Are cyanobacteria total, specific and trait abundance regulated by the same environmental variables?

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Abstract – In this study we analyzed if cyanobacteria total, specific and trait abundance are regulated by the same environmental variables in a Neotropical urban lake that recurrently suffers harmful cyanobacteria blooms. To assess the predictor variables for cyanobacteria total and species density we performed a multiple regression (GLM) and a redundancy analysis (RDA), respectively. Temperature and oxygen were the main predictor variables for both total and species abundance. Conductivity was an exclusive predictor for cyanobacteria total density (GLM) and light availability ($Z_d;Z_{eu}$) for species abundance (RDA). Nutrients were unnoticeable predictor variables for both. Cyanobacteria blooms showed high recurrence (8 blooms in 12 months) and occurred within 17–28°C. Blooms were mostly dominated by one species, and less frequently co-dominated by two species. These blooms were more recurrently dominated by dispersive non-fixing filamentous species (mainly Raphidiopsis curvata) linked to lower light availability. Less frequently, blooms were dominated by filamentous nitrogen fixers which develop scum blooms (mainly Anabaenopsis arnoldii) related to better light availability and lower dissolved oxygen concentration. The nitrogen fixing species showed high heterocyte density, suggesting nitrogen fixing behavior and probably giving this an advantage when inorganic nitrogen was low. Our results indicate that in absence of nutrients limitation, cyanobacteria total and species abundance can be regulated by different environmental variables. These results also show that species phylogenetically related (R. curvata and A. arnoldii) can respond differently to the prevailing environmental variables; highlighting the importance of considering cyanobacteria to a specific level when assessing their possible control factors.

Keywords: cyanobacteria / temperature / light availability / oxygen concentration

1 Introduction

Massive cyanobacteria growths constitute harmful algal blooms which can cause severe economic (Merel et al., 2013), ecological (Huisman et al., 2005), and health problems (Drobac et al., 2013; Carmichael and Boyer, 2016). The scenarios of global climate change forecast enhanced frequency and magnitude of such blooms, mostly due to increased global temperatures and eutrophication (Paerl and Huisman, 2009; Paerl and Otten, 2013). Thus, currently, great efforts are being invested in mitigating, preventing and predicting cyanobacteria harmful blooms (Paerl et al., 2016).

A wealth of studies has helped to unravel the main factors which control cyanobacteria biomass. That is, blooms are mostly favored by high nutrients, high temperatures, high water stability and high water residence time (O’Neil et al., 2012; Paerl et al., 2016), among other factors. Although many studies have assessed the responses of particular species to particular environmental triggers (e.g. de Tezanos Pinto and Litchman, 2010a; Bonilla et al., 2012); or reviewed the eco-physiological responses of nuisance species (Burford et al., 2016; Cires and Ballot, 2016; Gobler et al., 2016; Li et al., 2016), it is still unclear if the environmental variables that drive cyanobacteria total abundance affect species and trait abundance in a similar way. The latter would be the case if blooms were composed by the same species or if all species within a bloom responded in the same way to environmental triggers. Nevertheless, cyanobacteria capable of developing harmful blooms encompass a diverse group of organisms (three taxonomical Orders: Chroococcales, Oscillatoriales and Nostocales) and of ecological traits (morphologies,
physiologies and life cycles). Because the traits that may help cyanobacteria dominance are not shared by all taxa, different species may respond differently to environmental variables. For example, Dolman et al. (2012) analyzed the importance of nitrogen versus phosphorus in explaining total and specific cyanobacterial biovolume in 102 German lakes, and found bloom-forming species may display diverse responses to differential N versus P concentrations, even within species that shared the trait of nitrogen fixation. Also, Gobler et al. (2016) showed that beyond total cyanobacteria biomass, N loading selectively promoted the abundance of non-fixing cyanobacteria (Microcystis and Planktothrix). Hence, Cyanobacteria should not be treated as a single group when considering the effects of changes in nutrient loading on phytoplankton community structure (Dolman et al., 2012).

This probably also happens along light gradients, as certain cyanobacteria bloom mostly forming surface scums (e.g. Dolichospermum, Aphanizomenon, Microcystis) while others are usually found throughout the water column (e.g. Planktothrix, Limnotrix) (Chorus and Bartram, 1999; Paerl et al., 2016).

