

## Drivers of the *Ceratium hirundinella* and *Microcystis aeruginosa* coexistence in a drinking water reservoir

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### ABSTRACT

#### Drivers of the *Ceratium hirundinella* and *Microcystis aeruginosa* coexistence in a drinking water reservoir

The spatial and temporal patterns of phytoplankton in relation to physical and chemical properties were studied in a drinking water reservoir - the Lázberc Reservoir - located in north-east Hungary. The main objectives were to determine the role of the hydrologic regime in structuring algal growth and the effects of physical and chemical variables on the coexistence of a dominant species: cyanobacteria, *Microcystis aeruginosa* (Kützing) Kützing and an eukaryotic dinoflagellates, *Ceratium hirundinella* (O.F. Müller) Dujardin. The results suggest that nutrients (TP, NH<sub>4</sub>-N and NO<sub>3</sub>-N), turbidity, and the hydrologic regime play an important role in regulating the occurrence of investigated species. The rainy summer period resulting in a mixing of the water column, and the low level of nitrogen coupled with the internal release of phosphorus from the lake sediment under brief periods of anoxia promote cyanobacterial bloom.

During this period, the water column was characterised by high turbidity, which created favourable conditions for developing a huge *C. hirundinella* biomass and the simultaneous occurrence of *M. aeruginosa*. This study also demonstrated - that contrary to what was previously known, deep standing waters in the temperate zone are not only dimictic (mixing twice a year during the spring and the fall), but they can also be mixed during the summer period due to continued rainfall, which equalizes the temperature in the whole water column. This can promote the occurrence of cyanobacterial and eukaryote planktonic organisms.

**Key words:** *Microcystis aeruginosa*, *Ceratium hirundinella*, phosphorus, seasonal variation, water management, lake-poly-mixis in temperate zone

### RESUMO

#### Efeito da flor de *Ceratium hirundinella* e *Microcystis aeruginosa* no reservatório de água potável

Os padrões espaciais e temporais do fitoplâncton e sua correlação com as especificidades variáveis físicas e químicas, foram examinados no nordeste da Hungria, localizados em um reservatório típico de água potável no reservatório de Lázberc. Nosso principal objetivo foi para esclarecer o papel da hidrologia, e os diferentes especificidades físicas e químicas na coexistência de espécies dominantes: cianobactéria, *Microcystis aeruginosa* (Kützing) Kützing e Dinoflagellata eucariótica, *Ceratium hirundinella* (OF Müller) Dujardin. De acordo com os resultados, os nutrientes (TP, NH<sub>4</sub>-N, NO<sub>3</sub>-N), turbidez e os condições hidrológicas desempenham um papel importante na regulação da ocorrência das espécies examinadas. O período de verão chuvoso que resulta um equilíbrio do nível da água, o baixo nível de nitrogênio, juntamente com a liberação interna de fósforo do sedimento, durante um curto período anóxico promove a floração de cianobactérias. Durante este período, a coluna de água foi caracterizada por alta turbidez, criando condições favoráveis para o surgimento de uma enorme expansão da biomassa.

sa *C. hirundinella* e a aparição simultânea de *M. aeruginosa*. Este estudo mostrou também que as águas profundas nas áreas da zona moderada, não tem apenas dimictic especialidade (misturando duas vezes por ano, na primavera e no outono), mas também durante a estação do verão pode ser misturada por chuvas contínuas que compensam a temperatura em toda a coluna da água. Isso ajuda a presença de cianobactérias e organismos eucariotas planctônicos.

**Palavras chave:** *Microcystis aeruginosa*, *Ceratium hirundinella*, fósforo, variação sazonal, manejo da água, lago-polimixis em zona temperada

## INTRODUCTION

Over recent years it has become clear that eutrophication is a significant problem in many freshwater reservoirs used as drinking water supply. Eutrophication includes high levels of chlorophyll-*a* (Boyn-ton *et al.*, 1982; Nixon & Pilson, 1983; Conley & Malone, 1992), excessive macrophyte biomass and algal blooms, the occurrence of anoxia and hypoxia (Gerlach, 1990), and harmful and toxic algal blooms (Franks, 1997; Seda *et al.*, 2000; Oudra *et al.*, 2002; Jeppesen *et al.*, 2015).

