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Estimating future cyanobacterial occurrence and importance in lakes: a case study with *Planktothrix rubescens* in Lake Geneva

Nicole Gallina[1] · Martin Beniston[1] · Stéphan Jacquet[2]

Abstract Among the multiple forms of freshwater pelagic cyanobacteria, the phycoerythrin-rich species *Planktothrix rubescens* is well adapted to temperate, deep and large lakes. In Lake Geneva, this filamentous and microcystin-producing species has been the dominant cyanobacterial species observed since the early years of this century. In addition to the trophic state (e.g., the phosphorus level), the influences of air and water temperature on the occurrence and development of cyanobacteria are particularly relevant in the context of global climate change. The latter may indeed be particularly marked for lakes in the Alpine region, with a rate of warming that may be twice as large as the global average. The impact of climate change on *P. rubescens* is thus an important challenge and it has been analysed in this study through two different approaches: (1) the extreme air temperature events as a proxy for future climate and (2) the multi adaptive regression splines (MARS) model to predict future *P. rubescens* biomass. These methods allowed us to determine whether Lake Geneva will still sustain an important biomass of *P. rubescens* in forthcoming years, provided there is no severe over-enrichment with nutrients in the future. The outcomes strongly suggest that the fraction of cyanobacterium could increase with respect to the total phytoplankton community by as much as 34 % by the end of this century and induce a significant change in the microalgal composition.

Additionally, the results point to the fact that spring is a key period during which air temperature and nutrients become the determinant factors for outbreaks of this species in the subsequent seasons.

Keywords Lake Geneva · Global warming · Statistical model · Cyanobacteria · *Planktothrix rubescens* · Lake ecology

Introduction

Lake Geneva is the largest natural lake in Western Europe and represents an important resource for drinking water supply, and is home to many recreational activities. It is therefore an important task for water resource managers to maintain Lake Geneva's water quality in a good to excellent state. Long-term monitoring of aquatic ecosystems is likely to provide useful information to address key questions dealing with causes and consequences of changes in water quality. Lake Geneva has been surveyed since 1957 as part of the international programme of water protection led by the Commission Internationale pour la Protection des Eaux du Léman (CIPEL; International Commission for the Protection of Lake Geneva Waters). Several studies highlighting the changes in Lake Geneva's water quality have already been published (Anneville and Leboulanger 2001; Anneville et al. 2002, 2007; Tadonléké 2010; Jacquet et al. 2012, 2014a, b; Berthon et al. 2013). Lake Geneva has begun to recover from the 1990's, and went from being highly eutrophic to today's mesotrophic state, mainly due to restoration measures which led to a progressive decline in phosphorus concentration. As a response, seasonal changes in the phytoplankton community occurred and have been documented as well as

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changes in the relationships between primary production, nutrients and global warming. However, only a few studies have focused on one particular phytoplankton species or group of species. To the best of our knowledge, this has only been the case a couple of times in the past, for diatoms (Druart and Rimet 2009; Rimet et al. 2009) and the green conjugate *Mougeotia* sp. (Tapolczai et al. 2015). So far, and compared to other neighbouring lakes no particular focus has been devoted to a special group of potentially blooming toxic cyanobacterial species such as *Planktothrix rubescens*. However, this species represents a key concern for lake management authorities and a large debate exists nowadays related to its possible evolution in response to global warming (Jacquet et al. 2005; Shatwell et al. 2008; Paerl and Huisman 2009; Gallina et al. 2011, 2013; Huber et al. 2012; Anneville et al. 2015; Savichtcheva et al. 2014).

Cyanobacteria are oxygenic photosynthetic prokaryotes and these microorganisms have often been reported to proliferate excessively to form blooms. The increased biomass during a bloom episode increases the turbidity of lakes which in turn affects the transparency and therefore restricts the light availability necessary for the aquatic vegetation. This may lead to habitat disappearance for fish and benthic flora and fauna (Scheffer et al. 1997). The shading due to population outbreaks can result in the selection or suppression of the phytoplankton via the competition for light (Jöhnk et al. 2008), potentially leading to a drastic reduction of the phytoplankton diversity. During nighttime, dense blooms of cyanobacteria are able to cause oxygen depletion through respiration and bacterial decomposition, which can result in massive fish mortality and food chain loss (Vanni et al. 1997). A major concern related to cyanobacteria concerns risks to human health and the ability of these algae to produce toxic compounds harmful for livestocks, pets and humans (Chorus and Bartram 1999; Dokulil and Teubner 2000; Briand et al. 2003). These toxins can be grouped into three families, depending on their toxic effects: hepatotoxins, neurotoxins and dermatotoxins. Numerous hypotheses have been formulated about the reasons underlying the production of these toxins (Wiegand and Pflugamcher 2005; Schatz et al. 2007) including the allopathic effect that is designed to harm potential grazers or competitors (Paerl and Millie 1996; Tillmans et al. 2008). It is noteworthy that the impact of cyanotoxins on aquatic ecosystems still remains largely misunderstood. This has created the need for a better understanding of the conditions favouring cyanobacterial growth and development, with the goal of providing a basis for the control and management of their occurrence and abundance (Chorus and Bartram 1999). As cyanobacteria are very tolerant to changes in their environmental conditions, they could be favored under a changing climate, an outcome that is indeed expected for Lake Geneva in the course of the 21st century (Perroud and Goyette 2010). Thus the question is asked whether changes in climate (long-term warming or shorter extreme events) could favour the development of the cyanobacteria and counteract the evolution of the re-oligotrophication of Lake Geneva's ecosystem. This represents a critical issue because of the ecological and socio-economic importance of such ecosystems, especially when one consideres the fact that Lake Geneva supplies drinking water to more than 1.5 million inhabitants, contains stocks of commercially important fishes such as the Arctic char, perch and whitefish, and is used for multiple recreational activities.

Among the different species of cyanobacteria, *Planktothrix rubescens* (Anagnostidis and Komarek 1988, synonym *Oscillatoria rubescens* Gomont 1892) produces mainly variants of the hepatotoxin microcystin, known to be associated with oncological and endocrinological risks. It is a red-colored, filamentous cyanobacterium with gas vesicles, which is able to adjust its buoyancy and thus its position in the water column, in order to obtain its preferred low light environment (and possibly also in response to other resources). It often forms deep-water maxima in the stratified lakes of temperate latitudes (Feuillade 1994; Bright and Walsby 2000; Jacquet et al. 2005, 2014c). *P. rubescens* achieves relatively high growth rates even at low or variable light intensities (Oberhaus et al. 2008), and its morphology (frequently elongated or trichal) provide a high surface/volume ratio, thus enabling rapid exchange of metabolites through the cell surface. These features make *P. rubescens* a perfect biological model to test the impact of global warming.

Under current warming trends at the global and regional scales, extreme events such as heat waves are becoming more frequent (IPCC 2007) and are projected to become the norm in a "greenhouse climate" by 2100. Therefore, the use of current climate extremes as a proxy for future climate allows assessment of possible impacts on the natural environment (Beniston 2007), and such a methodology has already been applied successfully to other deep sub-alpine lakes (Gallina et al. 2011). If many studies have already pointed out the increasing risk of cyanobacterial blooms with climate change and that recent accumulating evidence has indeed suggested that global warming will favor cyanobacteria (e.g. Paerl and Huisman 2008; Elliott 2010), other studies have also reported that heat waves and extreme hot weather periods may not necessarily promote cyanobacterial blooms. This is because of the importance of critical thresholds for some abiotic drivers (Huber et al. 2012) and thus high temperatures could be of limited value in forecasting the structure of phytoplankton communities in a warmer context (Anneville et al. 2015).