Exploring the effects of varying chemical, physical and biological variables beyond total biomass will broaden our understanding of the ecology of the group, and our abilities to forecast bloom composition in different scenarios. In this paper we assessed cyanobacteria total bloom, species and trait abundance in a Neotropical shallow lake which recurrently suffers cyanobacteria blooms throughout one year. We aimed to answer if the abundance of total cyanobacteria and the abundance of the species which develop blooms (and its ecological traits) are regulated by similar chemical and physical variables.

2 Material and methods

2.1 Study area

The shallow urban Lake Quillá (31°39’ S, 60°42’ W, Argentina) has a surface of 12 hectares and its basin has flatbed topography, a mean depth of 2.7 m and a maximum depth of 4 m in its central area (Fig. 1). This lake has a high recreational value as it is used for rowing, mostly during the warm seasons, recurrently suffering cyanobacteria blooms throughout the year.

2.2 Sampling and assessment of environmental variables and cyanobacteria

From June 2014 to May 2015, several environmental variables were monthly measured in situ in five sampling points (four littoral and one limnetic) to encompass the spatial heterogeneity produced by the effect of wind and the characteristics of the littoral (presence of vegetation and shorter water column) and the limnetic area (without vegetation and deeper water column) (n=60 samples) (Fig. 1). The physical–chemical variables considered were: temperature (°C), dissolved oxygen (DO) (mg L⁻¹ and saturation percentage), pH and conductivity (µS cm⁻¹), depth (Zd) (meters) was measured with an ultrasonic probe. The photic zone (Zeu) was estimated according to Koenings and Edmundson (1991) for turbid environments as Zeu = Secchi depth (SD) (m) × 3.5. The Zd:Zeu ratio was calculated as a measure of light availability in the water column. High values of this ratio indicate that the relative amount of time that phytoplankton spends in darkness increases (Reynolds, 1984). Water volume (m³) entering the lake was estimated using the criteria suggested by UNESCO (2006). Water samples for dissolved inorganic and total nutrient concentration: nitrate + nitrite (N-NO₃⁻ + N-NO₂⁻), ammonium (N-NH₄⁺), soluble reactive phosphorus (SRP), total phosphorus (TP) and total nitrogen (TN) were taken using 1 L bottles. Concentration estimations (µg L⁻¹) were done in laboratory following the protocols indicated in APHA (2005).

Phytoplankton samples were also collected monthly throughout a year (June 2014 to May 2015) at the same sampling points (four littoral and one limnetic) considered in physico-chemical sampling (n=60 samples) (Fig. 1). In each
Table 1. Mean values of the environmental variables analyzed, sorted by seasons. Values within parentheses denote the standard deviation (for each season and variable n = 5 sites × 3 months = 15, total n for each variable = 60).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temp. (°C)</td>
<td>15.0 (±0.7)</td>
<td>19.4 (±1.8)</td>
<td>27.3 (±0.7)</td>
<td>24.0 (±3.1)</td>
</tr>
<tr>
<td>pH</td>
<td>7.4 (±0.4)</td>
<td>7.6 (±0.7)</td>
<td>7.7 (±0.5)</td>
<td>7.7 (±0.6)</td>
</tr>
<tr>
<td>Cond (μS cm⁻¹)</td>
<td>2447.0 (±774.4)</td>
<td>3380.0 (±366.8)</td>
<td>3296.3 (±373)</td>
<td>5918.8 (±4485)</td>
</tr>
<tr>
<td>Z₄</td>
<td>1.3 (±0.8)</td>
<td>1.1 (±1.1)</td>
<td>1.1 (±0.9)</td>
<td>1.4 (±1.2)</td>
</tr>
<tr>
<td>DO (mg L⁻¹)</td>
<td>14.2 (±3.8)</td>
<td>12.1 (±2.3)</td>
<td>8.8 (±2.9)</td>
<td>9.8 (±1.1)</td>
</tr>
<tr>
<td>sat. DO (%)</td>
<td>100 (±19)</td>
<td>91 (±32)</td>
<td>79 (±9)</td>
<td>84 (±47)</td>
</tr>
<tr>
<td>Water vol. (m³)</td>
<td>5687.9 (±2724.07)</td>
<td>8405.5 (±4098.9)</td>
<td>20350.1 (±12511.3)</td>
<td>23383.7 (±26590.7)</td>
</tr>
<tr>
<td>TN (μg L⁻¹)</td>
<td>2475.3 (±1870.7)</td>
<td>1326.4 (±837.4)</td>
<td>959.3 (±216.1)</td>
<td>894.7 (±155.8)</td>
</tr>
<tr>
<td>DIN (μg L⁻¹)</td>
<td>2083.7 (±1602.96)</td>
<td>152.2 (±104.48)</td>
<td>120.4 (±102.68)</td>
<td>195.8 (±218.33)</td>
</tr>
<tr>
<td>TP (μg L⁻¹)</td>
<td>212.1 (±25.1)</td>
<td>269.2 (±104.3)</td>
<td>357.1 (±125.6)</td>
<td>400.6 (±157.3)</td>
</tr>
<tr>
<td>SRP (μg L⁻¹)</td>
<td>109.9 (±31.75)</td>
<td>66.0 (±52.25)</td>
<td>97.4 (±63.96)</td>
<td>89.9 (±31.69)</td>
</tr>
</tbody>
</table>

