Succession and interaction of surface and subsurface cyanobacterial blooms in oligotrophic/mesotrophic reservoirs: a case study in Miyun Reservoir

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Abstract

Subsurface cyanobacterial blooms, are a significant source of odor problems in source water and have been recorded in many oligotrophic/mesotrophic drinking water reservoirs. In this study, we explored the key driving forces responsible for the succession between surface and subsurface cyanobacteria using ecological niche modelling based upon a case study in Miyun Reservoir, China. The results suggest a negative effect of water depth and surface light irradiance (I_0) on subsurface *Planktothrix* sp. growth (p-values < 0.001), and a unimodal effect of surface water temperature (T_0) with the optimum at 23 °C (p-value < 0.001). While the surface *Microcystis* spp. shows a strong positive relationship with temperature (T_0 ; p-value < 0.001), and significant effects for the interaction between T_0 and I_0 (p-value < 0.01). In addition, we identified the extent and type of interaction between subsurface and surface cyanobacteria and conclude that the high irradiance surface water combined with sufficient nutrients at the pre-bloom stage are key factors responsible for the preferential growth of surface cyanobacteria, while the gradual decline of the surface cyanobacteria in post-bloom stage is associated with nutrient reduction. This decline and loss of surface populations enhanced underwater irradiance and thus promoted the growth and allowed for succession of subsurface cyanobacteria in deeper layers where the nutrient supply was still adequate. Based upon this, the growth potentials for the subsurface and surface cyanobacteria are different under different environmental conditions: the subsurface cyanobacteria have greater growth potential than surface cyanobacteria in shallow oligotrophic and deep eutrophic reservoirs during median light irrigation seasons.

31 *Keywords: Generalized Additive Model, Ecological niche, Surface cyanobacteria, subsurface*
32 *cyanobacteria, Source water, Taste and odor*

33 1. Introduction

34 Cyanobacteria have developed advantages and strategies through evolution that allow them
35 to flourish in aquatic environments, producing massive blooms, scums and mats (Huisman and
36 Hulot, 2005). They also produce a diverse range of compounds that include tastes (Yang et al.,
37 2008, Kehoe et al., 2015, Bai et al., 2017, Survey et al., 2017) and toxins (MacKintosh et al.,
38 1990, Molica et al., 2005, Dittmann et al., 2013, Buratti et al., 2017), which degrade water qual-
39 ity. For example, globally the two most prominent cyanobacteria that produce striking sur-
40 face blooms: *Microcystis* spp. produces microcystin toxins, and *Dolichospermum* spp. (formerly
41 named as *Anabaena* spp.) can produce both anatoxin and saxitoxin neurotoxins in addition to the
42 earthy smelly odor compound geosmin; and attract extensive concern and attention (Acuña et al.,
43 2012, Liu et al., 2011, Chia et al., 2018). Surface-living cyanobacteria are able to regulate their
44 buoyancy and therefore maintain a particular vertical position according to their needs, which
45 can potentially provide an advantageous competitive strategy over non-buoyant phytoplankton
46 (Mur et al., 1999, Yao et al., 2017, Wang et al., 2017). However, aesthetic and toxin-induced wa-
47 ter quality problems are known to occur in some drinking water reservoirs, sometimes with low
48 nutrient concentrations, and are not always associated with or explained by the occurrence
49 of surface bloom-forming cyanobacteria.

50 Example of cyanobacterial blooms that are not strongly buoyant such as the filamentous types
51 *Oscillatoria* spp., *Phormidium* spp. etc., have been recorded in many reservoirs (AWWA, 2010,
52 Dokulil and Teubner, 2012, Watson et al., 2016). These may have large biomass accumulations
53 present either as mats on the sediment surface (Noffke et al., 2003) or are present as blooms
54 deeper in the water column that produce high chlorophyll concentrations well below the epil-
55 imnion (Dokulil and Teubner, 2012). This behavior may seem paradoxical, since the surface-
56 living cyanobacteria with access to sufficient irradiance would be expected to outcompete the

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57 types with a preference for living in a subsurface zone (Davis et al., 2003). For water qual-
58 ity management, it is important to understand the combination of conditions or environmental
59 changes that allow subsurface cyanobacteria to outcompete surface cyanobacteria.