In this paper, we tested the hypothesis that the biomass of *P. rubescens* may become higher in Lake Geneva under warmer climatic conditions projected for the coming decades of the 21st century, provided phosphorus concentrations remain in non-limiting conditions for growth and development (Jacquet et al. 2014c). To address this goal, we employed two methods based on (1) a descriptive approach in which we used current climate extremes as a proxy for future mean climate and (2) a quantitative analysis in which we used a statistical model (multivariate adaptive regression splines, MARS) (Leathwick et al. 2005) to predict of the future biomass.

Methods

Study site and sampling strategy

Lake Geneva is a deep peri-alpine lake, located on the border between France and Switzerland. It is situated at an altitude of 372 m, with an area of 582 km^2, a maximum width of 13 km and length of 72 km, representing a volume of approximately 89 km^3 for a theoretical average residence time of about 11 years. Lake Geneva is composed of two basins, a deep central eastern basin, also called the "large lake" ("Grand Lac"), whose deepest point is 309 m below the surface, and a western and more shallow basin, the "small lake" ("Petit Lac"), with a maximum depth of 74 m (Fig. 1). Defined as a warm monomictic lake, temperatures seldom drop below 6 °C in winter and this lake never freezes. Between 1974 and 2010, full mixing of the water column occurred only seven times (1979, 1981, 1984, 1986, 1999, 2005 and 2006). Lake Geneva underwent rapid eutrophication in the 1960's, reaching approximately 90 µgP L^{-1} around 1980. Following a program designed to reduce phosphorus loading, initiated in the early 1970's, the lake recovered and is an example of a restored ecosystem "in progress". Lake Geneva is now defined as a mesotrophic ecosystem (Jacquet et al. 2012, 2014a).

Water sampling was performed using an integral sampler (Pelletier and Orand 1978) at the reference station "SHL2", located above the deepest point of the lake (Fig. 1), with a monthly frequency from November to February, and twice per month from March to October, when the biological activity is more important. Although the data cover the period since 1974 for the phytoplankton time series, we only considered for this study the 2001–2008 period in order to avoid bias in the data. Indeed, the sampling strategy changed in 2000. Before this year, samples were collected in the upper euphotic layer (0–10 m) and this depth was increased to 20 m after 2001. After Lugol fixation and sedimentation in Utermöhl chambers (Utermöhl 1958), phytoplankton counts were carried out using reversed microscopy (Zeiss) to perform a qualitative and quantitative examination of the phytoplankton. The abundances found were converted into biomass (expressed in µg L^{-1}) starting from the biovolumes of each species (Druart and Rimet 2008). For *P. rubescens*, cell dimensions varied between 5 and 6 µm on average, and biovolumes were obtained from filament length using the
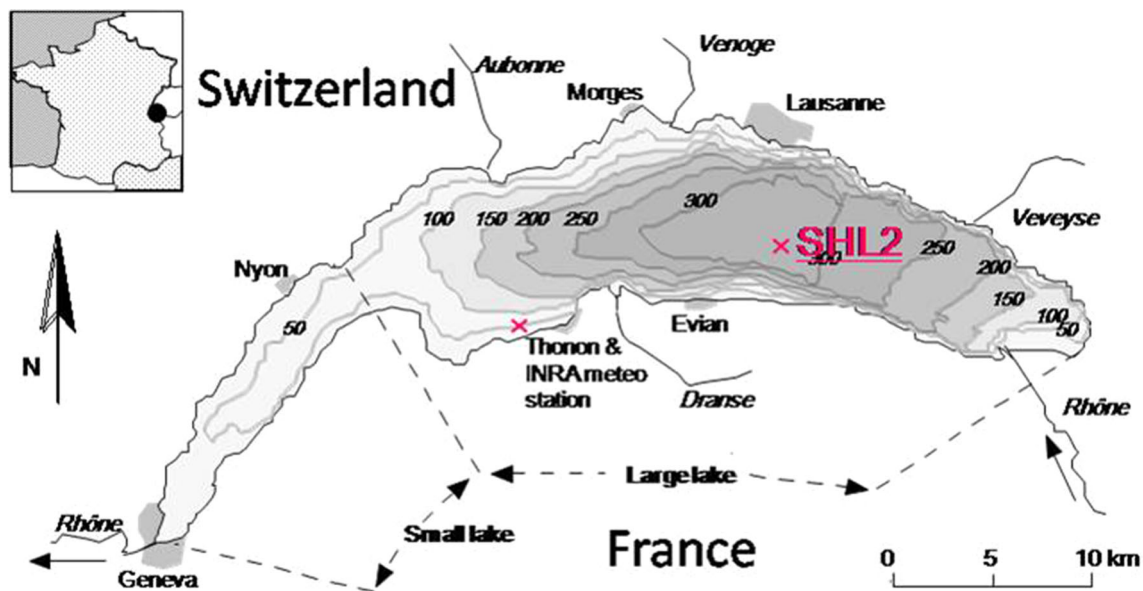

Fig. 1 Study site: location of Lake Geneva located between France and Switzerland. The reference station named SHL2 corresponds to the deepest zone of the lake. The meteorological station is also indicated and is situated at the INRA limnological research station in Thonon-les-Bains, France

formula PI $\times$ radius^2 $\times$ height of the filament. Such biovolumes were then used to estimate biomass.

Physical and chemical parameters were sampled at discrete depths (0, 1, 2.5, 5, 7.5, 10, 12.5, 15, and 20 m) at the same date and frequency as the phytoplankton samples. The details related to the sampling procedures and analyses are provided elsewhere (Jacquet et al. 2012, 2014a, b). To allow the comparison between environmental and phytoplankton data, the weighted averages of the physical and chemical parameters were calculated over the first 20 m of the water column.

Data

To assess the relative importance of the cyanobacteria during extreme events, their biomass was converted into their percentage relative to the total phytoplankton community, in order to better demonstrate their contribution to the entire phytoplankton community. For further modelling purposes, we analysed the biomass of *P. rubescens*, as it was the most abundant species within the cyanobacterial community of Lake Geneva, representing over 45 % of the total cyanobacterial biomass during the selected period of this study, i.e., from 2001 to 2008 (Fig. 2b).

For modelling purposes, predictors were generated using parameters known to influence the phytoplankton community (Nôges et al. 2010; Gallina et al. 2013). To exclude co-linearity among predictors and to avoid inference with the fitting process, only 13 predictors were selected from an initial set of 22 constructed predictors. The selection was performed upon the graphical outcome of a PCA analysis and the correlation coefficients between the descriptors. Descriptors having a correlation coefficient of $r > 0.8$ were excluded, as for descriptors exhibiting an overlapping gradient in the resulting PCA analyses, pointing either to the same or to the opposite direction (negative correlation) with the same strength. PCA analysis was performed using the ade4-package in R (Dray and Dufour 2007). The selected predictors were grouped into five categories, namely into predictors related to nutrients (total nitrogen and total phosphorus, and the nitrogen to phosphorus ratio), water physical characteristics (temperature, water column stability), light availability (euphotic depth and underwater climate index), competition (number of species present in the sample, total phytoplankton biomass of the previous sample) and meteorological predictors (rainfall, wind speed and global radiation) (Table 1).