2.3 Statistical analyses

To assess the environmental variables which influenced total cyanobacteria abundance, a multiple regression model with Gaussian adjustment was run. This model was used after proving several environmental combinations. The best model was chosen according to its statistical significance and the Akaike Information Criterion (AIC). The density of total cyanobacteria during the whole sampling period (n = 60) was used as response variable. To assess the environmental variables which influenced the abundance of the cyanobacteria species which developed blooms, a Redundancy Analysis (RDA) was run. This method was used because the Detrended Correspondence Analysis (DCA) revealed that the gradient length of the response data was <3 (Leps and Šmilauer, 1999). Only variables that had a variance inflation factor (VIF) less than 20 were considered in the RDA analysis (Leps and Šmilauer, 1999). Environmental variables were considered predictive variables and were chosen with a forward selection. The densities (cell mL⁻¹) of each cyanobacteria species which developed blooms were used as response variables. All statistical analyses were performed using the software CANOCO for windows v. 5.10 (ter Braak and Šmilauer, 2012).

3 Results

3.1 Environmental and phytoplankton assemblage characterization

The most rainy and hot seasons were summer and autumn (564 mm – 30 °C and 1085 mm – 23 °C, respectively) while the least were winter and spring (136 mm – 14 °C and 25 mm – 20 °C, respectively). Water temperature, water volume and TP concentration were higher in summer and autumn than in winter and spring (Tab. 1). The opposite pattern occurred for TN (Tab. 1). TN was between two fold to one order of magnitude higher than TP (Tab. 1). DIN and SRP fractions were very high in winter, but dropped to lower concentrations in spring, summer and autumn (Tab. 1). In the latter period, DIN concentrations were one order of magnitude lower than in winter (Tab. 1). SRP concentrations, however, were always above 14 μg L⁻¹, with mean values ranging from 66 to 109 μg L⁻¹ (Tab. 1). Dissolved oxygen values were always
higher than 8 mg L\(^{-1}\) (Tab. 1); its concentrations were lower in autumn and summer compared to winter and spring. A similar pattern was observed for dissolved oxygen saturation (% sat. DO) (Tab. 1). Conductivity was high and ranged in average from 2400 to 5900 \(\mu\)S cm\(^{-1}\); pH remained rather neutral throughout the study period (Tab. 1). The \(Z_{\text{d:Z}_{\text{eu}}}\) ratio was, in average, higher than one across seasons, yet \(Z_{\text{d:Z}_{\text{eu}}}\) also reached values of one within each season, as evidenced by the high standard deviation (Tab. 1).

Phytoplankton density was 4500 ind mL\(^{-1}\) during the winter season, but increased one order of magnitude (> 50 000 ind mL\(^{-1}\)) for most part of spring — in particular in September and October — and then dropped to about a half (18 000 ind mL\(^{-1}\)) throughout summer and autumn. During winter and spring the phytoplankton assemblage was dominated in density (ind mL\(^{-1}\)) by Chlorophyta (40–80% relative density), while in summer and autumn it was dominated by Cyanobacteria (30–80% relative density) (Fig. 2A).

3.2 Cyanobacteria dynamics throughout the study period

The total number of phytoplankton species recorded throughout the studied period was 115. Out of the phytoplankton richness, 15 species were Cyanobacteria (Tab. 2). From the latter, 5 reached bloom densities (> 50 000 cell mL\(^{-1}\)) at least once during the studied period (Tab. 2). We recorded cyanobacteria blooms in 8 out of the 12 months analyzed, throughout spring (except in October), summer and autumn, with a magnitude of 100 000–800 000 cell mL\(^{-1}\) (mode 10 000 cell mL\(^{-1}\)) (Fig. 2B). High variability in abundance was registered during seasons, especially during February and May (Fig. 2B), reflecting a heterogeneous distribution of blooms in the lake. In winter

![Fig. 2](image-url)
there was lack of cyanobacteria blooms and its absolute and relative densities were almost zero (Fig. 2A and B).

Regarding bloom dominance patterns, these were most of the times (5 out of the 8 blooms) dominated by a single species (mono-specific). Less frequently blooms (3 out of the 8 blooms) were co-dominated by two species (poly-specific), without following a straightforward temporal pattern (Fig. 3). The dominant species in the assemblage was rarely the same across sampling periods (Fig. 3).

The five mono-specific blooms were composed either by: *Dolichospermum circinale* (90% of total cyanobacteria density, in September), *Anabaenopsis arnoldii* (84% of total cyanobacteria density, in December) and *Raphidiopsis curvata* (88%, 80% and 70% of total cyanobacteria density in November, March and April, respectively). The three poly-specific blooms occurred in: January (60% *R. curvata* and 33% *Glaucospira laxissima*), February (55% *Microcystis aeruginosa* and 38% *A. arnoldii*), and May (52% *G. laxissima* and 30% *A. arnoldii*) (Fig. 3). In September, *D. circinale* reached the maximum bloom density registered (746 279 cell mL\(^{-1}\)) (Fig. 3A). While *A. arnoldii* (Fig. 3B) reached the threshold of absolute abundance considered as a bloom; its relative contribution to total cyanobacteria abundance in September was lower than 15%. Hence, this case September sampling was excluded from the assessment of bloom dominance pattern (mono and/or polyspecific).

*R. curvata* and *A. arnoldii* were the species with the highest bloom recurrence; each species reached bloom densities four times throughout the study, with similar magnitude (range: 75 000–100 000 cell mL\(^{-1}\)) (Fig. 3). In *A. arnoldii*, only one out of the four blooms was mono-specific (Fig. 3B), whereas in *R. curvata* three out of the four blooms were mono-specific (Fig. 3C). These species were the only ones which developed both mono-specific and poly-specific blooms (Fig. 3). Their absolute densities showed opposing patterns and never co-dominated in a poly-specific bloom (Fig. 3).

Regarding the trait of nitrogen fixation, *D. circinale* and *A. arnoldii* developed heterocysts during blooms: in the *D. circinale* bloom, heterocyte density was very high (ca. 20 000 hets mL\(^{-1}\)) whereas in the latter it was much lower.

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**Fig. 3.** Monthly cyanobacteria absolute abundance (cell mL\(^{-1}\)) of the species which bloomed throughout the study period (vertical lines indicate standard deviation). For the nitrogen fixing cyanobacteria *Dolichospermum circinale* and *Anabaenopsis arnoldii* the secondary axis shows heterocyte abundance (het mL\(^{-1}\), dotted line). The horizontal line denotes the threshold of >50 000 cell mL\(^{-1}\) used in the study to consider a cyanobacteria bloom. M = Mono-specific bloom, P = poly-specific bloom. * A. arnoldii* surpassed the threshold of 50 000 cell mL\(^{-1}\), yet it contributed with less than 15% of total bloom abundance in September.
Nevertheless, both species showed similar ratio of vegetative to heterocyte cells (about 25 vegetative cells per heterocyte).

Despite differences in species composition within and across blooms (Fig. 3), blooms were mostly (7 out of the 8 blooms) of filamentous morphology (Tab. 3). Blooms were dominated by species capable of either dispersive development (R. curvata and G. laxissima, in 4 out of 8 blooms) or scum-type development (D. circinale, A. arnoldii and/or M. aeruginosa in 3 out of 8 blooms), without following a straightforward pattern (Tab. 3). One bloom was co-dominated by dispersive and scum forming species (Tab. 3). The trait of nitrogen fixation (heterocyte presence) was dominant in 2 of the 8 blooms (Tab. 3).

### 4 Discussion

#### 4.1 Controlling factors of cyanobacteria total abundance

Cyanobacteria blooms were recurrent throughout spring, summer and autumn with high magnitude (always surpassed Table 3. Trait characterization of the cyanobacteria blooms: morphology, eco-strategy and nitrogen fixing ability are indicated. Key: Dolichospermum circinale (Dolich.), Anabaenopsis arnoldii (Anabaen.), Raphidiopsis curvata (Raphid.), Microcystis aeruginosa (Microcys.), Glaucospira laxissima (Glaucos.).

<table>
<thead>
<tr>
<th>Samples</th>
<th>Species</th>
<th>Morphology</th>
<th>Eco-strategy</th>
<th>N Fixation (heterocyte-lack heterocyte)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jun</td>
<td>NB</td>
<td>NB</td>
<td>NB</td>
<td>NB</td>
</tr>
<tr>
<td>Jul</td>
<td>NB</td>
<td>NB</td>
<td>NB</td>
<td>NB</td>
</tr>
<tr>
<td>Aug</td>
<td>NB</td>
<td>NB</td>
<td>NB</td>
<td>NB</td>
</tr>
<tr>
<td>Sep</td>
<td>Dolich.</td>
<td>Filament</td>
<td>Scum</td>
<td>Hets</td>
</tr>
<tr>
<td>Oct</td>
<td>NB</td>
<td>NB</td>
<td>NB</td>
<td>NB</td>
</tr>
<tr>
<td>Nov</td>
<td>Raphid.</td>
<td>Filament</td>
<td>Dispersive</td>
<td>No hets</td>
</tr>
<tr>
<td>Dec</td>
<td>Anabaen.</td>
<td>Filament</td>
<td>Scum</td>
<td>Hets</td>
</tr>
<tr>
<td>Jan</td>
<td>Raphid. + Glaucos.</td>
<td>Filament</td>
<td>Dispersive</td>
<td>No hets</td>
</tr>
<tr>
<td>Feb</td>
<td>Microcys. + Anabaen.</td>
<td>Colony + filament</td>
<td>Scum</td>
<td>No hets + hets</td>
</tr>
<tr>
<td>Mar</td>
<td>Raphid.</td>
<td>Filament</td>
<td>Dispersive</td>
<td>No hets</td>
</tr>
<tr>
<td>Apr</td>
<td>Raphid.</td>
<td>Filament</td>
<td>Dispersive</td>
<td>No hets</td>
</tr>
<tr>
<td>May</td>
<td>Glaucos. + Anabaen.</td>
<td>Filament</td>
<td>Scum + dispersive</td>
<td>No hets + hets</td>
</tr>
</tbody>
</table>

NB = No bloom event.

Table 4. Multiple regression model (GLM) using total Cyanobacteria abundance as response variable. Statistically significant values ($p < 0.05$) are indicated in bold.

<table>
<thead>
<tr>
<th>Term</th>
<th>b</th>
<th>SE</th>
<th>T</th>
<th>$p(T)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>0.845707</td>
<td>0.9568586</td>
<td>0.88</td>
<td>0.38078</td>
</tr>
<tr>
<td>Temp</td>
<td>0.162782</td>
<td>0.03084941</td>
<td>5.28</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td>pH</td>
<td>−0.00150902</td>
<td>0.00107495</td>
<td>−1.4</td>
<td>0.16621</td>
</tr>
<tr>
<td>Cond</td>
<td>0.00013851</td>
<td>4.24E−05</td>
<td>3.27</td>
<td>0.00189</td>
</tr>
<tr>
<td>$Z_{mix}:Z_{eu}$</td>
<td>−0.126665</td>
<td>0.1037133</td>
<td>−1.2</td>
<td>0.22738</td>
</tr>
<tr>
<td>DO</td>
<td>−0.1391</td>
<td>0.04088931</td>
<td>−3.4</td>
<td>0.00128</td>
</tr>
<tr>
<td>WT</td>
<td>−1.36E−05</td>
<td>9.14E−06</td>
<td>−1.5</td>
<td>0.14313</td>
</tr>
</tbody>
</table>

WT = Water volume.

The multiple regression model was statistically significant ($F=21.08, p < 0.001$) and 3 variables ($p < 0.05$ for each one) out of 6 variables analyzed (Tab. 4) explained 70.5% of the changes observed in total cyanobacteria abundance. In the model, cyanobacteria abundance was positively linked with temperature and conductivity, but negatively linked with dissolved oxygen (Tab. 4). The RDA analysis (Fig. 4), run with the density of the 5 Cyanobacteria species which developed blooms was statistically significant ($F=17.9, p=0.001$) and explained 43.8% of total variation. The first and second axis of the RDA explained the 81.2% and 16.6%, respectively. The significant variables were: temperature, $Z_{mix}:Z_{eu}$ ratio and dissolved oxygen. Temperature explained 30.5% of total variance ($F=17.9, p=0.001$) and had a positive association with all cyanobacteria species, especially with M. aeruginosa and G. laxissima (Fig. 4). Dissolved oxygen (5.3%, $F=2.9, p=0.02$) had a negative link with all cyanobacteria species, especially with A. arnoldii and D. circinale. The $Z_{mix}:Z_{eu}$ ratio (5.9%, $F=2.2, p=0.048$) showed a high and negative association with the densities of D. circinale and A. arnoldii (both developed scum type blooms), but showed a strong an positive link with the densities of R. curvata (developed dispersive type blooms).

4.3 Environmental variables which affected cyanobacteria total and species abundance

The multiple regression model was statistically significant ($F=21.08, p < 0.001$) and 3 variables ($p < 0.05$ for each one) out of 6 variables analyzed (Tab. 4) explained 70.5% of the changes observed in total cyanobacteria abundance. In the model, cyanobacteria abundance was positively linked with temperature and conductivity, but negatively linked with dissolved oxygen (Tab. 4). The RDA analysis (Fig. 4), run with the density of the 5 Cyanobacteria species which developed blooms was statistically significant ($F=17.9, p=0.001$) and explained 43.8% of total variation. The first and second axis of the RDA explained the 81.2% and 16.6%, respectively. The significant variables were: temperature, $Z_{mix}:Z_{eu}$ ratio and dissolved oxygen. Temperature explained 30.5% of total variance ($F=17.9, p=0.001$) and had a positive association with all cyanobacteria species, especially with M. aeruginosa and G. laxissima (Fig. 4). Dissolved oxygen (5.3%, $F=2.9, p=0.02$) had a negative link with all cyanobacteria species, especially with A. arnoldii and D. circinale. The $Z_{mix}:Z_{eu}$ ratio (5.9%, $F=2.2, p=0.048$) showed a high and negative association with the densities of D. circinale and A. arnoldii (both developed scum type blooms), but showed a strong an positive link with the densities of R. curvata (developed dispersive type blooms).

WT = Water volume.

(2500–4500 hets mL$^{−1}$) (Fig. 3A, B). Nevertheless, both species showed similar ratio of vegetative to heterocyte cells (about 25 vegetative cells per heterocyte).

Despite differences in species composition within and across blooms (Fig. 3), blooms were mostly (7 out of the 8 blooms) of filamentous morphology (Tab. 3). Blooms were dominated by species capable of either dispersive development (R. curvata and G. laxissima, in 4 out of 8 blooms) or scum-type development (D. circinale, A. arnoldii and/or M. aeruginosa in 3 out of 8 blooms), without following a straightforward pattern (Tab. 3). One bloom was co-dominated by dispersive and scum forming species (Tab. 3). The trait of nitrogen fixation (heterocyte presence) was dominant in 2 of the 8 blooms (Tab. 3).
and dissolved oxygen concentration (DO). e.g. high ion concentrations (known that several cyanobacteria species are well adapted to the second alert level established by the World Health Organization (WHO, 2003) for drinking water and recreational use. The temporal distribution of the species which developed blooms may, at least in part, be explained by their temperature growth optimum. For example, M. aeruginosa only bloomed at high temperatures (∼27 °C); this is consistent with previous studies which reported optimum growth for this genus between 25 and 35 °C (Nalewajko and Murphy, 2001; Lürling et al., 2013). However, D. circinale bloomed at much lower temperatures (∼17 °C), in accordance with what was reported in laboratory experiments by Zapomělová et al. (2008). A. arnoldii and R. curvata bloomed at a wider temperature range (from 17 to 27 and 21–27 °C, respectively). The range found for R. curvata agrees with the results found by Li et al. (2008) (from 10 to 35 °C). The coincidence of temperature as a predictor variable for total and species abundance reflects that cyanobacteria have high temperature optima (median ca. 27 °C, Lürling et al., 2013). It also suggests that within the range of temperature optima, different species have particular growth optima values.

For this hyper-eutrophic lake (mean range of TP = 200–400 µg L⁻¹ and TN = 890–2500 µg L⁻¹) soluble reactive phosphorus concentration was always above limiting concentrations for phytoplankton development (<5 µg L⁻¹, Reynolds, 2006). Dissolved inorganic nitrogen (DIN) despite being above limiting concentrations (<100 µg L⁻¹, Reynolds, 2006), recurrently reached limiting concentrations as can be inferred by the large variation observed in the mean values (see Tab. 1). This great variation, however, could be explained by the large concentrations of total nitrogen (TN) registered with low DIN concentrations.

Bloom distributions were mostly dominated by one species or co-dominated by two species. Dominance patterns changed without following a straightforward temporal pattern, which may relate to the different Zₐ/Zₑu ratios (light availability) which was a significant variable in the RDA analysis. Reynolds (1997) stated that species morphologically attenuated in light availability. The predominance of filamentous forms probably reflects the periodic light restriction for phytoplankton in this water body. Also, blooms were mostly of disperse type, and less frequently of scum forming type. When the water is stagnant, buoyant Cyanobacteria accumulate in the surface, whereas when there is turbulence and the water is mixed, species are evenly distributed throughout the water column (Paerl and Huisman, 2009).

The trait of nitrogen fixation (expressed in D. circinale and A. arnoldii) was dominant with better light availability, low DIN concentration and low dissolved oxygen concentration. This result may reflect the high dependence of light and anoxic conditions for nitrogen fixation. It is acknowledged that the rates of nitrogen fixation increase with light levels (Mugidde et al., 2003; Agawin et al., 2007) and poor oxygen conditions since it inhibits or reduce nitrogenase activity (enzyme responsible of nitrogen fixation) (Fay, 1992). These results are consistent with laboratory experiments which showed that in the absence of nitrogen supply, nitrogen fixation was about three times higher in light sufficiency than in light limitation (de Tezanos Pinto and Litchman, 2010a).

In this study, R. curvata and A. arnoldii bloomed with higher recurrence. Though these species share a monophyletic origin (order Nostocales, filamentous morphology) when A. arnoldii bloomed, R. curvata had very low densities, and vice versa. This opposite behavior may settle in their contrasting ecologies. R. curvata was dominant with high DIN concentra-
trations and low light availability while *A. arnoldii*, as a nitrogen fixer, was dominant with low DIN concentrations (high TN concentration) and high light availability. The relation low DIN and high TN could be indicating a high phytoplankton inorganic catching rate; which in this study may be favoring the growth of *A. arnoldii* as a nitrogen fixer. On the other hand, *Raphidiopsis* is the only genus within the order Nostocales that is unable to fix nitrogen, as it lacks part of the genes involved in the synthesis of the heterocytes and of the nitrogenase (Stucken et al., 2010). Therefore, we would not expect to find blooms of *R. curvata* in low DIN and high TN scenarios.

5 Conclusions

The results of the present study suggest that cyanobacteria total and species abundance are not necessary regulated by the same environmental variables. While cyanobacteria total and species abundance responded in a similar way to several environmental variables (especially temperature), certain variables affected in particular cyanobacteria total density (conductivity) and others the abundance of the species which developed blooms (light availability). We observed that closely related cyanobacteria (*e.g. A. arnoldii* and *R. curvata*, both from the order Nostocales), which were also the most recurrent species developing blooms, showed contrasting distributions in the studied environment. Their different ecologies, despite sharing a similar phylogeny, seem to be explained by a contrasting set of morphological and physiological traits (particularly related with light and nitrogen fixation). This highlights the importance of avoiding treating cyanobacteria as a single group when assessing the effects of environmental variables on the ecology of this group.

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