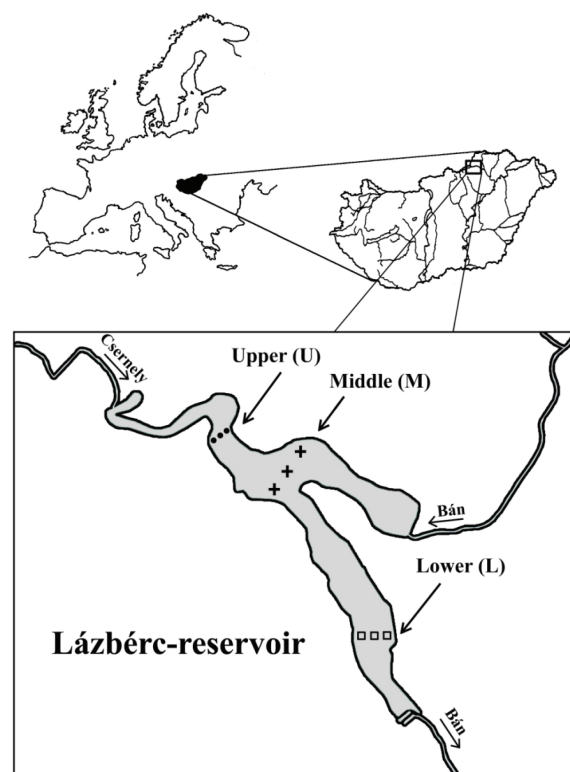
The understanding of the factors behind the abundance patterns of microbial species in nature are a central issue in environmental sciences. Planktonic microorganisms, as the primary producers, can mirror changes in aquatic ecosystems and carry the basic information needed to assess the trophic status and water quality of aquatic environments. In freshwater phytoplankton assemblages, it is often observed that the phytoplankton undergoes a series of seasonal changes in individual numbers and biomass, as well as shifts in composition. Succession has acquired a wide meaning in plankton ecology, covering the pattern of annual development, and the sequential changes in species dominance (Smayda, 1980). Planktonic microorganism development occurs at different temporal scales: eg. short-term variations induced by local weather are driven by stochastic disturbances, while annual variations lead to seasonal succession. Their development is the outcome of the interplay between both internal community-directed processes and external forcing (Kiss, 1996; Reynolds, 2000; Reynolds, 2003), and at the same time, abiotic and biotic factors. Nutrient enrichment often leads to increases in microbial biomass (Jones & Knowlton, 1993), and in particular cyanobacterial production and dominance (van

Liere & Walsby, 1982; Izaguirre, 1992; Izaguirre *et al.*, 1998, 2007; Bouvy *et al.*, 2003; Izydorczyk *et al.*, 2009; Noyma *et al.*, 2016).

*C. hirundinella* is also widespread in lakes and ponds in temperate regions. It is often dominates the warm water period and at times also results in blooms also. (Reynolds 1976, Heaney 1976), However there has been little investigation on its population dynamics in reservoirs. Based on a literature review, *C. hirundinella* is a ubiquitous, relatively large and slow-growing species characteristically found during late summer in reservoirs, and in water bodies with a warm stable epilimnion and low nutrient concentrations (Nicolls *et al.*, 1980; Whittington *et al.*, 2000; Inkel *et al.*, 2001; Pérez-Martínez & Sánchez-Castillo, 2001, 2002; Grigorszky *et al.*, 2003). Under these low-turbulence conditions, its ability to undertake significant diel vertical migration enables an optimal exploitation of light and nutrients – two essential resources – whose availability contrasts directly in the vertical dimension during stratification (Heaney, 1976; Heaney & Furnass, 1980; James *et al.*, 1992; Whittington *et al.*, 2000). The seasonal periodicity of *C. hirundinella* is variable. Pérez-Martínez and Sánchez-Castillo (2001) reported clear winter maxima for an array of Spanish reservoirs, but subsequently further highlighted the variability of its occurrence, as reported in the literature. Notwithstanding its putative advantage at low nutrient levels (Whittington *et al.*, 2000), *C. hirundinella* also occurs in eutrophic lakes (e.g. Frempong, 1984), and was typified as a component of late-summer phytoplankton associations in oligotrophic, mesotrophic and eutrophic temperate waters (Reynolds, 1996). In South Africa, *Ceratium* blooms have been recorded in 17 of 57 reservoirs (van Ginkel *et al.*, 2007). Among these reservoirs, blooms occurred in all