The stability of the water column was calculated using the Brunt–Väisälä frequency, according to the following formula:
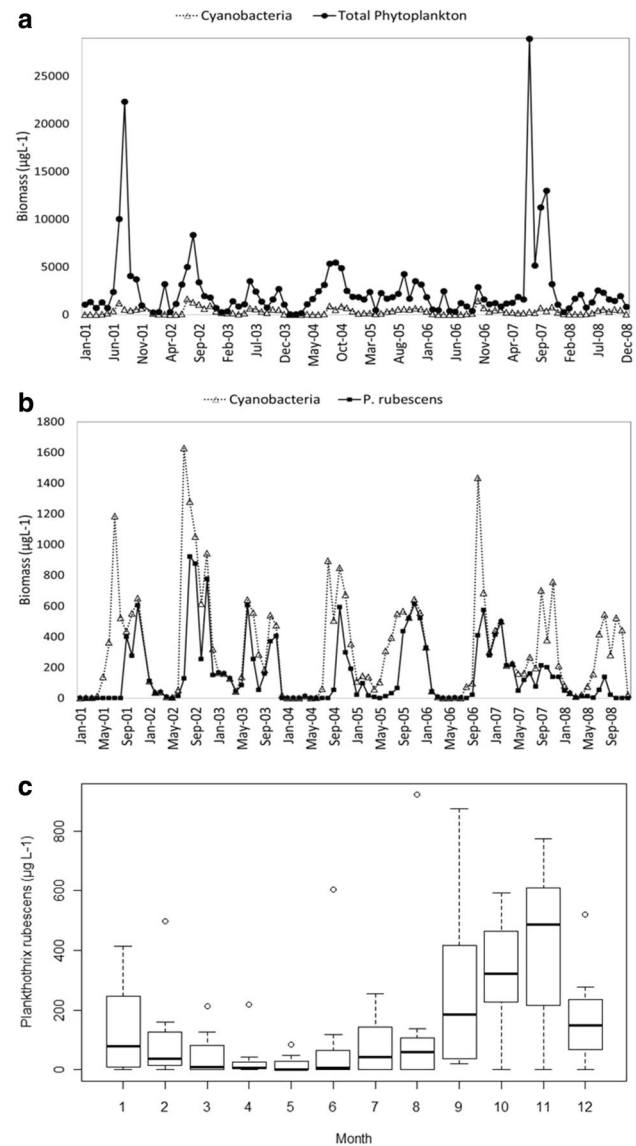

Fig. 2 **a** Monthly average concentrations of the total phytoplankton vs. the cyanobacteria biomass and **b** monthly evolution of the total cyanobacteria vs. *Planktothrix rubescens* biomass, in Lake Geneva between 2001 and 2008. **c** Illustrates the monthly biomass variation of *P. rubescens* assessed from 2001 to 2008, indicating the main growth period starting at the end of the summer, reaching the maximum biomass by the end of autumn, and subsequently decreasing in winter and disappearing in the following spring

$$N^2 = \frac{g}{\rho}\left(\frac{d\rho}{dz}\right)$$

where N^2 is the stability coefficient (in s^{-2}), g is the gravitational acceleration (9.81 m s^{-2}), ρ is the water density (kg m^3), z is the depth (in m), and the pressure was calculated according to Lemming (1978) as follows: $\rho(T) = 1000 - 7 \times 10^{-3} (T - 4)^2$ and where T is the temperature (°C). We used the log of the maximum value of N^2.

Table 1 Predictors used to fit *P. rubescens*

Predictors	Autocorrelation correction LAG-*P. rubescence* (µg L^{-1}) AUTOCORR	Nutrients related predictors			Physical related predictors		Light related predictors	
		Total nitrogen (mg L^{-1}) TN	Total phosphorus (mg L^{-1}) TP	Total nitrogen to total phosphorus ratio TP:TN	Water temperatures (°C) WT	Log of Brunt–Väisälä frequency LogN2	Euphotic depth (m) Z_{EU}	Underwater climate index Z_M/Z_{EU}
Mean	141.2	0.54	0.003	35.44	11.5	7.19E−04	16	0.6
Range	0–784	0.2–0.9	0.035	14.2–82.9	5.7–19.3	1.36E−06–4.42E−03	3.8–38.5	0–4.01
AUTOCORR	**1**	0.25	**−0.27**	**0.23**	−0.02	−0.16	0.19	0.19
TN		**1**	**0.44**	**0.28**	**−0.57**	**−0.46**	0.18	**0.51**
TP			**1**	**0.51**	**−0.67**	**−0.41**	0.02	**−0.53**
TP/TN				**1**	**0.31**	**0.23**	0.14	0.18
WT					**1**	**0.79**	**−0.42**	**0.7**
LogN2x						**1**	**−0.44**	**0.53**
Z_{eu}							**1**	**−0.47**
Z_m/Z_{eu}								**1**
DivNB								
TotalBM-1								
RAIN								
LogV								
Vx								
RAD								

Predictors	Phytoplankton community related predictors		Meteorological related predictors			
	Numbers of species present in the sample DivNB	Total Phytoplankton BM present at the previous sampling Total BM-1	Rainfall (mm) RAIN	Log of the windspeed (m^{-1}) LogV	Maximum windspeed (ms^{-1}) Vx	Global radiation (J cm^{-2}) RAD
Mean	*18.1*	*3.17*	*0.43*	*0.41*	*7.9*	*1457.6*
Range	*4–33*	*1.61–4.25*	*0–1.19*	*0–0.71*	*1.5–20*	*126.8–3117*
AUTOCORR	0.16	**0.22**	0.02	−0.07	−0.15	**−0.47**
TN	**0.56**	**−0.35**	−0.16	0.1	0.08	−0.15
TP	**−0.63**	**−0.37**	−0.2	0.07	0.08	0
TP/TN	0.12	0.18	0.08	0.01	−0.06	−0.06
WT	**0.67**	**0.48**	**0.23**	−0.14	0	**0.46**
LogN2x	**0.51**	**0.29**	0.09	**−0.22**	0.09	**0.72**
Z_{eu}	**−0.48**	**−0.234**	−0.13	0.08	−0.03	**−0.48**
Z_m/Z_{eu}	**0.41**	**0.4**	0.09	−0.12	−0.03	0.2
DivNB	**1**	**0.43**	−0.05	−0.09	−0.08	0.13
TotalBM-1		**1**	0	−0.08	−0.05	0.13
RAIN			**1**	0.13	−0.04	−0.11
LogV				**1**	**0.37**	**−0.22**
Vx					**1**	−0.04
RAD						**1**

Mean, range (minimum and maximum values) of the predictors from August to February 2001–2008 are shown in the first two lines in italics, followed by the Spearman rank correlation coefficient matrix. The significant correlations ($\alpha < 0.01$, $n = 64$) are represented in bold and larger font

To include light condition and limitation for phytoplankton growth, the euphotic depth (Z_{eu}) was calculated by multiplying the Secchi depth by 2.5 (Vollenweider and Kerekes 1982), which corresponds to the depth at which the light irradiance is theoretically below 1 % of that at the surface (Talling 1957). The mixing depth (metalimnion) referred to as Z_m, which was estimated with the help of the graphical and the numerical outputs of the temperature profiles, was defined as the depth where the temperature gradient changes suddenly (1 °C per m) following Wetzel (2001). The underwater light climate index translated as the Z_m/Z_{eu} ratio.

