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Phytoplankton response to experimental thermocline deepening: a mesocosm experiment

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Abstract

A number of modelling results suggested thermocline shifts as a consequence of global climate change in stratifying lakes. Abundance and composition of the phytoplankton assemblage is strongly affected by the stratification patterns, therefore, change in the thermocline position might have a substantial effect on this community or even on the whole lake ecosystem. In this study, thermocline depths in large mesocosms installed in Lake Stechlin (Germany) were deepened by 2 meters and phytoplankton changes were analysed by comparing changes to untreated mesocosms. Higher amounts of SRP were registered in the hypolimnion of treatment mesocosms than in the controls, and there were no differences in the epilimnion. Small but significant changes were observed on the phytoplankton community composition related to the effect of deepening the thermocline; however, it was weaker than the yearly successional changes. The most remarkable differences were caused by *Planktothrix rubescens* and by chlorophytes. *P. rubescens* became strongly dominant at the end of the experiment in the mesocosms, and in the open lake as well. The results of the experiment cannot clearly support the proliferation of cyanobacteria in general; however, the deepened thermocline can modify the behaviour of some species, as was observed in case of *P. rubescens*.

Introduction

Global climate change has a significant effect both on terrestrial and aquatic ecosystems and its consequences will accelerate in the future (IPCC, 2007; IPCC, 2013). One of the most significant effects of climate change on phytoplankton communities in stratifying lakes will be presumably related to changes in stratification patterns. 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). Several key variables, which are driving the phytoplankton community assembly 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 in itself results in complex physical and chemical gradients, which increase the heterogeneity of the water column, thus increase habitat heterogeneity (Selmeczy et al., 2016). The turbulence is supressed in a stratified waterbody (Turner, 1979), which favours motile

(Gervais, 1997) or buoyant phytoplankton species (Huisman et al., 2004) and negatively affects most planktonic diatoms with high sinking rates (Reynolds, 2006) and also some green algal species (Huisman et al., 2004). Thus, it is expected that mainly because of the physical processes altered by climate change diatoms and other non-motile species will be replaced by other groups, which are able to cope with reduced mixing (Findlay et al., 2001). Though in a few other cases diatoms dominated over other taxonomic groups (Winder et al., 2009; Medeiros et al., 2015) in stratifying lakes, according to most of the scenarios increase of cyanobacteria is foreseen.

Cyanobacteria have several unique abilities to surpass other taxonomic groups in different environments affected by climate change. The most important eco-physiological features, which help them to adapt to 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 of akinete production, (vi) very good light harvesting in a wide range of wavelengths by chromatic adaptation, (vii) good UV resistance (Ehling-Schulz and Scherer, 1999; Carey et al., 2012), (viii) high level of ecophysiological plasticity (Üveges et al., 2011) and different antipredator properties. Obviously, not all cyanobacteria species possess all 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. Increase of dominance of cyanobacteria as a consequence of climate change has been an overall emerging issue in phytoplankton ecology (Salmaso et al., 2015; Sukenik et al., 2015).

The main goal of the joint experiment was to mimic a deepened thermocline during the summer stratification in large size mesocosms and to follow the changes in the food web and matter transport (Fuchs et al., 2017). This study tries to 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?

Materials and methods

Lake Stechlin is a dimictic, meso-oligotrophic, hardwater lake in Northern Germany, which is one of the best studied lakes in the region. The mean depth of the lake is 23.3 m, the maximum depth is 69.5 m, and the surface are is 4.25 km^2 (Casper, 1985). The phytoplankton community of Lake Stechlin has been studied since 1959, however, regular surveys are performed only from 1994 (Padisák et al. 2010). Seasonal patterns of the phytoplankton show a bimodal distribution. The spring assemblages are dominated by species of Codon **B** (such as *Stephanodiscus neoastraea* Håkansson & Hickel) and the most common species during summer belong to the **H1** and **Lo** coda in the epilimnion. In most years, the metalimnion and/or upper hypolimnion is dominated by picocyanobacteria species (codon **Z**), although in some years *Planktothrix rubescens* (De Candolle ex Gomont) Anagnostidis & Komárek population (codon **R**) were present in the upper hypolimnion with significant biomass (Padisák et al. 2010; Selmeczy et al., 2016).

An experimental setup consisting of 24 large-sized enclosures and a central reservoir was built in the south basin of Lake Stechlin (Bauchrowitz, 2012). This facility is called “LakeLab” (http://www.lake-lab.de). 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 horizontal under the LakeLab, the depths of the enclosures vary between 17 and 20 m. Twelve enclosures were randomly selected for the experiments from Fields I-III (Fig. 1). Prior to the experiment, water exchange was performed in all mesocosms to ensure the possible highest similarity. The thermocline was deepened by 2 m experimentally in 6 of 12 mesocosms; the other six mesocosms served as controls. The water exchange and the alteration of the stratification was performed by submerged pumps (SUPS 4-12-5, SPECK Pumpen Verkaufsgesellschaft GmbH, Neunkirchen am Sand, Germany) transporting nearly 6 $m^3 h^{-1}$ of water via aluminium release rings. The graphical design of the system is found in Fuchs et al. (2017). During the experiment surface water was pumped down to a given depth only during daytime to allow the natural cooling over nights. During the first month, rhythm of pumping activity was 8 h per day, then until the end of the experiment it was increased to 12 h per day. In the control mesocosms, aluminium rings were placed in the depth of the lake's thermocline in order to affect equally all systems by pumping activities. The depth of the release rings were moved 1 m down at 24 July, 25 July and 04 September to follow the natural thermocline depth in the lake.

