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Blue-Green Algae in a "Greenhouse Century"? New Insights from Field Data on Climate Change Impacts on Cyanobacteria Abundance

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Abstract

Climate warming is likely to impact phytoplankton communities by providing a habitat in which cyanobacteria have competitive advantage over other phytoplankton taxa. We used extreme hot weather periods to investigate the potential impact of climate change on cyanobacteria abundance in three large and deep peri-alpine lakes, Lakes Geneva, Annecy, and Bourget. Between 2000 and 2011, there were four extreme warm weather periods: spring and summer 2003, autumn 2006 and winter 2007. We found that the consequences of extreme air temperatures on cyanobacteria abundance and phytoplankton composition depend on the time of year in which the extreme temperatures occur. In all three lakes studied, a warm summer did not clearly promote cyanobacteria blooms, whereas a warm autumn promoted cyanobacteria growth in the mesotrophic Lakes Geneva and Bourget, but not in the oligotrophic Lake Annecy. A warm winter was associated with high cyanobacteria abundance and a high contribution of cyanobacteria to total phytoplankton biomass. Our results reinforce the idea that lakes have an ecological memory by showing that a warm winter can influence subsequent seasonal succession in the cyanobacteria community. In both mesotrophic lakes studied, cyanobacteria abundance was strongly influenced by phosphorus concentrations and winter air temperatures. We conclude that although extreme hot weather periods can be used to analyze various aspects of the impacts of climate change, they are of limited value in forecasting the structure of phytoplankton communities in a warmer future.

Key words: climatic forcing; extreme events; temperature; warming; phytoplankton; lakes; heat wave; water quality; eutrophication.

Introduction

Global average air temperature increased by approximately 0.6°C in the twentieth century (IPCC 2001; Cubasch and others 2013) and global circulation models predict that it may increase by 1.7 to 4.9°C over the next century (Wigley and Raper 2001). Cyanobacteria, formerly referred to as

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blue-green algae, are autotrophic oxygenic prokaryotes. They comprise a large variety of species and possess a number of morpho-functional traits that could make some of them well adapted to the environmental conditions associated with global warming, such as high nutrient loading, rising temperatures, enhanced stratification, increased residence time, and salinization (Pearl and Huisman 2008; Carey and others 2012; Ekvall and others 2013). Consequently, speculations that climate change may increase cyanobacteria abundance has given rise to increasing concerns over lake use and management because cyanobacteria are known for their ability to form blooms (Reynolds 2006) and produce toxins (Sivonen and Jones 1999). In the past decade, the impact of climate change on cyanobacteria populations has become a major concern in environmental sciences, leading to a steadily increasing number of studies on the topic.

It has been proposed that the impact of warming on lakes is modulated by the amount of nutrient resources (Winder and Sommer 2012), and hence trophic status of the lake and/or climate-related changes in nutrient loading (Elliott 2012; Arheimer and others 2005).

Modelling studies generally predict increased cyanobacteria biomass and/or dominance with increasing water temperature and climate-induced changes in the thermal regime (Jöhnk and others 2008; Trolle and others 2011; Elliott 2012). Although several time series analyses of plankton data have shown a tight link between climatic forcing and variability in phenology (Scheffer and others 2001; Edwards and Richardson 2004; Winder and Schindler 2004; Adrian and others 2009), only a few studies based on field observations of phytoplankton communities have clearly shown an increase in cyanobacteria abundance in response to climate warming. Comparative and long-term studies have shown that warmer conditions are indeed associated with higher cyanobacteria abundance. For example, the percentage of cyanobacteria in the phytoplankton community is higher in warm than in cold shallow lakes (Kosten and others 2012), warmer winters favor growth and inoculum production in certain species (Anneville and others 2004; Weyhenmeyer 2001; Adrian and others 1995; Jacquet and others 2014b). The above-mentioned field and modelling studies, as well as the experimental work (De Senerpont Domis and others 2007), provide some evidence that climate warming likely favors cyanobacterial forms. There is also the general finding that cyanobacteria grow better at higher temperatures and possess morphological, physiological, and behavioral traits that confer advantages in strongly stratified environments (Winder and Sommer 2012). Distinct competitive advantages of cyanobacteria over other taxa would principally arise from the ability of cyanobacteria to efficiently capture and utilize spatially segregated resources (light and nutrients). Cyanobacteria should gain advantage from their capacities to (1) regulate their position through buoyancy, (2) capture light at low intensities over a wide range of wavelengths thanks to the accessory pigmentation and the structural organization of their light-harvesting antenna, (3) access organic phosphorus thanks to phosphatases, and (4) to store luxury phosphorus (Carey and others 2012).

In support of this hypothesis, recent comparative studies show that water temperature is indeed a predictor of cyanobacteria abundance. However, at the same time, these studies emphasize the role played by nutrients, trophic status (Beaulieu and others 2013; Rigosi and others 2014) or even mixing regime of the lake (Taranu and others 2012), and demonstrate that the response of cyanobacteria to climate change relies upon complex interactions between nutrient availability and climate-related variables (Kosten and others 2012). Some empirical evidence from long-term data point to the impact of confounding factors, such as phosphorus concentrations, that are stronger than, or act in synergy with, meteorological fluctuations and atmospheric modes of variability, to explain observed changes in phytoplankton communities (Jeppesen and others 2003; Anneville and others 2002, 2004; Shatwell and others 2008; Stich and Brinker 2010; Salmaso and Cerasino 2012).

This is largely due to a lack of homogeneous phytoplankton time-series that cover a time-period long enough to include strong hydrological modifications which might induce significant changes in cyanobacteria abundances. Indeed, very few phytoplankton time-series extend back to before the 1960s, and phytoplankton time-series usually cover a time-period that is long enough to capture important changes in key environmental parameters, like phosphorus concentrations (Jeppesen and others 2005), whose effects are often stronger or combine with those induced by climate change (for example, Stich and Brinker 2010; Pomati and others 2012).

Paleolimnology has helped solve this problem by broadening the time-period studied (for example, Alric and others 2013; Berthon and others 2013). Furthermore, cyanobacterial biomarkers like pigments and DNA are starting to be included in

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paleolimnological approaches, revealing the relative importance of nutrients and warming on cyanobacteria dynamics (Domaizon and others 2013; Savichtcheva and others 2014).

An alternative way of studying the impact of climate warming on cyanobacteria abundance is to focus on extreme meteorological events (Gallina and others 2011; Huber and others 2012). Most of the global warming debate focuses on changes in global average temperature anomalies. However, climate change is characterized by important interannual variability and the occurrence of extreme conditions at certain periods of the year. As statistical methods summarize patterns within data, such extremes are usually lost in temporal averages, and the impact of climate variability has long been neglected. Only recently have researchers started analyzing the impact of extreme weather events (Jentsch and others 2007). In fact, a number of studies have shown that extreme weather events strongly impact hydrodynamics and plankton communities (Jankowski and others 2006; Straile and others 2010; Anneville and others 2010; Gallina and others 2011). Research also suggests that the impact of climate extremes is different from the impacts of mean climate change such as the increase in mean water temperature for instance (Mearns and others 1997; Straile and others 2010).

It is crucial to assess the impact of warm extreme events because such events are expected to occur more frequently in the future and are characteristic of global warming (Beniston 2007). The present study addresses the impact of such events on cyanobacteria abundance in deep peri-alpine lakes. Our objective is to test, using historical data, if cyanobacteria perform better and bloom during exceptional hot weather periods (EHWPs). To answer these questions, we analyzed long-term phytoplankton data from Lakes Geneva, Annecy, and Bourget. These three lakes differ in trophic status and morphology (Jacquet and others 2014a). We examined data for a ten-year period to determine if: (i) the occurrence of an EHWP significantly impacts the seasonal dynamics of cyanobacteria, (ii) an EHWP increases the abundance of cyanobacteria and induces a change in the composition of the phytoplankton community, and (iii) at the interannual scale, cyanobacteria abundance is driven by air temperature.

What is today considered an extreme meteorological condition may become the norm in a future warmer climate (Beniston 2007). It has therefore been suggested that an EHWP may be a useful tool for predicting the impact of climate warming (Jankowski and others 2006; Huber and others 2010; Gallina and others 2011). However, the general applicability of an EHWP is unclear; for example, we know that it cannot be used for all variables and it is inappropriate for predicting changes in water temperature (Straile and others 2010). Drawing on our results for Lakes Geneva, Annecy, and Bourget, we discuss two main questions regarding the use of EHWPs: can they serve to analyze the impact of climate change and, can they be used to empirically test models and conceptual predictions about the impact of climate warming on cyanobacteria.