seasons and across the trophic status range. These studies show that *C. hirundinella* is a common organism in different seasons and in different trophic statuses, but no precise explanation is yet available for its occurrence. Furthermore, although the two species *M. aeruginosa* and *C. hirundinella* are frequently found together, accurate explanations for their co-occurrence are still lacking. However, the turbid conditions created by the heavy rain and the wind disturbance may have been more favorable for cyanobacterial growth since some taxa have a greater tolerance for turbid conditions (Kosten *et al.*, 2011). In addition, there may have been a positive feedback in the reservoirs with the increased biovolume of cyanobacteria caused by diel vertical migration promoting more turbid conditions, which in turn, enhanced cyanobacterial growth (Kosten *et al.*, 2011). Presing (1996) found that low light conditions created by cyanobacterial blooms facilitated their persistence. Nuisance cyanobacterial blooms are common in drinking water reservoirs and have been associated with the occurrence of objectionable taste and odor events (Saadoun 1999; Smith *et al.*, 2002). *Microcystis aeruginosa* is one of the dominant species of cyanobacteria that form surface water blooms in eutrophic lakes and has received much attention as a result of the water management problems associated with its blooms (Dokulil & Teubner 2000). The distribution and abundance of *M. aeruginosa* are to a large extent affected by factors such as light and nutrient availability acting synergistically with other physical and chemical factors. Nitrogen and phosphorus are generally considered to be the main nutrients for algal growth in temperate standing waters. It has been suggested that the lower ratio between these two nutrients may promote the development of cyanobacterial blooms (Smith, 1983). There is also an interesting theory, accompanied by some investigations that positively buoyant cyanobacteria, such as *Microcystis*, have an ecological advantage in light-limited waters due to buoyancy regulation (Huisman *et al.*, 2004;). Therefore it is thought that low light and low nitrate concentrations may create conditions more favourable to the dominance of *M. aeruginosa*. However, little information is available about the

combined effects of nitrogen, phosphorus concentration, and light intensity on population dynamics and coexistence with other population of *M. aeruginosa*. We conducted a field experiment to evaluate the nutrient concentrations and the hydrological regime in combination with light intensities on the growth/coexistence of *C. hirundinella* and *M. aeruginosa* in a drinking water reservoir. The objectives of this study were to determine (i) temporal and spatial patterns in the relationships between water quality and cyanobacterial and dinoflagellates growth, (ii) the role of the hydrologic regime in structuring cyanobacterial growth and (iii) which variables make it possible for the two dominant taxa, *M. aeruginosa* (cyanobacteria) and *C. hirundinella* (eukaryotic alga, dinoflagellate), to coexist. In addition, we discuss the implication of our results with respect to management strategies for the Lázbérci Reservoir and drinking water reservoirs in general.



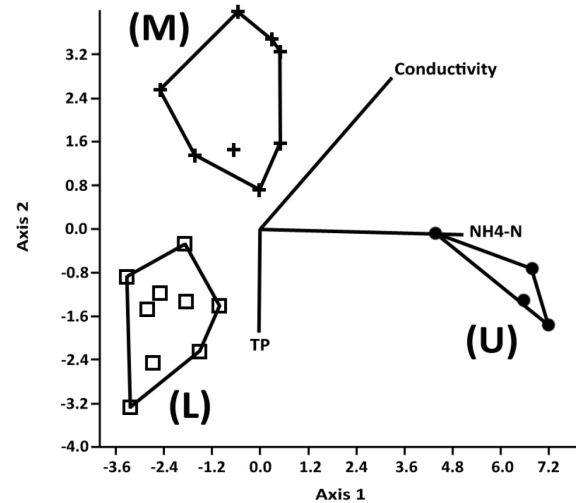
**Figure 1.** Sampling sites at the studied Lázbérci Reservoir. *Locais de amostragem no reservatório de Lázbérc.*

## MATERIAL AND METHODS

Lázbérci Reservoir is located in the North-Eastern part of Hungary, in a low mountain region (48.1226 ° N, 20.2752 °E, Fig. 1). It was constructed in period between 1967 and 1969 to assure the drinking water supply for the fast-growing region of North-Hungary. The reservoir volume is 5.9 million m<sup>3</sup>. Its average depth is 7.5 m and its maximum depth is 17.2 m. The reservoir has a surface area of 77 ha that can be extended to 92.2 ha during flood control operations. The 23.9 km long Bán Stream and the 17.2 km long Csernelly Stream flow into the reservoir. The retention time of the reservoir is approximately 1 year. The watershed encompasses nearly 217.5 ha. Annual precipitation in the reservoir area was 806 mm in 2007 and 911 mm in 2008. The average annual precipitation in Hungary is 500-700 mm. The temperature reached its maximum value in July, in both years. By contrast, wind intensity increased in spring (April–June) and late summer to autumn (September to November). Reservoirs exhibit distinct longitudinal gradients in their physical, chemical, and biological properties due to their “river-lake hybrid” nature. In order to characterize these gradients, nine sampling sites based on lake morphology (i.e., location and depth) were selected and divided into three general categories (upper, middle and lower regions, Fig.1).