To consider the phytoplankton community, we recorded the species present in the samples at each sampling date and labeled this index DivNB, representing diversity in the numbers of species present. Another index used was the biomass which was present at the previous sampling date and which was labeled totalBM-1.

The meteorological data were obtained from the meteorological station situated at Thonon-les-Bains (France) in the southern part of Lake Geneva, which belongs to the INRA Research Institute CARRTEL (Fig. 1). Rainfall (mm), global radiation (J cm^{-2}), wind speed (log transformed) as well as the maximum wind speed (m/s) were considered. As air temperature was highly correlated with the water temperature, this parameter was not integrated into the model. For all predictors, we averaged the values of the 5 days prior the sampling of the phytoplankton in order to integrate the possible response time of phytoplankton to meteorological events.

Simulated water temperature profiles for the period 2082–2089 were used for the projections of change in a future climate, with the aim of testing the sensitivity of *P. rubescens* to warmer water conditions. These profiles were obtained from the model simulations reported by Perroud and Goyette (2010), in which future temperature profiles for Lake Geneva were simulated under the IPCC A2 Scenario, using a one dimensional lake model applied to the SHL2 sampling point. The results of Perroud and Goyette (2010) suggest that with an increase in air temperature of 4 °C, an average increase of 2 °C in the first 20 m may be expected, inducing a longer lasting stratification period, as well as an increase in lake stability. The published thermocline values represent a reliable estimate of future water temperature conditions. In a second step the values of predictors which were selected by the MARS models were also integrated, and estimated from published literature. By modeling time-series, the seasonal cycles represent an auto-correlation structure in the data, which needs to be taken into account to avoid any misinterpretation. Therefore, to avoid data redundancy, we integrated a synthetic auto-regressive variable, which we determined as the time-lag

of the biomass of *P. rubescens* (named as AUTOCORR) and which corresponds to the biomass of *P. rubescens* from the previous sampling.

The goodness-of-fit measures the discrepancy between the observed responses and the fitted responses from model outcome; it was assessed using a linear regression model calculating the correlation between the two datasets.

Method used to define extreme temperatures and the corresponding cyanobacteria biomass variation

Our goal was to define the extreme seasons during the investigated period 2001–2008. We therefore defined a 30-year reference period from 1971 to 2000, representing the 'normal climate situation', to compare current air temperature to that of the past. Furthermore, the reference seasons from 1971 to 2000 were defined as follows: winter (December to February), spring (March to May), summer (June to August) and autumn (September to November). For each reference season, the 99th percentile of the air temperature distribution was calculated, as an objective threshold of extreme hot temperatures. These percentiles or extreme values were then compared to the annual seasonal air temperature average from 2001 to 2008. A season was defined as extremely hot when its average value was above the 99th percentile value. It was considered as normal when the average temperature value was between the 1st and the 99th percentile. Once extreme seasons were defined, we compared the response of cyanobacteria biomass during these "extreme" seasons vs. the "normal" seasons. Finally, with help of the box-plot graphical presentation, we expressed as a percentage the variation of the cyanobacteria among the total phytoplankton community during extreme and normal seasons. The statistical difference of the responses of cyanobacteria to extreme and normal seasons was tested with the Wilcoxon Rank Sum Test using the statistical software R, version 2.1.14 (R Development Core Team 2012).

Multiple adaptive regression splines (MARS) model description

In freshwater ecosystems, non-linear responses of phytoplankton dynamics are common (Malchow 1993; Stollenwerk et al. 2001). Therefore, it is crucial to use and apply appropriate statistical models to be able to represent phytoplankton patterns in response to a variety of biotic and abiotic drivers. We used the MARS model because it is a flexible non-parametric regression modeling method (Friedman 1991), with the capacity to model complex and non-linear relationships between

response and explanatory variables with similar levels of complexity to that of generalized additive models (GAM) (Hastie and Tibshirani 1990). Our choice was also motivated by the study of Elith et al. (2006) who tested and compared 16 predictive techniques, revealing that MARS was appropriate for our purposes. Its originality consists in the hinge functions breaking the full range of the predictors into subsets of linear segments using knots. The model fitting in MARS has the advantage of being very rapid and consists of two main phases: the forward and the backward pass, with the latter evaluated by using generalized cross-validation (GCV). This two-stage approach is the same as that used by recursive partitioning trees. The MARS function, implemented in the "mda"-package (Hastie and Tibshirani 2011), was applied using the free statistical software package R, version 2.1.14 (R Development Core Team 2012). In our study the code written by Leathwick et al. (2005) was used, which has the added ability of fitting a least-squares MARS model, followed by the extraction of the basic functions and the refitting of the model as a general linear model (GLM), adding the ability to specify a "family" distribution. Further statistical details can be found in Friedman (1991) and Leathwick et al. (2006).

In using MARS, we could determine (1) which predictors contribute the most to fit the response of *P. rubescens* biomass, and (2) what should its biomass be under expected in a warmer climate in the future. The model was fitted to the biomass data of *P. rubescens* from January 2001 to December 2008. The Poisson family error distribution was selected, upon analyses performed using histograms based on the distribution of *P. rubescens* biomass. The selected model was evaluated by the correlation coefficient derived from the relationship between the observed and the fitted values as well as a k-fold ($k = 10$) cross validation algorithm of the MARS/GLM model (Hastie et al. 2001), which is better at estimating the expected prediction error across training sets. The residuals were checked for homogeneity and plotted against the fitted values.

Two scenarios were considered. For the first scenario, the prediction of *P. rubescens* biomass was applied to a dataset in which all the selected predictors remained constant except for water temperature. For this scenario, we used the forecasted water temperature profiles of the period 2082–2089, i.e., using the outcomes of the work of Perroud and Goyette (2010). These water profiles were averaged for the 0–20 m layer, on the same days as the phytoplankton where sampled during the 2001–2008 period. This allowed us to investigate the response of *P. rubescens* under a global warming scenario and, simultaneously, to assess its sensitivity of to warmer water temperatures. For the second scenario, we not only changed the values of the water temperature, but also the other predictors which were selected by MARS and which most contributed to fit and best predict the biomass of *P. rubescens*. As no forecasted values of the period 2089–2089 exist for these selected predictors for Lake Geneva, they were estimated based on published literature, by adding or subtracting a constant value to the observed values of the period 2001–2008. By integrating the expected changes of all the selected predictors of MARS, this second scenario leads to a more representative picture of *P. rubescens* and what can be expected at the end of the 21st century.

Results

Phytoplankton and *P. rubescens* biomass variation in Lake Geneva

Figure 2 illustrates the succession of the total phytoplankton community, the cyanobacteria community, and *P. rubescens* in Lake Geneva during the investigated period (i.e. 2001–2008). Cyanobacteria were not a dominant group among the phytoplankton community as they represented 9 % of the total phytoplankton biomass. However, their contribution increased to 11.7 % with respect to the period of 1974–1999. Although the lake has experienced a re-oligotrophication process since the end of 1980's, the monthly phytoplankton biomass increased and almost doubled between 1974 and 2000 (1500 µg L^{-1}) and 2001–2008 (2650 µg L^{-1}) (Fig. 2a). The potential causes can not be evaluated because as the sampling strategy for phytoplankton changed during this period (see "Methods"). *P. rubescens* represented the dominant species among the cyanobacteria community (48 %), and its contribution also increased between the two periods 1974–1999 and 2001–2008. *P. rubescens* was responsible for most of the cyanobacteria proliferation events as their respective biomass coincided (Fig. 2b). In terms of population dynamics, we observed that *P. rubescens* started its growing phase in the middle of the summer and its biomass gradually increased until it reached its highest biomass concentration in November, with a median concentration of 490 µg L^{-1}. In December, the biomass abruptly decreased (median: 150 µg L^{-1}) and disappeared by the end of March of the following year (Fig. 2c).

The extreme seasons during the period 2001–2008

The yearly seasonal air temperature averages are shown in Fig. 3. The dotted lines represent the 99th percentile of the air temperature distribution, calculated for each season based on the reference period (1971–2000). These percentiles represent the threshold above which a season is

Fig. 3 *Bar charts* of the yearly seasonal mean air temperature registered at the INRA weather station in Thonon-les-Bains. The *dashed horizontal line* represents the value of the 99th percentile of the seasonal air temperature computed from 1971 to 2000, the 30-year reference period (*sum* value of the 99th summer percentile, *aut* same for autumn, *spr* same for spring, *win* same for winter). The *arrows* indicate the three seasons which were identified as extreme seasons
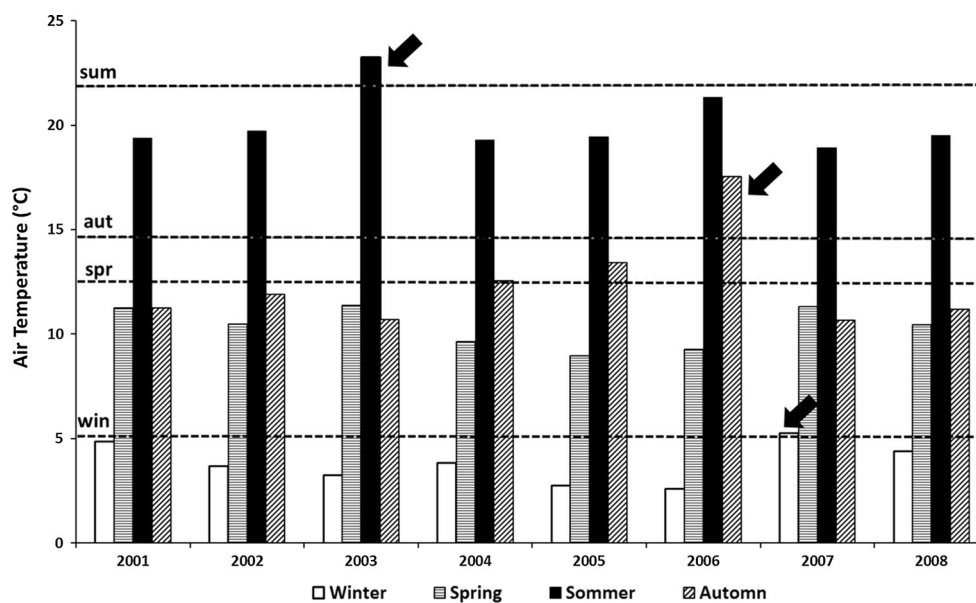
defined as being extreme, and have a value of 5.08, 12.51, 21.51 and 14.17 °C for winter, spring, summer and autumn, respectively. During the investigated years, only three out of the 32 seasons could be defined as extreme seasons, namely the summer of 2003, the autumn of 2006 and the winter of 2007. The 2003 summer and the 2006/2007 winter were clearly above the threshold. Furthermore, the winter of 2001, as well the springs of 2001, 2003 and 2007, were relatively warmer seasons. In 2003 and 2007, springs were even warmer than autumns.

Cyanobacterial behaviour during extreme seasons

Cyanobacteria started their growing phase slowly in summer (10 %) and contributed to 20 % of the total phytoplankton biomass in autumn before decreasing by half in winter (the following year), and ultimately reaching less than 5 % in spring. Their contribution to the remaining phytoplankton communities varied from less than 5 % to around 20 % during normal seasons (Fig. 4a). However, during the three defined extreme hot seasons, the biomass contribution of the cyanobacteria was significantly more important when compared to the normal seasons. It doubled during the autumn of 2006 and the summer of 2003 and was three times more important during the 2006/2007 winter. The null hypothesis of the Wilcoxon Ran sum test of equal distribution was rejected at a *p* level <0.01, indicating a significant increase during these extreme periods.

In order to analyse the behaviour and adaptation of the cyanobacterial community, its biomass variation was investigated during the seasons following an extreme hot event (Fig. 4b). After the summer heat wave in 2003, cyanobacteria represented a high fraction of the total

community until the autumn of the same year, despite the recorded "normal" temperatures (Fig. 3). The spring of 2007 was particular in this case, since it followed two consecutive extreme hot seasons (the autumn of 2006 and the winter of 2006/2007) and was recorded to be relatively warm. During this spring, the cyanobacteria community represented up to 20 % of the total phytoplankton community, a relatively important contribution, compared to a percentage close to zero under normal air temperature conditions.

The season prior to an extreme season was also analysed in order to investigate the presence of a cyanobacterial inoculum that could potentially contribute to their further development as recently shown in Lake Bourget by Jacquet et al. (2014c). Spring 2003 was a warm season and the cyanobacteria were already present at 10 %, a higher percentage level than during normal springs. Therefore the cyanobacterial pool was already present before the summer 2003 heat wave began to impact the community. However in the summer of 2006, prior to the extreme warm autumn of 2006 and winter of 2006/2007, the conditions were seen to be completely different. The cyanobacterial community contribution increased rapidly from near 0 % in summer to about 40 % in autumn. This interesting behaviour is reinforced by the fact that the cyanobacteria community was even smaller than for summers in which air temperatures were "normally" distributed.

Predictors and their contribution to the fitted *P. rubescens* model

Table 1 represents the statistical summary of the predictors used to fit *P. rubescens* to the MARS model, namely the

Fig. 4 a Seasonal variation of the percentage of cyanobacteria biomass among the total biomass of the phytoplankton community. The variation of the cyanobacteria was investigated during "normal" seasons and compared to extreme hot seasons. The *stars highlight* the three identified extreme seasons, the *numbers* indicate the year of the extreme season. **b** extends **a** in adding the seasons which either proceed or succeed an extreme seasons, to investigate the behavior of the cyanobacteria beyond the extreme seasons
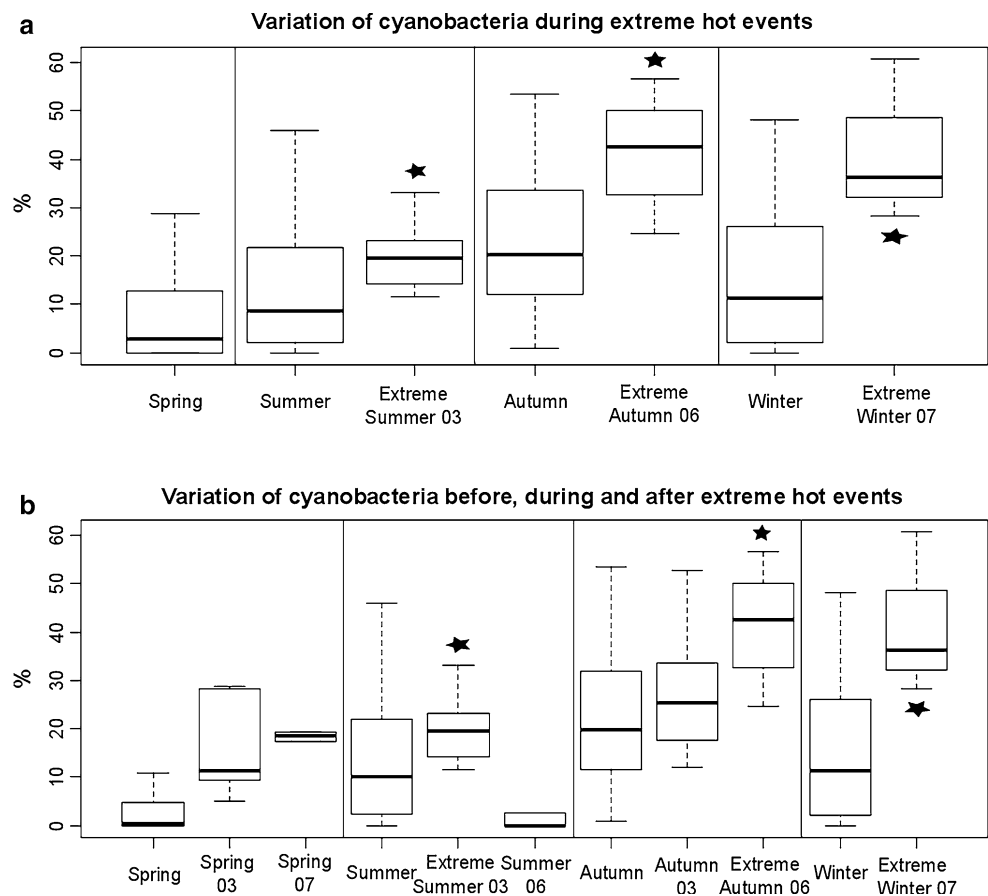
mean and the range of the predictors with their maxima and minima from 2001 to 2008. The Spearman rank correlation coefficient r between the predictors is listed in the second half of Table 1, highlighting significant correlations ($\alpha < 0.01$, $n = 64$) with larger bold font. As already stated, correlations having a coefficient $r > 0.8$ were excluded to avoid co-linearity. 13 predictors were selected and could be subdivided into five different classes related to nutrient availability, physical conditions, light availability, competition pressure, and meteorological conditions.

The nutrients (TP, TN) were neither correlated to the meteorological predictors nor to the euphotic depth. However, they were related to water temperature, as well as to the diversity of the species present and the biomass gathered from the previous sampling and the underwater physical characteristics. The negative correlation with the stability of the water column and the water temperature revealed that the highest nutrient concentrations were present in the upper layers during colder periods, when de-stratification and mixing were occurring. There was no significant relationship between the water temperature and wind whereas water temperature was correlated to all the remaining predictors ($p < 0.05$). This might indicate that the wind speed is clearly a stochastic predictor and unable

to affect the first 20 m of the water column. Water temperature was highly correlated to the water column stability, nutrients and light as well as the competition-related predictors. The correlation of the water temperature to almost all the other predictors highlighted the importance of water temperature as a potential predictor. The stability of the water column was highly correlated to predictors related to light, such as the underwater climate index and global radiation, indicating that factors governing the stability of the water columns are associated to light conditions. Light-related predictors did not significantly correlate with the meteorological predictors wind and rainfall, but had a significant relation to competition related predictors. No significant relationships were found between predictors related to competition and meteorology. Rainfall was only significantly correlated with water temperature.

Selection and validation of the *P. rubescens* model

Our results indicate that the MARS model was able to reproduce the succession of *P. rubescens* biomass during the investigated period. The final configuration of the model that we retained from this study selected four predictors contributing the most to fit the response of *P.*

a Selected Predictors by the MARS (Multi-Adaptive Regression Splines)

Water temperature

Global Radiation

Rainfall

b

$y= 15.42+0.86x$
$R=0.79$
$p<0.0001$
$AME=32$
$N=134$

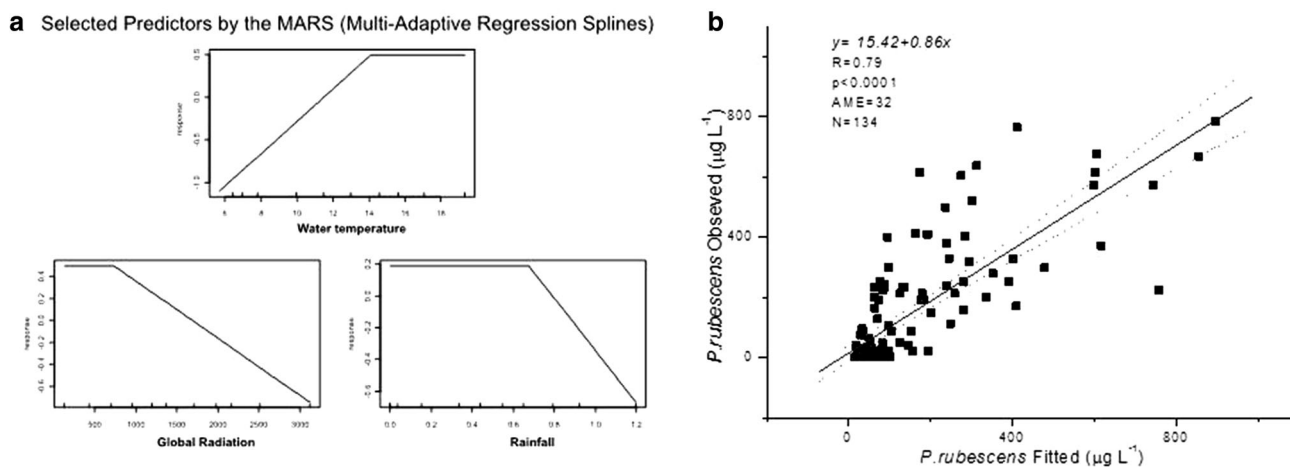*P.rubescens* Fitted (µg L^{-1})

Fig. 5 **a** Illustrations of the selected predictors of MARS contributing to the best fit of the *P. rubescens* biomass. They are shown in order of the importance of their contribution to the model: (1) water temperature, (2) global radiation and (3) rainfall. For each predictor, the form of the response function of *P. rubescens* is shown. **b** Output of the linear regression model and its upper and lower confidence limit of the fitted and observed biomass of *P. rubescens* (µg L^{-1}). The Regression Model is significant (F-statistics $p < 0.0001$, $R = 0.79$, with an absolute mean error (AME) of 32 µg/L, based on 134 observations (*N*)

rubescens, which are listed hereafter according to their contribution to the model: the AUTOCORR predictor, water temperature, rainfall and global radiation. The selected predictor's response curves suggested that *P. rubescens* has a strong positive response to warmer water temperature, but a declining response when the global radiation and rainfall increase up to a certain threshold (Fig. 5a).

The goodness-of-fit of the linear regression model between the observed and fitted biomass of *P. rubescens* was significant (F-statistics $p < 0.0001$), with a correlation coefficient of $r = 0.79$ indicating that 62 % of *P. rubescens* variation could be explained by the model. The absolute mean error (AME) was 33 µg L^{-1}. Further, the accuracy estimation of the selected model was tested via a 10-fold cross-validation test, and the full test score achieved an $r = 0.75$ whereas the mean score of the subsets reached a score of $r = 0.58$.
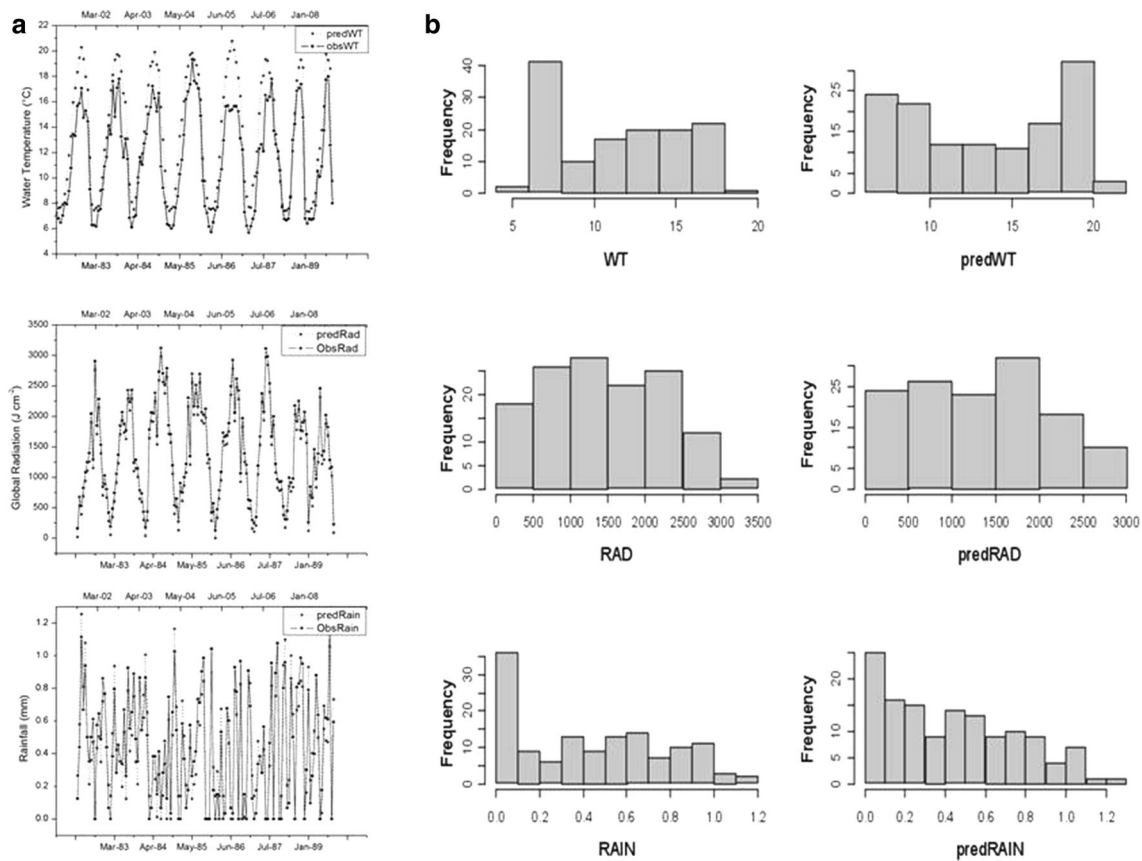
Prediction of *P. rubescens*

With the first scenario (in which only temperature is selected), the outcome indicated clearly the sensitivity of *P. rubescens* to warmer water temperatures. The resulting biomass of *P. rubescens,* averaged per month, was further compared to the observed data (2001–2008) (Fig. 6b). During the whole year, except for September, higher biomass of *P. rubescens* under future water temperature was forecasted. The increase became more important from the end of spring (May) but *P. rubescens* was primary affected during its main growth period, i.e., in the autumn (October to December). The predicted changes did not however affect the succession pattern of *P. rubescens*. All in all, a total increase of 432 µg L^{-1} was simulated for *P. rubescens*, corresponding to a total increase of 23 % by the end of the century compared to the 2001–2008 period.

With the second scenario, not only water temperature but also the selected predictors of the MARS model, i.e., global radiation and rainfall, were changed (Fig. 6a). In the future, the yearly rainfall pattern is predicted to increase in winter and decrease in summer (IPCC 2007). To run the predictions, a constant increase of 0.14 mm was added to the observed value from December to March, in order to enable the resulting increase to lie within the expected range of the median and the third quantile of the observed values (Table 1). The same value was subtracted from May to September so that the predicted rainfall values are also located between the 1st quantile and median of the observed values. To follow the forecasted rainfall pattern from the literature (IPPC 2007), no changes were undertaken in April and November. Future global dimming changes can be expected to be closely tied to emissions of atmospheric pollution and greenhouse gas warming. Warming of higher levels of the atmosphere leads to increased atmospheric water vapor, which in turn absorbs some of the sun's energy before it reaches the surface. If future global warming proves to be substantial, widespread dimming by water vapor could be a consequence. A constant value of 280 J cm^{-2} was subtracted from the observed global radiation throughout the year, representing 20 % less radiation compared the median values of 1458 J cm^{-2}, (Table 1). The frequency distribution was performed to represent the applied changes (6b). This second scenario, as for the previous scenario, resulted in a

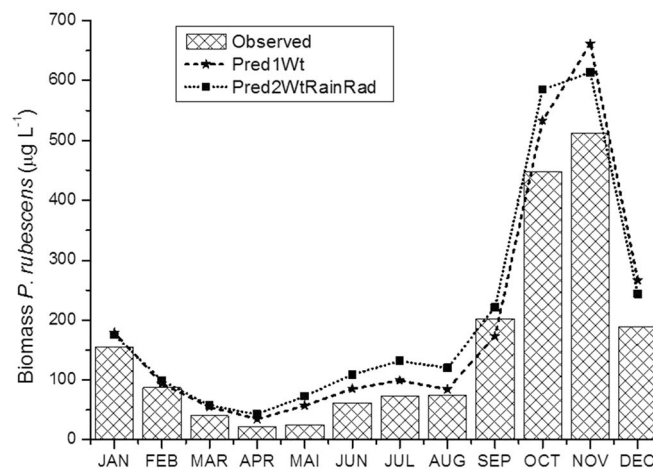**Fig. 6** **a** Observed (2001–2008) and predicted (2082–2089) values of the selected predictor implemented in MARS to run the simulations. **b** Histograms of the frequency distribution of the observed and predicted values for water temperature, rainfall and global radiation. **c** Comparison of the model outcomes to the observed biomass of *P.* *rubescens* (2001–2008) using the water temperature predicted by the end of this century (2082–2089) (Pred1WT) and the values suggested in the scientific literature for the MARS model selected predictors rainfall and global radiation (Pred2WtRainRad) (*WT* water temperature, *Rain* rainfall, *Rad* global radiation)

monthly increase in biomass throughout the year, during the main growth period (i.e. October and November) but also from May to August. The total monthly biomass increase for *P. rubescens* of the predicted period was about 583 µg L^{-1}, thus resulting in an increase of 31 % compared to the 2001–2008 period. Integrating all the selected predictors rainfall and global radiation resulted in forecasted biomass increase.

Discussion

The method proposed in this study using 'extreme events' represents a powerful tool to address questions related to future climatic conditions, especially when long data sets are missing. The outcome of this research confirmed our initial hypothesis that cyanobacteria, especially *P. rubescens*, might become more abundant in Lake Geneva under a warmer climate in the future (Beniston 2007; Perroud and Goyette 2010). This result holds provided phosphorus does not drop below a certain threshold that would prevent growth and development of the species (Jacquet et al. 2014c).

A main conclusion of our study is the confirmation that extreme air temperatures are likely to impact cyanobacterial growth and development. This indirect effect of air temperature on freshwater biological communities has been previously highlighted for other peri-alpine lakes (Gallina et al. 2011), British and Irish lakes (Georg et al. 2010), boreal lakes (Graham and Vinebrooke 2009), or some Dutch lakes (Jöhnk et al. 2008). The present research thus represents a new and concrete case study highlighting the potential importance of air temperature on phytoplankton, keeping in mind the fact that this parameter may also depend on the importance of many others such as lake morphology, its geographic position or again the mixing regime (Livingstone 1993, 1997; Blenckner 2005). In addition, as each lake has its own specific phytoplankton community, the effect of extreme events may have different repercussions for cyanobacterial communities (Gallina et al. 2013). In the case of Lake Geneva, we found an increased contribution of cyanobacteria to the total phytoplankton biomass in situations of extreme hot seasons, suggesting that warmer air temperature induces more favorable conditions for the development of this group. This result seems logical regarding cyanobacterial physiology and ecology (Huisman 2005; Reynolds 2006). However, our finding seemed to be in contradiction with the results of Huber et al. (2012) who documented that extreme summer temperatures may not always be the cause for cyanobacterial biomass increase and highlighted the importance of the differences in the intensity and duration of thermal stratification. In fact, the same conclusion might be drawn in the present study. Each of the investigated extreme hot seasons was preceded by a warmer spring, known to positively influence the stratification strength and duration. Therefore it is suggested that in years where the air temperatures were 'extremely hot', a warm spring might be the decisive factor to trigger an enhanced cyanobacterial proliferation. This is especially relevant for *P. rubescens*, a metalimnic species adapted to low underwater light climate and able to regulate its buoyancy to search for optimal nutrient and light conditions in the deeper metalimnion (Jacquet et al. 2005, 2014). It is noteworthy that our data also pointed out that the two exceptional biomass peaks occurring in 2001 and 2007 were both due to the massive bloom of *Mougeotia gracillima* (Tapolczai et al. 2015). Again, these events were associated with a warmer-than-average spring, which might have led to an earlier onset and longer duration and particularly deeper water column stratification, thereby resulting in an earlier and deeper depletion of the nutrients in the water column (Anneville and Leboulanger 2001; Nõges 2004). This situation, suitable for the development of *P. rubescens*, may thus have favoured *M. gracillima*, also known to be tolerant of low light levels and capable of developing deeper in the water column, where phosphorus is abundant (Anneville et al. 2002; Tapolczai et al. 2015). It is therefore possible that warm spring events could be favourable to species other than *P. rubescens*, such as *M. gracillima*, and that strong competition may well occur between these species. Our analysis seemed also in contradiction with recent findings of Anneville et al. (2015) who did not find a significant increase for cyanobacteria in peri-alpine lakes in response to higher temperatures. However, such discrepancies could be easily understood: (1) their analyses were performed in more recent years where the warming might have already impacted the community; (2) the seasons were not defined as for meteorological-climatological studies, so that the link with the cyanobacteria may have been missed.

The model results for temperature fit with the physiology of *P. rubescens* since the cyanobacterium has been experimentally shown to display a relatively large optimal temperature range for growth, i.e. between 15 and 25 °C (Oberhaus et al. 2008). With this temperature increase, it would however be interesting to test the impact on species interactions and competition since it is possible that the niche in temperature could also favor other groups. In particular, new ecological approaches like the theory on functional diversity, have introduced the trait-based concept to understand the mechanisms related to the response of species and communities to multiple environmental stressors like a changing climate (Litchman et al. 2007, 2010; Litchman and Klausmeier 2008; Gallina et al. 2013). In line with our results, those approaches should represent further objectives for future research in Lake Geneva. The idea is to use major functional traits of phytoplankton and combine them with the data on species' distribution along major environmental gradients with the goal to map ecological niches.

In our investigation, nutrients were not selected to contribute as important predictors to the final model, which best fitted *P. rubescens* growth throughout the year. However, it is acknowledged since the earliest days of

phytoplankton ecology research, that nutrients (especially phosphorus) are an important driver of cyanobacterial bloom (Whipple and Jackson 1899; Tonaru et al. 2015) and responsible for seasonal phytoplankton successions (Reynolds 1984; Sommer 1986; Anneville et al. 2002) and cyanobacterial growth (Pearl et al. 2001; Briand et al. 2005; Havens 2008; Gallina et al. 2013; Jacquet et al. 2014c). Likewise, recent studies suggested the importance of the nutrient concentration during the spring season, as being the main nutrient pool responsible for phytoplankton growth during its main growth period in summer and autumn (Gallina et al. 2013). Salmaso (2012) stated that nutrients will change their role during the seasonal succession depending on the season; in spring, nutrients could be considered as an explanatory variable and once absorbed in summer—autumn by the phytoplankton, they become a response variable. This fact could explain why nutrients were not selected by the MARS model, because they may have already been considered as a response variable. Similar results were obtained by Dupuis and Hahn (2009), who stated that of several factors influencing phytoplankton dynamics, total dissolved nutrients [nitrogen (N), phosphorus (P) and N:P] and water column stability were absent.

This study clearly highlighted the additional important role of the meteorological predictors that are capable not only of influencing biological in-lake processes, but also of altering the phytoplankton community composition. The predictors selected by the MARS model that contributed the most to the growth of *P. rubescens* were meteorological variables (rainfall and global radiation) together with water temperature, which is in addition directly related to meteorological variables such as air temperature (Perroud and Goyette 2010; Gallina et al. 2013). The decreasing response of *P. rubescens* to increasing radiation suggested its preference for low insolation as found under conditions typical in the metalimnon and during autumn. This is due to their large light antennae that capture enough light under such conditions (Reynolds 1997), and also because as a phycoeythrin-rich species, it thrives under green light conditions (Micheletti et al. 1998; Jacquet et al. 2005). *P. rubescens* also showed a similar decreasing response to higher rainfall. The reason may be that, as a metalimnic species (Davis et al. 2003; Reynold 1984), it is favored by a stable water column (Dokulil and Teubner 2000), so that increasing rainfall events (associated with stronger wind conditions) could act as a disturbance factor of such habitat preference. In contrast, a strong positive response was observed by *P. rubescens* biomass in connection with the increase in water temperature. Water temperature is a major driving factor in aquatic ecosystems (Robarts and Zohary 1987; De Stasio 2009; Gallina et al. 2013) and Dubuis (2009) also stated that water temperature was in

general related to changes in the phytoplankton community and the percentage of cyanobacterial biovolume.

Our results suggest that in the future, under higher water temperature regimes, a composition change may occur in the phytoplankton where *P. rubescens* may be more abundant throughout the year, more especially during summer and late autumn. The increase of *P. rubescens* biomass in stratified lakes under warmer conditions has already been reported, and explained by the synergetic effects of increased transparency due to the reduction in the phosphorus loads, the deepening of the P-depleted zone and water column stability (Jacquet et al. 2005; Nõges et al. 2010). Here it is important to note that for both methods, namely the extreme events "analog method" as well as the MARS model, displayed the same results, thereby confirming the increasing cyanobacteria hypothesis in Lake Geneva. Furthermore, both analyses predicted a more important increase at certain periods of the year, likely to result in phytoplankton composition modifications as a consequence of new niche adaptation. Our results are based on physical factors but it is clear that biological interactions should also be changed in view of their importance in these complex processes.

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