60 The competitive exclusion principle (Hardin, 1960) has long been the tenet for predicting out-
61 comes of competition between algal populations (Klausmeier and Litchman, 2001, Rothhaupt,
62 1996, Tilman et al., 1982). Huisman et al. (1999), have demonstrated that the species with “min-
63 imal resource requirements” should be the superior competitor. Dynamic competition models
64 built around this principle and based upon differential equations usually work well for controlled
65 conditions, and have been extensively used to explain competitive relationships among algal
66 species in experimental laboratory systems (Huisman and Weissing, 1995, Huisman et al., 1999,
67 Rothhaupt, 1996). However, with regard to the natural environment, the models are not neces-
68 sarily applicable where the resources for their growth vary spatially and also seasonally. The
69 application of mechanistic models in field studies can be challenging owing to the complex in-
70 terplay between physical and chemical properties of the aquatic environment and the responsive-
71 ness of the individual species (Huisman and Hulot, 2005). By contrast ecological niche models
72 utilize associations between environmental variables and known species’ occurrence localities
73 to define abiotic conditions within which populations can be maintained (Guisan and Thuiller,
74 2005), and have already been integrated into a broad variety of research disciplines (reviewed
75 by Raxworthy et al. (2007)). The niche hypervolume, defines the multi-dimensional space of
76 resources (e.g., light irradiance, nutrients, temperature, etc.) available to (and specifically used
77 by) organisms (Hutchinson, 1957) is constrained by a multivariate species’ response function of
78 the habitat vector. McKane et al. (2002) successfully used resource-based niches to analyze the
79 plant species diversity and dominance in arctic tundra.

80 In this investigation we attempt to extend the niche space to include time scales, and hence
81 integrate all the spatial and seasonally dependent vectors into a unified niche space. Since the or-
82 ganisms response at each point in the niche is specified, it is possible to model interspecies com-
83 petition by comparing response vectors of competing species at points of niche overlap (Wuens-
84 cher, 1969). In this study, the niche concept is employed to evaluate and determine the driving
85 forces responsible for the seasonal succession between the surface and subsurface cyanobacte-
86 ria, using ecological niche modeling (Generalized Additive Models, a non-parametric statistical
87 method; (Hastie and Tibshirani, 1990)) in a major Chinese drinking water reservoir. This is

88 novel and unique application of the niche concept model to achieve improved understanding of
89 the behavior of cyanobacteria for source water management.

90 Miyun Reservoir, the most important surface water resource for the city of Beijing, has been
91 subject to major taste & odor problems for several years due to the development of subsurface-
92 living blooms of *Planktothrix* sp. (Su et al., 2015). Hereby we perform niche modeling by using
93 the long-term monitoring data in Miyun Reservoir, to assess the seasonal dynamics of surface
94 and subsurface cyanobacteria, and identify the environmental constraints responsible for their
95 seasonal succession. This can be used for the development of possible strategies for the pre-
96 vention of subsurface cyanobacteria based upon their ecological niche in various environment
97 conditions.

98 2. Methods

99 2.1. Study area and sampling strategy

100 The Miyun Reservoir is situated in the northeastern part of Beijing, China (40°30'N, 116°55'E,
101 Figure A1). It was initially constructed for flood control, irrigation and fisheries, but is now the
102 major water source for the city of Beijing. The reservoir encompasses a large area, with a total
103 storage capacity of 437.5 GL and a surface area of 188 km², as well as a complex bathymetry
104 classified as a mountain valley reservoir type (Su et al., 2014). Miyun Reservoir's major natural
105 replenishment is from the Bai and Chao Rivers that contribute mean flow of 111 GL yr⁻¹ and
106 203 GL yr⁻¹, respectively (data from Beijing Water Authority, 2010 to 2013). The main outflow
107 is a channel in the South Region of the reservoir at 18 m depth, where water is removed via
108 pumping stations to waterworks.

109 The water samples were collected during 2006 and 2012. No sample was collected during
110 January and February owing to the security limitation during the ice-covered period. Samples
111 were collected from eight sites (MY01, MY02 ... MY08) before 2008; more sample sites were
112 involved and more samples were collected during September and October when the off-flavor
113 problems occurred between 2009 to 2012. Water samples were collected using a kemmerer
114 water sampler from three different depths; surface and middle water samples were collected at
115 0.5 m and 5 m (for shallow water areas) or 8 m (for deep water areas) depth. The bottom water
116 samples were collected above the sediment floor or at a maximum depth of 15 m. Nutrients,

117 phytoplankton cell counting and online monitoring including Secchi depth, surface water tem-
118 perature, water depth were simultaneously monitored except very limit amount of unsuccessful
119 detections, which were removed during the model construction in later sections.