Each of the nine sampling sites was sampled monthly from April to November. A 2 L Van-Dorn sampler was used to collect water samples at a series of discrete depths that were determined by the maximum depth at each site (surface/0.25 m, 1.5 m, 3 m, 6 m, 9 m and 12 m). Phytoplankton counting was done according to Utermöhl (1931) in an inverted microscope (Axiovert-100). At least 400 units were counted giving a counting accuracy, expressed in terms of 95 % confidence limits of, < 10 % for the whole phytoplankton. The phytoplankton biomass determination was based on the calculation of the species volume.

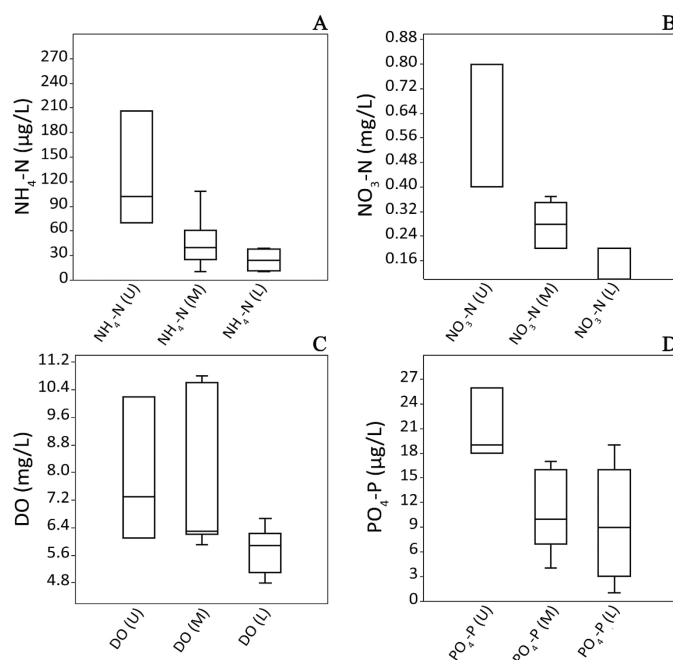
Samples for NO<sub>3</sub>-N, NO<sub>2</sub>-N, NH<sub>4</sub>-N, and PO<sub>4</sub>-P were filtered through ion chromatography acrodisc 0.45 µm filters before analysis. Temperature, conductivity, oxygen, pH were measured when sampling. Total nitrogen (TN) and total



**Figure 2.** Canonical Variate Analysis (CVA) of the sampling sites in correspondence with environmental variables in Lázbérc Reservoir. Canonical Variate 1 was significant ( $p < 0.0001$ ) and comprised 74.76 % of the total variation. Canonical Variate 2 was also significant ( $p < 0.0001$ ) and comprised 25.24 % of the total variation. (• = no species; + = *C. hirundinella* only; □ = *M. aeruginosa* and *C. hirundinella*). *Análise canônica multivariada (AVC) dos locais de amostragem em ligação de variáveis ambientais do reservatório Lázbérc. A variação canônica 1 foi significativa ( $p < 0.0001$ ) e 74.76 % da variação total. A variação canônica 2 também foi significativa ( $p < 0.0001$ ) e contém 25.24 % da variação total. (• = Nenhuma espécie; + = apenas *C. hirundinella*; □ = *M. aeruginosa* e *C. hirundinella*).*

phosphorus (TP) concentrations were determined using photometric procedures (Ebina *et al.*, 1983). The total alkalinity was measured titrimetrically (APHA, 1995). All laboratory analysis was performed within 48 hours of sample collection. The concentration of chlorophyll-*a*, corrected for pheophytin-*a*, was determined photometrically.