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, OH, USA) and PAR sensors. These data were recorded in half a meter increments from the surface (0.5 m) to the bottom in every hour. Integrated water samples were taken on 25 June, 10 July, 23 July, 06 August, 20 August, and 11 September 2013 both from the epi- and hypolimnion using an integrated water sampler (IWS II, Volume: 5L, Hydro-Bios, Kiel, Germany). Concentrations of TP, SRP, TN, NO_2^-, NO_3^-, NH_4^+ and SRSi were measured according to APHA (1998) in these samples. 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). Samples for phytoplankton analyses were taken on 25 June, 23 July, 20 August 2013. These samples were preserved in Lugol's solution and were stored in a dark at room temperature. Phytoplankton numbers were determined with the classical methodology by Utermöhl (1958) and Lund et al. (1958). Altogether 400 settling units (cells, filaments and colonies) were counted at minimum in each sample using an inverted microscope (Zeiss Axiovert 100, Oberkochen, Germany). 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 mm^3L^{-1} = 1 mgL^{-1} conversion factor. Opticount cell counting software (Opticount, 2008) was used to estimate the biomass. Phytoplankton species were sorted into different functional groups (FG) according the classification of Reynolds et al. (2002) and Padisák et al. (2009).

Analysis of variance using distance matrices was used to test how depth (epilimnion or hypolimnion), month of the sampling (June, July, August) and treatment (control, treatment) influence the community composition using function ADONIS in R software (R Core Team, 2015). 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.

Results

The alteration of the thermocline depth resulted in multiple changes in the stratification pattern: the border between hypolimnion and metalimnion sank, and according to the temperature the epilimnion had two parts. The temperature of upper part (from the surface until 4 meter) was homogenous and the lower part had a small temperature decrease until metalimnion. The temperature was rather smooth in the epilimnion of control mesocosms. The typical temperature profile of the treatment and control mesocosms are shown in Fig. 2. Similar patterns were observed in the control and treatment mesocosms related to SRP values: at the beginning, the amounts of SRP fall near to the detection limit in both in the epilimnion and hypolimnion, later SRP in the epilimnion remained low during the whole experiment, but it increased in the hypolimnion after mid-July. In spite of the similar pattern, the medians of SRP were higher in the hypolimnion of treatment mesocosms compared to the controls (Fig. 3), however there were no significant differences between the treatment and control mesocosms according to t-test analyses. 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. 4). Later, 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 decreased in the epilimnion and alternated in the hypolimnion.

Altogether 78 samples were analysed and 130 taxa were found in these samples. Species can be categorised in 21 functional groups of which **F**, **H1**, **X2**, **X3**, and **Y** were the most frequently occurring FGs present in 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 1.

Cryptophytes were the most dominant phytoplankton group in the epilimnetic samples at the beginning of the experiment (Fig. 5 A, C). Later 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. The biomass of cyanobacteria showed increasing pattern during the experiment, and reached the highest amount during August as well.

Maximum abundance of cryptophytes was registered during July in the hypolimnion of both types of mesocosms (Fig. 5 B, D). Biomass of dinoflagellates showed increasing pattern in the treatment and control mesocosms as well. Similar amount of Chlorophytes were present in the two types of mesocosms 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 chrysophytes were observed in negligible amounts. Diatoms occurred rarely in our experiment, although higher amounts were registered in the hypolimnetic samples but remaining below 12% of the total biomass.

The changes of the seven most dominant functional groups are shown on Figure 6. At the beginning, **H1**, **X2** and **Y** coda dominated in the epilimnetic samples. The abundance of the latter was higher in the epilimnion of control mesocosms, than in the treatment one (Fig. 6 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 high amounts 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 and started to increase from the beginning of the experiment and became the most dominant by 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 in the hypolimnion. However, in the epilimnia *P. rubescens* reached 8% (32.9±62.2) in the control mesocosms and 44% (342.3±381.6) in the treatment enclosures (Fig. 7). This difference was significant according to Wilcoxon test: W=2, p=0.03175.

Phacotus lenticularis (Ehrenberg) Deising was the only member of $\mathbf{X_{Ph}}$ codon, and did not belong to the frequently occurring functional groups. However, during July it became the dominant member of the phytoplankton community in mesocosm T6; while remaining low in other mesocosms (not shown) and nearly disappeared from T6 during August. Thus this codon caused the highest uncertainty during the experiment.

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 2). INDVAL analyses were performed to investigate, which functional groups indicate the different categories of months, depths and treatment (Table 3). Six functional groups (**X2**, **L_0**, **X1**, **Y**, **F** and **H1)** were indicators of epilimnetic samples and 3 coda (**R**, **X3** and **C)** were indicators of hypolimnetic samples (Fig. 8). Interestingly, INDVAL did not find any indicator codon for treatment or control mesocosms.

NMDS analyses (Fig. 9) were carried out to visualize differences between samples belonging 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.

Discussion

The heat-balance of lakes is determined basically by meteorological forcing at the air-water interface, therefore, it is possible to raise general predictions for 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 and chemical changes as well. For example, both shrinking and deepening of thermoclines were predicted and observed in a number of studies. Model predictions for four Finish lakes suggested thermocline deepening in three cases and a shallower thermocline in one case (Elo et al., 1998). In North-temperate lakes in Wisconsin (USA), analyses of 10-year 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 Canadian boreal lakes 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 increase in Secchi-depths was the consequence of decreasing DOC level because of the less precipitation runoff caused by longer periods of droughts.

The general findings of numerous studies is that warmer air temperatures result in warmer surface water temperature and this layer of warmer and lighter water weakens wind induced mixing, thus shallower and warmer epilimnia are predicted in the future (Robertson and Ragotzkie, 1990; King et al., 1997; Vincent, 2009; De Senerpont Domis et al., 2013). 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 the reasons remained unrevealed. Straile et al. (2003) and Livingstone (2003) analysed long dataset from deep European lakes (Lake Constance and Lake Zürich) 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 quite 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 deepened by 2 meters 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 position of the 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. Moreover, the amounts of chlorophytes were higher in the epilimnion of control mesocosms during the last month, as a consequence of the considerable abundance of **F** and **MP** coda.

Similar, but more spectacular results were found by Cantin et al. (2011) 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 towards dominance of chlorophytes in the epilimnion in response to thermocline deepening. In our experiment we did not observe this phenomenon, although green algae belonging to codon **F**, such as *Oocystis lacustris* Chodat, frequently occurred in epilimnetic samples, and reached higher biomass in the control mesocosms.