Materials and Methods

Lakes

Lakes Geneva, Annecy, and Bourget are located in the western part of the Alps (Figure 1). They are large, never freeze over, and are thermally stratified during much of the year (Table 1). These three lakes differ in mixing regime and trophic status. Although Lake Geneva does not undergo complete mixing every year, Lakes Annecy and Bourget regularly undergo winter mixing over the entire water column. Finally, in contrast to Lake Annecy, which has not suffered from large increases in phosphorus concentrations over the past 40 years, Lakes Geneva and Bourget have been eutrophic for several years (Jacquet and others 2014a). In all three lakes, measures to reduce phosphorus loading in the watersheds were implemented in the 1970s, leading to a decrease in phosphorus concentrations starting in the early 1980s. In Lake Geneva, annual average total phosphorus concentration dropped from 89.5 to 21.6 $\mu g\ P\ l^{-1}$ (Lazzarotto and others 2013), in Lake Bourget winter average total phosphorus concentration dropped from 150 to 14 $\mu g\ P\ l^{-1}$ between 1980 and 2012 (Jacquet and others 2013). In Lake Annecy, the annual concentrations of total phosphorus remained rather stable over the last 30 years with an average of $6 \pm 1.9\ \mu g\ P\ l^{-1}$ (Domaizon and others 2014). Lakes Annecy, Bourget, and Geneva are now respectively oligotrophic, oligo-mesotrophic, and mesotrophic (Jacquet and others 2014a).

Sampling

Lakes Annecy, Bourget, and Geneva are currently being monitored as part of a long-term water quality and biological monitoring program. As new sampling protocols for measuring physical and chemical parameters, as well as plankton abundance and composition were implemented in 2000 (Jacquet and others 2014a), we use only data

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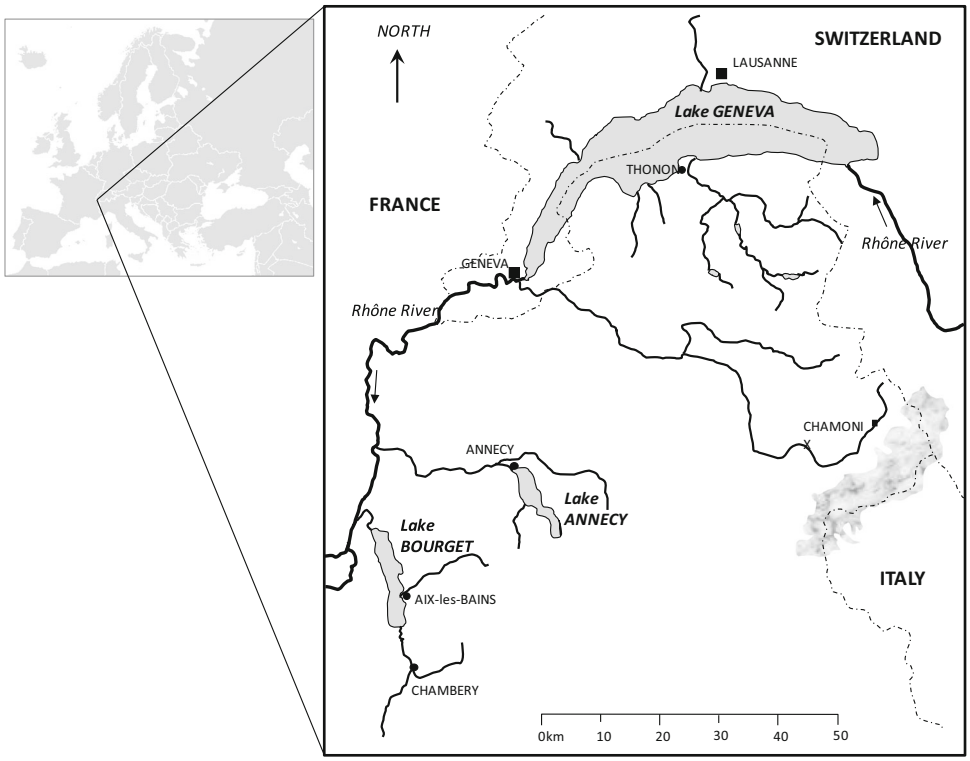

Figure 1. A map showing the location of the studied lakes in the western range of the Alps (from north to south: L. Geneva, Annecy and Bourget).

Table 1. Geographical Location and Morphological Characteristics of the Lakes Geneva, Bourget, and Annecy (from Jacquet and others 2014a)

Lake	Latitude	Longitude	Elevation (m)	Mean depth (m)	Max. depth (m)	Surface area (km^2)	Watershed area (km^2)
Geneva	46°27′N	6°32′E	372	153	310	580	7,419
Bourget	45°76′N	5°86′E	231	80	145	44	588
Annecy	45°51′N	6°10′E	447	41	65	27	278

collected following this, from 2000 to 2011. This limits any bias due to changes in sampling protocol.

The lakes were sampled at a single station located at the deepest point in the lake basin. Sampling was carried out once a month in winter and twice a month in spring, summer, and autumn. Water temperature was measured using a multiparameter probe. Water for nutrient concentration measurements was sampled at a series of discrete depths between the surface and bottom of the lake. The analytical methods used are detailed in a CIPEL annual report (Monod and others 1984) and on the website dedicated to the observatory of alpine lakes (''http://www6.inra.fr/soere-ola'').

The water samples for identification and estimation of phytoplankton abundance and composition were collected using a custom-made integrating bell sampler (Pelletier and Orand 1978). The samples were taken in the upper 18 and 20 m in Lakes Geneva and Annecy, respectively. In Lake Bourget the depth integration was 2.5 times the transparency found using the white disc until 2005 and 0–20 m subsequently (Jacquet and others 2014a). Phytoplankton identification and cell counts were done in sedimentation chambers under an inverted microscope using the Utermöhl technique (1958), which has been standardized (Afnor 2006). Species biovolumes were derived from cell numbers and mean cell volumes using geometrical models. We then estimated total biomass by adding the biovolumes for each species, assuming a fresh weight of 1 g cm^{-3}. No data for phytoplankton abundance were available in 2003 for Lake Bourget, except for the cyanobacterium *Planktothrix rubescens* at discrete depths (2, 6, 10, 15, and 20 m).

Identification of EHWPs

We identified years with extreme meteorological conditions using air temperature measured at the

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INRA meteorological station, which is located at the western fringe of the Alps, on the south coast of Lake Geneva (46°22′N–6°27′17″E). Air temperature seasonal means were calculated for each year: winter (January, February, March), spring (April, May, June), summer (July, August, September), and autumn (October, November, December). An EHWP was identified for each season according to the method described in Gallina and others (2011). We calculated 99th percentiles for seasonal mean air temperature for the period 2000–2011 and for each season. An EHWP was then identified as a period of time whose seasonal mean was higher than the 99th percentile recorded for the study period (2000–2011).

Analyses

We used principal component analysis (PCA) to examine the impact of EHWPs on the annual dynamics of cyanobacteria. The PCA was run on the abundance of phytoplankton groups (PPG) as identified based on Bourelly's classification (Bourrelly 1972, 1981, 1985) which relies on morphology and pigment content. We have identified nine PPG in the studied lakes: Zygophyceae, Chlorophyceae, Diatomophyceae, Xanthophyceae, Chrysophyceae, Euglenophyceae, Cryptophyceae, Dinophyceae, and Cyanobacteria. Values for PPG biomass were ln-transformed and centred. We ran a PCA for each year and each lake to identify annual variability in cyanobacteria compared to other phytoplankton taxa. If an EHWP favors cyanobacteria, there should be higher variability in cyanobacteria abundance during a year with an EHWP versus other years. In terms of the PCA, if an EHWP favors a cyanobacterial bloom, the relative contribution of cyanobacteria to the formation of the PCA axis should be higher during years with an EHWP.

Inter-annual changes in phytoplankton composition were analyzed using between-groups PCA. The goal of the method is to describe between-group variability (Dolédec and Chessel 1989). The method consists of running a PCA on the group-weighted mean values of the variables. The weight of each group is computed during the analysis and is proportional to the number of samples in the group. In our study, the years constituted the groups, and PPG biomass the variables. We performed the analysis for each season and each lake separately. Taxa biomass was ln-transformed and centered before being entered in the analyses. We chose to use between-group PCA because this method effectively removes any background noise related to phytoplankton variability over the season and focuses, instead, on inter-annual changes.

Results

Identification of Seasonal EHWPs

Although air temperature showed pronounced seasonal changes, no long-term increase in annual mean air temperature could be observed between 2000 and 2011 (Figure 2A). Within this time period there was, however, strong inter-annual variability (Figure 2B). The identified EHWPs were: winter 2007, spring and summer 2003, and autumn 2006. Air temperature anomalies were rather similar during these EHWPs: +1.9, +1.5, +1.9 and +1.8°C in winter, spring, summer, and autumn, respectively (Figure 2B).

Cyanobacteria Community Structure

In total, 97% of the cyanobacterial biomass was made up of three species in Lake Bourget, four species in Lake Annecy, and seven species in Lake Geneva (Table 2). In both Lakes Geneva and Bourget, the three dominant genera were *Planktothrix*, *Aphanizomenon*, and *Aphanocapsa*. The cyanobacteria community was strongly dominated by *Planktothrix* and, more specifically *P. rubescens*. This species also dominated in Lakes Bourget and Geneva during the four identified EHWPs. In Lake Annecy, the composition was different: *Aphanocapsa* along with *Chroococcus* dominated the community, that is, they were more abundant than the other species during the EHWPs. It is noteworthy that the picocyanobacteria were an abundant group in all three lakes (Personnic and others 2009; Jacquet and others 2013). However, this group, merely represented by small-sized phycoerythrin-rich *Synechococcus* spp. (Personnic and others 2009), were not considered in this study.

Impact of EHWPs on Annual Variability in Cyanobacteria Abundance

In Lake Annecy, cyanobacteria tended to show an annual dynamic characterized by higher abundances at the end of the year. However, no clear recurrent and characteristic annual pattern could be identified because differences between months were not significant (Figure 3). In Lake Geneva and Bourget, where cyanobacteria were more abundant, their biomass showed a pronounced annual pattern with significant differences between some months (Figure 3). In these lakes, cyanobacteria demonstrate clear seasonal patterns char-

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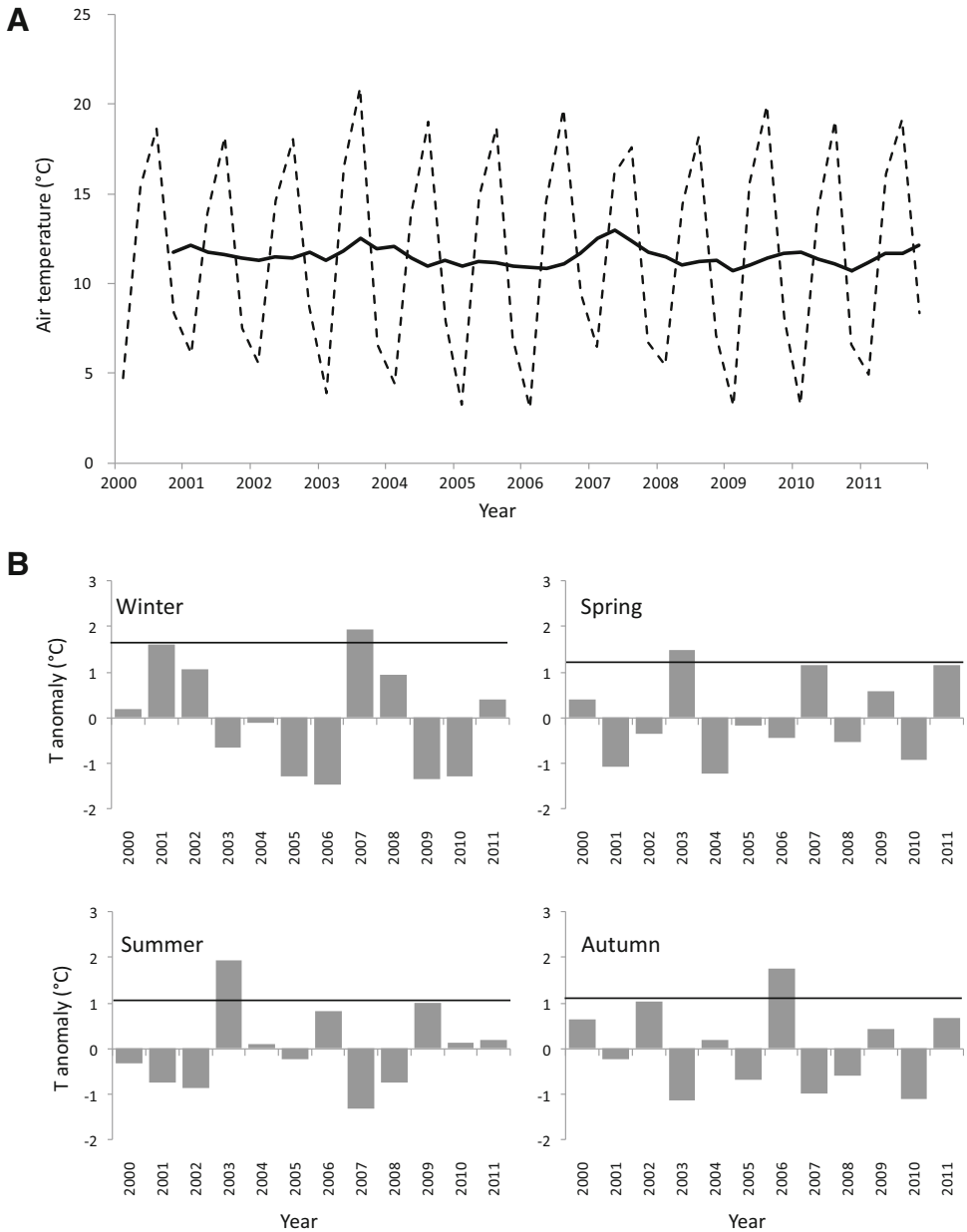

Figure 2. A Long-term changes in seasonal mean air temperature (*dotted line*) and 4-year moving average air temperature (*solid line*). **B** Long-term changes in seasonal air temperature anomalies measured at the INRA meteorological station from 2000 to 2011. The horizontal line indicates the 99th percentile for seasonal air temperature.

acterized by low biomass in winter and maximum biomass in summer and autumn.

The relative contributions of cyanobacteria to the formation of the first, second, and third PCA axes are proportional to the size of the circles shown in Figure 4A. The relative contribution of cyanobacteria to the formation of the first three axes was not exceptionally high during years of an EHWP. Rather, the contributions were generally low, except in 2006 (Figure 4A). In 2003 and 2007, low contributions indicated low annual variability in cyanobacteria abundance and, thus, no occasional blooms during the EHWP associated with these years. Indeed, in 2003, cyanobacteria were abundant in winter and spring in Lake Geneva but then decreased during the summer, even though an EHWP occurred during the summer. In Lake Annecy, a decrease in cyanobacteria abundance was also observed during the warm summer of 2003. During the 2007 winter EHWP, an exceptionally high biomass of cyanobacteria was observed in all three lakes (Figure 4B). Cyanobacteria maintained a high abundance throughout the year, resulting in a low contribution to the formation of the PCA axes (Figure 4A). In 2006, cyanobacteria abundance exhibited high annual variability; the 2006 autumn EHWP was associated with a strong increase in cyanobacteria abundance in autumn in

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Table 2. Dominant Genera of Cyanobacteria in Lakes Geneva, Bourget, and Annecy

Lakes	Taxa	% Total	% Spring 2003	% Summer 2003	% Autumn 2006	% Winter 2007
Geneva	Planktothrix	42	75	51	66	97
	Aphanizomenon	18	19	14	34	2
	Aphanocapsa	15	2	5	0	0
	Psuedanabaena	14	2	25	1	1
	Aphanothece	4	0	0	0	0
	Oscillatoria	2	0	0	0	0
	Pannus	1	0	0	0	0
	Others	3	2	5	0	0
Bourget	Planktothrix	85			97	99
	Aphanocapsa	9			1	0
	Aphanizomenon	3			1	1
	Others	3			1	0
Annency	Aphanocapsa	72	43	33	25	46
	Chroococcus	19	40	63	69	41
	Aphanothece	3	0	0	0	10
	Psuedanabaena	3	17	0	0	3
	Others	3	0	4	7	0

The contribution of each dominant taxa to total cyanobacteria biomass is indicated as a percentage. Percentages are given for the study period (% TOTAL), and for each EHWP (% SPRING 2003, % SUMMER 2003, % AUTUMN 2006, and % WINTER 2007).

Lakes Geneva and Bourget (Figure 4B). In Lake Annecy, there was a high biomass at the beginning of the year but it was not maintained for the rest of the year. In this lake cyanobacteria were observed at a very low abundance during the autumn EHWP (Figure 4B).

Influence of EHWP on Seasonal Phytoplankton Composition

During the warm winter 2007, cyanobacteria showed high abundances in all three lakes and contributed substantially to total phytoplankton abundance in Lakes Geneva and Annecy (Figure 5). The results of the between-group PCA underscored the peculiarity of 2007 that was segregated on axis I during winter in both Lakes Geneva and Bourget (Figure 6A). Cyanobacteria and Zygophyceae had a strong contribution to that axis. In Lake Annecy, 2007 was also associated with cyanobacteria, although this year was close to 2004 in the first plane (Figure 6A).

In spring, 2007 remained different from the other years and was still associated with cyanobacteria in Lake Annecy and with cyanobacteria and conjugates (Figure 6B) in the other lakes. Indeed, after the 2007 winter EHWP, cyanobacteria remained abundant and contributed greatly to phytoplankton biomass in all three lakes, but especially in Lakes Bourget and Annecy, where cyanobacteria biomass was exceptionally high (Figure 5). In Lake Geneva the highest abundance and contribution were recorded during the 2003 spring EHWP (Figure 5). In 2003, no data were available for Lake Bourget, although counts for *P. rubescens* suggest a very low biomass (Jacquet and others 2013).

In Lake Geneva, cyanobacteria made a high, but not an exceptional, contribution to phytoplankton biomass in summer 2003. Absolute biomass was low in both lakes Geneva and Annecy. The results of the between-group PCA indicate that phytoplankton composition in 2003 was no different from that in other years (Figure 7A). In Lake Annecy, 2003 belongs to a group of years in which cyanobacteria are present but in very low abundance in summer.

In 2006, autumn biomass of cyanobacteria reached the highest values recorded during the studied period in Lakes Geneva and Bourget (Figure 5). However, Figure 5 indicates a high, but not exceptional, contribution of cyanobacteria to total phytoplankton biomass. Indeed, although there were large differences in cyanobacteria abundance between the years studied, the PCA revealed that the autumn EHWP had no impact on phytoplankton composition, as suggested by Figure 7B, showing that the year 2006 did not segregate from the other years on the first plane.

Drivers of Cyanobacteria Abundance

We tested for linear and second order polynomial relationships between cyanobacteria biomass and

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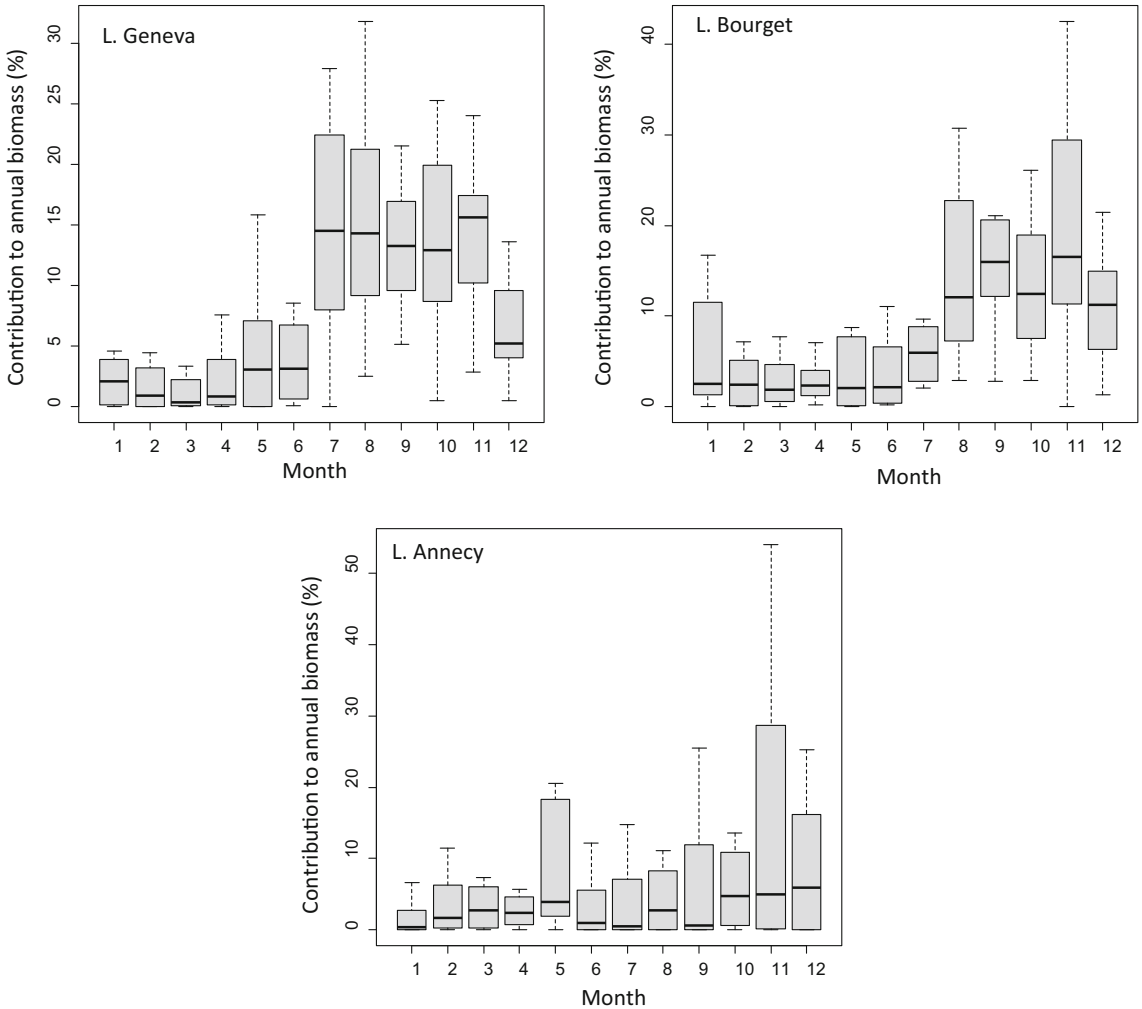

Figure 3. Monthly percentage contributions to the annual cumulative cyanobacteria biomasses in Lakes Geneva, Bourget, and Annecy. *Boxes* and *whiskers*, respectively, represent the 25th–75th and 5th–95th percentiles.

phosphorus concentrations, measured in February during the winter mixing. A second order polynomial model fitted the data most closely, indicating a hump-shaped relationship between phosphorus concentration and cyanobacteria abundance in Lakes Geneva and Bourget (Figure 8). Significant relationships between the residual and winter air temperatures were observed for these two lakes (P value < 0.05; Spearman coefficient, Lake Bourget: rho = 0.809; Lake Geneva: rho = 0.608). Both in Lake Geneva and Bourget, warm winters were associated with high annual cyanobacteria biomass.

Discussion

No significant increase was detected in the 2000–2011 temperature measurements considered in this study. This stability in air temperature was also observed at a more global scale and is referred to as a ''global warming hiatus''. This hiatus can be attributed to a weather pattern in the Pacific associated with the La Nina phase of the El Nino phenomenon (Kosaka and Xie 2013).Our study period was, however, characterized by the occurrence of some hot extreme weather events, some of which have also been identified over the longer reference period of 1971–2000 (Gallina 2012) and at a more global scale: a warm winter in 2007 (Straile and others 2010), a warm summer in 2003 (Jankowski and others 2006; Jöhnk and others 2008; Huber and others 2010). Such convergence in the identification of the extreme meteorological conditions support the relevance of the EHWPs identified in our study and which resulted in the warmest seasons ever observed in central Europe in the past 30 years.

Regional extreme weather and climate events, such as heat waves, heavy precipitation, droughts

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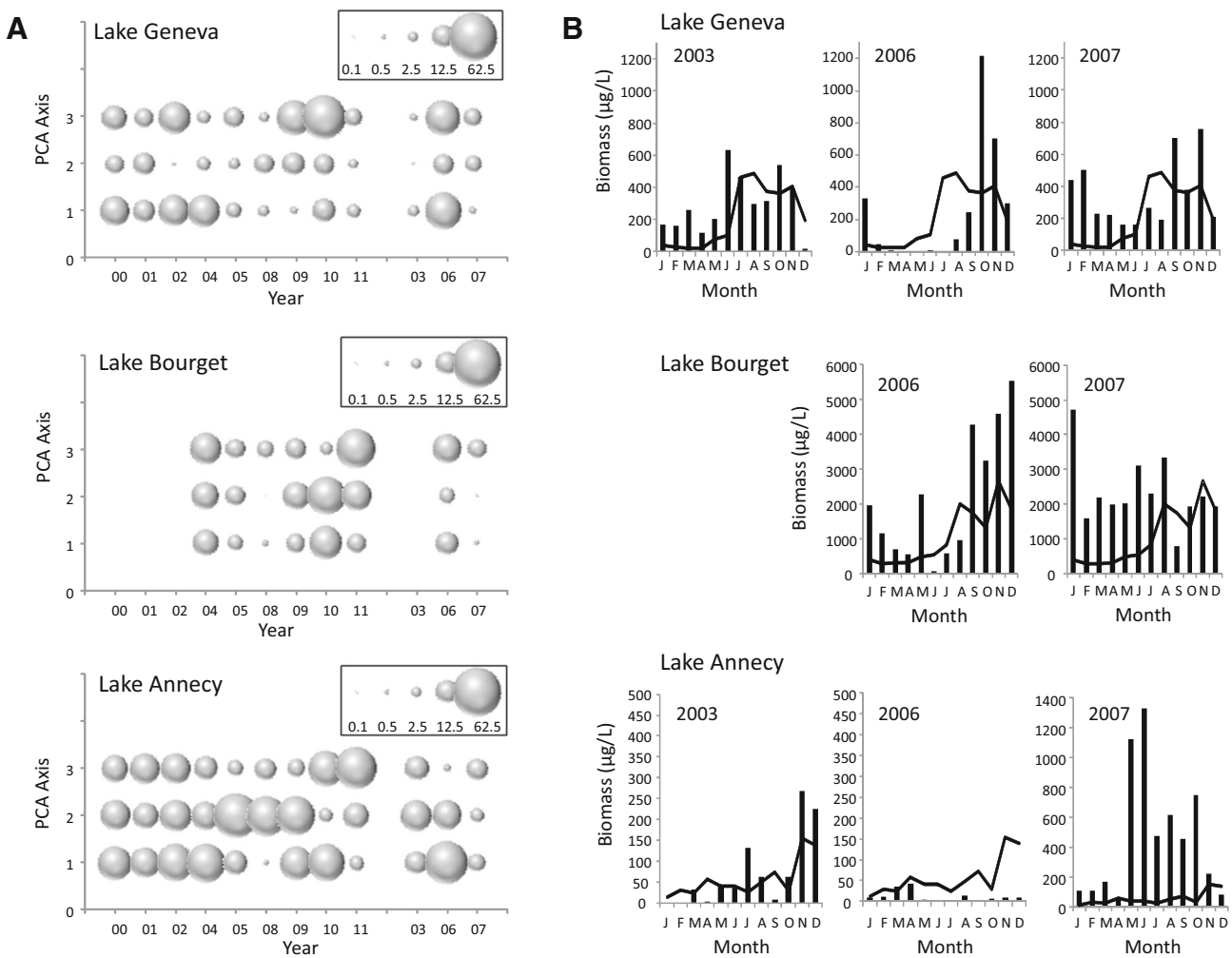

Figure 4. **A** Percentage of the relative contribution of cyanobacteria to the formation of the PCA axis. The size of the circle represents the relative strength of the contribution. **B** Annual changes in monthly biomass of cyanobacteria during years with an EHWP (*bar*) compared to the mean annual pattern of cyanobacteria abundance during years without an EHWP (*line*).

and wind storms, have a great impact on both ecosystems and human society. For example, heat waves, whose frequency and intensity are likely to increase through the twenty-first century (Beniston and others 2007; Kirtman and others 2013), are now being carefully considered in the framework of global warming (Cubasch and others 2013). In general, extreme weather events are emerging as one of the most important facets of climate change. Consequently, analyzing the effect of EHWPs might be used to investigate past impacts of climate warming on ecosystems. However, despite the growing interest in the impact of extreme events (Jentsch and others 2007), few studies have analyzed their impacts on cyanobacteria abundance, a taxonomic group which is expected to be favored by global warming (Pearl and Huisman 2008).

This research aims to address this lack by focusing on the annual dynamics and inter-annual variability of cyanobacteria in response to EHWPs. We have chosen to sequence the years into seasonal periods to examine the variability in the ecological response to EHWPs (Huber and others 2010). Finally, contrary to Gallina and others (2011), who analyzed the impact of extreme weather events on cyanobacteria at the larger scale of European alpine lakes, we focused on a few lakes located in the same ecoregion (Jacquet and others 2012). Although our results may be less powerful in terms of generalizability, our approach in which each lake is analyzed separately, means the results can be synthesized and interpreted based on the biotic and abiotic properties specific to each lake. This approach enables us to better formulate

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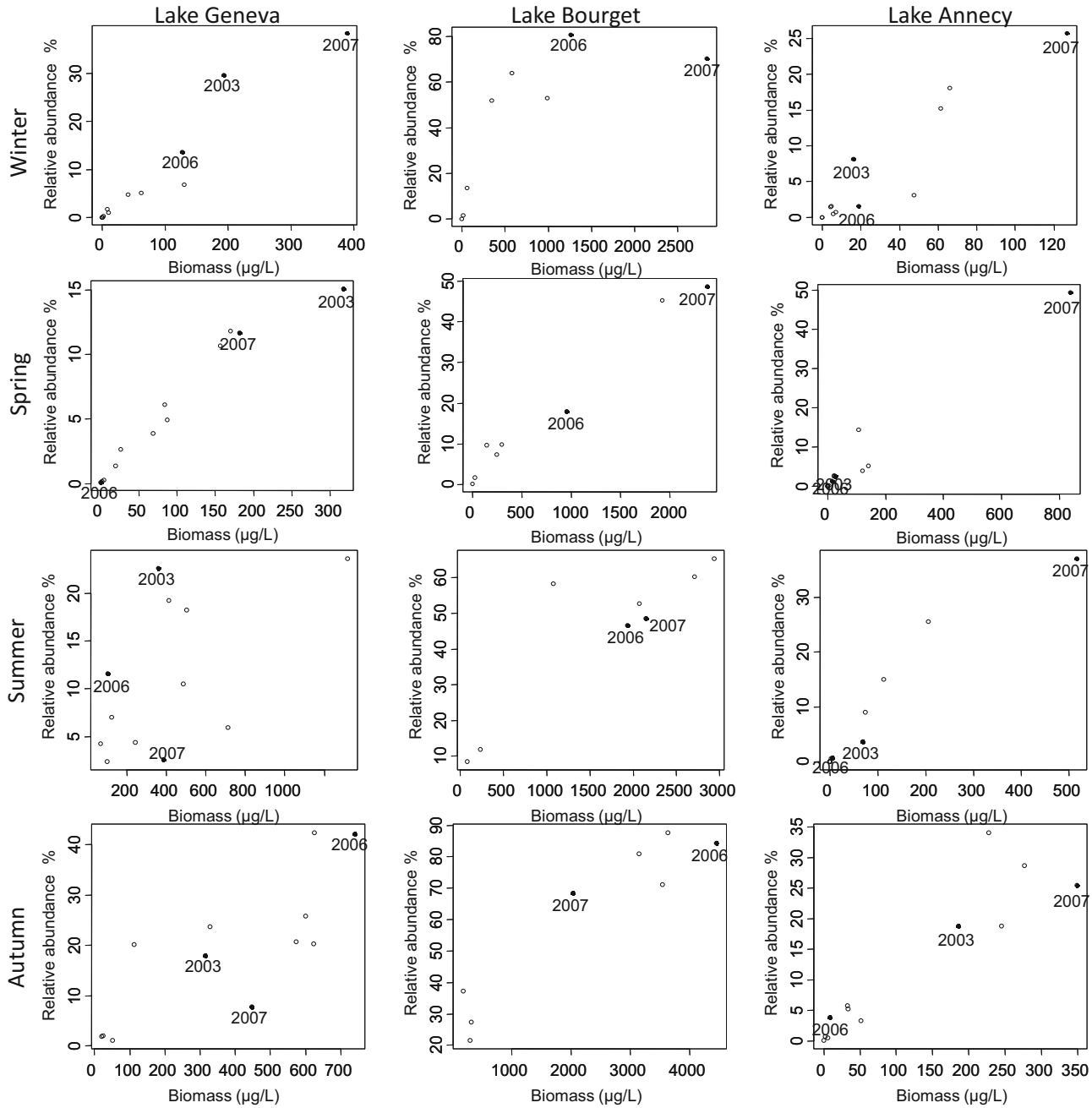

Figure 5. Interannual comparisons of the contribution of cyanobacteria to total phytoplankton biomass (as a percentage) versus absolute biomass of cyanobacteria in Lakes Geneva, Bourget, and Annecy by season.

hypotheses to explain variability between sites that differ in morphology, trophic status, and composition of the cyanobacterial community.

Importance of Nutrients and Trophic State

Based on the criteria of the European Water Framework Directive, according to the Austrian BI and German PSI indices, the species composition of the phytoplankton community indicates that Lake Annecy, an ultra-oligotrophic lake, is of good ecological quality (Kaiblinger and others 2009). Its cyanobacteria abundance was low compared to that of Lakes Geneva or Bourget, and in terms of cyanobacteria assemblages' composition, Lake Annecy is mainly characterized by the presence of Chroococcales, whereas the cyanobacteria com-

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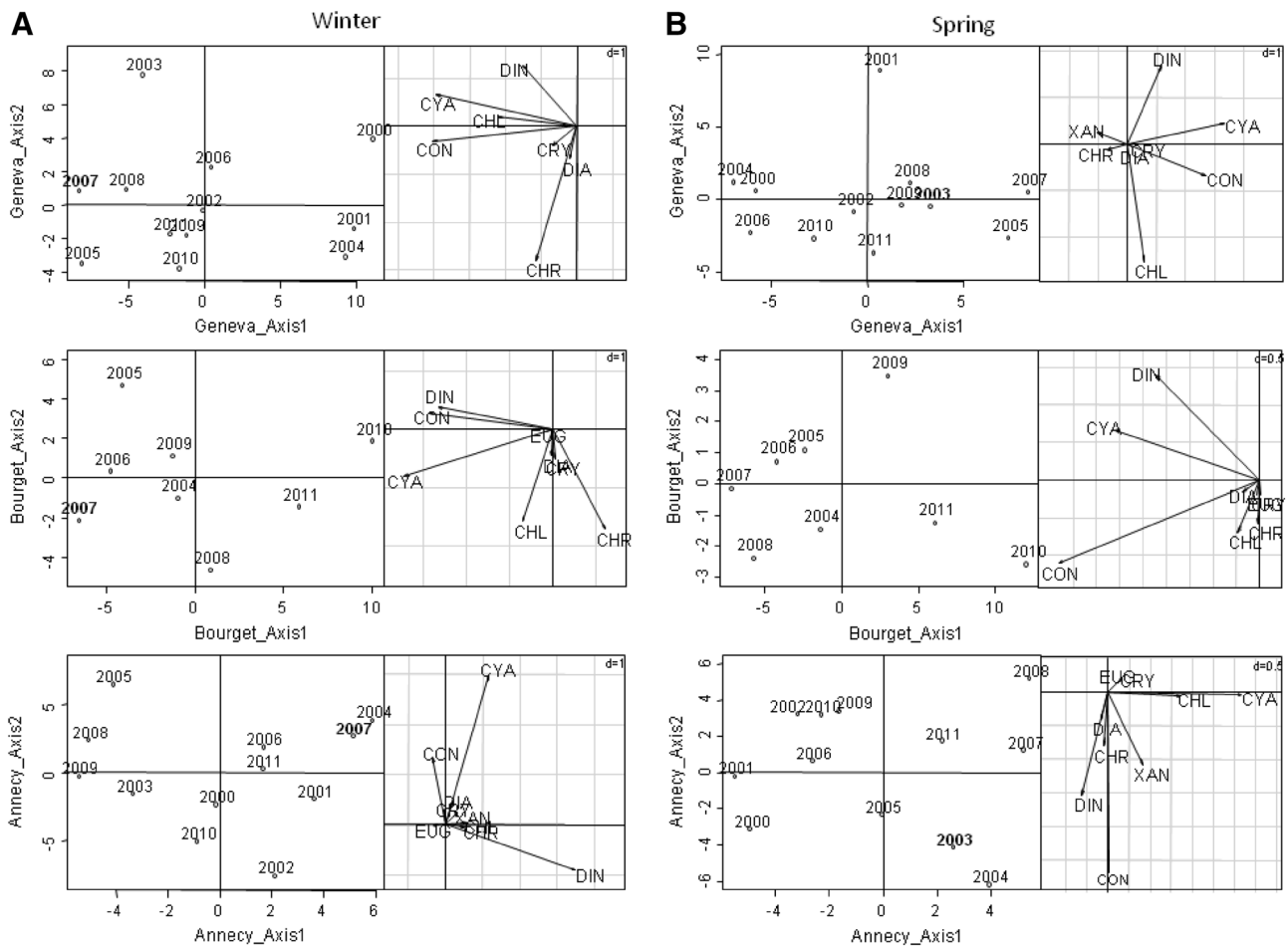

Figure 6. Distribution of the center of gravity of years for winter (**A**) and spring (**B**) within the first plane (defined by axes I and II) from the between-group PCA run separately on data from Lakes Geneva, Bourget, and Annecy. Warm years are indicated in *bold text*. *Right hand side* of each panel shows the scores of the phytoplankton taxa on the associated factorial map, indicating the contribution of the taxa to the formation of the axes. Abbreviations for phytoplankton taxa are: *CON* Zygophyceae, *CHL* Chlorophyceae, *DIA* Diatomophyceae, *XAN* Xanthophyceae, *CHR* Chrysophyceae, *EUG* Euglenophyceae, *CRY* Cryptophyceae, *DIN* Dinophyceae, *CYA* Cyanobacteria.

munity in Lakes Bourget and Geneva, is comprised mainly of Oscillatoriales and Nostocales. Although for the mesotrophic Lakes Bourget and Geneva, we observed a relationship between cyanobacteria and phosphorus concentrations, no such relationship was found for Lake Annecy. This may be explained by the fact that in Lake Annecy, phosphorus concentrations were low and did not change substantially during the study period (Jacquet and others 2014a). In Lake Geneva and Bourget, the relationship between phosphorus and cyanobacteria was hump-shaped. In these lakes, the cyanobacteria community was dominated by *P. rubescens*. Such a relationship supports the finding that the proliferation of *P. rubescens* is greatest in meso to moderately eutrophic conditions (Dokulil and Teubner 2012; Jacquet and others 2014b). Indeed, this species is used in the European Water Framework Directive as an indicator of medium quality state (Brettum 1989), as opposed to other species like *Microcystis* or *Limnothrix redeckei*, which are associated with very rich nutrient habitats (Brettum 1989). Such a habitat preference may explain the long-term dynamics of *P. rubescens* in Lake Bourget. *P. rubescens* appeared in the middle of the last century when phosphorus concentrations started to increase (Laurent 1970), then decreased strongly at the height of eutrophication, formed blooms again in the late 1990s, and finally collapsed in recent years (Jacquet and others 2014b). Finally, in the lakes where phosphorus concentrations were high enough to support a *P. rubescens* population, winter air temperature was the second driver of its abundance. This relationship between *P. rubescens* and winter air temperatures suggests that mild winters and winter EHWPs have a positive impact on this

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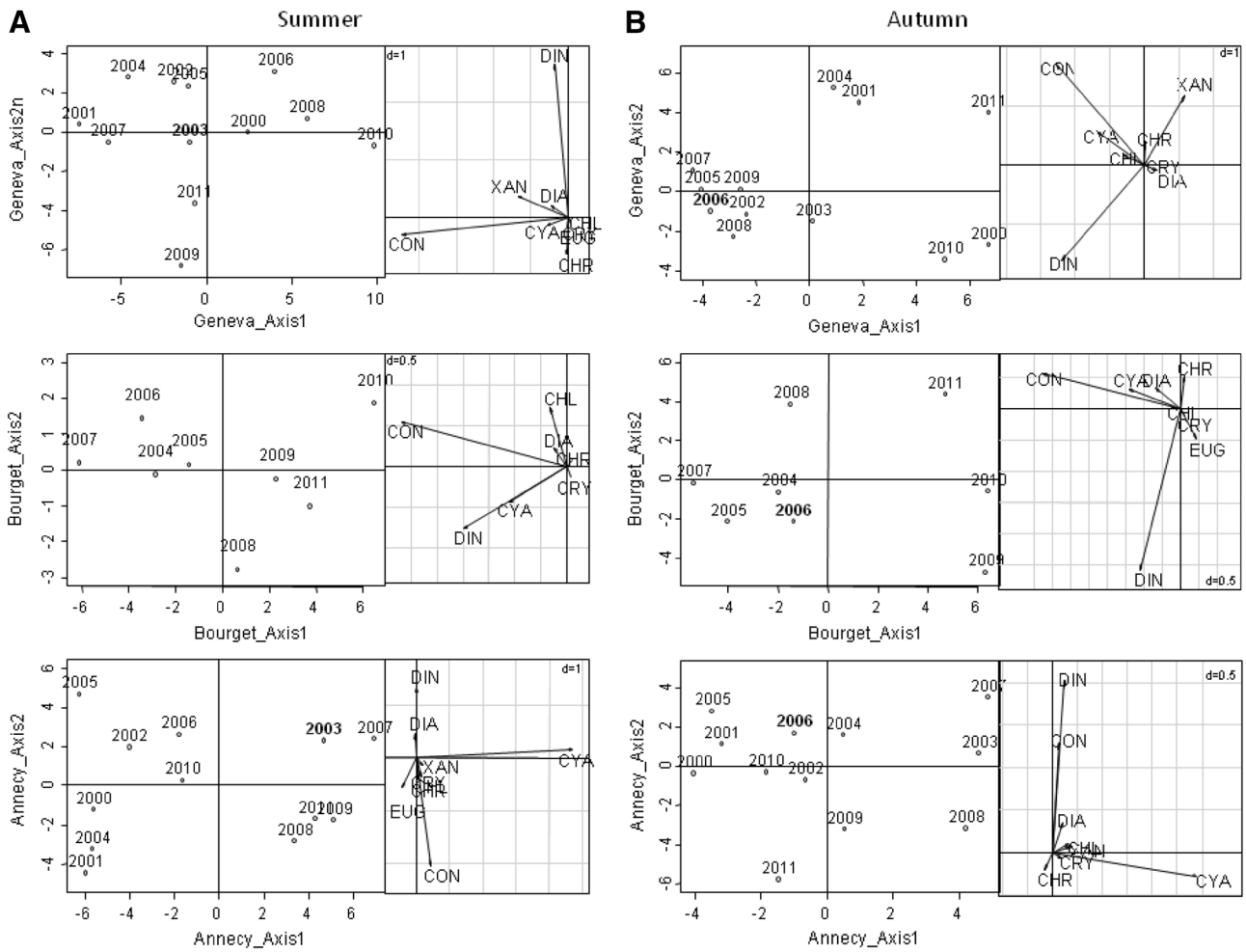

Figure 7. Distribution of the center of gravity of years for summer (**A**) and autumn (**B**) within the first plane (defined by axes I and II) from the between-group PCA run separately on data from Lakes Geneva, Bourget, and Annecy. Warm years are indicated in *bold text*. *Right hand side* of each panel shows the scores of the phytoplankton taxa on the associated factorial map, indicating the contribution of the taxa to the formation of the axes. Abbreviations for phytoplankton taxa are: *CON* Zygophyceae, *CHL* Chlorophyceae, *DIA* Diatomophyceae, *XAN* Xanthophyceae, *CHR* Chrysophyceae, *EUG* Euglenophyceae, *CRY* Cryptophyceae, *DIN* Dinophyceae, *CYA* Cyanobacteria.

population (Anneville and others 2004; Jacquet and others 2005; Dokulil and Teubner 2012; Jacquet and others 2014b).

The Impacts of Exceptionally Hot Meteorological Conditions are Season Dependant

The importance in the timing of meteorological events has already been underlined (Huber and others 2010), and our observations support this assertion: according to our findings, the impact of an EHWP depends on the season in which it occurs. Our results show that phytoplankton composition is particularly sensitive to the winter EHWP. In our analysis, a year characterized by an extreme warm winter was associated with a high cyanobacteria biomass and high proportion of cyanobacteria in the phytoplankton community during winter (Table 3). In short, a winter EHWP favored cyanobacteria abundance during winter in the three lakes studied. In Lakes Geneva and Bourget, according to the priority effects (Louette and De Meester 2007) and the idea that past events play an important role in structuring communities (Drake 1991), the high abundance of cyanobacteria probably resulted from the extremely high biomass that occurred during the warm autumn 2006. The following mild winter may have served to maintain this population. Furthermore, our results show that favorable conditions during the winter can impact cyanobacteria abundance right through into spring. Indeed, the

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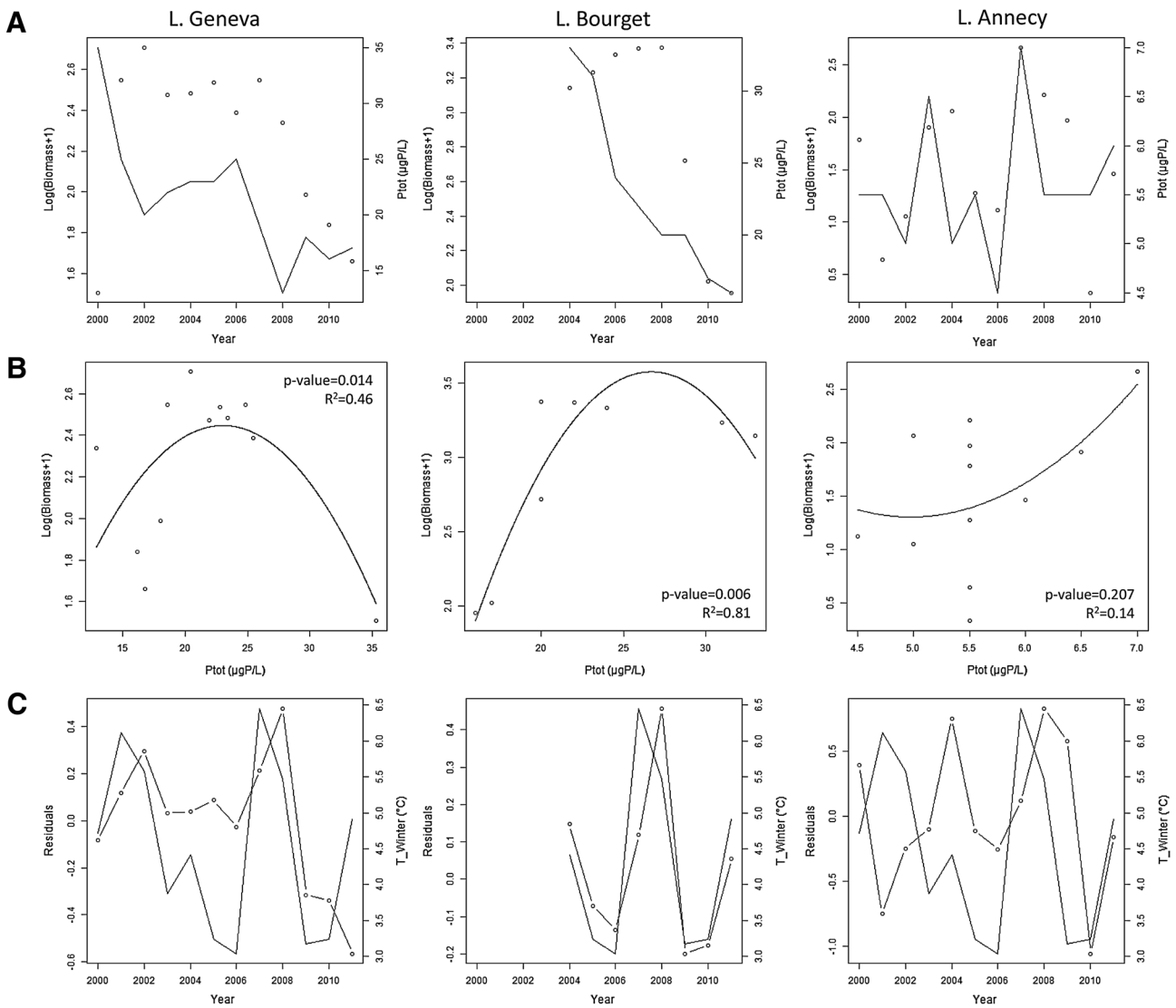

Figure 8. **A** Long-term changes in cyanobacteria abundance (*dots*) and total phosphorus concentrationmeasured in February (*line*). **B** Relationship between phosphorus and annual cyanobacteria biomass. **C** Long-term changes in the residuals of the relationship between cyanobacteria and phosphorus (*dotted line*), and long-term changes in winter water temperature (*solid line*).

Table 3. The Impact of EHWPs on Cyanobacteria (Summary of Results Presented in Figures 4, 5, 6, 7)

	Spring EHWP (2003)			Summer EHWP (2003)			Autumn EHWP (2006)			Winter EHWP (2007)		
Lake Geneva	B	C%	–	–	–	–	B	–	–	B	C%	C
Lake Bourget	NA	NA	NA	NA	NA	NA	B	–	–	B	–	C
Lake Annecy	–	–	–	–	–	–	–	–	–	B	C%	C

''B'' indicates an effect on cyanobacteria biomass, ''C%'' indicates an effect on the relative contribution of cyanobacteria to total phytoplankton biomass, and ''C'' indicates an effect on phytoplankton composition. ''NA'' indicates no data were available.

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literature suggests that warm winters favor *P. rubescens*(Anneville and others 2004; Jacquet and others 2005; Dokulil and Teubner 2012; Jacquet and others 2014b) because this organism's success is related to the timing of the onset of stratification (Dokulil and Teubner 2012) and the depth of winter mixing, which in turn influences spring inoculum abundance (Walsby and others 1998). Inoculum is known to play an important role in structuring the community; the species already present in largest numbers because they had the largest residual population from the previous episode, or were recruited by germination of the greatest number of resting propagules, are likely to become prominent after stabilization of a deep-mixed water column (Reynolds 1999). Our result strongly supports the concept of ecological memory (Padisak 1992), defined as the capacity of the ecosystem or its experiences from past states to influence present or future responses of the community. Ecological memory can involve various mechanisms and it can be the manifestation of priority effects, according to which temporal priority of a species may confer a competitive advantage over other taxa (Hodge and others 1996). To resume, our results put forward that the successions of events may have considerable implications for the abundance of phytoplankton taxa and they suggest that phytoplankton communities appear as historically derived structures. In Lake Annecy, cyanobacteria were not abundant in autumn 2006. However, they reached a high biomass in winter 2007, when the cyanobacteria community was dominated by *Aphanocapsa*, *Aphanothece*, and *Chroococcus*. *Aphanocapsa* abundance increased and managed to dominate throughout the year. *Aphanocapsa* is quite ubiquitous and some papers have reported its ability to use organic compounds (Beauclerk and Smith 1978). Thus, the mixotrophic capacities of these taxa may explain their presence in Lake Annecy, a strongly phosphorus-limited ecosystem. We have shown that a warm spring had a positive effect on cyanobacteria in Lake Geneva; unfortunately, we have no data comparable to the data from the other years for Lake Bourget. In Lakes Geneva and Annecy, the summer EHWP did not promote blooms and did not favor cyanobacteria over other taxa. During the monitoring of Lake Bourget, a very low biomass of cyanobacteria was reported for summer 2003 (Jacquet and others 2013; Vinçon-Leite 2014). These results differ from that of Jöhnk and others (2008); they showed that the 2003 summer heat wave had a strong influence on water temperature and hydrodynamics, boosting the growth of cyanobacteria and shifting the competitive balance in favor of buoyant cyanobacteria. Such contrasting results may be due to differences between the lakes in morphology, nutrient availability, and dominant cyanobacterial taxa. The three lakes we studied have much lower phosphorus concentrations, different stratification dynamics due to their greater depth (Z_{max} = 30 m in Jöhnk and others vs. Z_{max} = 65 m in Lake Annecy, the shallowest of our three lakes) and different morpho-functional properties of the dominant cyanobacterial forms. An increase in air temperature intensifies stratification (Livingstone 2003; Kerimoglu and Rinke 2013), which, in deep water bodies, can result in a substantial reduction in nutrient replenishment in the surface layer and lead to a decrease in primary production, especially if the intensified stratification leads to incomplete mixing during winter (Straile and others 2010). Historical and paleolimnological data suggest that climate change has contributed to diminished productivity (O'Reilly and others 2003). Furthermore, the cyanobacteria consist of many different species exhibiting a great diversity of traits and physiological characteristics. Different cyanobacteria species would be expected to respond in different ways to changes in environmental conditions (Rigosi and others 2014). In Lakes Bourget and Geneva, where the cyanobacterial community was dominated by *P. rubescens* (Table 2), our findings are in agreement with other authors who have observed a decline of the *P. rubescens* population in Lake Zurich (Posch and others 2012) and low *P. rubescens* biomasses in Muggelsee (Huber and others 2012) during the extremely hot 2003 summer. Finally, our results illustrate that an autumn EHWP can promote cyanobacterial growth in mesotrophic lakes (Table 3). It impacts cyanobacteria biomass but not the composition of the phytoplankton community. This would suggest that milder autumn temperatures benefit the entire phytoplankton community rather than just cyanobacteria. Gallina and others (2011) found similar results, and they hypothesized that lake temperature must reach a critical threshold to induce a change in phytoplankton composition. An autumn EHWP has no effect on oligotrophic lakes, probably because phosphorus concentrations are not high enough to support high phytoplankton biomass in this type of lake.

Impacts of Exceptional Hot Weather Periods are Informative But Unlikely to be Used to Forecast Future Changes in Cyanobacteria Abundances

Model projections for the temperate climatic zone point to higher air temperatures, increased stability

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of the water column, increased duration of the stratified period, and a reduction in vertical turbulent mixing. In such a habitat, the eco-physiological properties of some cyanobacteria species should enable them to maintain and out-compete other phytoplankton taxa (Carey and others 2012). Indeed, at relatively high temperatures, the growth rate of cyanobacteria typically reaches an optimum where other groups are severely inhibited (Butterwick and others 2005; Jöhnk and others 2008), and many cyanobacteria can regulate their position in the water column and so resist intensified stratification and exploit nutrients reaching metalimnic layers. Finally cyanobacteria may benefit from an increase in the duration of their optimal growth period. All in all, global warming is anticipated to favor cyanobacteria. However, there are a few caveats to keep in mind. First, it is unlikely that all cyanobacteria will respond in the same way to global warming, and taking the cyanobacteria as a group rather than considering species individually may bias our interpretation. Second, phosphorus runoff and availability may act in combination with internal loading and lake morphology to mediate the effect of EHWPs on cyanobacteria.

Our results suggest that EHWPs can be used to study past impacts of global warming. Extreme meteorological conditions are a way to track the consequences of warming during a period in which there is no increase in air temperature. They can be used at a large scale to identify exceptional years for inter-lake comparisons. Our results provide evidence that air temperature has an impact on cyanobacteria biomass in deep peri-alpine lakes (Gallina and others 2011) and supports the claim that climate change favors some phytoplankton taxa over others. But we have also showed that the timing of the EHWP is crucial and so it may not always favor cyanobacteria. Furthermore the impact of an EHWP can extend through several seasons and thereby influence the annual succession of communities. Such a constraint from historical states supports the concept of ecological memory, which has been shown to be important in shaping phytoplankton dynamics in aquatic ecosystems (Padisak 1992).

As recent record temperatures have been comparable to temperatures in a greenhouse climate (Beniston 2007), various authors have suggested using EHWPs as a tool for forecasting future impacts (Jankowski and others 2006; Gallina and others 2011) but Straile and others (2010) showed that direct extrapolations can be misleading, as the sequence of meteorological events are also relevant. Furthermore, ecological memory and sensitivity to nutrient concentrations are two properties of aquatic ecosystems that are crucial constraints on this approach. Furthermore, in deep aquatic ecosystems, reduced winter mixing reduces euphotic layer fertilization with deep water (O'Reilly and others 2003). Consequently, extreme events that occur today cannot be expected to occur under the same conditions in the future, nor have the same impacts on a phytoplankton community whose structure has been shown to be influenced by past events. Thus, extreme events are not suitable for predicting the future abundance of cyanobacteria; nor can they be used as proxy for forecasting future effects on the phytoplankton community.

What is the Future for Cyanobacteria in a Warmer World?

Our study did not provide any evidence that higher summer air temperatures promote cyanobacterial growth (Table 3). However, this does not mean that some cyanobacteria taxa will not in fact proliferate more than others in such a situation. To better address this issue, future research should (i) take into account changes in the watershed that could potentially impact runoff and future phosphorus availability, and (ii) consider individual cyanobacteria species rather than the cyanobacteria as one homogeneous group. For example, one could distinguish among cyanobacteria based on shape and/or size, or focus on picocyanobacteria, which are expected to be favored by a temperature increase and nutrient decrease (Callieri 2008, 2010). In general, nutrient limiting conditions are expected to favor picocyanobacteria over larger phytoplankters (Agawin and others 2000). Indeed, the relative contribution of picocyanobacteria to total phytoplankton abundance has been shown to increase with decreasing trophic state (Agawin and others 2000). In addition, increased summer temperatures, combined with lowered soluble reactive phosphorus levels, could provide picocyanobacteria with an ecological advantage over other phytoplankton classes in various aquatic systems, including lakes (Agawin and others 2000; Collos and others 2009; Fu and others 2007). However, it is still difficult to disentangle the effects of reoligotrophication and concomitant global warming in the response of lacustrine picocyanobacteria, partly due to the lack of long-term monitoring data (Jacquet and others 2013). A recent study based on a DNA-paleolimnological approach suggested a significant effect of summer temperature on picocyanobacteria dynamics in Lake Bourget (Domaizon and others 2013). In light of this result, we

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emphasize the need to analyze picocyanobacteria, which is not regularly monitored and often excluded from the majority of long-term monitoring programs. Finally, there is still a great challenge in understanding how the combined effects of the drivers (nutrient supply rates, light, temperature, oxidative stressors, interactions with other biota) impact cyanobacteria blooms and cyanotoxin production (Pearl and Otten 2013), and the diversity of responses of native and invasive cyanobacteria species to local and global drivers has to be taken into account to better understand the impact of climate change on these communities.

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