The Shapiro-Wilks test was used to analyze the normality of conductivity, TP and NH<sub>4</sub> within the groups. Multivariate normality conditions for the multivariate Canonical Variate Analysis (CVA) were analysed by the Mardia test for conductivity, TP and NH<sub>4</sub>. Since the latter test gave very similar results to the normal distribution, the upper, middle and lower parts of the reservoir were compared by CVA. The groups were compared with one-way ANOVA and Tukey post hoc (normal distribution) tests, or with the Kruskal-Wallis and Mann-Whitney tests (non-normal distribution).



**Figure 3.** The physical and chemical variables in the various parts of the reservoir (U = upper region, M = middle region, L = lower region): A,  $\text{NH}_4\text{-N}$ ; B,  $\text{NO}_3\text{-N}$ ; C, dissolved oxygen; D,  $\text{PO}_4\text{-P}$ . *Especialidades físicas e químicas estudadas em três regiões do reservatório (U = região superior, M = região média, L = região inferior): A,  $\text{NH}_4$ ; B,  $\text{NO}_3\text{-N}$ ; C oxigênio dissolvido; D,  $\text{PO}_4\text{-P}$ .*

## RESULTS

The CVA of the biomass of *M. aeruginosa* and *C. hirundinella* as regards to Total Phosphorous (TP), ammonium-ion ( $\text{NH}_4\text{-N}$ ) and conductivity showed that the studied sites of the reservoir could be divided into three different groups (Fig. 2). Sampling sites, – the upper part of the reservoir, U – with high concentrations of ammonium-ion correlated with sites where neither *M. aeruginosa* nor *C. hirundinella* was present. The second group of sampling sites – middle part of the reservoir, M – was characterized by high conductivity and the presence of *C. hirundinella* only. The third group contained locations – the lower part of the reservoir, L –, where both species were present, and where the principle of separation was based on the low phosphorous content.

Based on the average concentrations of ammonium-ion, nitrate-ion and orthophosphate-ion the sampling sites were split into two groups (Fig. 3). The first group was composed of upper region samples with no presence of *C. hirundinella* or *M.*

*aeruginosa* and with high concentration of the ammonium-ion, nitrate-ion and orthophosphate-ion. The second group represented sites from the middle and lower regions where *C. hirundinella* occurred on its own or sites where both species were found. In the second group the ammonium-ion, nitrite ion and orthophosphate-ion concentrations were low (Fig. 3),

Based on the average concentrations of dissolved oxygen, the sampling sites were split into two groups (Fig. 3C). Higher dissolved oxygen concentrations characterized sites where neither of the two species occurred or sites where *C. hirundinella* occurred on its own. Lower dissolved oxygen concentrations were measured at sites where both species were found.

Furthermore, we examined the variables that were influential in terms of the co-occurrence of the two species in the lower part of the reservoir, especially concerning the low dissolved oxygen concentrations. In May, dissolved oxygen levels were low (0-3 mg/L) in the lower regions (below 9 m depth) of the reservoir (Fig. 4A). In June and