120 2.2. Data collection and laboratory analysis

121 Field measurements and water samples were collected in a program from Miyun Reservoir to
122 collect data on water temperature, optical properties, nutrient concentrations and cyanobacterial
123 numbers. Samples for nutrient analyses were first filtered through a 0.45 μm filter and then sub-
124 sampled and analyzed for each individual nutrient using continuous flow analyzer (CFA, Skalar
125 San++, Netherlands), according to standard methods (APHA, A., 1998). Water transparency,
126 expressed as Secchi depth (SD), was measured with a Secchi disk (diameter: 20 cm, black and
127 white). Water temperature was measured in situ with a multi-parameter probe (YSI-6600, USA).
128 Light irradiance on each sampling date in Miyun Reservoir was extracted from China Mete-
129 orological Data Service Center (CMDSC) (CMDSC, 2018) using the downwelling short wave
130 radiation. Subsamples (100 mL) for cell enumeration were preserved with 5 % Lugol's iodine
131 (Sherr and Sherr, 1993). After static settlement over 48 h, the resulting 10-fold pre-concentrated
132 samples were kept in dark until cell counting. The algal cell density was determined using
133 the Utermöhl technique with a Sedgewick-Rafter counting chamber under an upright micro-
134 scope (Nikon Eclipse 50i) with phase contrast and bright field illumination (Hasle, 1978) using
135 the self-developed cell counting tool (CCT v1.4, China, <http://suming.me/cc/publish.htm>). The
136 number of filamentous algal cells was calculated by dividing the measured filamentous length by
137 the mean cell length. The number of cells in colony species such as *Microcystis* was estimated
138 based upon colony volume and mean cell density. The colony volume was measured using built-
139 in micrometer in CCD (couple-charged device) cameras' software (Olympus DP80, Japan), and
140 the mean cell density was estimated by measuring certain number of colonies and corresponding
141 cell numbers accomplished by CCT v1.4 according to $\rho = \sum_{i=1}^n (\frac{N_i}{V_i})/n$; ρ : mean cell density, N_i :
142 cell number of the i_{th} colony, V_i : volume of the i_{th} colony, n : number of colonies. The detailed
143 cell enumeration and identification has been described in Su et al. (2015).

144 2.2.1. Statistics analysis

145 Generalized Additive Models (GAMs) is a generalized linear model in which the linear pre-
146 dictor depends linearly on unknown smooth functions of some predictor variables, and interest

147 focuses on inference about these smooth functions (Hastie and Tibshirani, 1990). Analysis using
 148 GAMs was performed to evaluate the effects of the spatial and temporal patterns of environmen-
 149 tal factors as well as the regression models for the biomass of surface and subsurface cyanobac-
 150 teria. Variance inflation factor (VIF) quantifies the severity of multicollinearity in an ordinary
 151 least squares regression analysis. VIF analysis was used for evaluate the collinearity of involved
 152 environmental factors as the predictors. GAMs, VIF analysis, descriptive statistics and data vi-
 153 sualization has been performed using **mgcv**, **car**, **vegan** and **graph** package in R 3.3.2 (Wood,
 154 2006, 2011, Fox and Weisberg, 2011, Oksanen et al., 2014, R Core Team, 2016).

155 2.3. Temporal-spatial pattern fit of environmental factors

156 Most environmental factors are affected by both long-term trends and within-year variation;
 157 as shown in Eq. (1), GAMs were used to decompose the temporal variation into seasonal patterns
 158 and inter-annual trends.

$$y = \beta_0 + f_{seasonal}(x_1) + f_{trend}(x_2) + \varepsilon, \varepsilon \sim N(0, \sigma^2 \Lambda) \quad (1)$$

159 where β_0 is the intercept, $f_{seasonal}$ and f_{trend} are smooth functions for the seasonal and trend
 160 features. Seasonal components were represented by cyclical splines (Adams, 1974) to avoid dis-
 161 continuity between the beginning and the end of a year. The seasonal indicator, x_1 , is represented
 162 by the sampling week number, while the long-term trend indicator, x_2 , is the sampling date in
 163 units of decimal years.

164 GAMs were also used to represent spatial patterns in the complex bathymetry of Miyun
 165 Reservoir. The spatial patterns were represented with two-dimensional smoothers of horizontal
 166 and vertical position referring to the stations in Figure A1. Each of these sites have a depth (z_{max})
 167 and a spatial position, but the 2-dimesnional (x, y)-position is reduced to a 1-dimensional position
 168 along with the main water flow pattern from the west reservoir dam via the north shallow region
 169 (channel) to the south reservoir dam, formed by a transect line (see Figure A3a). The distances
 170 along this transect line for those sites represents the horizontal position variation, and the vertical
 171 water depth of those sites (see Figure A3b) presents the vertical water depth variation.

$$y = \beta_0 + f_{horizontal}(x_3) + f_{vertical}(x_4) + \varepsilon, \varepsilon \sim N(0, \sigma^2 \Lambda) \quad (2)$$

172 where x_3 represents the horizontal transect distance and x_4 the water depth ($z_{\max}$; vertical
173 distance to the bottom at the sampling sites).

174 2.4. Niche modeling

175 2.4.1. Response variables and predictors

176 A general approach to niche modeling is to predict conditional abundance distribution by
177 smooth functions of one or more predictors. Phytoplankton count data typically contains a high
178 abundance of zeros (in our case, 44.8 % for *Planktothrix* spp. and 26.1 % for *Microcystis* sp.).
179 Since the zeros are consequences of the natural spatio-temporal dynamics of the phytoplankton
180 populations, it is important that this feature of the data be represented properly. Zero-inflated data
181 cannot be analyzed by standard statistical distributions (e.g., log-normal, Poisson, etc.) because
182 of the high proportion of zeros (Zuur et al., 2007). The Tweedie distribution with variance scaling
183 parameter, $1 < p < 2$, is especially appealing to model zero-inflated data, and has recently been
184 used in range of fields including ecology studies (Candy, 2004, Shono, 2008, Tascheri et al.,
185 2010, Arcuti et al., 2013) and rainfall prediction (Dunn, 2004). We used the variance inflation
186 factor (VIF) analysis to quantify collinearity of the model predictors.

