech et al. (2012). Primers CYA361f and CYA785r (Nübel et al., 1997) were employed for the amplification of the V3–V4 regions of the 16S rRNA gene. Amplification of the 16S rRNA gene fragment was carried out as follows: initial three min at 94 °C, 30 cycles of one min at 94 °C, 30 s at 55 °C, 45 s at 70 °C, and a final elongation step at 72 °C for five min. Amplification of the aminotransferase (AMT) domain situated on the modules *mcyE* and *ndaF* of the microcystin and nodularin synthetase enzyme complexes was performed using HEPF and HEPF primers (Vasas et al., 2013) with a PCR protocol described earlier (Dittmann et al., 1997). Besides testing the *mcyE* gene for microcystin in the samples, other toxin-producing genes for saxitoxin and anatoxin were examined using suitable primers that had been utilized by earlier workers (Ballot et al., 2010a, b). The PCR cycling protocol for each primer pair was applied as previously described by the authors.

The amplified products were cleaned using QIAquick PCR purification columns according to the manufacturer's protocol and were examined on a 1% agarose gel. Cleaned PCR products of field samples were cloned using the Zero Blunt® Topo® PCR cloning kit (Invitrogen, Darmstadt, Germany) according to the manufacturer's instructions. The positive clones selected were PCR amplified and then cycle sequenced to retrieve the sequence of the AMT domain for the *mcyE* gene. Uncultured *Planktothrix* sp. clones that were sequenced were designated as ST_*mcyE*_plank. Likewise, the uncultured *Microcystis* sp. clones that were sequenced were entitled ST_*mcyE*_micro. Both strands of purified products were sequenced on an ABI 3100 Avant Genetic Analyzer using BigDye Terminator Cycle Sequencing Kit v3.1 (Applied Biosystems, Applied Biosystems GmbH, Darmstadt, Germany), as described in the manufacturer's manual. The sequences of the 16S rRNA gene belonging to *Dolichospermum*, *Aphanizomenon*, *Planktothrix* and *Microcystis* taxa, and for the AMT domain related to the *Microcystis* and *Planktothrix* taxa, were retrieved from the nucleotide NCBI database and aligned with sequences obtained in the present study using the MUSCLE software (Edgar, 2004). Alignment was visually checked using the Manual Sequence Alignment Editor, Align v05/2008 (SequentiX, Klein Raden, Germany, 2001) (Hepperle, 2008). The phylogenetic trees were constructed by the maximum likelihood (ML) method using the programme MEGA

version 6.0 (Tamura et al., 2013) with the default settings, applying a suitable model of nucleotide substitution. Confidence values for the edges of the maximum-likelihood tree were computed by bootstrapping of 1000 replications. The nucleotide sequences reported in this study were deposited in the NCBI database under the GenBank accession numbers KM376423–KM376430 (16S rRNA gene), and KM376431–KM376433 (*mcyE* gene).

Toxin and MALDI-TOF MS Analysis were performed by Gábor Vasas (University of Debrecen).

The first step of the quantification of the MCYSTs was that, cells were collected on glass fibre filters from a known volume were frozen and stored at $-20\text{ }^{\circ}\text{C}$. Prior to freezing, the samples were divided into two parts; the first part (for analysis of cyanotoxins) was frozen ($-20\text{ }^{\circ}\text{C}$) and thawed twice and then filtered through a microfibre filter (GF/C, Whatman), while the second part was lyophilised for determination of dry mass. Microcystin variants were analysed in the whole extracts of the samples. The toxin concentration of the extracts was determined by micellar electrokinetic chromatography, as published earlier (Vasas et al., 2004, 2006) (MEKC) (Prince CEC-770 instrument; polyimide coated fused silica capillary (Supelco, 60 cm, 50 μm id., effective length: 52 cm); hydrodynamic injection 100 m bar 9 s⁻¹; applied voltage: +25 kV; 25 mM sodium-tetraborate-100 mM SDS buffer, pH: 9.3; detection by diode-array detector at 239 nm). DAX 3D version 8.1 software (PrinCE Technologies; Emmen; The Netherlands) was used for the evaluation of the electropherograms. MC-LR was used as a standard (purified in our laboratory, purity approx. 97% (HPLC-DAD)).

Lyophilised waterbloom-samples were screened for microcystins by MALDI-TOF MS. For the analyses, five mg of the lyophilised sample was mixed with 200 μL of 50% aqueous methanol, sonicated for five min, and allowed to stand for one h. The samples were examined in the positive-ion mode using a Bruker Biflex MALDI-TOF mass spectrometer equipped with delayed-ion extraction. A 337-nm nitrogen laser was used for desorption/ionisation of the sample molecules. Spectra from multiple (at least 100) laser shots were summarised using a 19-kV accelerating and 20-kV reflectron voltage. External calibration was applied using the $[\text{M}-\text{Na}]^+$ 1 peaks of malto-oligosaccharides dp 3–7, m/z values 527.15, 689.21, 851.26, 1013.31, and 1175.36, respectively. The measurement was performed in the 2,5-dihydroxybenzoic acid (DHB) matrix by mixing 0.5 μL of the matrix solution with 0.5 μL of the sample on the sample target and allowing it to dry at room temperature. The DHB matrix solution was prepared by dissolving DHB (10 mg) in a mixture (0.5 mL) of ethanol and water (1:1, v/v). The compounds were identified on the basis of the mass of $[\text{M} + \text{H}]^+$ peak. After the determination of mass values, post-source decay (PSD) measurements were performed directly from the same sample on the template, and microcystins and other peptides were identified by the PSD fragment structure analysis (Welker et al., 2002).

5.3.3. Results

The P- and N-concentrations on the two sampling dates (Table 6) were typical for oligo- to mesotrophic lakes. In November, at the end of the stratification period, an accumulation of the nutrients in the hypolimnion was found (e.g., TP 0.113 mg L⁻¹ and SRP 0.104 mg L⁻¹). A decrease in oxygen saturation from 103.8%–49.6% was observed in the deep layers. Two peaks of phytoplankton biomass were found during 2011 (Fig. 20). The first peak occurred in April and was dominated by centric diatoms, such as *Stephanodiscus neoastraea* (maximum: 1779 µg L⁻¹). The second peak occurred in July and was dominated by *Dolichospermum* species, mainly *Dolichospermum circinale* (maximum: 1198 µg L⁻¹), and additionally by the dinoflagellate *Ceratium hirundinella* (510 µg L⁻¹). Notably, *Microcystis* cf. *aeruginosa* existed in Lake Stechlin above the observation limit, mainly during the second half of 2011 (Fig. 21).

Table 6 P- and N-concentrations; physical properties in July 2011 and November 2012.

Sampling time	Water Layers	TP (mgL ⁻¹)	SRP (mgL ⁻¹)	TN (mgL ⁻¹)	DIN (mgL ⁻¹)	pH	Conductivity (µS cm ⁻¹)	O ₂ (mgL ⁻¹)	O ₂ (%)	Secchi depth (m)
July 2011	Epilimnion	0.011	0.002	0.376	0.039	8.70	285	10.87	122.4	5.7
	Hypolimnion	0.020	0.009	0.334	0.064	8.17	292	11.99	99.5	
Nov 2012	Epilimnion	0.010	0.003	0.393	0.024	7.92	282	10.52	91.3	5.5
	Hypolimnion	0.113	0.104	0.425	0.155	7.02	298	4.27	34.0	

In 2012, three peaks were observed. Large centric diatoms, like in 2011, established the first peak of the year. The second peak was lower and the phytoplankton assemblage was more diverse than in 2011. *Asterionella formosa* was the dominant species during early June, and later cryptophytes and dinoflagellates were observed with high biomass. The third peak was a very unusual event regarding the general phytoplankton succession of Lake Stechlin, since the phytoplankton assemblage was dominated by *Aphanizomenon flos-aquae* with >80% contribution to total biomass. Besides, *Planktothrix rubescens* occurred in increasing amounts (60 µg L⁻¹) (Fig. 21). At both field samplings of the lake, which took place in July 2011 and November 2012, cyanobacteria dominated the pelagic phytoplankton community (Fig. 22).

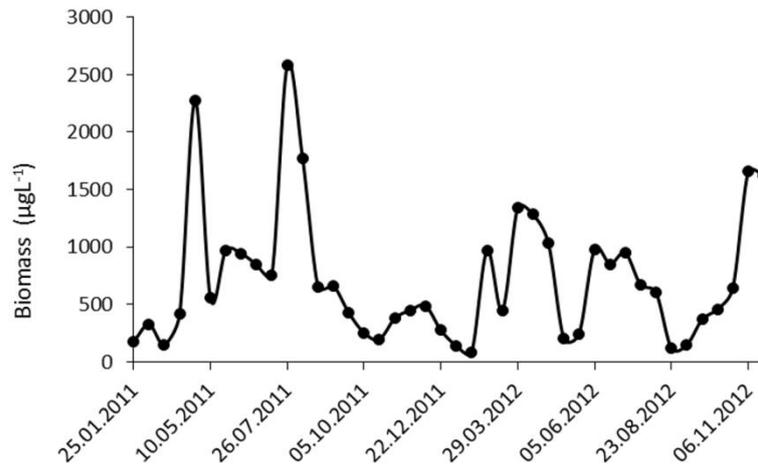


Fig. 20 Phytoplankton biomass in Lake Stechlin during 2011 and 2012. ($\mu\text{g L}^{-1}$)

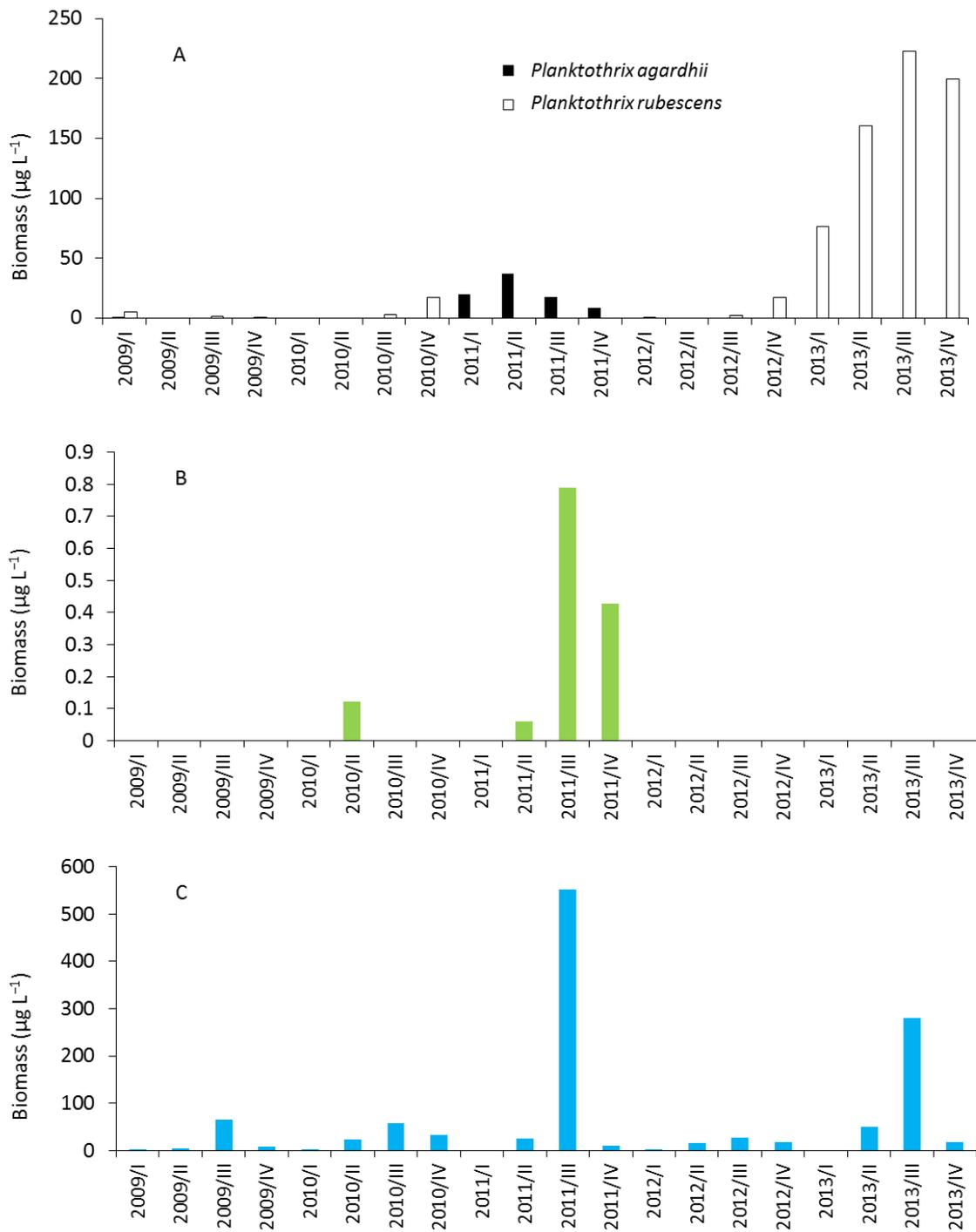


Fig. 21 Average biomass of *Planktothrix rubescens*, *Planktothrix agardhii* (A); *Microcystis* cf. *aeruginosa* (B); and *Dolichospermum* spp. (C) between 2009 and 2013 in Lake Stechlin. I, II, III, and IV stand for quarters of years

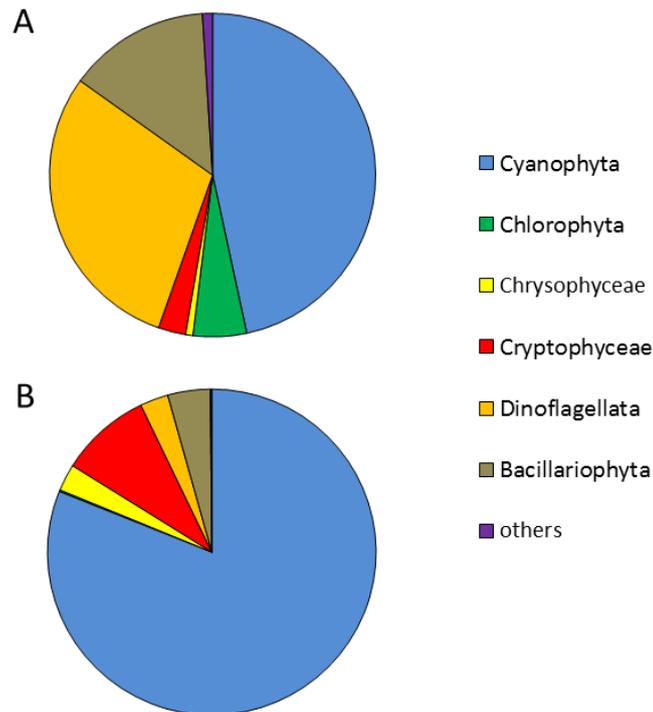


Fig. 22 Ratio of pelagic phytoplankton communities in July 2011 (A) and November 2012 (B).

The revealed and 386 bp long determined sequences of the AMT domain of *mcyE* gene from field samples showed the highest similarity to *Microcystis* and *Planktothrix* in the BLASTN analysis. 351 positions were used in a phylogenetic comparison in which two groups were detected. One of the groups contains sequences mostly from *Microcystis* and the other includes sequences of *Planktothrix* and *Oscillatoria*. The group in case of *Microcystis* was supported by a 100% bootstrap value and in case of *Planktothrix* was supported by a 98% bootstrap value.

Other *mcyE* gene fragment was amplified with HEPF/HEPR primers belonging to *Microcystis* and *Planktothrix*, however it was not available in GenBank for comparison. Isolated strains of *Dolichospermum circinale* (A1, A5 & A7), *Aphanizomenon flos-aquae* (AP1) were also tested with HEPF/HEPR primers, but without any amplification for the *mcyE* gene. Further specific primers for saxitoxin and anatoxin-a were tested on the field samples and strains as well, however any amplification were detected.

V3 and V4 regions of 16S rRNA gene were sequenced to evaluate the phylogenetic position of the isolated strains. 396 bp were determined from the 16S rRNA gene from all the studied strains and the same number of position used for the phylogenetic analysis. The sequence of *Aphanizomenon flos-aquae* fell in a clade containing sequences from worldwide origins (China, France and UK). Strains of *Dolichospermum* corresponded to *Anabaena lemmermanni* with 100% similarity isolated in the UK. The sequences of *Microcystis* cf. *aeruginosa* grouped together sequences from different countries around the world (Vietnam, Japan, Canada and Mexico) and *Planktothrix rubescens* strains showed the highest similarity with sequences from China and UK. However, there were not

available sequences of V3 and V4 regions in the GenBank belonging to *Planktothrix* and *Microcystis*, which originated from Germany.

MC content was measured and calculated as MC-LR equivalent, thus in case of field sample from July 2011 was 27.32 μgL^{-1} and 4.25 μgL^{-1} was from November 2012 according to the cyanotoxin analyses. Several microcystin variants were detected in the environmental samples, further in one of the *P. rubescens* strain (Table 7).

Table 7 Microcystin variants and contents detected in field samples and cyanobacterial strains from Lake Stechlin, (n.d.: not detected).

Sample/strain	Dominant taxon in field sample	other taxa	Microcystin content (μgL^{-1} LR Equivalent)	Microcystin variants	Toxin gene detected
July 2011	<i>Dolichospermum circinale</i>	<i>Microcystis</i> cf. <i>aeruginosa</i>	27.32 μgL^{-1}	MCYST-LL, -LR, -LW, -RR,	<i>mcyE</i> <i>Microcystis</i>
November 2012	<i>Aphanizomenon flos-aquae</i>	<i>Planktothrix rubescens</i>	4.25 μgL^{-1}	MCYST-LW, [Dha7]MCYST-RR	<i>mcyE</i> <i>Planktothrix</i>
<i>Dolichospermum circinale</i> A1			n.d.		n.d.
<i>Dolichospermum circinale</i> A5			n.d.		n.d.
<i>Dolichospermum circinale</i> A7			n.d.		n.d.
<i>Aphanizomenon flos-aquae</i> AP1			n.d.		n.d.
<i>Microcystis</i> cf. <i>aeruginosa</i> M1			n.d.		n.d.
<i>Microcystis</i> cf. <i>aeruginosa</i> M2			n.d.		n.d.
<i>Planktothrix rubescens</i> P1			n.d.	[Dha7]MCYST-RR	<i>mcyE</i> <i>Planktothrix</i>
<i>Planktothrix rubescens</i> P2			n.d.		n.d.

5.3.4. Discussion

The annual phytoplankton biomass distribution pattern of Lake Stechlin is typically uni- or bimodal. In case of unimodal pattern a spring peak can be observed, if the distribution bimodal a lower biomass peak occurs in the late summer followed by the higher one in spring (Padisák et al., 2003b). The Year 2011 was exceptional: the summer peak was higher than the spring peak. The fact that cyanobacteria dominate in summer assemblage and could reach a higher biomass than the diatoms dominating in the spring assemblage indicates a shift from oligo-mesotrophic towards a eutrophic state (Sommer et al., 1986). In

recent years, the highest phytoplankton biomass peak was regularly caused by *Dolichospermum* species and *Aphanizomenon flos-aquae*. It is well-known that the physiological optima for the photosynthesis of many cyanobacteria species are above 20 °C (Konopka and Brock, 1978; Baker and Bellifemine, 2000). A long-term monitoring study (Kirillin et al., 2013) shows the surface water temperatures at Lake Stechlin are increasing by a rate of 0.37 °C per decade, thus the duration of periods with at least a 20 °C surface temperature is waxing, which may open a new ecological niche and contribute to the increased biomass of the *Dolichospermum* species. However, other reasons like the effect of forestry management or the changing groundwater inflow can contribute as well, but none of these hypotheses have yet been tested (Padisák et al., 2010).

After the exceptional 2011, another unusual event was observed in the phytoplankton succession in autumn 2012. In most cases, the phytoplankton biomass shows a minimum level after autumnal overturn around November-December (Padisák et al., 2003b), however in 2012 the phytoplankton biomass reached a minimum value in September, then it started to increase until early November, when *Aphanizomenon flos-aquae* was the dominant member of the phytoplankton community. *Planktothrix rubescens* showed a similar increasing pattern, however during winter reached a higher biomass, than *Aphanizomenon flos-aquae*.

Mass development caused by *Dolichospermum circinale* and *Aphanizomenon flos-aquae* was observed in July 2011 and November 2012. Microscopic analysis showed that the cyanobacterial assemblage included other potential microcystin-producing taxa: *Microcystis* sp. and *Planktothrix agardhii* in July 2011 and *P. rubescens* in November 2012. Although microscopic analysis is a good base to monitor toxin-producing potential in blooms, it is, in many cases, insufficient. Using molecular markers is a very effective tool to detect toxic populations, independently of their taxonomic identity (Bittencourt-Oliveira, 2003). Selective primers were used for environmental samples and isolates to detect genes for the synthesis of cyanotoxins such as anatoxin-a, microcystin or saxitoxin. The *mcyE* gene was detected in the amplified products, which is a frequently used region to reveal toxic cyanobacteria (Wiedner et al., 2001). This region is necessary for microcystin production (Dittmann et al., 1997), that is why this region suitable to detect microcystin-producers in environmental samples (Padisák et al., 2003a; Vaitomaa et al., 2003; Mbedi et al., 2005; Krienitz et al., 2013) or even in sediment samples (Dadheech et al., 2009). Our results showed, that microcystin was produced by *Microcystis* and *Planktothrix*, which were present that time only in very low biomass in Lake Stechlin.

Interestingly, *Dolichospermum* and *Aphanizomenon*, the two dominant cyanobacterial taxa, did not show any potential to produce toxins and toxin-producing genes corresponding to these species were not detected. Earlier findings show that there is no correlation between the presence and amount of cyanotoxins and the composition of cyanobacterial community (Elder et al., 1993), because not all the species, even more not all the strains are toxic in a waterbody. Different variants of microcystin (LR, LL and LW) were detected in the field samples from Lake Stechlin by us. These variants produced by *Microcystis* and *Planktothrix* were found in water bodies of Germany in a previous study (Fastner et al., 1999), moreover a microcystin producing genotype of *P. rubescens* was reported from Lake Stechlin (Mbedi et al., 2005). In our study, we could detect the *mcyE*

gene in one of the *P. rubescens* (P1) strains, and it was confirmed by toxicological analysis, because the [Dha7]MCYST-RR variant were found in the P1 isolated strain. Cyanotoxin producing genes were not found in any strains of *Dolichospermum circinale*, *Aphanizomenon flos-aquae* and *Microcystis* cf. *aeruginosa*. However presence of potential toxin producing *Microcystis* was shown for the first time as we could detect a sequence of the *mcyE* fragment from a field sample, and the presence of microcystins in Lake Stechlin was also confirmed by analytical results of field samples.

A much higher microcystin amount ($27.32 \mu\text{gL}^{-1}$ LR equivalent) was detected in July 2011 than in the environmental sample from November 2012 ($4.25 \mu\text{gL}^{-1}$ LR equivalent). The lower value of microcystin could be resulted by several reasons in the sample, which was taken during autumn. One of them could be the higher temperature ($20.6 \text{ }^\circ\text{C}$) in July, compared to November ($9.3 \text{ }^\circ\text{C}$), because the optimum temperature for toxin production is between 20 and $25 \text{ }^\circ\text{C}$ (Watanabe and Oishi, 1985). Moreover, the toxin production can vary temporally and spatially at a particular site, or even within the bloom itself (Ressom et al., 1994). Other studies show that toxin production is affected by light as the second most important factor after the temperature (Van der Westhuizen and Eloff, 1985). Besides light and temperature, other factors can influence the production of cyanotoxins such as nutrients (Sevilla et al., 2010) or iron (Sevilla et al., 2008).

Determination of cyanobacteria by microscopic analyses was confirmed by molecular markers. V3 and V4 hypervariable regions of 16S rRNA gene are among the most capable regions to distinguish bacterial taxa, including cyanobacteria (Nübel et al., 1997; Mühling et al., 2008). The result on the regions of 16S rRNA gene is an addition to phylogeny of *Microcystis*, because the sequence of these regions was not available in GenBank. Phylogenetic analyses of *Microcystis* strains show that there is no geographic restriction of *Microcystis* spp., which verify the truly cosmopolitan distribution of this cyanobacterial taxon (Van Gremberghe et al., 2011). Our study also provides some information about phylotypes of *Planktothrix*, *Dolichospermum* and *Aphanizomenon*. Interestingly, the *Aphanizomenon* phylotype of Lake Stechlin did not cluster with sequences from Germany, which suggests a remarkable genetic divergence of *Aphanizomenon*.

5.4. Spatial-and niche segregation in Lake Stechlin⁴



⁴ This chapter based on the following article:

Selmeczy GB; Tapolczai K; Krienitz L; Casper P; Padišák J (2016): Spatial- and niche segregation of DCM forming cyanobacteria in Lake Stechlin (Germany). *HYDROBIOLOGIA*, 764: 229-240

5.4.1. Specific introduction

Stable stratified water columns especially at low trophic status offer favourable conditions for sufficiently adapted phytoplankton species to form deep chlorophyll maxima (DCM). Reports of deep living populations of a phytoplankton species appeared in the early years of the 20th century (i.e. Juday, 1934) and since that time, a number of papers were published dealing with this phenomenon. DCM were found nearly everywhere in the world where water bodies meet the requirements of their appearance.

DCM typically occurs in stratified lakes with trophic state ranges from ultra-oligotrophic to mesotrophic (e.g. Abbott et al., 1984; Larson et al., 1987; Bird and Kalff, 1989; Queimaliños et al., 1999) and in few cases also in eutrophic systems (Gervais, 1997a). The distribution of deep layer population maxima spans a wide geographical scale including both temperate (i.e. Barbiero and Tuchman, 2004; Halstvedt et al., 2007) and tropical lakes (Padisák et al., 2003a) and large lakes (i.e. Barbiero and Tuchman, 2004) or small oxbows (Grigorszky et al., 2003). Deep layer maxima by picocyanobacteria are common even in the Antarctic region (Holm-Hansen and Hewes, 2004).

A wide range of phytoplankton taxa can form DCM such as diatoms (e.g. Fahnenstiel and Glime, 1983;), cryptophytes (Gervais, 1997a), cyanoprokaryotes (Padisák et al., 2003a) or chlorophytes (Clegg et al., 2012).

The mechanisms of forming deep layer maxima are diverse. According to Camacho (2006) there are six main mechanisms: (i) different predation pressure between top and deep layers; (ii) passive depth-differential sinking of epilimnetic populations; (iii) symbiotic association of algae with protozoa, followed by blooming in the metalimnion; (iv) photo-acclimation of the phytoplankton living in deep layers can cause elevated biomass specific Chl-a concentrations (without significant biomass increase); (v) vertical migration of cryptophytes, and (vi) *in situ* growth of phototrophs. Latter can be observed in lakes with oligo- or mesotrophic conditions when stratification during summer results in epilimnetic nutrient depletion and low standing crop of phytoplankton allows light to penetrate into the metalimnion and the upper hypolimnion (Reynolds, 2006). These conditions result a narrow stratum with relatively high nutrient pool and sufficient light availability allowing for *in situ* growth of certain species (Camacho, 2006). Species that can occupy this habitat with its harsh conditions (i.e. low light intensity, strong physical and chemical gradients combined in the temperate region with cold temperatures) have successful adaptive strategies to exist at the limit of their ecological tolerance (Clegg et al., 2012).

In this study, we investigate whether or not the three (*Aphanizomenon flos-aquae*, *Cyanobium* sp., *Planktothrix rubescens*) populations were vertically segregated, and if yes, niche segregation did or did not occur between them taking ambient ranges of some main environmental variables into account.

5.4.2. Specific material and methods

The investigation period was between May and September 2013. Data of this study derive from two sampling stations: SP in the southern basin of the lake and DP in the center of the

lake (Fig. 1). Physical and chemical parameters (temperature, conductivity, pH, redox potential, oxygen concentration, oxygen saturation and the photosynthetically available radiation - PAR), pigment concentrations of different algal groups (chlorophytes, cyanobacteria, diatoms, cryptophytes) and yellow substances were measured with a BBE (biological, biophysical, engineering) fluoroprobe and a YSI (Yellow Springs Instruments) sensor. These data were recorded in half a meter intervals from the surface (0.5 m) to the bottom (20.5 m). Integrated phytoplankton samples were taken biweekly from the epilimnion and the hypolimnion with integrating water sampler (HYDRO-BIOS IWS III, Kiel, Germany). Concentrations of TP, SRP, TN, NO₂⁻, NO₃⁻, NH₄, and Si were measured according to APHA (1998). All inorganic N fractions (NO₂⁻-N, NO₃⁻-N and NH₄⁺-N) were added for estimating dissolved inorganic nitrogen (DIN), and their proportion relative to SRP (DIN/SRP) was calculated. Additionally, water samples were taken in monthly intervals from the deepest part of the lake (sampling site DP) in 5 m increments. Phytoplankton composition, biomass, APP numbers, physical and chemical parameters were measured in these samples. Further, phytoplankton samples were taken biweekly from May until October in 5 meter increments from the surface until 25m and these subsamples were mixed equally to make integrated samples. Euphotic depth was calculated as 3 × Secchi depth (Koenings and Edmundson, 1991). Relative water column stability (RWCS) (Welch, 1992) was calculated using the formula:

$$RWCS = \frac{D_b - D_s}{D_4 - D_5},$$

where D_b is the density of bottom water, D_s is the density of surface water, and $D_4 - D_5$ is the density difference between 4 and 5°C water. Autotrophic picophytoplankton (APP) was counted by epifluorescence method as described in Padisák et al. (1997). Surfer 9 was used for diagram of interpolated depth profiles.

5.4.3. Results

Prior to the studies, the ice covered period started late and lasted unusually long: after a two weeks period, ice melted in early February 2013 then the lake froze again in middle March which condition lasted for a month. Thermal stratification started in early May and the most stable stratification occurred on 27 July with an RWCS value of 346 (Fig. 23).

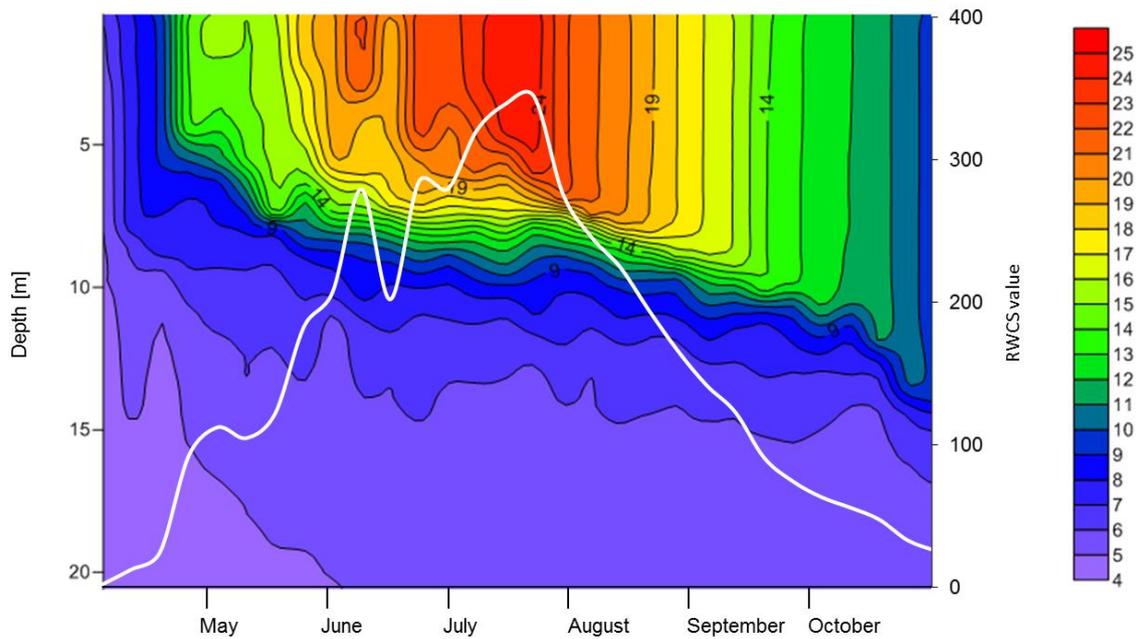


Fig. 23 Relative water column stability values (white) and depth profiles of temperature (°C) in the south basin of the lake from 22 April 2013 to 11 November 2013

Phytoplankton development of Lake Stechlin showed a basically unimodal distribution during 2013 (Fig. 24). Until early February, the phytoplankton assemblage was dominated by *Rhodomonas lens* Pascher & Ruttner and *Gymnodinium helveticum* Penard. During spring, the big centric diatoms, especially *Stephanodiscus neoastraea* Håkansson & Hickel peaked, then overall biomass decreased in May being *Gymnodinium helveticum* ($831 \mu\text{gL}^{-1}$) the dominant member of the phytoplankton assemblage. Phytoplankton biomass reached an annual maximum level in July ($1711 \mu\text{gL}^{-1}$) and after that it decreased continuously until the end of the year. *Aphanizomenon flos-aquae*, *Dolichospermum solitarium* (Klebahn) Wacklin, *D. circinale* (Rabenhorst ex Bornet & Flahault) Wacklin, *Planktothrix rubescens* and *Gymnodinium helveticum* were the characteristic species in the summer phytoplankton community. *Fragilaria crotonensis* Kitton 1869 and *Synedra acus* Kützing 1844 (82 and $477 \mu\text{gL}^{-1}$) provided a slight diatom peak early in September. Contribution of *Planktothrix rubescens* to the total biomass increased from September to November, when it became the dominant species.

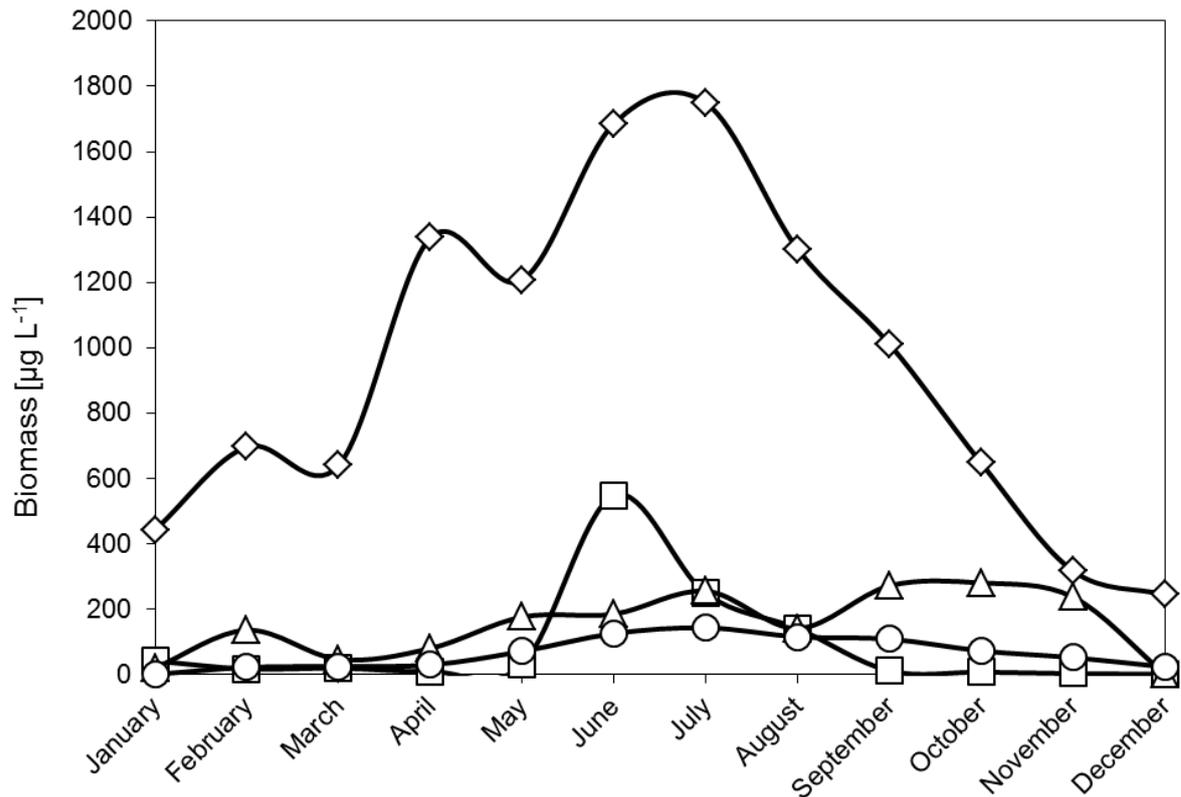


Fig. 24 Monthly average phytoplankton biomass and *Aphanizomenon flos-aquae*, *Planktothrix rubescens* and *Cyanobium* sp. in Lake Stechlin (station DP) during 2013 (diamond: total biomass, square: *Aphanizomenon flos-aquae*, triangle: *Planktothrix rubescens*, circle: *Cyanobium* sp.).

At the deepest part of the lake, *Aphanizomenon flos-aquae*, *Planktothrix rubescens* and *Cyanobium* sp. formed a distinct DCM (Fig. 25). At the beginning of the stratification period (early May) biomass of *Cyanobium* sp. peaked at 10 m, biomass of *Aphanizomenon flos-aquae* was less than $30 \mu\text{g L}^{-1}$ and distributed evenly in the whole water column and *Planktothrix rubescens* did not show clear vertical distribution (Fig. 25, A). In early June, the peak of *Cyanobium* sp. deepened to 15 m; the maximum biomass of *Aphanizomenon flos-aquae* was observed close to the surface and *Planktothrix rubescens* peaked between 20-25 m (Fig. 25, C). This pattern was not observed in the shallower south basin of Lake Stechlin (sampling site SP). During July, *Aphanizomenon flos-aquae* formed a distinct DCM at 10 m together with *Cyanobium* sp., and *Planktothrix rubescens* clearly separated from them (Fig. 25, E). *Cyanobium* sp. (maximum: $1764 \mu\text{g L}^{-1}$) and *Aphanizomenon flos-aquae* (maximum: $980 \mu\text{g L}^{-1}$) showed the highest biomass during August at 10 m (Fig. 25, G), however *A. flos-aquae* in the south basin of the lake reached a much higher biomass (10.090 mg L^{-1}) in a point sample from 7.5 m on 21 June, 2013. By early September, the DCM of *A. flos-aquae* eroded and its biomass was very low in the whole water column. The DCM of *Cyanobium* sp. and *Planktothrix rubescens* were still present, moreover the biomass of *P. rubescens* increased and reached a maximum level of $440 \mu\text{g L}^{-1}$ (Fig. 25, I).

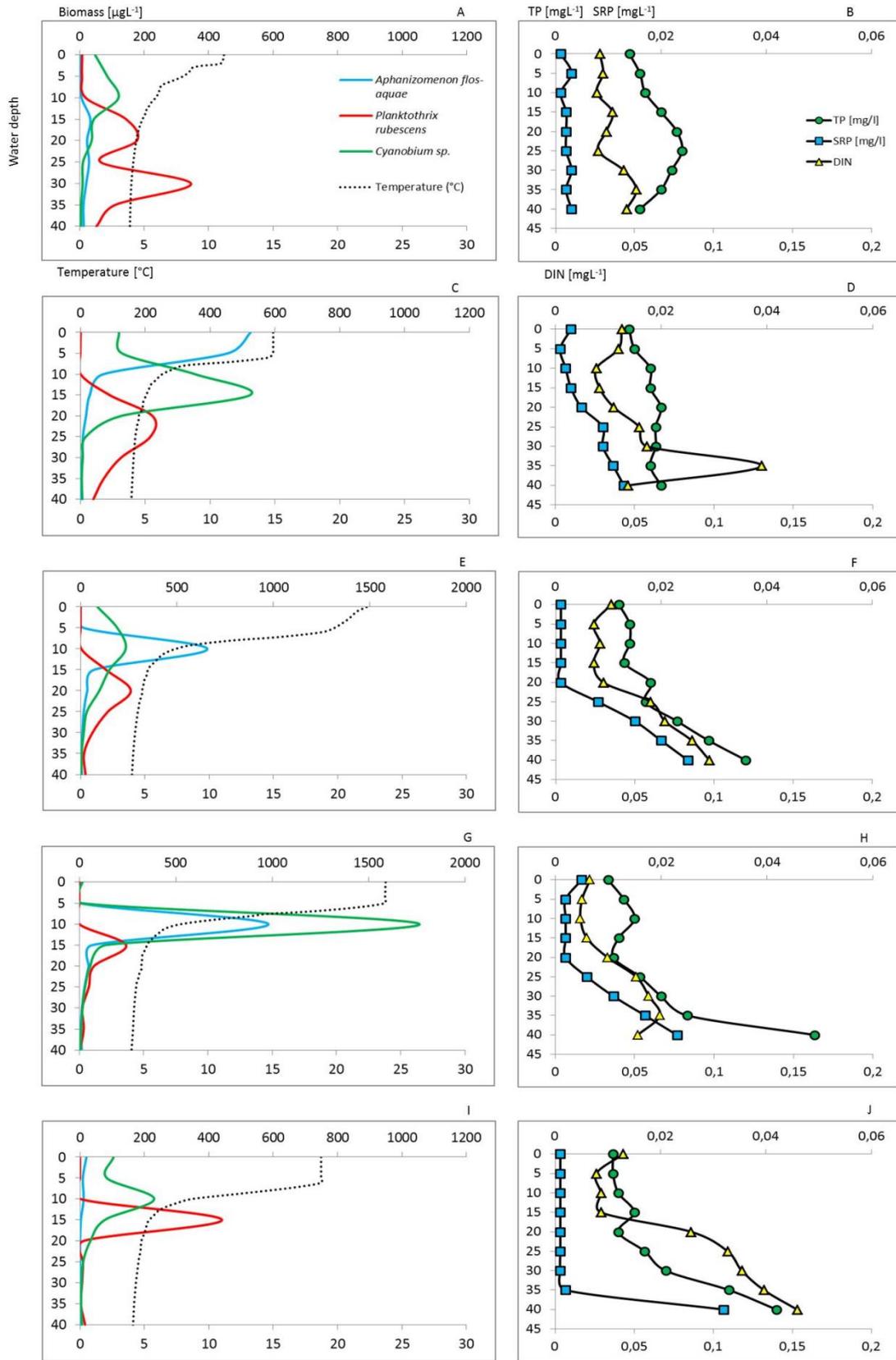


Fig. 25 Depth profiles of *Aphanizomenon flos-aquae*, *Planktothrix rubescens*, and *Cyanobium sp.* biomass (μgL^{-1}), temperature and TP, SRP, DIN gradient in the deepest

point of Lake Stechlin (DP) at different dates. A, B: 07 May 2013; C, D: 04 June 2013; E, F: 09 July 2013; G, H: 08 August 2013; I, J: 03 September 2013

DIN/SRP ratio varied from 6 to 81 (Table 8). The lowermost value of DIN was measured in August at 10 m (0.016 mgL^{-1}) and during the whole study period the lowest values were recorded in the 5-10 m depths. The highest values were measured in September at 65m (0.3 mgL^{-1}). Levels of DIN showed a bimodal distribution in May (Fig. 25, B). During May and June the amounts of NH_4^+ and NO_3^- were quite similar, however from July NH_4^+ decreased and NO_3^- was the most abundant form of DIN. Interestingly, the lowest (0.004 mgL^{-1}) and the highest (0.256 mgL^{-1}) NO_3^- values were measured in September at 10 and 65 m. Nitrite was rather even from May to September with a mean value of 0.0024 mgL^{-1} . The amounts of SRP were quite low in the whole water column during May (average: 0.002 mgL^{-1}), however during June the values of SRP increased in the hypolimnion. From the next month on, the vertical profile of SRP changed and showed similar distribution between July and September (Fig. 25, F, H, J). During these months SRP was present in small amounts (mean: 0.002 mgL^{-1}) from the surface until 20 m depth – in September until 35m - and in deeper water layers concentration increased dramatically.

During the investigated period, the highest Secchi depth was measured in May (6.8 m), than it decreased continuously until August (5.1 m), and increased in September (6.65 m). The highest estimated euphotic depth occurred in May (20.4 m) and the lowest value in August (15.3 m).

Table 8 DIN/SRP ratio at deepest point of Lake Stechlin (DP)

Month	Epilimnion	Hypolimnion
May	19.0	18.9
June	27.0	9.0
July	29.5	16.4
August	6.5	8.7
September	32.7	81.6

Amount of phycocyanin at SP is displayed on Fig. 26 and data clearly show the amount of *Aphanizomenon flos-aquae*. DCM of *A. flos-aquae* and *Planktothrix rubescens* occurred in this part of the lake too, however some interesting differences were observed between the two sites of the lake. *Aphanizomenon flos-aquae* started to develop between 7 and 14 June, when the epilimnetic water temperature reached $19 \text{ }^\circ\text{C}$ (Fig. 23), thus stratification was quite strong (RWCS= 190). On 30 July when the RWCS showed the highest values (around 340) it started to decrease, however the thickness of the metalimnion also started to decrease. DCM of *A. flos-aquae* practically disappeared between 13 and 20 August when the first signals of the annual overturn appeared. Maximum abundance of *A. flos-aquae* occurred in the middle of the metalimnion just above the thermocline at 7.5 m. Maximum of the phycocyanin ($11.6 \text{ } \mu\text{gL}^{-1}$) was observed on 02 July 2013. From early September until the end of October, the maximal phycocyanin value was around $3 \text{ } \mu\text{gL}^{-1}$ at 12-14 m depth and this maximum was caused by *Planktothrix*

rubescens. This DCM eroded when the epilimnion reached this depth, because of the process of autumnal overturn around 30 October. Microscopic observations on the integrated epi- and hypolimnetic samples indicated the clear presence of *P. rubescens* DCM in the upper hypolimnion even in periods when the species was not detected by the fluoroprobe. Epilimnetic samples did not contain any *P. rubescens* filaments from May until August. It was present in the hypolimnion in May ($218 \mu\text{gL}^{-1}$), and somewhat decreased in June ($75 \mu\text{gL}^{-1}$). Then continuously increased until August, when the level of the biomass was $372 \mu\text{gL}^{-1}$. The vertical pattern of oxygen saturation reflected the pattern of the cyanobacterial biomass with a stable oxygen peak between the 5-10 m depth (Fig. 27).

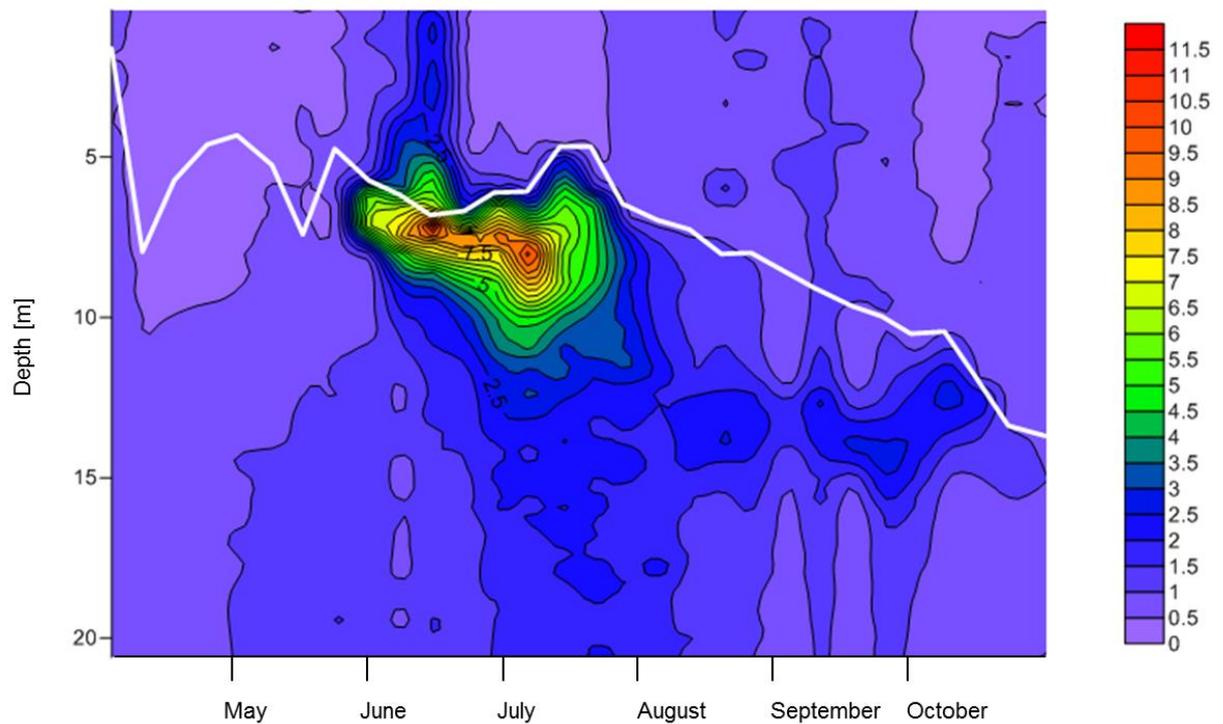


Fig. 26 Depth profiles of cyanobacterial biomass (phycocyanin (μgL^{-1})) in south basin of Lake Stechlin (station SP) from 22 April 2013 to 11 November 2013 (the white line indicates the border of the epilimnion and metalimnion)

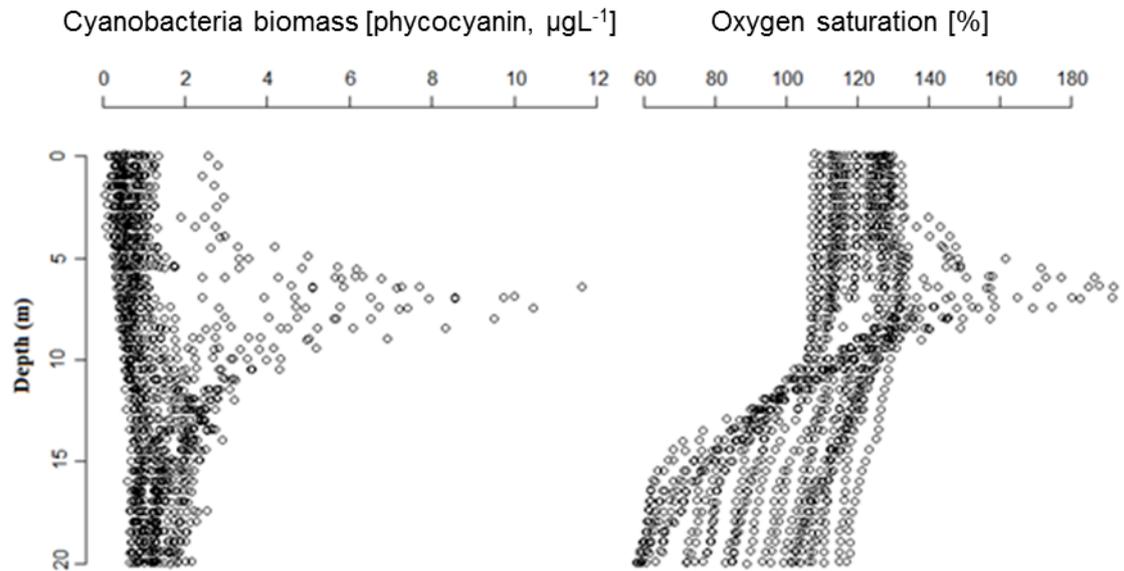


Fig. 27 Cyanobacterial biomass, estimated as phycocyanin and oxygen saturation data in different depths between May and September 2013 in the south basin of Lake Stechlin (SP)

Light intensities were estimated in the south basin of Lake Stechlin; they ranged from 35 to 55 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR in water layers where *Aphanizomenon flos-aquae* reached its maximum biomass and in layers with *Planktothrix rubescens* maxima of PAR from 2 to 4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 28) were characteristic.

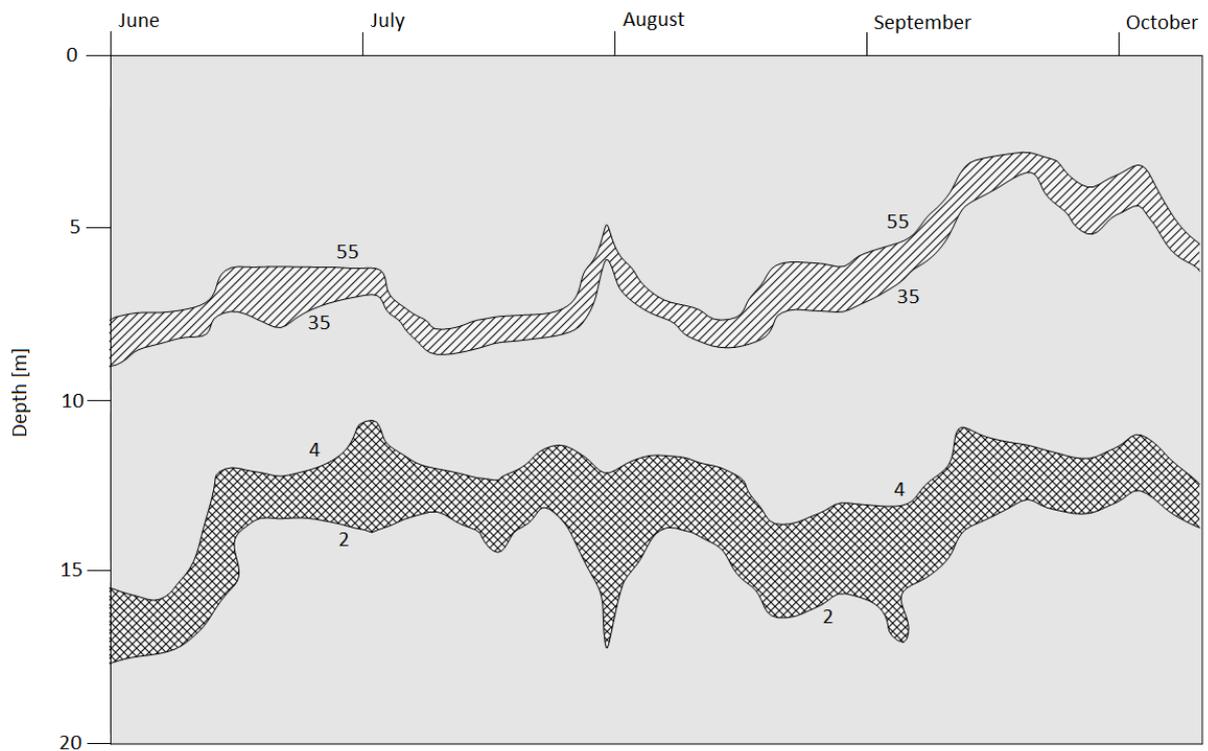


Fig. 28 Striped regions indicate light intensity where *Aphanizomenon flos-aquae* (35-55 $\mu\text{mol m}^{-2} \text{s}^{-1}$) *Planktothrix rubescens* (2-4 $\mu\text{mol m}^{-2} \text{s}^{-1}$) reached its maximum biomass in the south basin of Lake Stechlin (SP)

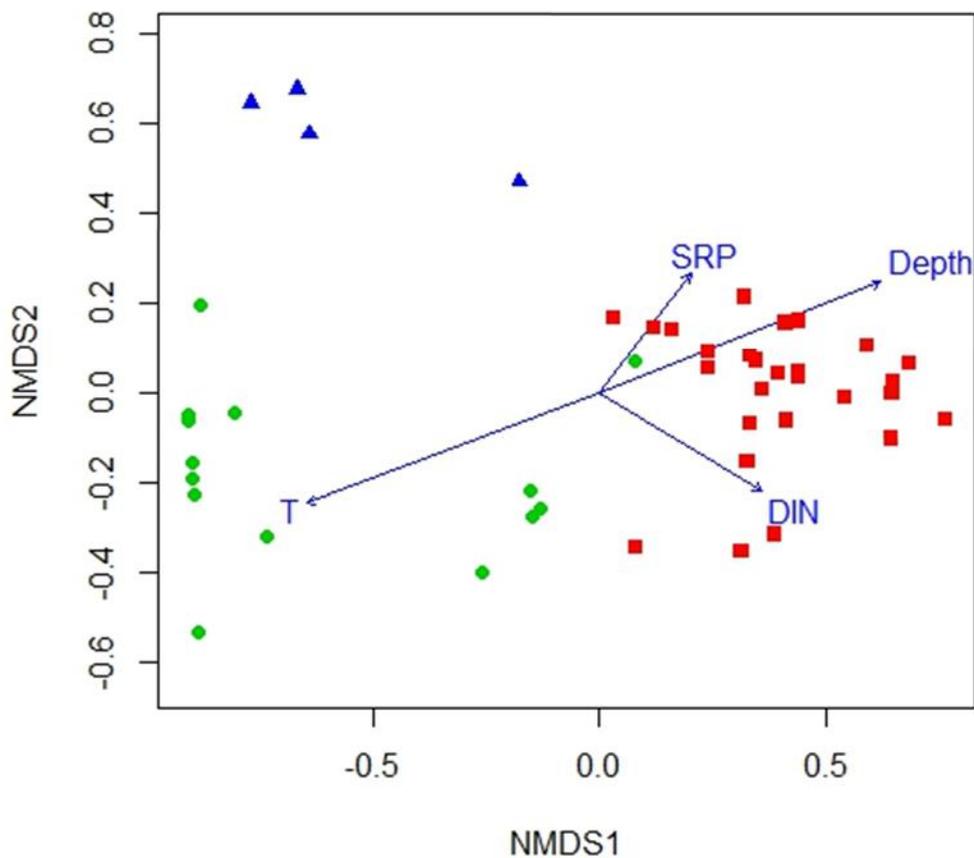


Fig. 29 Ordination of some environmental parameters and phytoplankton species at different sampling dates and depths based non-metric multidimensional scaling (NMDS). Every symbol represents one sample: green circles if *Cyanobium* sp., blue triangles if *Aphanizomenon flos-aquae* and red squares if *Planktothrix rubescens* had the highest biomass

The strongest relationships ($p < 0.01$) between the samples and environmental variables according to the non-metric multidimensional scaling (NMDS) are given in Fig. 29. The direction and the length of the arrows were proportional with the direction and the strength of the environmental gradient. The samples were encamped in three groups, which were characterized by the highest biomass of *Planktothrix rubescens*, *Aphanizomenon flos-aquae* and *Cyanobium* sp., respectively. The two strongest gradients were the temperature and the depth. Samples with highest biomass of *Planktothrix rubescens* characterized by higher SRP, DIN and lower temperature than those with the highest biomass of *Cyanobium* sp.

5.4.4. Discussion

During summer of 2013, a rarely observed phenomenon occurred in Lake Stechlin: *Planktothrix rubescens*, *Aphanizomenon flos-aquae* and *Cyanobium* sp. formed DCM, however with spatial segregation. Although significant differences of the vertical and horizontal distribution of phytoplankton community are observable in many stratified lakes (e.g. Pelechaty and Owsiany, 2003; Borics et al., 2011), the observed phenomenon represents a unique situation in the pelagic zone.

According to Hardin's principle of competitive exclusion (Hardin, 1960) as many species can coexist in a constant environment as the number of limiting factors. Since the metalimnetic or upper hypolimnetic layers during stratification are relatively long-lasting and the limiting factors are few, they provide ideal circumstances for selection of steady-state phytoplankton assemblages (Naselli-Flores et al., 2003). Additionally, values of physical and chemical parameters existing in these deep layers fall aside the ecological niche of most of the species. Thus, only a few species with special adaptations have the chance to take part in this competition. These species need to have specialized ecological tolerances which involve capability to perform net photosynthesis under low light intensity and low temperature combined with good buoyancy regulation to sustain position around a defined depth layer along the vertical profile.

Planktothrix rubescens is a native, and in some periods dominant member of the phytoplankton community in Lake Stechlin since it was mentioned (as *Oscillatoria rubescens*) in the first description of the flora (Krieger, 1927). The first quantitative record of *P. rubescens*, as well as the first observation in deep layers in Lake Stechlin is from 1963 (Casper, 1985b). Further investigations on *P. rubescens* deep-layer populations were published by Padisák et al. (2003a) supporting the consistency of this phenomenon with observations in other deep lakes. Though the species occurs regularly in the plankton, in most years it remains "quiet" and reaches high biomasses only in certain years or series of years. It was hypothesized that mass appearance of *P. rubescens* is driven by mainly mesoclimatic cycles since the observed dominance of the species was related to unusually cold winters with long lasting ice cover (Padisák et al., 2010). This hypothesis is corroborated by our observations too, since the ice break up happened during mid-April. In these cases, *P. rubescens* growth starts in autumn when the thermocline erodes, continues during the isothermal period and the winter stagnation at a low rate, with a filament number increase in the whole water column. When the thermocline establishes in spring, part of the population sinks to the bottom but the bulk accumulates and continues growth in the upper hypolimnion forming a DCM. This pattern was characteristic in the 1997-1998 (Padisák et al., 2003a) and in 2012-2013 (this study). As shown in many studies, *P. rubescens* is well adapted to build up substantial populations in metalimnia or upper hypolimnia (Konopka, 1982; Padisák et al., 2003a; Camacho, 2006; Hastvedt et al., 2007). Its effective buoyancy by aerotopes enables the species to regulate its vertical position and to stay in the depth of favorable conditions. Since *P. rubescens* contains both phycoerythrin and phycocyanin, it is able to utilize the shorter wavelength of the radiation spectrum which is a successful adaptive feature to survive under low light conditions. Several authors reported that *Planktothrix rubescens* is able to grow at $2 \mu\text{mol m}^{-2} \text{s}^{-1}$

(Bright and Walsby, 2000; Davis et al., 2003) corresponding to light intensities observed in this study. These features give this species adaptive advantage under these harsh conditions of light limitation.

The presence of *Cyanobium* sp. deep-layer maxima in Lake Stechlin was described for the first time in a picophytoplankton survey in 1994 (Padisák et al., 1997) and since that time the phenomenon is recurrent every year, though its intensity varied (Padisák et al., 2010). The species starts growing in the period prior to the onset of stratification, and when the lake stratifies the population concentrates in a narrow layer in the upper hypolimnion where it continues growth. During the maximum growth period, *Cyanobium* population may double every third day (Padisák et al., 1997). As most studies on unicellular freshwater picocyanobacteria refer to “*Synechococcus*”, a complex of genotypes, it is difficult to find data characterizing ecological preferences/tolerances of *Cyanobium*. One of the first measurements in oligotrophic lakes within this topic was provided by Gervais et al. (1997). According to this study, *Cyanobium* exhibited an I_k of $3.6 \mu\text{E m}^{-2} \text{s}^{-1}$ on cloudy days in the DCM and therefore this species may outcompete other species because of its high S/V ratio and consequently very high nutrient uptake affinity. Other available data also support association of autotrophic picoplankton with low light environments and sensitivity of high PAR and UV (Callieri, 2008).

Aphanizomenon flos-aquae appeared in Lake Stechlin (Padisák et al., 2010) in 2000. In the following years it typically appeared in the plankton in June-July and persisted until the autumnal destratification. The species gradually increased its overall dominance (Padisák et al., 2010). In 2010-2011 its temporal pattern was exceptional. It peaked in August then, after a decline in September-October, a second growth started and it formed a bloom under ice (Üveges et al., 2012). After the ice-break its biomass decreased but another bloom occurred in May-June 2011. In summary, the species was perennial for a year independent of season with some oscillations. First observations of *A. flos-aquae* DCM are from 2009 and 2010 (Tapolczai et al., 2013). The only documentation of *Aphanizomenon* DCM in other lakes is from Konopka's (1989). At each case *A. flos-aquae* population accumulated in the metalimnion at about the depth of the thermocline. In principle, *A. flos-aquae* is a common bloom-forming cyanobacterium and typical in eutrophic ecosystems (e.g. Yamamoto, 2009) in the temperate region. However, it provided a winter bloom and as disclosed in studies by Üveges et al. (2012), the species' remarkable ecophysiological plasticity enables it being successful either in cold and low light or warm and high light environments. At temperatures 5-20 °C its I_k ranged between $38-102 \mu\text{E m}^{-2} \text{s}^{-1}$.

Two of the above discussed species, *Planktothrix. rubescens* and *Cyanobium* sp., contributed to DCM in 1998, however, with spatial segregation: the light limited *Cyanobium* sp. in the metalimnetic and the P-limited *Planktothrix* in the upper hypolimnetic layer (Gervais et al., 1997; Padisák et al., 2003a). In the cited references spectral distribution of light, shape (greatest axial linear dimension, GALD) and S/V differences of the two species were used to explain limitation background. The population of the two species could coexist because of the spatial separation was supported by the different limiting factors.

As shown above, all the three species building up the DCM in Lake Stechlin in 2013 share a common feature: ability to photosynthesize and grow under low temperatures, however, none of them starts population increase in the DCM. A competitive advantage of *P. rubescens* population lies in the fact that, as starting growth after erosion of the thermocline in the previous year, the species can use the whole cold season with relatively good nutrient availability for growth. This pattern is observable in other lakes e.g. Lake Zürich (Micheletti et al., 1998) as well. Thus *P. rubescens* can accumulate nutrients in its biomass before the next DCM species, *Cyanobium* would start to grow. Then both species form upper hypolimnetic maxima with spatial segregation thus avoiding further competition for nutrients. Though *Aphanizomenon flos-aquae* may overwinter and existing populations can even bloom in winter, the akinetes need temperatures of 16-17 °C for germination (Gorzó, 1987). Therefore, in lack of perennial populations, population growth can start in late spring-early summer as observed in Lake Stechlin in most of the years and also supported by other studies (Wildman et al., 1975; Karlsson-Elfgren and Brunberg, 2004; Yamamoto and Nakahara, 2009). Such temperatures in Lake Stechlin develop in June, corresponding to mass appearance of *A. flos-aquae*. Its massive growth takes place first in the epi- then in the metalimnion and supported by its dinitrogen fixing ability, which represents an adaptive advantage against *Planktothrix rubescens* at DIN/SRP ratios < 16 (Teubner et al., 1999). The P demand of growth might have been sufficed by P stored in the akinetes as suggested in other studies (e.g. Barbiero and Kann, 1994).

Establishment of the *Aphanizomenon* DCM in the metalimnion imposed a substantial shade on the species forming DCM below and triggered different response. *Cyanobium* lifted from 15 m to 10 m thus avoiding light limitation and coexisted with *Aphanizomenon*. Due to the small cell volume, its SRP uptake might have been more efficient than that of *Aphanizomenon*, however, limitation by DIN was likely. In this metalimnetic layer, *Aphanizomenon* might have been limited both by SRP and light while *Cyanobium* by DIN which situation allowed relatively stable coexistence (Hardin, 1960). Since having lower I_k , light limitation of *Cyanobium* in the similar layer might be less severe as that of *Aphanizomenon*.

According to experiences with *Planktothrix* DCM in Lake Stechlin, the population occupies the deepest layer that is allowed by its low light demand to gain nutrients which, especially DIN, show an increasing trend along the hypolimnion. This depth was 20-25 m in 1998 (Padisák et al., 2003a) with light intensities of < 5 $\mu\text{E m}^{-2} \text{s}^{-1}$ in accordance with observations by Halstvedt et al. (2007) reporting on a stable *P. rubescens* at < 1 Wm^{-2} light intensity corresponding to 4.76 $\mu\text{mol m}^{-2} \text{s}^{-1}$. In May-June 2003, the population started to grow at similar depths as in 1998, however, after the *Aphanizomenon* and *Cyanobium* populations established in the metalimnion it emerged to 15 m, but growth remained suppressed. It allows concluding, that despite its extreme shade tolerance the *Planktothrix* population was limited by light as long as the metalimnetic populations prevailed. After decline of *Aphanizomenon* and *Cyanobium*, the *Planktothrix* population escaped of light limitation and started to grow. The increase of *Planktothrix* might have been due not only to growth, but also to entrainment by enlarging epilimnetic layers during the autumnal thermocline erosion.

As discussed above, growth of *Planktothrix rubescens*, *Aphanizomenon flos-aquae* and *Cyanobium* sp. could be limited by different environmental factors when all the three exhibited DCM: *Planktothrix* (despite its excellent shade tolerance) by light, *Aphanizomenon* (after an initial growth based on cellular P storage) by SRP and *Cyanobium* by DIN. Another species-specific feature might have contributed to the observed patterns: buoyancy regulation. Both *Cyanobium* and *Planktothrix* possess excellent buoyancy regulation mechanisms as being able to adjust their vertical position within the upper hypolimnion as shown in cases when only these two species contributed to DCM (Padisák et al., 2003a). During September 2013, the relative water column stability continuously decreased and it was paralleled by biomass decrease of *Aphanizomenon flos-aquae*. It suggests that *Aphanizomenon* probably uses the strong density gradient for maintaining its steady-state. It supports Camacho's hypothesis on the combined effect of the different DCM forming mechanisms (Camacho, 2006).

Deep chlorophyll maxima are typically provided by a single species being *Planktothrix rubescens* the best known and most studied freshwater example (Dokulil and Teubner, 2012; Akçalan et al., 2014; Hingsamer et al., 2014; Solis and Wojciechowska, 2014). The species appears to expand within its traditional NW European distributional range (Salmaso et al., 2014), additionally signals of radiation became also apparent for example by a massive bloom in a small, shallow pit pond (Vasas et al., 2013) in Hungary. Descriptions on spatial segregation of more than one species are rare, especially because such analyses need labour intensive microscopic countings with high spatial and temporal resolution. Fluorimetric methods offer an excellent opportunity to study DCM. In this study, both fluorimetry and microscopy were used to detect DCM, however, with somewhat different results. In the fluorimetric image, the metalimnetic DCM appeared very distinct which, nevertheless, was provided by two species (*Cyanobium* and *Aphanizomenon*) with different ecological adaptations and the upper hypolimnetic *Planktothrix* DCM remained hidden. Underlying reasons, though were not studied here, may involve different biomass specific pigment contents and different sensitivity of the fluoroprobe to detect phycoerythrin and phycocyanin, which depends on the calibration (Leboulanger et al., 2002). If only one species forms a DCM, with its simplicity and high spatial/temporal resolution, fluorimetry is an excellent study method. In cases of multispecies DCM, fluorimetric results with or without occasional sampling for species composition need care in interpretation because disregarding of different ecological adaptations of contributing species diminishes explanatory value of underlying factors (Barbiero and Tuchman, 2001), or may even lead to misinterpretations.

6. General discussion and further perspectives

6.1. Climate change and the phytoplankton community of Lake Stechlin

Number of papers dealing with climate change have been impressively increasing after the year 2000 and mainly after 2003, when a serious heat wave shocked Europe. Although no similarly hot summer was observed since this year, hotter summers and milder winters are forecasted in our area according to model predictions (IPCC, 2007).

The two main consequences of climate change are the changing air temperature and the amount and distribution of precipitations, which contribute to the increased number of extreme weather events. These changes obviously affect the abiotic environment of lakes, such as light climate (e.g. Beaver et al., 2013), stratification pattern (e.g. Danis et al., 2004) or the concentration of nutrients (Cantin et al., 2011). Numerous papers dealing with climate change focus on the effects of these changes on aquatic communities (Stewart et al., 2013).

In our case, mesocosm experiments were used to test the possible effects of climate change such as extreme weather events or the deepened epilimnion. At present, it is not possible to get general predictions about how climate change will affect the phytoplankton community in lakes as each aquatic ecosystem is unique, and can respond differently to the climate change due to the very high number of contributing or consequential environmental factors. However, from these experiments we can get some predictions concerning the phytoplankton community of Lake Stechlin. According to our results, extreme weather events will very likely have stronger effect on the phytoplankton community of Lake Stechlin, than the changing depth of epilimnion. During the experiment of extreme weather event a Cryptophyte (species in **X2** and **Y** codon) and later a Cyanobacteria (species in **H1** group) dominated community was observed (Chapter 5.1.4), thus our results confirm that these two groups have a good competitive abilities to become more and more abundant in Lake Stechlin in the future.

The high abundance of **H1** group in the summer assemblage has started after 2000 and it became the dominant group instead of the previous **L₀** codon after 2006 (Padisák et al., 2010), even taking part in the DCM (Chapter 5.4). The reason of the increasing abundance of **H1** is unclear, although it can be the effect of forestry management or the changing groundwater inflow, but these hypotheses have not yet been tested (Padisák et al., 2010). However, there are signs, that the mass appearance of **H1** group can be connected to the effects of climate change. The annual mean surface water temperature of Lake Stechlin increase significantly by 0.37 °C per decade clearly because of the climate change (Kirillin et al., 2013), thus appearance of those species are expected from southern climate zones (Parmesan, 2006), which has recruitment of warmer water temperature. In the near past, several invasive species were observed in north-eastern Germany, such as *Cylindrospermopsis raciborskii*, *Anabaena bergii* or *Aphanizomenon aphanizomenoides* (Stüken et al., 2006) Notice, that the current name of *Anabaena bergii* is *Chrysochloris bergii* (Zapomělová et al., 2012) and after a revision of *Aphanizomenon aphanizomenoides* became *Sphaerospermum aphanizomenoides* (Zapomělová et al., 2009). The origin of

Cylindrospermopsis raciborskii is the tropical region, but this species successfully could conquer the temperate zone and now it is widely distributed (Padisák, 1997). This species has a great physiological plasticity (Komárek and Komarková, 2003) and is able to produce akinetes, which features are very likely to play important roles in the expansion of *C. raciborskii*. The other two mentioned species have akinetes as well, thus they can survive unfavourable conditions too. According to Stüken et al. (2006) *C. raciborskii* and *Chrysochloris bergii* were found mainly in shallow waterbodies in north-eastern Germany, which supports the necessity of warm water temperature requirements of these species, but no any explanatory factor was revealed for expansion of *Sphaerospermum aphanizomenoides*. However, it is important to notice, that the deepest lake where *Cylindrospermopsis raciborskii* was registered is the dimictic Lake Scharmützel with a maximum depth of 29.5 m (Stüken et al., 2006). However, this lake has a shallow northern basin with a maximum depth of 7 m, thus stable stratification does not occur in this basin and this part of the lake behaves as a polymictic lake. This morphological condition is very likely a key factor for *C. raciborskii*, because this species is one of the typical representatives of S_N functional group (Reynolds et al., 2002), and this codon comprises several cyanobacteria taxa, which prefer warm mixed environments (Padisák et al., 2009). If we compare the morphometry of Lake Stechlin and Lake Scharmützel, we can recognize the strong difference of relief between the two lakes. The thermocline develops in Lake Stechlin around 8 meter, thus at 10 meter the water temperature is rarely warmer than 5°C – 6 °C. According to the bathymetric map (Fig. 1) less than 10% of the lake is shallower than 10 m, which is mostly in the littoral zone, plus a small bay in the eastern side of the lake, which reach the pelagic zone. The two most important factors for the akinete germination of numerous cyanobacteria are the proper light and temperature conditions (Fay, 1988; Baker and Bellifemine, 2000; Karlsson-Elfgren and Brunberg, 2004). The akinete germination of *C. raciborskii* is occurred at 22 °C in Lake Balaton (Padisák, 1997), however the high adaptability of the species (Dokulil, 2016) is shown by the occurrence of the vegetative filaments in North German lakes (Wiedner et al., 2007), where the water temperature was 15-17 °C, which indicate the germination at lower temperature. Tingwey (2009) reports akinete germination at 13°C, which one of the lowest available record, however, this results is still much higher, than at least the 90% of the sediment surface of Lake Stechlin. It is very likely, that resting propagules of this species reach Lake Stechlin, but because of the high relief of the lake, the appearance of *C. raciborskii* is not probable in the near future, in spite of the warming summer epilimnion, which could offer an adequate habitat for them. Additionally, we should notice if the epilimnion will strongly increase in the future, very likely it will offer a better condition for the germination of *C. raciborskii* and the other two mentioned species. Moreover the unusual weather events can help the propagation of these species, because, there are examples, when tropical species after unusual weather conditions become dominant such as in France (Cellamare et al., 2010), or in Lake Balaton in Hungary (Padisák, 1998; Padisák and Koncsos, 2002). Until now there is no documentation of *C. raciborskii* and *Chrysochloris bergii* from Lake Stechlin, however Ramm (2014) reported the appearance of *Sphaerospermum aphanizomenoides* in 2008 from Lake Stechlin, but during the last 8 years there was no any confirmation, thus this species probably hasn't got a stable population in the lake.

These 3 cyanobacteria species are able to produce toxins. Cylindrospermopsin or analogs produced by strains of *Cylindrospermopsis raciborskii* reported in numerous papers and Antunes et al. (2015) published a distribution map summarizing these observations. Cylindrospermopsin synthesis by strains of *Chrysochloris bergii* was reported by Schembri et al. (2001) from Australia and toxic *Sphaerospermum aphanizomenoides* was found in Lake Oued Mellah (Morocco) (Sabour et al., 2005). There is no information about toxin production of these two species in European waterbodies, thus it is unlikely, that if these species appear in Lake Stechlin, will produce toxins. However, there are several European lakes where toxins produced by *Cylindrospermopsis raciborskii* were registered, thus it is possible, but very pessimistic scenario, that if one day *C. raciborskii* appear in Lake Stechlin, may produce toxins as well.

The presence of potentially toxic cyanobacteria in Lake Stechlin is already proved by Mbedi et al. (2005). The found genes responsible for toxin production were related to the native *Planktothrix rubescens*. However, microcystins and microcystin genes were detected by Dadheech et al. (2014) (Chapter 5.3) in field samples of the lake for the first time. It is very important to notice that these toxins were produced by *P. rubescens* and *Microcystis aeruginosa*. In spite of these species were present with low abundance in the summer assemblage, toxins produced by them were measured, which confirm if a new, potentially toxin producer species, such as *Cylindrospermopsis raciborskii* appear in the lake, we can predict increasing amounts of toxins in Lake Stechlin. Thus, the continuous monitoring of phytoplankton community is very important, not just with fluorimetric methods, but with microscopic analyses (Chapter 5.4.4.), supplemented with toxicological analyses.

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9. Thesis points

1st Thesis point: Extreme weather events, which are able to reach and erode the thermocline can have drastic effects on the phytoplankton community of Lake Stechlin.

Depending on the speed of wind, increasing amount of nutrients, decreasing water temperature and decreasing amount of phytoplankton biomass will occur immediately after the weather event most probably. After the decreasing period, dominance of **X2** and **Y** functional groups are expected, following an **H1** codon dominance. Diatoms with mixing preferences can appear for short time, however after several shifts the phytoplankton community may return to its common successional sequence, which driven by seasonality. Additionally, this experiment highlights, that successional events during such periods are sensitive to the system memory in the sense that seed populations might get an opportunity to emerge.

2nd Thesis point: Deepened thermocline (with two meters) has a significant effect on the phytoplankton community.

The alteration of stratification caused multiple changes in the stratification pattern: the border of the hypolimnion and metalimnion sank, and in the epilimnion a weak, secondary thermocline developed. During the experiment **F**, **H1**, **X2**, **X3**, and **Y** were the most frequently occurring FG's, which showed up more than 90 % of the samples. However **R**, **H1** and **Y** were the most dominant ones. Small, but strongly significant ($P < 0.001$) differences were observed between the phytoplankton community composition of the treated and control enclosures. The most obvious difference between the control and treatment mesocosms is the high abundance of *Planktothrix rubescens* in the epilimnion of treatment and in the hypolimnion of control enclosures.

3rd Thesis point: The species number and biomass of cyanobacteria increase in Lake Stechlin that raise concern about potential toxicity.

Microcystin and microcystin producing genes were for the first time detected in environmental samples from Lake Stechlin according to toxicological and molecular analyses. It was proved, that toxins were produced by *Microcystis* cf. *aeruginosa* and *Planktothrix rubescens* present with low biomass, and not by the dominant *Dolichospermum circinale* and *Aphanizomenon flos-aquae*.

4th Thesis point: Equilibrium conditions can offer spatial- and niche segregation for DCM-forming cyanobacteria.

Rarely occurring deep chlorophyll maximum was observed in Lake Stechlin caused by three species: *Cyanobium* sp., *Planktothrix rubescens* and *Aphanizomenon flos-aquae*. *A. flos-aquae* and *Cyanobium* sp. caused a metalimnetic maximum and *Planktothrix rubescens* were observed in the hypolimnion. Growth of *Planktothrix rubescens*, *Aphanizomenon flos-aquae* and *Cyanobium* sp. could be limited by different environmental factors when all the three exhibited DCM: *Planktothrix* (despite its excellent shade tolerance) by light, *Aphanizomenon* (after an initial growth based on cellular P storage) by SRP and *Cyanobium* by DIN.

10. List of Publication

10.1. Publication related to the Dissertation

- Tapolczai K; Üveges V; **Selmeczy GB**; Peter C; Krienitz L; Padisák J (2013): Az Aphanizomenon flos-aquae vertikális eloszlása egy mély, oligo-mezotróf tóban: Stechlin-tó, Németország. Hidrológiai Közlöny 93/5-6: 75-77.
- Dadheech PK; **Selmeczy GB**; Vasas G; Padisak J; Arp W; Tapolczai K; Casper P; Krienitz L (2014): Presence of potentially toxin producing cyanobacteria in an oligo-mesotrophic lake in Baltic Lake District, Germany: An ecological, genetic and toxicological survey. TOXINS (BASEL) 6: 2912-2931. **IF 2.13/ Independent citation: 2**
- **Selmeczy GB**; Tapolczai K; Krienitz L; Casper P; Padisák J (2016): Spatial- and niche segregation of DCM forming cyanobacteria in Lake Stechlin (Germany). HYDROBIOLOGIA, 764: 229-240. **IF: 2.275**
- Kasprzak P; Shatwell T; Gessner MO; Gonsiorczyk T; Kirillin G; **Selmeczy GB**; Padisák J (submitted): Extreme weather event triggers cascade towards extreme turbidity in a clear-water lake, Ecosystems
- **Selmeczy GB**; Berger SA; Nejstgaard JC; Giling DP; Grossart HP; Kasprzak P; Casper P; Gessner MO; Padisák J (in prep): Simulating an extreme weather event in large mesocosms: changes phytoplankton community dynamics and an example of the memory effect
- Szabó B; Padisák J; **Selmeczy GB**; Krienitz L; Stenger-Kovács CS (submitted): Benthic diatom flora and its spatial and temporal patterns in Lake Stechlin, Germany, Turkish Journal of Botany
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10.2. Other publications

- Pék AS; **Selmeczy GB**; Balassa M; Padisák J; Kovács K (2010): Egy dombvidéki patak szakasz ökológiai állapotbecslése különböző módszerekkel, *Acta Biologica Debrecina, Supplementum Oecologica Hungarica Fasc. 21*: 163-175.
- Kovács K; **Selmeczy GB**; Kucserka T; Nassr-Allah H. Abdel-Hameid; Padisák J (2011): The effect of stream bed morphology on shredder abundance and leaf-litter decomposition in Hungarian midland streams, *Pol. J. Environ. Stud.* 20/6: 1547-1556. **IF: 0,888/ Independent citation: 4**
- **Selmeczy GB** (2011): Avarlebontási kísérletek dombvidéki kisvízfolyásokon, *Pannon Egyetem Mérnöki Kar, Bagoly Almanach.* pp. 106-115. ISBN: 978-615-5044-17-5.
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- Pálmai T; **Selmeczy GB**; Szabó B; G.-Tóth L; Padisák J (2016) A *Microcystis flos-aquae* fotoszintetikus aktivitása a Balaton keleti medencéjében 2015 nyarán. Hidrológiai Közlöny 96:75-78 .

10.3. Edition of books

- **Selmeczy GB**; Dr. Üveges Viktória (2012): XIII. Országos Felsőoktatási Környezettudományi Diákkonferencia Konferencia Kiadvány, Pannon Egyetem, Környezettudományi Intézet, Veszprém. ISBN: 978-615-5044-53-3.

11. Appendix

Table 9 Species list of the mesocosms in the experiments in 2013 and 2014

codon	Taxon	codon	Taxon
MP	<i>Achnanthes minutissima</i>	F	<i>Radiococcus</i> sp.
C	<i>Asterionella formosa</i>	J	<i>Scenedesmus aculeolatus</i>
C	Centrales 0-5	J	<i>Scenedesmus armatus</i>
A	Centrales 10-15	J	<i>Scenedesmus costato-granulatus</i>
B	Centrales 15-20	J	<i>Scenedesmus ecornis</i>
B	Centrales 20-25	J	<i>Scenedesmus</i> sp.
B	Centrales 25-30	X1	<i>Schroederia</i> big
B	Centrales 30-35	X1	<i>Schroederia</i> small
A	Centrales 5-10	X1	<i>Selenastrum</i> sp.
MP	<i>Cymbella</i> sp.	F	<i>Sphaerocystis</i> sp.
D	<i>Diatoma elongatum</i>	MP	<i>Spyrogyra</i> sp.
MP	<i>Epithemia</i> sp.	N	<i>Staurastrum cf. planktonicum</i>
MP	<i>Eunotia</i> sp.	N	<i>Staurastrum paradoxum</i>
P	<i>Fragilaria capucina</i>	J	<i>Tetraedron minimum</i>
P	<i>Fragilaria crotonensis</i>	W2	<i>Trachelomonas</i> sp.
P	<i>Fragilaria cyclosum</i>	F	<i>Treubaria</i> sp.
P	<i>Fragilaria</i> sp.	MP	<i>Ulothrix</i> sp.
MP	<i>Gyrosigma</i> sp.	F	<i>Westella botryoides</i>
MP	<i>Navicula</i> sp.	MP	<i>Zygnema</i> sp.
MP	<i>Rhopalodia gibba</i>	X2	Chryso crescent
D	<i>Synedra</i> sp.	X2	Chryso with long tail
D	<i>Synedra</i> sp. long	X2	Chrysocyst
D	<i>Synedra ulna</i>	X2	Chrysoflagellata
N	<i>Tabellaria fenestra</i>	E	<i>Dinobryon acuminatum</i>
X1	<i>Ankyra</i> sp.	E	<i>Dinobryon</i> cyst
X1	<i>Ankyra</i> sp. big	E	<i>Dinobryon divergens</i>
F	<i>Botryococcus braunii</i>	E	<i>Dinobryon sociale</i>
X2	<i>Carteria</i> sp.	X2	<i>Epipyxis</i> sp.
X1	<i>Chlamydomonas</i> sp.	X2	<i>Kephyrion</i> sp.
X1	<i>Chlorella</i> sp.	E	<i>Mallomonas</i> sp.
P	<i>Closterium aciculare</i>	X3	<i>Ochromonas</i> sp.
P	<i>Closterium acutum</i> var. <i>variable</i>	X2	<i>Pseudokephyrion ellipsoideum</i>
P	<i>Closterium cynthia</i>	X2	<i>Pseudopedinella</i>
P	<i>Closterium gracile</i>	Y	<i>Cryptomonas</i> sp. small
P	<i>Closterium</i> sp.	Y	<i>Cryptomonas</i> sp.
J	<i>Coelastrum</i> sp.	Y	<i>Cryptomonas</i> sp. huge
F	<i>Coenocystis polycocca</i>	X3	<i>Katablepharis ovalis</i>
N	<i>Cosmarium binoculatus</i>	X2	<i>Rhodomonas lacustris</i>
N	<i>Cosmarium botrytis</i>	X2	<i>Rhodomonas lens</i>
N	<i>Cosmarium granatum</i>	H1	<i>Aphanizomenon flos-aquae</i>

N	<i>Cosmarium meneghinii</i>	L0	<i>Aphanocapsa</i> sp.
N	<i>Cosmarium monoliforme</i> var. <i>monoliforme</i>	L0	<i>Chroococcus</i> sp. small
N	<i>Cosmarium phaseolus</i>	L0	<i>Chroococcus distans</i>
N	<i>Cosmarium reniforme</i>	L0	Cocoid cyano
N	<i>Cosmarium turpinii</i>	L0	<i>Coelosphaerium kuetzingianum</i>
J	<i>Crucigenia rectangularis</i>	S1	Cyano filament
F	<i>Elakatothrix gelatinosa</i>	S1	Cyano filament short
N	<i>Euastrum gemmatum</i>	H1	<i>Dolichospermum</i> sp.
G	<i>Eudorina</i> sp.	H1	<i>Dolichospermum akinete</i>
J	<i>Franceia</i> sp.	H1	<i>Dolichospermum circinalis</i>
J	<i>Golenkinia</i> sp.	H1	<i>Dolichospermum flos-aquae</i>
X1	Green colony	H1	<i>Dolichospermum lemmermanni</i>
X1	Green other	H1	<i>Dolichospermum macrospora</i>
F	<i>Kirchneriella aperta</i>	H1	<i>Dolichospermum mendotae</i>
J	<i>Lagerheimia</i> sp.	H1	<i>Dolichospermum planctonica</i>
X1	<i>Monoraphidium contortum</i>	H1	<i>Dolichospermum solitaria</i>
X1	<i>Monoraphidium griffithii</i>	MP	<i>Gloeocapsa</i> sp.
X1	<i>Monoraphidium</i> sp.	L0	<i>Merismopedia</i> sp.
MP	<i>Mougeotia</i> sp. thick	M	<i>Microcystis aeruginosa</i>
MP	<i>Mougeotia</i> sp. thin	L0	picocyano
F	<i>Nephrocystium limneticum</i>	S1	<i>Planktothrix agardhii</i>
F	<i>Oocystis borgei</i>	R	<i>Planktothrix rubescens</i>
F	<i>Oocystis lacustris</i>	S1	<i>Pseudanabaena</i> sp.
F	<i>Oocystis solitaria</i>	L0	<i>Radiocystis</i> sp.
G	<i>Pandorina morum</i>	X3	<i>Rhabdogloea scendesmoides</i>
J	<i>Pediastrum boryanum</i>	L0	<i>Ceratium</i> cyst
J	<i>Pediastrum duplex</i>	L0	<i>Ceratium hirundinella</i>
J	<i>Pediastrum integrum</i>	Y	<i>Glenodinium</i> sp.
J	<i>Pediastrum tetras</i>	X3	<i>Gymnodinium helveticum</i>
X _{ph}	<i>Phacotus lenticularis</i>	X3	<i>Gymnodinium lacustre</i>
F	<i>Planktosphaeria</i> sp.	L0	<i>Peridinium aciculiferum</i>
F	<i>Pseudosphaerocystis</i> sp.	L0	<i>Peridinium</i> sp.
X1	<i>Pseudotetraedriella kamillae</i>	X2	<i>Chrysocromulina parva</i>
F	<i>Quadrigula pfitzerii</i>	X1	<i>Trachydiscus sexangulatus</i>