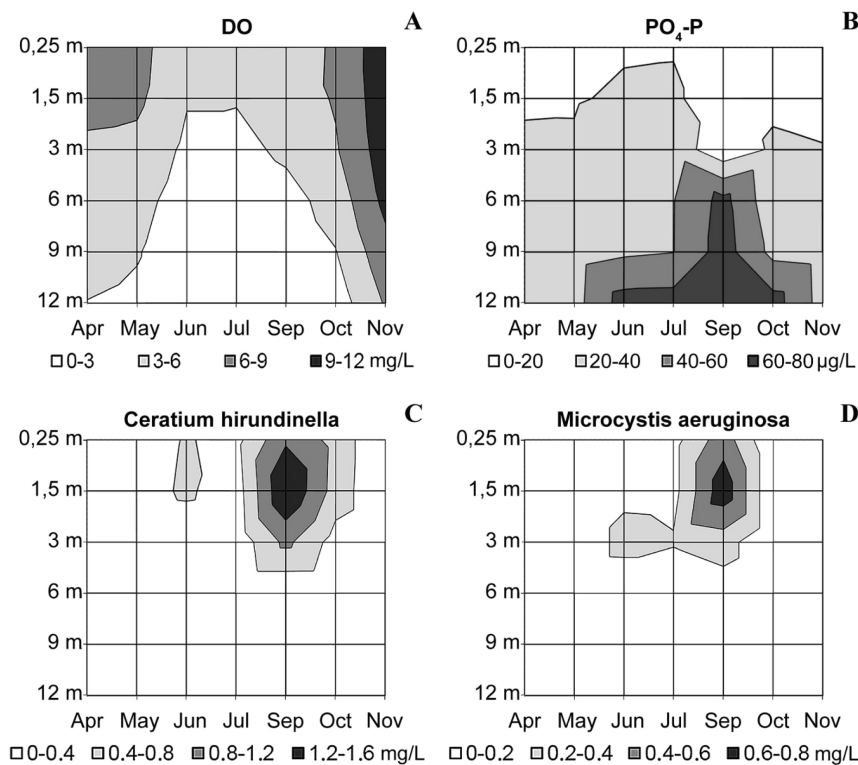


July, the low oxygen content became characteristic of shallower depths, up to 1.5 m. By September, this low oxygen zone descended again below 3 m, and continued to descend below 9 m in October. In November, the dissolved oxygen content of the entire water column was significantly higher. In May and June, the orthophosphate-ion concentration was typically low both close to the surface and in deeper water layers (Fig. 4B). The observed orthophosphate-ion concentration increase in June and July was almost characteristic for the entire water column (Fig. 4B). In September, the orthophosphate deficient water layer was sank down to a depth of about 4 meters (Fig. 4B), while this layer was characterized by a mass occurrence of the examined species (Fig. 4. C, D). In April and May, *C. hirundinella* did not occur at any depth (Fig. 4C). In June, there was a minor occurrence of the species at the upper two

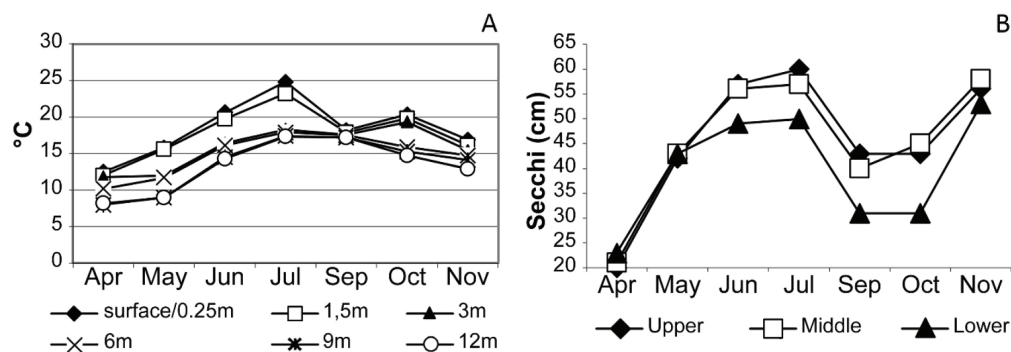
sampling depths, while it disappeared again in July. In September, the *C. hirundinella* biomass became significant in all three upper sampling depths, reaching the maximum value of the study period at 1.5 m (1.6 mg/L). In October, *C. hirundinella* only occurred at the upper two sampling depths with a low biomass.

In April and May, *M. aeruginosa* did not occur at any depth (Fig. 4D). In June, the species occurred at the 3 m depth in moderate numbers, which remained the same in July. In September, the biomass of *M. aeruginosa* increased significantly at all depths down to 3 m, reaching the maximum value (0.8 mg/L) at 1.5 m. The species did not occur in October and November.

In April, water temperature was at its minimum. All layers of water reached their maximum values in July. By this time, the temperature of the near-surface and the 1.5 m layer was higher



**Figure 4.** The dissolved oxygen (A), PO<sub>4</sub>-P (B), biomass of *C. hirundinella* (C) and *M. aeruginosa* (D) at various depth in the lower region of the reservoir. *O teor de oxigênio dissolvido (A), PO<sub>4</sub>-P (B), o C. hirundinella (C) e o M. aeruginosa (D) biomassa em diferentes profundidades na parte inferior (L) do reservatório.*



**Figure 5.** Temperature and transparency changes of the reservoir: A) temperature changes at various depths in the lower region of the reservoir (L); B) Secchi depth changes in the various regions of the reservoir. *Mudança da temperatura e transparência do reservatório: A) mudança de temperatura em diferentes profundidades na parte inferior do reservatório (L); B) mudanças de profundidade de Secchi em diferentes áreas do reservatório.*

and completely separated from the maximum temperature of the deeper layers. In September, the temperature of all layers decreased markedly to the same value at all layers (Fig. 5A). In October, the water temperature at the surface, at 1.5 m and at 3 m started to increase slightly, while it decreased in all the other layers. In November, the temperature of the entire water body decreased to nearly the same value.