187 2.4.2. GAM modeling

188 Among the many different strategies developed for ecological niche modeling, we will here
189 focus on generalized additive models (GAMs). In this study, GAMs were used to identify the
190 environmental constraints on the abundances of *Microcystis* spp. and *Planktothrix* sp.. Models
191 for our zero-inflated continuous responses are specified as follows:

$$E(y_i) = \beta_0 + \sum_{j=1}^m s_j(x_{ij}) = \eta(x_i) \quad (3)$$

192 Where E is the function linking the mean response y_i to the additive predictor $\eta(x_i)$. Semi-
193 parametric smooth functions of observed covariates s_j 's are specified as piecewise polynomial
194 basis functions.

195 Interaction terms were represented by tensor product smoothers (**te()** terms), which are less
196 sensitive to scaling differences between interacting predictors than other representations (Wood
197 et al., 2013). We investigated the importance of the interaction effect by comparing models with
198 and without an explicit tensor product interaction (**ti()**) term. Model selection was based on

199 combining generalized cross-validation with a penalty-based method for model simplification
200 (Marra and Wood, 2011).

201 3. Results

202 3.1. Temporal-spatial patterns of environmental conditions

203 The nutrient concentrations indicate that Miyun Reservoir is mesotrophic with a total dis-
204 solved nitrogen (total N, TN) concentration of $967 \pm 317 \mu\text{g L}^{-1}$ (mean $\pm$ Variance, $N = 1447$),
205 ammonia (NH_4) concentration of $250 \pm 142 \mu\text{g L}^{-1}$ ($N = 1447$), total phosphorus (total P, TP)
206 concentration of $14 \pm 11 \mu\text{g L}^{-1}$ ($N = 1447$) and water transparency Secchi depth (SD) of $2.34 \pm 0.86 \text{ m}$
207 ($N = 1465$). Most limnological parameters in the Miyun Reservoir showed significant tempo-
208 ral variation (Figure 1), but with “rugs” in January and February owing to unevenly distributed
209 sampling dates over seasons. Judging from the seasonal splines, total N, nitrate and nitrite con-
210 centration exhibited very similar seasonal fluctuation patterns, with highest concentrations in
211 spring, and lowest concentrations during July and August (only TN splines is shown in Figure
212 2). Ammonia, whose utilization is energetically more favorable for phytoplankton, is typically
213 consumed more quickly and thus shows a different seasonal pattern from other nitrogen species.
214 In our study, concentrations decrease from March through June, then increase until the end of
215 October before again decreasing. The water level, represented by z_{max} , shows strong seasonal
216 fluctuations, but indicates a clear decreasing inter-annual trend during the investigated years,
217 which could probably cause the ammonia increases and SD decreases.

218 [Figure 1 about here.]

219 The 95 % predictive intervals suggesting T_0 (surface water temperature) and I_0 (light irra-
220 diance above water surface) do not vary by sampling sites, while z_{max} and other factors show
221 non-negligible spatial variations, due to complex bathymetry and large surface area of Miyun
222 Reservoir. Figure 2 shows that the nutrient concentrations and Secchi depth in September varies
223 along with the geographical position (presented by transect distance) and water depth (present by
224 z_{max}), respectively. The results suggesting the area in the middle of the transect line (correspond-
225 ing to the north reservoir region) shows different environmental conditions from the beginning
226 to the end of the transect line (corresponding to west reservoir and south reservoir regions).

227 [Figure 2 about here.]

228 3.2. Distributions of *Microcystis* and *Planktothrix*

229 In total 162 genera/species of cyanobacteria and eukaryotic algae were detected during the
230 entire study (data not shown). Here we focus on *Microcystis* and *Planktothrix*, as they are the
231 main nuisance genera in the Miyun Reservoir. The mean concentrations of *Microcystis* and
232 *Planktothrix* over the four year study period were 1251 cells mL⁻¹ and 224 cells mL⁻¹, respec-
233 tively, indicating a higher concentration of *Microcystis* than *Planktothrix*, although this does
234 not take into account cell volume, which varies approximately 1.6-fold (*Microcystis* 48 µm³;
235 *Planktothrix* : 77 µm³, data from Su et al. (2014)) between the two cyanobacteria. Both genera
236 exhibited seasonal variations (Figure 1 (n-o)). *Microcystis* had rapid growth in summer followed
237 by a gradual decline in autumn. The concentration of *Planktothrix* remained low in spring and
238 summer, while peak concentrations were generally observed in September and/or October and
239 subsequently decreased during the following months. Vertical distributions of *Microcystis* and
240 *Planktothrix* in the north shallow area (NSR, see Figure A1) during September (September 7
241 and September 23 in 2012, sampling time around 10:00-12:00 AM) are shown in further de-
242 tail (Figure 3). The top 2 m contained greater concentrations (54 %) of *Microcystis* cells, while
243 *Microcystis* cell number contributed only 6 % in the layer of “6-8 m”. In contrast to this, only
244 9 % *Planktothrix* cells were found in top 2 m while cells in the lower layers (“2-4 m”, “4-6 m”
245 and “6-8 m”) contributed a higher concentration of about approximately 24 %, 41 % and 26 %
246 respectively to the total cell number of *Planktothrix* in the water column, respectively.