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 the increase of diatoms, because this group never exceeded a 12% contribution to the total biomass, though in more than 80% of the samples the SRSi concentration was higher than 0.1 mgL^{-1} but none of them was higher than 0.5 mgL^{-1}. According to Reynolds (2006) silica concentration below 0.5 mgL^{-1} begins to interfere the growth of diatoms, but the growth-limiting threshold is 0.1 mgL^{-1} or less in most lacustrine environments. Sommer (1988) reviewed a number of experimental and field observations and concluded that the limitation is strongly species-specific and ranges between 0.9 μM Si (~0.023 mgL^{-1}) and 20 μM Si (~0.5 mgL^{-1}). Others indicate 0.5 mgL^{-1} as limitation threshold for *Asterionella formosa* Hassall, (Lund, 1950; Vaccari et al., 2006), which was the most dominant diatom species during our experiment.

At beginning of the experiment cryptophytes were the dominant taxonomic group in all the epilimnetic samples in the treatment and control mesocosms as well, which can be explained by the effect of pumping activity which can be considered as a kind of disturbance. This group can be prominent in post-stratification community or can peaks after disturbances such as precipitation periods or wind activity (Reynolds and Reynolds, 1985; Bicudo et al., 2009). During July cryptophytes increased in the hypolimnetic samples and decreased in the epilimnion. The epilimnetic decline could be related to the increasing zooplankton grazing and may the deepened thermocline favoured to cryptophytes to increase their biomass in the hypolimnion. Cryptophytes can have competitive advantage there, because in case of deeper thermocline the nutrient-rich hypolimnion has lower light levels, which they can utilize with special pigments such as carotene or phycoerythrin (Gervais, 1997) or they can compensate with mixotrophic strategy (Cantin et al., 2011). However, the reason of the cryptophytes increase was most probably their disturbance tolerance.

Planktothrix rubescens is an important member of the phytoplankton community of Lake Stechlin for a long time (Krieger, 1927). The abundance of this species is commonly low, however, if the circumstances are appropriate it can become the dominant taxon in the lake, such as in 1998 (Padisák et al., 2003) or in the year of this study (2013) (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 deep-chlorophyll maximum (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 a more or less 10-15 meter thick water layer available for DCM formation. If the thermocline will 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 flosaquae* Ralfs ex Bornet & Flahault, 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, 2003; Selmeczy et al., 2016) mainly spatially separated from the population of *Planktothrix rubescens*. However, if the thermocline depth will increase, the amount of available light will decrease, which basically influences the community of DCM forming species. Consequently, *P. rubescens* may outcompete the above mentioned species, if the thermocline depth increases until a certain point, because *P. rubescens*, can utilize low light levels much more effectively than either *Aphanizomenon flosaquae* or *Cyanobium* sp. Additionally, *Planktothrix rubescens* can produce cyanotoxins in Lake Stechlin (Dadheech et al., 2014), which justifies the necessity of regular monitoring of the species. In spite of the typical characteristic of this species, according to our experiment *P. rubescens* can be a good competitor in the epilimnion as well, because during August it became the dominant species in the epilimnion of treatment mesocosms. This phenomenon is interesting, because it was rarely described (e.g. Anneville et al., 2014) that higher or at least comparable biomass of *P. rubescens* occurred in the epilimnion, as in the meta,- or upper hypolimnion in case of deep lakes. A possible explanation is that the lower part of epilimnion offered good conditions for *P. rubescens*. This zone had a slightly lower temperature compared to the same depths of the control mesocosms, however, because of the lack of samples from different depth increments, it is not possible to confirm this hypotheses.

IndVal analyses did not detect any functional group which would be specific to the phytoplankton assemblage of either the treatment or the control mesocosms, however statistically significant differences were registered between them. Thus, the differences between the two communities related to numerous smaller or bigger differences in the proportion of different functional groups, instead of emerging one or few groups, which are present just in one type of mesocosms. However, on species level, significant difference was found related to the biomass of *P. rubescens,* but only in the epilimnetic samples during August. This was the most remarkable difference, which was registered during end of the experiment and this can be explained by the high resilience of the community. Additionally, according to IndVal analyses the temporal changes (different months) and different depths have a stronger effect on the community, than the altered thermocline.

As a conclusion, the artificial deepening of the thermocline led to small, but significant changes in the epilimnetic phytoplankton community: higher level of biomass of *Planktothix rubescens* (codon **R**) and lower amounts of coda **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 a deepened thermocline, because in 2013, when the study was conducted, *P. rubescens* were present with high biomass during the whole vegetation period, similarly to 1998 (Padisák et al., 2010), therefore presumably the summer phytoplankton assemblage was considerably affected by *P. rubescens*.

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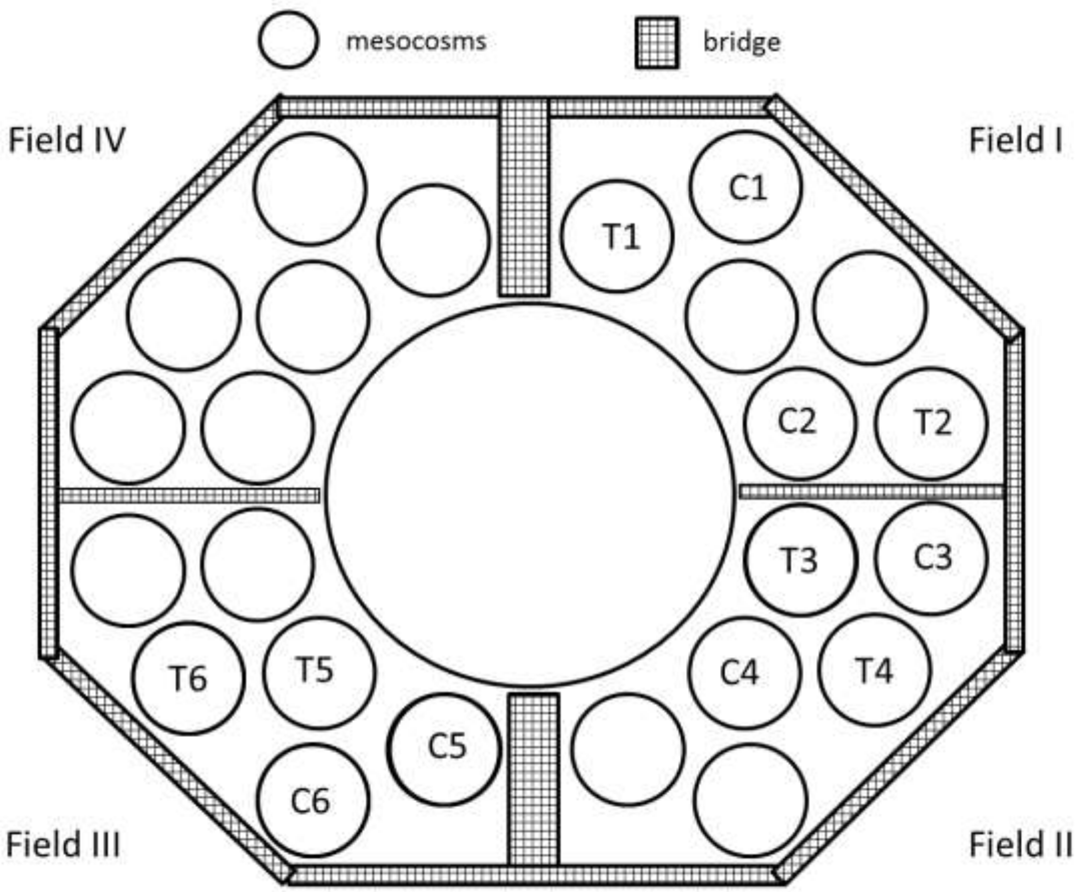