The transparency of the water was the lowest in April at all three sampling sites (Upper, Middle, Lower), and then strongly increased in May (Fig. 5B). In June and July, the the transparency of the water at the sampling sites increased, while as a result of rainfall in September it reduced significantly (Fig. 5B). In October, the transparency of the water increased at the middle sampling site, however, while at the upper and lower sites it remained low. The transparency of the water in November increased strongly at all three investigated sites.

## DISCUSSION

Based on our Canonical Variance Analysis (CVA) with the consideration of the chemical variables, it can be observed that the individual sampling sites and the associated two algae species are separated in the reservoir area. The reservoir was divided into three different parts. A discrete group is composed of those samples that originate from

the upper part of the reservoir and during the year none of the two species occurred in this region (U). Samples from the middle part of the reservoir were grouped separately, i.e. locations where only *C. hirundinella* occurred (M), and the lower part of the reservoir (L) where the co-occurrence of *C. hirundinella* and *M. aeruginosa* was typical. The ammonium-ion concentration over the entire year was the highest at the sampling site where one none of the examined species was not occurred. Here we found the greatest change in the ammonium-ion concentration over the investigated period. The annual average of the ammonium-ion concentration was significantly lower at those sampling points where just the *C. hirundinella* has occurred. The lowest ammonium-ion concentration was found at those sampling sites where both investigated species was occurred. Considering the average for the whole year, the concentration of the orthophosphate-ion with the consideration of the whole yearly average was the highest at those sampling sites where none of the studied species were occurred. The annual average of orthophosphate ion concentration was significantly lower at those sampling sites where only *C. hirundinella* occurred. The annual average concentration of the orthophosphate ion was even lower – the lowest – at those sampling sites where both two species occurred. Here, the concentration of the orthophosphate ion varied most during the study period.

Based on our results in a mesotrophic reservoir, we identified an additional process: the lowest parts of the reservoir were characterised by the highest algal biomass, but lower nutrient concentrations, because the large quantities of living organisms used the nutrients and thus the amount of nutrients in the water body decreased.

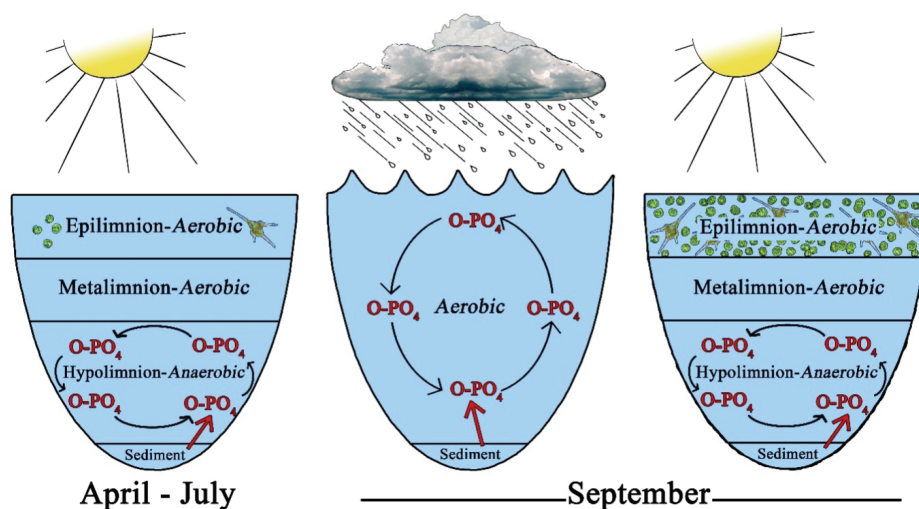
The characteristic species composition and the community formed by the dominant species of a reservoir depend on meteorological, physical and chemical characteristics. During our study we were able to describe the potential mechanisms facilitating the common cyanobacterial and eukaryotic algal blooms (Fig. 6). We observed increases in algal biomass concentrations in September after a rainy, cold period. During this period, the reservoir experienced a brief period of non-stratification and parts of the hypolimnion became anoxic potentially resulting in the internal release of nutrients from the sediment. As these special hydrological and climatic circumstances allowed phosphorus to move up from the anoxic bottom region to the upper, photic layers, cyanobacterial and eukaryotic algal blooms occurred.