247 [Figure 3 about here.]

248 3.3. Predictive parameters of the *Microcystis* and *Planktothrix*

249 Variance inflation factor (VIF) analysis (see Table A2), indicated that both nutrient sources
250 (represented by ammonia, total N and total P) and the physical environment (represented by
251 Secchi depth, water depth, surface temperature and irradiance) could be considered candidate
252 predictor variables.

253 [Table 1 about here.]

254 The model for *Planktothrix* indicates that four parameters (NH₄, z_{max}, I₀ and T₀) make statis-
255 tically significant contributions in the prediction of *Planktothrix* cell density; this model explains

in total 38.1 % of the total deviance (Table 1). On the other hand, three parameters including NH_4 , $z_{\max}$ and T_0 as well as the interaction between I_0 and T_0 are the major contributors to predicting *Microcystis* cell density. 51.0 % of total deviance is explained by this model (Table 1). The fitted GAM models suggest minimal effect of total N, total P or SD on either *Planktothrix* (all p-values > 0.40) or *Microcystis* (all p-values > 0.20), as shown in Table 1. Subsequently, we have simplified the two GAMs by removing inefficient predictors, as shown in Eq. (4).

$$\log(E[C_{pla}]) = \beta_0 + s_1(\text{NH}_4) + s_2(z_{\max}) + s_3(T_0) + s_4(I_0) + ti(I_0, T_0) \quad (4a)$$

$$\log(E[C_{mic}]) = \beta_0 + s_1(\text{NH}_4) + s_2(z_{\max}) + s_3(T_0) + s_4(I_0) + ti(I_0, T_0) \quad (4b)$$

where C_{pla} and C_{mic} denote the cell density distributions of *Planktothrix* and *Microcystis*. Cell densities are assumed to follow a *Tweedie* distribution with a logarithmic link function, such that the logarithm of the expectation (The $E[\cdot]$ operator) is a linear combination of smoothers for ammonia, water depth, surface temperature and irradiance.

3.4. Effects of environmental factors on *Planktothrix*

The updated GAMs for *Planktothrix* (Eq. 4a) have a lower akaike information criterion (AIC) value, and can also explain a higher percentage of the total deviance (39.4 %) compared to the original one, suggesting that the simplified model performs better. According to the results of the updated model (Figure 4-top), $z_{\max}$ has a negative effect on the growth of *Planktothrix* (p-value < 0.001). There was also very strong evidence showing a unimodal effect of surface temperature on *Planktothrix*, with the optimum around at 23 °C (p-value < 0.001), and a negative effect of surface light irradiance (p-value < 0.001).

[Figure 4 about here.]

3.5. Effects of environmental factors on *Microcystis*

As shown in Figure 4 (bottom), the updated model for *Microcystis* shows a strong positive relationship with surface water temperature (p-value < 0.001) and it primarily occurred under low-nutrient conditions (ammonia: $20 \mu\text{g L}^{-1}$ to $200 \mu\text{g L}^{-1}$ (p-value < 0.01). *Microcystis* tended to grow more in the north shallow region (6 m to 15 m) than the deep regions (15 m to 30 m) in the years in this study. Data also indicated that *Microcystis* showed lower cell density at water

281 depths less than 6 m, however this is mainly associated with samples collected in littoral area
282 in September when *Microcystis* tended to collapse. There was no effect of surface irradiance
283 alone on *Microcystis*, however there was a strong effect for the interaction between surface water
284 temperature and irradiance (p-value < 0.01).

285 3.6. Ecological niche analysis with predictive parameters

286 The GAM models suggest that the four environmental factors, ammonia, water depth, surface
287 irradiance and water temperature, are important predictors for cell densities of both *Planktothrix*
288 and *Microcystis*. We have developed contour maps for the GAMs to illustrate the temporal and
289 spatial interactive effects of the environmental factors (Figure 5 and 6). Amongst these factors
290 irradiance and surface water temperature show strong seasonal fluctuations that do not vary with
291 spatial location, water depth varies with location as expected, and ammonia shows both seasonal
292 fluctuation and spatial variation. Amongst these variables, irradiance is a lead driver which is
293 followed by surface water temperature as a lag; water depth is strongly determined by operational
294 requirements; whereas NH_4 will be seasonally influenced by both inflows and a biogeochemical
295 response to seasonal drivers (irradiance and water temperature).

296 As a consequence niche analysis was performed along with the seasonal trajectory (combi-
297 nations of two factors among NH_4 , T_0 and I_0) and spatial trajectory (combination of NH_4 and
298 z_{max}) of these factors in the Miyun Reservoir, and this is shown in Figure 5 and 6, respectively.

299 In terms of seasonal trajectory *Planktothrix* and *Microcystis* exhibit different seasonal pat-
300 terns in all bi-dimensional environmental niche spaces. *Microcystis* has a preferred growing sea-
301 son and blooms are observed in July and August while *Planktothrix* is generally absent during
302 this period; *Planktothrix* then increases towards the end of August and reaches a peak in Septem-
303 ber or early October, as *Microcystis* concentrations decline. In the $I_0 \times T_0$ plane, the seasonal
304 trajectory of these growth driving variables has an elliptic orbit in the anti-clockwise direction.
305 This is associated with the time required for water temperatures to increase over the spring and
306 summer. *Planktothrix* populations develop associated with modest surface temperatures and irra-
307 diance conditions (Figure 5 (a)), while *Microcystis* mainly occur in high temperature conditions
308 (Figure 5 (d)). In the $\text{NH}_4 \times T_0$ plane (Figure 5 (b, e)), both genera appeared to be more sensitive
309 to water temperature. The two genera exhibit reciprocal patterns in the $\text{NH}_4 \times I_0$ plane (Figure
310 5 (c, f)) with *Planktothrix* mainly present in lower irradiance conditions and *Microcystis* more

311 abundant at high light irradiance. This pattern is also reflected in the overall depth distribution
312 of the two genera (Figure 3).

313 [Figure 5 about here.]

314 The spatial trajectory of the niche space of both *Planktothrix* and *Microcystis* on the $\text{NH}_4 \times$
315 z_{max} plane indicate that ammonia concentration and z_{max} vary in different regions of the reservoir
316 with a controlling effect upon the spatial distribution of *Planktothrix* and *Microcystis*. (Figure
317 6). The greatest concentrations of both genera are generally observed in the north and northeast
318 shallow regions of Miyun Reservoir. *Planktothrix* is primarily found in the littoral areas ($z_{\text{max}} <$
319 5 m) of the shallow regions, whereas *Microcystis* is found in low concentrations in littoral areas.
320 Overall *Microcystis* shows higher concentrations in shallow north region compared to the deep
321 regions in the west and south.

322 [Figure 6 about here.]

323 4. Discussion

324 The *Microcystis* seasonal patterns show growth as early as April and it becomes the dominant
325 species by July (data not shown). *Planktothrix* is rarely observed before August and its growth is
326 greatest at a time that *Microcystis* is declining. Our findings indicate that ammonia, water depth,
327 surface water temperature and irradiance are the essential predictors of *Microcystis* and *Plank-*
328 *tothrix*, but they act in different ways. For example, elevated ammonia can be regarded as being
329 both a cause and an effect of a bloom. *Microcystis* is dependent upon surface water temperature
330 and water depth while *Planktothrix* is dependent upon these factors as well, but also dependent
331 upon surface light irradiance. The seasonal cycles of inorganic nutrients are also correlated with
332 the annual temperature cycle. It is possible that there is a confounding effect of water tempera-
333 ture with other seasonal signals. We nevertheless find that light irradiance and temperature are
334 robust and parsimonious predictors of the seasonal cycles of *Planktothrix* and *Microcystis* in the
335 Miyun Reservoir. The biomass of *Microcystis* is mainly limited by low concentrations of inor-
336 ganic nutrient resources (mainly P) that are depleted in late August (Figure 4 (a-d)). On the other
337 hand, the growth of *Planktothrix* density does not demonstrate this relationship, and is mainly
338 influenced by the combination of preferred water depth and irradiance. The *Planktothrix* growth

339 season commences in September as *Microcystis* begins to decline from the surface layer. What
340 we find is that *Planktothrix* shows a negative relationship with water depth, which is consistent of
341 ecotypes that can have distinct vertical and seasonal distribution in a Norwegian Lake (Rohrback
342 et al., 2008).

343 Vertical distribution of *Microcystis* in the water column has been widely studied over the
344 last 40 years (Brookes and Ganf, 2001, Wu and Kong, 2009). The vertical movement of *Microcystis*
345 is mainly driven by vertical mixing process of the water column in conjunction with
346 buoyancy adjustment. Morphological features have been used to explain the habitat of different
347 genera/species (Su et al., 2014); *Microcystis* tends to have greater concentrations at the
348 top of the water column where light irradiance is high but where nutrient concentrations can be
349 severely depleted (Liu et al., 2015). *Microcystis* cells also have both a small cross-sectional area
350 ($22.8 \mu\text{m}^2$, (Su et al., 2014)) and a high specific surface area $1.42 \mu\text{m}^{-1}$ that are associated with
351 low light-harvesting potential and high nutrient uptake affinity. Compared to *Microcystis*, *Planktothrix*
352 cells however have a higher cross-sectional area ($172 \mu\text{m}^2$) and lower specific surface
353 area ($1.06 \mu\text{m}^{-1}$) which results in higher light-harvesting potential and lower nutrient-utilization
354 capability. This allows for better adaptation by *Planktothrix* to lower irradiance in deeper layers.
355 This conclusion is consistent with another case study for *Planktothrix rubescens* in Lake Zürich
356 (Van den Wyngaert et al., 2011). Besides differences in morphological features, high temperature
357 has been regarded as a key factor predicting *Microcystis* blooms. Also in relation to temperature
358 preferences, *Planktothrix rubescens* appeared to be much more competitive than *Planktothrix*
359 *agardhii* in 15°C , while *Planktothrix agardhii* was more competitive at 25°C in competition
360 experiments (Oberhaus et al., 2007).

361 *Microcystis* and *Planktothrix* blooms have been frequently recorded and the niche of each
362 genera have also been widely analyzed (Walsby and Schanz, 2002, Oberhaus et al., 2007, Davis
363 et al., 2009, Cuypers et al., 2011, Van den Wyngaert et al., 2011, Gallina et al., 2017, Chaffin
364 et al., 2018); however, the interactions and resources competition including light irradiance
365 and nutrient between two genera have rarely been discussed. Our findings suggest that surface
366 irradiance is the main predictor determining the outcomes of competition between surface and
367 subsurface cyanobacteria. In Table 2, we speculated in more general terms the niche model pre-
368 dictions in relation to seasonal conditions and lake properties. Density stratification will typically
369 be weaker in shallow water bodies, resulting in strong vertical mixing and high nutrient supply

fluxes from the sediments. Surface-living cyanobacteria like *Microcystis*, which are well adapted to high light irradiance and nutrient conditions, will have frequent and serious blooms under such conditions, and a prominent example of this is in hyper-eutrophic Lake Taihu in Jiangsu, China (Qin et al., 2010). While the subsurface cyanobacteria have a higher growth potential under low light irradiance conditions, lower growth may occur in eutrophic water bodies because of competition from surface blooms of *Microcystis*, which may reduce the penetration of subsurface irradiance. This is consistent with findings of great *Planktothrix* abundance in the shallow areas of the Miyun Reservoir (Su et al., 2017). Light preferences and competitive access by two *Planktothrix* species was also confirmed in an earlier laboratory study (Oberhaus et al., 2007). This study found that pigmentation of these strains was of primary importance in determining the outcomes of the competition experiments under low irradiance. We found that subsurface growth *Planktothrix* is likely to be reduced or be limited by shading by surface dwelling *Microcystis* blooms under high light conditions in summer in Miyun Reservoir. The *Planktothrix* population has difficulty growing until subsurface light irradiance is able to increase (typically starting in September) associated with the collapse of *Microcystis*. Besides, cyanobacteria possess a buoyancy regulation mechanism to influence their vertical position along the water column (Medrano et al., 2013). Serizawa et al. (2010) compared the buoyancy regulation mechanism in surface scum cyanobacteria and filamentous cyanobacteria based on a shape factor referring to as the coefficient of form resistance (Reynolds et al., 1987), addressing that the buoyancy regulation of filamentous cyanobacteria was weakened owing to their slender shape compare with *Microcystis*. This provide another advantag of the surface *Microcystis* over the subsurface cyanobacteria.

These observations agree with the concept of the “critical light irradiance” required to support and sustain competitive growth of different phytoplankton species under light-limited conditions proposed by Huisman and Weissing (1994). They proposed a model which is applicable to competition for light under well-mixed water conditions, where each algal or cyanobacterial species has a different “critical light irradiance” which must be exceeded for the species to grow and increase in population size (Huisman and Hulot, 2005). In the case of *Microcystis* in Miyun Reservoir it has adequate light above this irradiance during summer growth under stratified conditions and continues to shade the water column and prevents *Planktothrix* from receiving its “critical light irradiance” threshold to initiate and sustain growth, until nutrient depletion causes *Microcystis* to decline.

401 This interaction with nutrient availability in deeper water is also critically important, In the
402 deeper regions of the reservoir, the water column will typically be stratified during the warm
403 summer months. This will reduce or eliminate vertical mixing which leads to reduction in supply
404 from sediments and results in nutrient limitation for the over-buoyant surface dwelling *Microcys-*
405 *tis* populations. This mechanism represents part of the explanation for the decline of *Microcystis*
406 in Miyun Reservoir and succession to sub-surface cyanobacteria. Thus, nutrients responsible for
407 the succession of surface and subsurface cyanobacteria become more important in deep water vs
408 shallow water.

409 [Table 2 about here.]

410 5. Conclusion

411 In this study, the main mechanisms driving the of the succession and interaction between the
412 surface and subsurface cyanobacteria in a major Chinese Reservoir have been proposed based
413 upon the ecological niche concept derived from the GAM modeling. Underwater light irradi-
414 ance, controlled by both surface light irradiance and water column transparency, is regarded as
415 a critical factor to control the growth of subsurface cyanobacteria in this reservoir, and might
416 be perhaps also applied to other shallow and oligotrophic/mesotrophic waters, while nutrients
417 may play a more important role in deeper waters with eutrophic conditions. The study has also
418 demonstrated the role of competitive interaction for light with surface bloom forming species
419 and sub-surface types that grow at depth, with summer surface blooms of *Microcystis* causing
420 shading that causes a delay to the onset of growth of sub-surface types until summer blooms
421 decline.

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598

Figure 1: The seasonal patterns (a-e, k-o; Annual Mean over 7 years) and inter-annual trend (f-j, p-t; 2007-2013) of major environmental variables influencing the ecology and population development of *Microcystis* (o,t) and *Planktothrix* (n,s) in Miyun Reservoir. Y-axis represents GAM modelled results corresponding to the seasonal and trend term of each parameter. Abbreviations - TN, total nitrogen; NH_4 Ammonia; TP, total phosphorus; PO_4 , Soluble Phosphorus; SD, secchi disk depth; T_0 , surface water temperature; I_0 , Surface light irradiance; $z_{\max}$, maximum depth; P, *Planktothrix* spp.; M, *Microcystis* spp..

Figure 2: Patterns of important environmental variables (a-e); (TN: total nitrogen; NH₄: ammonia; TP: total phosphorus; PO₄: soluble phosphorus; SD: Secchi Disk depth, respectively) demonstrating the horizontal variability and trend along a transect line (thalweg) from the west dam to the south dam in the reservoir; and the variation over depth (0-30 m) for these same variables (f-j). in Miyun Reservoir.

Figure 3: Vertical profile of cell numbers of *Microcystis* (a) and *Planktothrix* (b) in the north shallow area (NSR, see Figure A1) during September, 2012, when the 2-MIB concentrations are usually high. (samples were collected on Sep. 7 and 23; sampling time: 10:00-12:00).

Figure 4: Environmental effect size curves for important growth controlling variables from GAMs fitted to the cell density of *Planktothrix* (upper) and *Microcystis* (lower) in the Miyun Reservoir (—), with 95 % confidence bands (- - -). The Y-axis of the 8 figures (on the left) represent 4 environmental effect sizes of ammonia, $z_{\max}$, T_0 and I_0 for both strains, while the 2 figures on the far right are the effect sizes (present by contour lines) of interactions between I_0 (Y-axis) and T_0 (X-axis) on the two strains.

Figure 5: Niche analysis of *Planktothrix* (a-c) and *Microcystis* (d-f) in relationship to seasonally fluctuating environmental variables in the Miyun Reservoir. The contour colours and lines indicate the predicted logarithms of cell densities in the two genera (from low to high represented by green to bright orange); empty grey circles indicate absence, while white circles indicate presence; blue to dark red colour filled within white circles indicate observed cell density (from low to high); the gray - black lines indicate the long-term and seasonal (January to December) trajectories of the same environmental factors.

Figure 6: Miyun Reservoir niche analysis of *Planktothrix* sp. (a) and *Microcystis* spp. (b) on spatially varied factors (NH_4 and z_{max}) for average September conditions. The contour colour, lines, and circles represent the same as in Figure 5; the squares filled by four colours indicate the sampling sites in four regions: west reservoir region (green); north reservoir region (yellow); northeast reservoir region (red); south reservoir region (light blue). Detailed information can be found in Figure A1.

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Table 1: Significance of each predictor of *Planktothrix* and *Microcystis* in GAMs

Smooth terms	<i>Planktothrix</i>			<i>Microcystis</i>		
	F	p-value	sig. ^a	F	p-value	sig.
s(TN)	0.000	0.750		0.000	0.942	
s(NH ₄)	1.298	0.008	**	1.056	0.002	**
s(TP)	0.000	0.405		0.061	0.206	
s(SD)	0.000	0.430		0.000	0.409	
s(z _{max})	2.298	<0.001	***	10.307	<0.001	***
s(T ₀)	6.990	<0.001	***	7.122	<0.001	***
s(I ₀)	1.336	<0.001	***	0.000	0.249	
ti(T ₀ ,I ₀)	0.238	0.060	.	1.095	0.003	**
Summary	0.268 ^b 38.1% ^c			0.458, 51.0%		

^a ***: <0.001, **: <0.01, .: <0.1 ^b R-sq.(adj)

^c Deviance explained percentage.

Light irradiance ^a	Water depth ^b	Oligo-		Meso-		Eutrophic	
		SLC ^c	SSC ^d	SLC	SSC	SLC	SSC
High	Shallow	** ^e	*	****	*	*****	
	Median	*	*	***	**	*****	*
	Deep	*		**	*	***	**
Median	Shallow	*	**	***	**	*****	*
	Median	*	*	**	**	**	**
	Deep			*	*	*	**

a: High “light” represent relatively strong light irradiance such as in summer, median values represent lower light irradiance such as in autumn or spring; while low light irradiance is not included since both surface and subsurface cyanobacterial blooms are rarely recorded;

b: The water depth defined as deep represent the stratification may occur in the water column during summer, while shallow represent no stratification occurs.

c: SLC, surface-living cyanobacteria; d: SSC, subsurface cyanobacteria;

e: growth potential, *****: very high, *: low; empty: very low.