Fig. 1 Lake Lab platform with the experimental design, C1, C2, C3, C4, C5, C6 indicate control mesocosms and T1, T2, T3, T4, T5, T6 indicate treated mesocosms

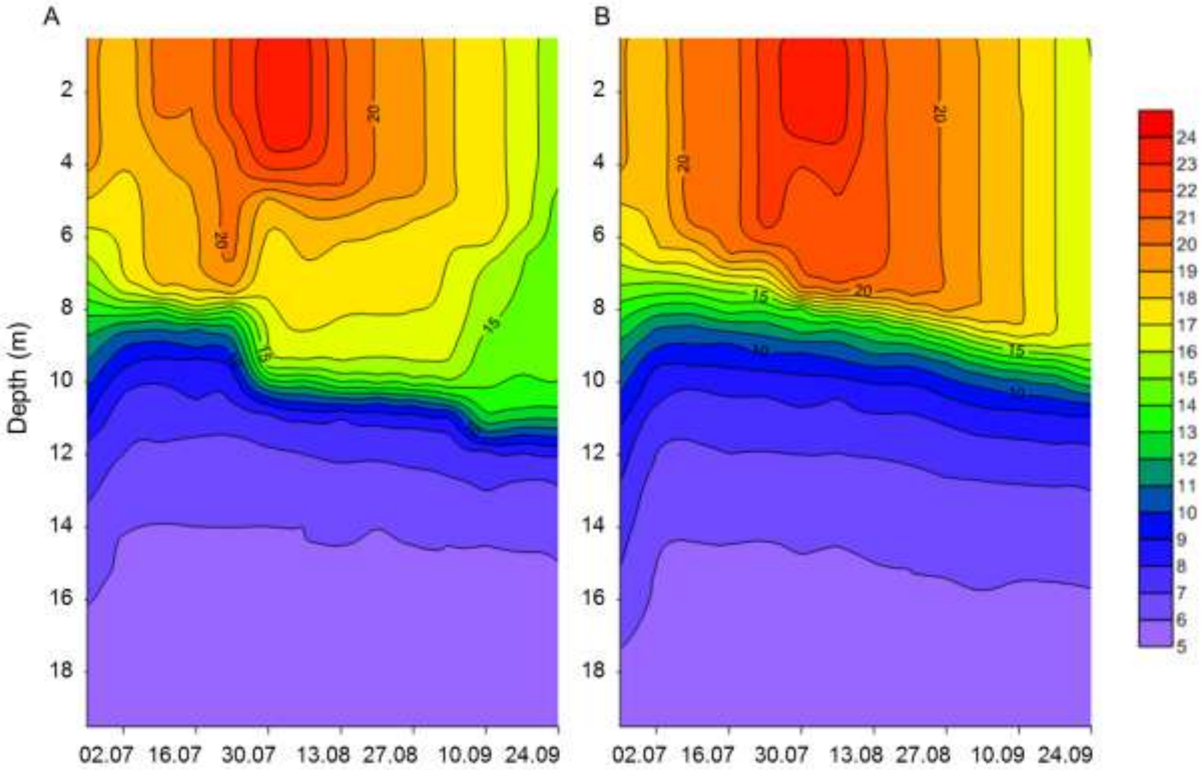

Fig. 2 Typical temperature profiles of treatment (A) and control (B) mesocosms established in Lake Stechlin between 25 June 2013 and 24 September 2013

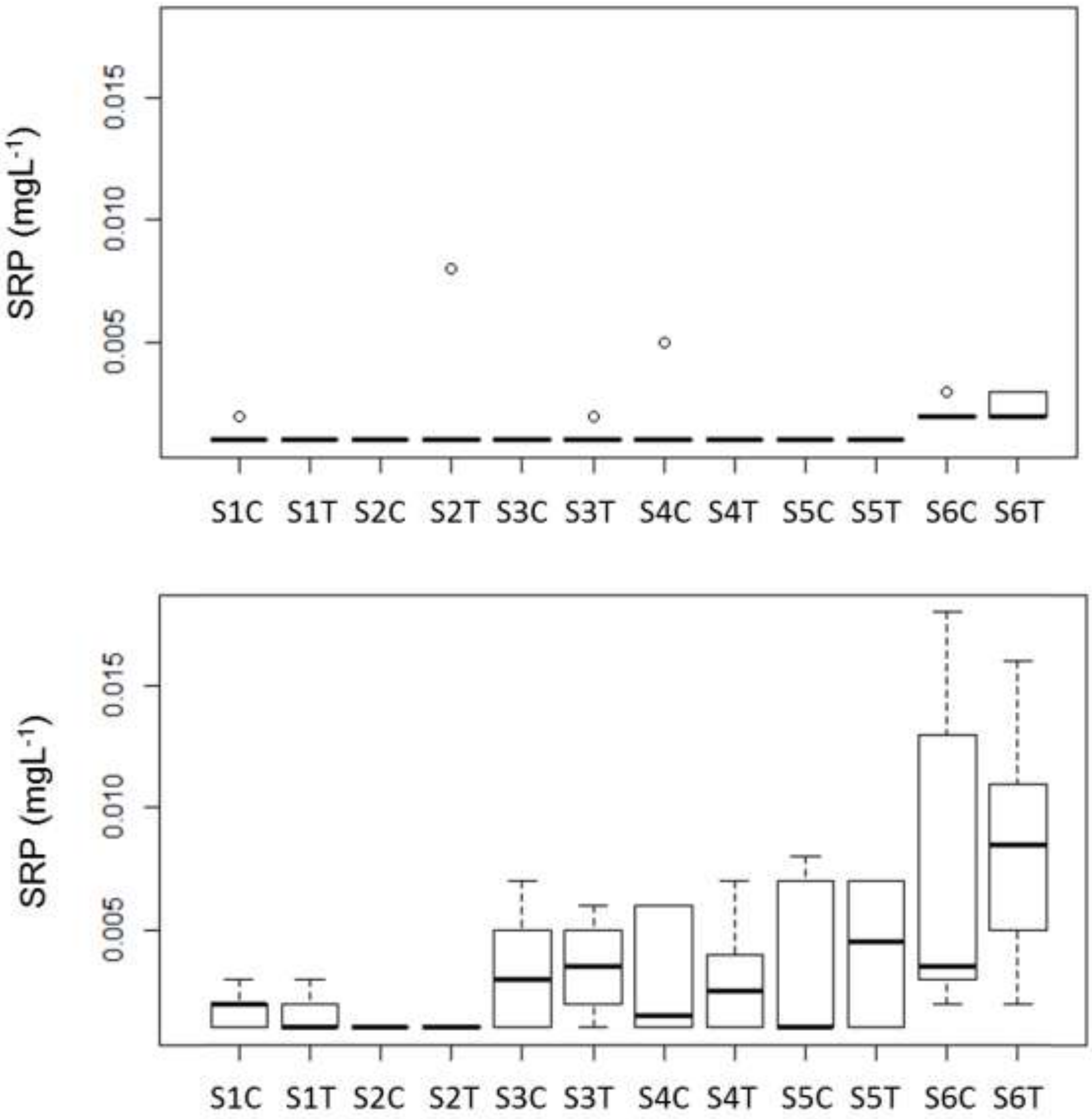

Fig. 3 Boxplots of SRP values during the experiment in the epilimnion (upper panel) and in the hypolimnion (lower panel), S1: 29 May, S2: 25 June, S3: 10 July, S4: 23 July, S5: 06 August, S6: 20 August; C indicates control, T indicates treatment mesocosms

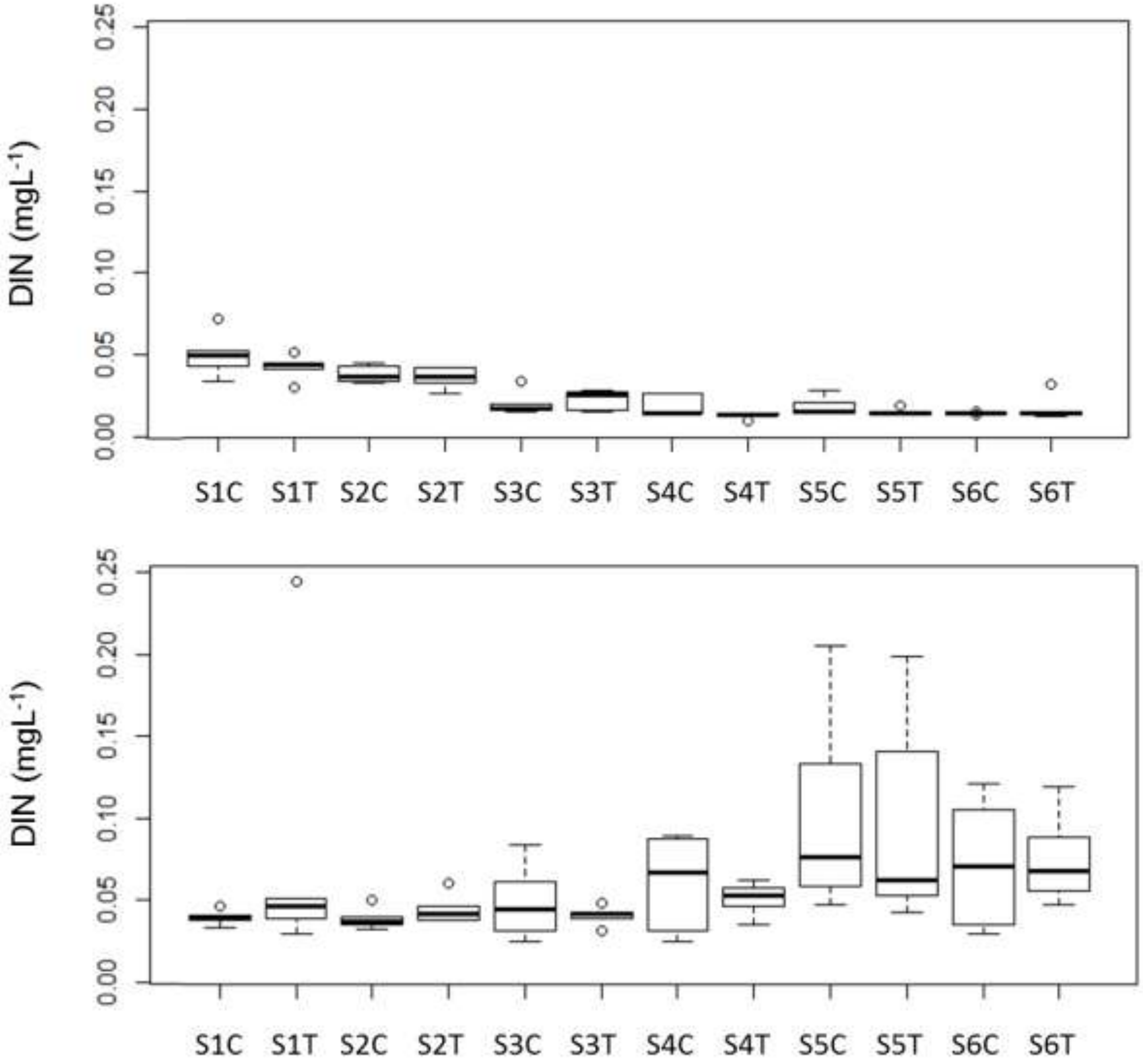

Fig. 4 Boxplots of DIN values during the experiment in the epilimnion (upper panel) and in the hypolimnion (lower panel), S1: 29 May, S2: 25 June, S3: 10 July, S4: 23 July, S5: 06 August, S6: 20 August; C indicates control, T indicates treatment mesocosms

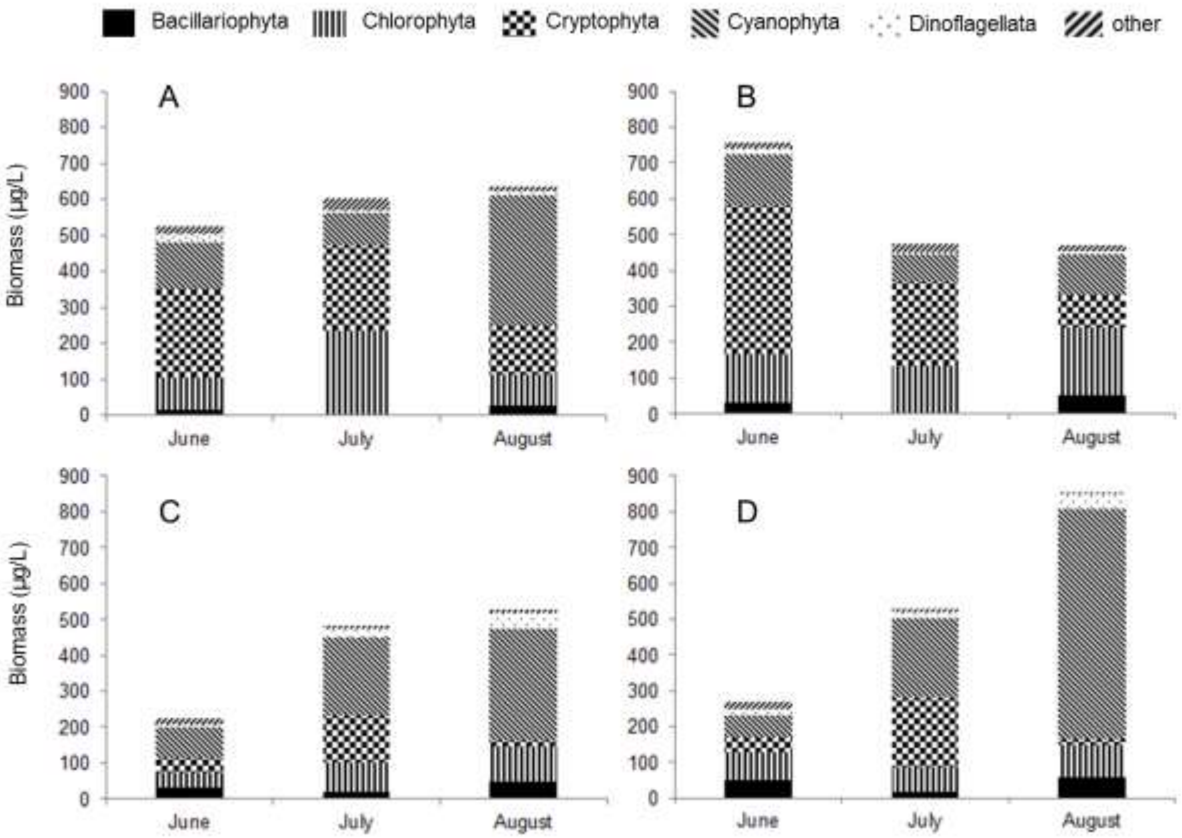

Fig. 5 Average biomass of the different taxonomical groups during the experiment (A: Epilimnion of treatment mesocosms, B: Hypolimnion of treatment mesocosms, C: Epilimnion of control mesocosms, D: Hypolimnion of control mesocosms)

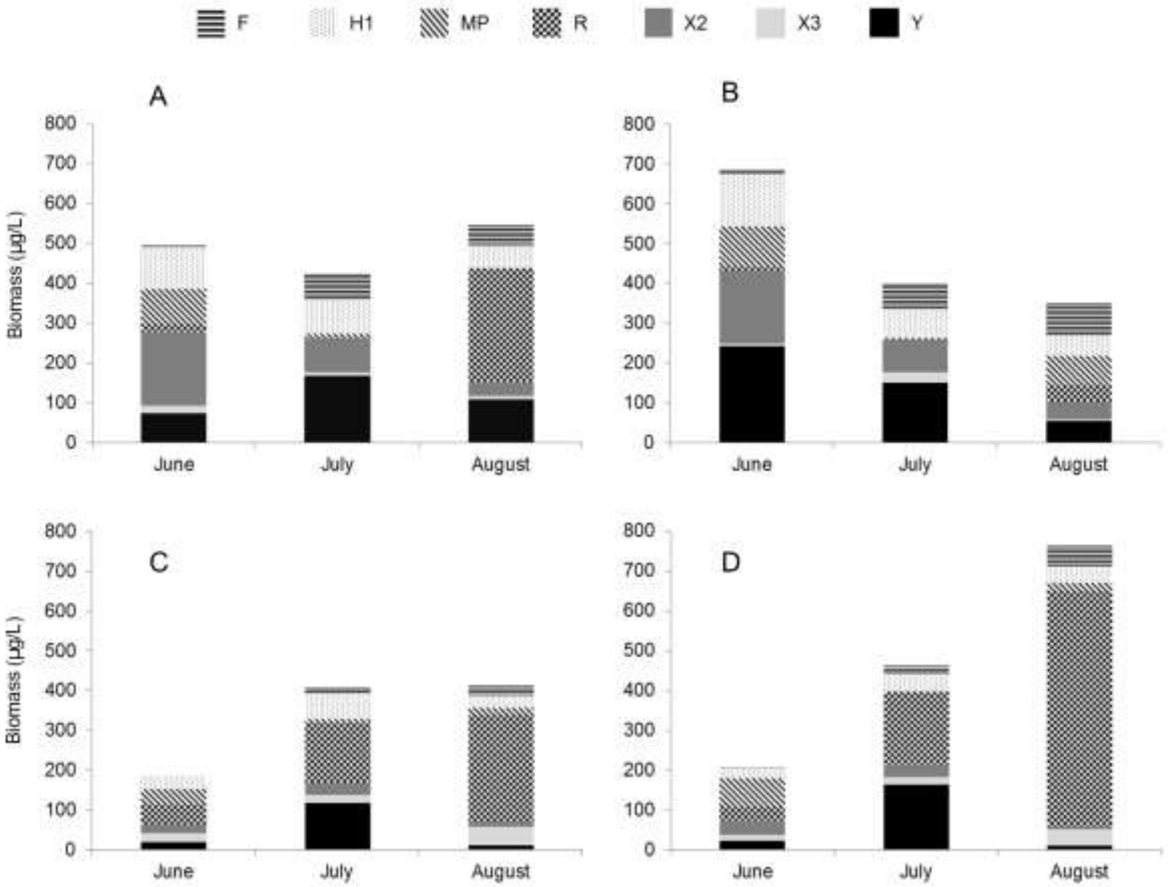

Fig. 6 Average biomass of the most dominant functional groups during the experiment (A: Epilimnion of treatment mesocosms, B: Hypolimnion of treatment mesocosms, C: Epilimnion of control mesocosms, D: Hypolimnion of control mesocosms)

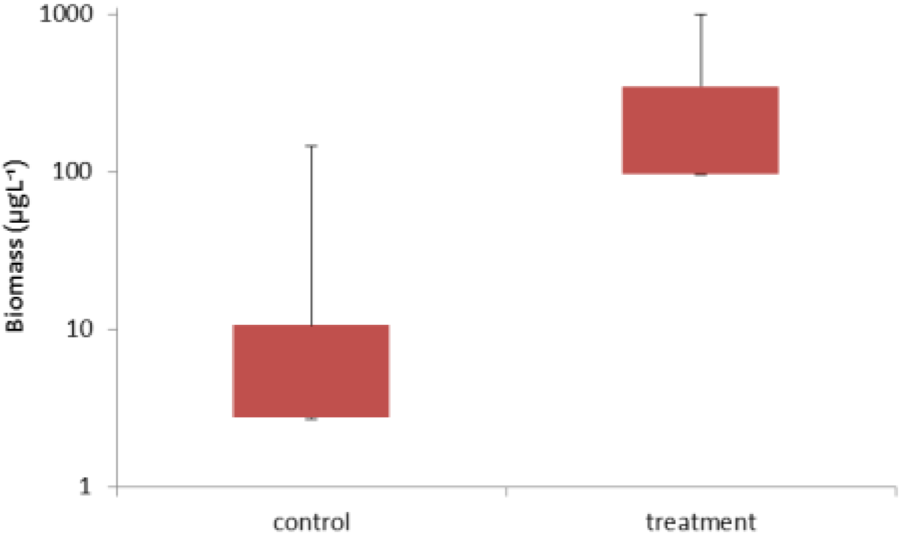

Fig. 7 Boxplots of biomass (µgL^{-1}) of *Planktothrix rubescens* in epilimnion during August

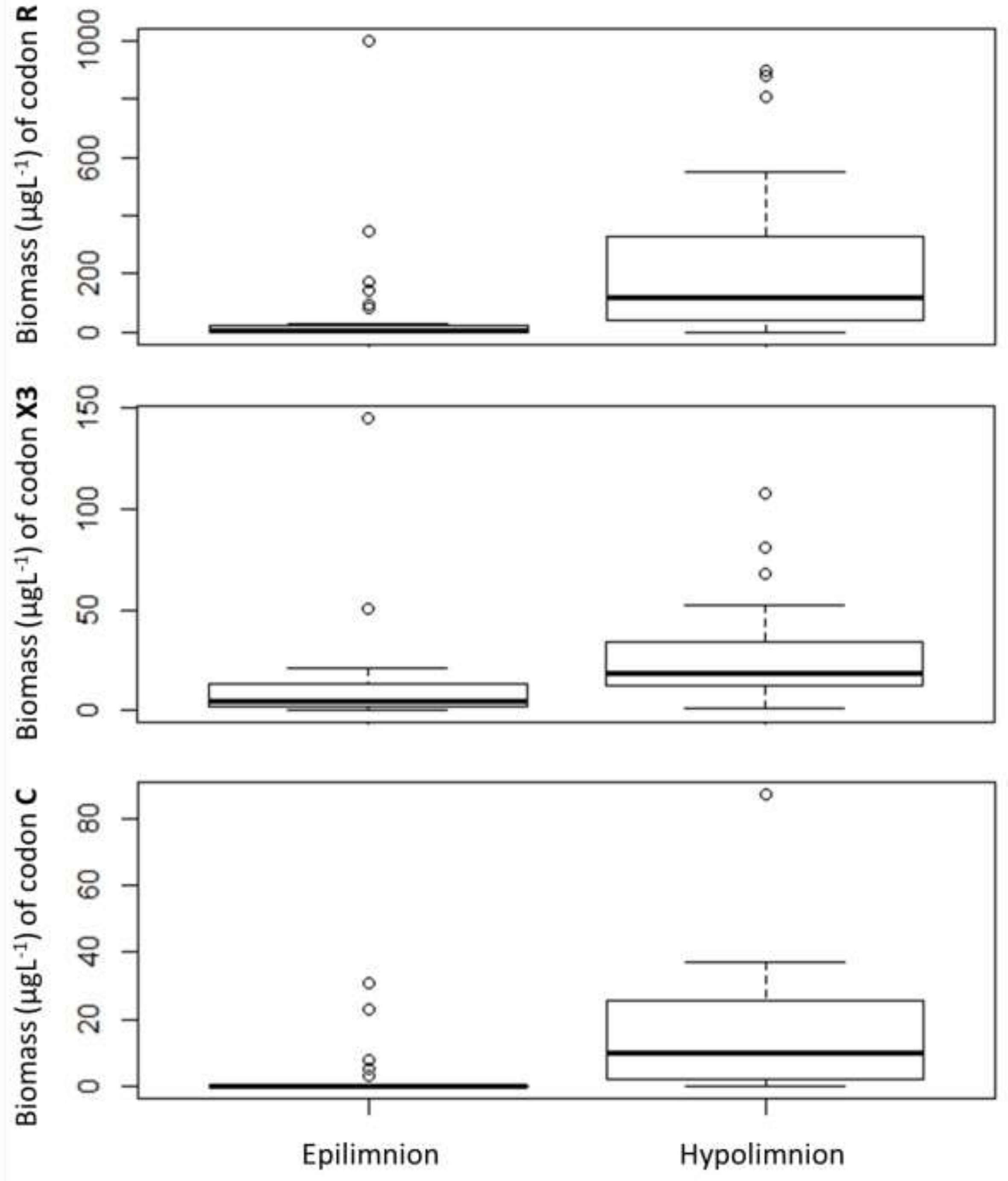

Fig. 8 Boxplots of biomass (μgL^{-1}) of coda **C**, **X3** and **R** in epilimnetic and hypolimnetic samples

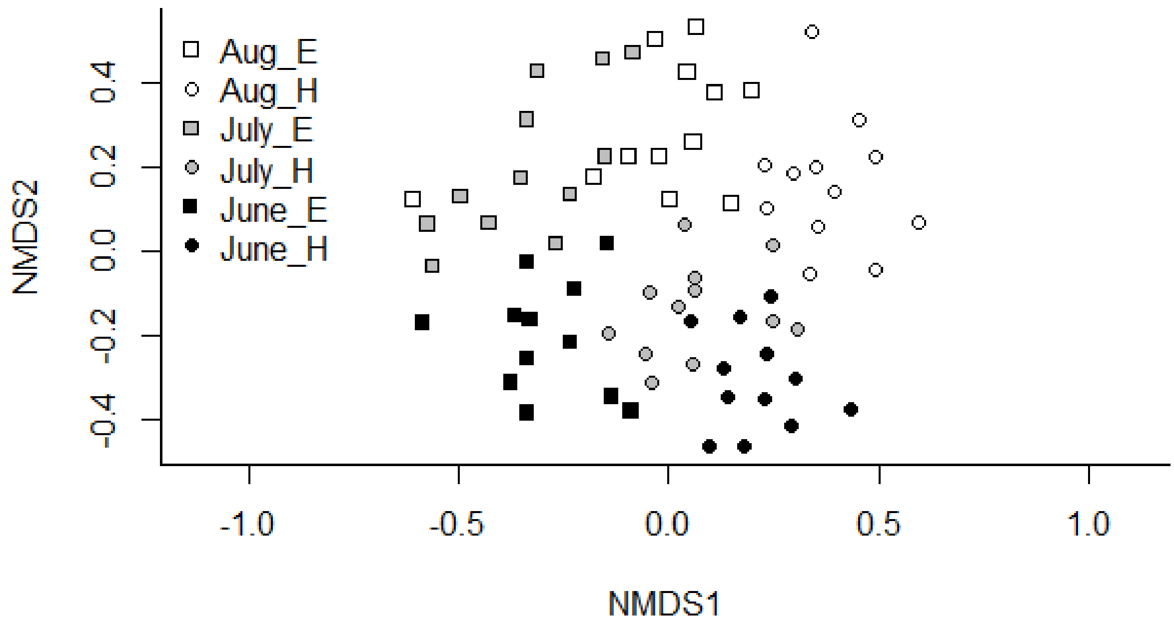

Fig. 9 NMDS ordination diagram based on the functional group composition of the samples. E= Epilimnetic samples, H=Hypolimnetic samples

Table 1 Most important representatives of the main functional groups with their typical habitat template according to Padisák et al. (2009)

Functional group	Typical habitat template	Dominant species
F	Clear, deeply mixed meso-eutrophic lakes	*Oocystis lacustris* Chodat *Coenochloris polycocca* (Korshikov) Hindák
H1	Eutrophic, both stratified and shallow lakes with low nitrogen content	*Aphanizomenon flosaquae* Ralfs ex Bornet & Flahault *Dolichospermum circinale* (Rabenhorst ex Bornet & Flahault) P. Wacklin, L. Hoffmann & J. Komárek *Dolichospermum solitarium* (Klebahn) Wacklin, L. Hoffmann & Komárek
X2	Shallow, meso-eutrophic environments	*Rhodomonas lacustris* Pascher & Ruttner *Rhodomonas lens* Pascher & Ruttner *Chrysocromulina parva* Lackey
X3	Shallow, well mixed oligotrophic environments	*Katablepharis ovalis* Skuja *Gymnodinium helveticum* Penard
Y	Almost all lentic ecosystems when grazing pressure is low	*Cryptomonas* sp.
R	In the metalimnion or upper hypolimnion of deep oligo-mesotrophic lakes	*Planktothrix rubescens* (De Candolle ex Gomont) Anagnostidis & Komárek

Table 2 Summary of analyses of variance using distance matrices (ADONIS) testing the individual and joint effects of month, treatment and depth on community composition. Significant factors are highlighted in bold.

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	

Table 3 Summary of IndVal analyses

Codon	Indication	Indicator value	P
X2	Epilimnion	0.81	0.001
$\mathbf{L_0}$	Epilimnion	0.81	0.001
X1	Epilimnion	0.71	0.004
Y	Epilimnion	0.70	0.004
F	Epilimnion	0.67	0.041
H1	Epilimnion	0.63	0.039
R	Hypolimnion	0.76	0.001
X3	Hypolimnion	0.70	0.002
C	Hypolimnion	0.69	0.001
MP	June	0.62	0.001
X2	June	0.56	0.001
C	June	0.39	0.009
Y	July	0.52	0.001
$\mathbf{X_{Ph}}$	July	0.52	0.007
A	August	0.76	0.001
R	August	0.72	0.001
J	August	0.62	0.009
P	August	0.56	0.001
$\mathbf{L_0}$	August	0.52	0.020
F	August	0.52	0.031