Considerable evidence suggests that nutrient conditions can facilitate the dominance of cyanobacteria. The explanations of the occurrence of Cyanobacteria taxa occurrence are quite obvious

if the given Cyanobacteria taxa tend to have a competitive advantage in low N environments because such taxa are able to fix atmospheric  $N_2$ . Therefore, our data provides support for the hypothesis that low N concentrations favour cyanobacterial dominance if the available phosphorus is present. While nutrient concentrations were important in facilitating cyanobacterial development, the hydrologic regime of the lake may also have played an important role in the biomass increase of *C. hirundinella*. There may have been a positive feedback in the reservoir with increased biomass of cyanobacteria and more turbid conditions, which in turn, enhanced *C. hirundinella* growth.

## CONCLUSION

Ecological communities are expected to be structured by a variety of stochastic and deterministic processes. Two deterministic processes are thought to play a major role in determining the coexistence of species in the same trophic level: interspecific competition and environmental filtering, where species are excluded from a community due to an inability to survive and reproduce in a given physical environment. The general rules for predicting the relative importance of



**Figure 6.** The cyanobacterial and eukaryotic algal bloom forming process in drinking water reservoir. *Formação da produção em massa de cianobactérias e algas eucarióticas no reservatório.*



these processes in different contexts are still largely unresolved. The results of this study strongly suggest that there is a positive association between the increase in the frequency of summer rainfall events, the resulting non-stratification and internal P-release, and cyanobacterial blooms. Therefore, identifying the causal factors related to cyanobacterial blooms is an important first step in managing the water quality problems of drinking water reservoirs. Low nitrogen levels in combination with internal phosphorus inputs from the watershed and sediment may have created conditions that were favourable for cyanobacterial production. Furthermore, mixing patterns helped to move up to the phosphorus up into the surface region to promote nitrogen-fixing cyanobacteria growth.

The complexity of the processes involved in the development of algal blooms cannot be completely understood with costly mesocosm or microcosm approaches. Therefore, it is extremely important to study and understand the phenomena that occur naturally in the reservoirs, and then use our experiences as a model on other water bodies. By doing so, we will be able to understand different ecosystem processes that control algal blooms and how they interact and respond to different inputs.

The co-existence of phytoplankton assemblages under similar environmental conditions has allowed the identification of functional groups made up of species with similar morphological and physiological characteristics. Fourteen groups of phytoplankton were identified in Reynolds's original study (Reynolds, 1980a,b). Some have been subdivided since, although the biggest change has been to re-label them (Reynolds, 1984). The Reynold's model includes such group – LM –, which together include the *C. hirundinella* and *M. aeruginosa*. The model will be redesigned, but these two species will remain in the given group. In some cases, the two species often occur together in large quantities in various types of standing water all over the world. At other times, from year to year one or the other become the dominant species in the same water. In addition, in many respects these two species have extremely different of ecological needs.

Cyanobacteria blooms are typically associated

with eutrophic and poorly flushed waters (Paerl, 1988; Paerl *et al.*, 2001; Phielers *et al.*, 2009; Quin *et al.*, 2010; Smith, 1983). As surface waters become enriched with nutrients, particularly phosphorus (P), there is often a shift in the phytoplankton community towards dominance by cyanobacteria (Smith, 1983, Wang & Wang, 2009, Zhai *et al.*, 2009). The nutrient release from the sediment may have helped to further facilitate cyanobacterial blooms as has been reported in other waterbodies (Forbes *et al.*, 2008, Paerl 2009). Johnston & Jacoby (2003) also hypothesized that internal nutrient release was an important factor in fueling cyanobacterial blooms in a large lake in Seattle, Washington. Following the period of stratification, the lake began to mix as wind speed and rainfall events increased, and temperature gradients were minimal in the early fall (Wang & Wang, 2009).

Finally, this study demonstrated that higher temperatures coupled with elevated P concentrations frequently yielded growth rates of toxic *Microcystis* cells which exceeded all other treatments and populations.

Our study might also be used as a predictive tool supporting inter-disciplinary ecosystem management to assist in previewing the consequences of different management decisions. We suggest that management efforts should focus on controlling mesotrophic/eutrophic reservoirs. Because of the high amount of phosphorus released from the bottom of the water body due to anaerobic conditions, the phosphorus concentrated water needs to be released from the hypolimnion at intervals. This might be especially important during the summer months, before long-lasting rains to prevent undesirable cyanobacterial and/ or algal blooms or mass production.

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Con el apoyo de:

