

# 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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60 blue-green algae, are autotrophic oxygenic pro- 115  
 61 karyotes. They comprise a large variety of species 116  
 62 and possess a number of morpho-functional traits 117  
 63 that could make some of them well adapted to 118  
 64 the environmental conditions associated with global 119  
 65 warming, such as high nutrient loading, rising 120  
 66 temperatures, enhanced stratification, increased 121  
 67 residence time, and salinization (Pearl and Huis- 122  
 68 man 2008; Carey and others 2012; Ekvall and 123  
 69 others 2013). Consequently, speculations that cli- 124  
 70 mate change may increase cyanobacteria abun- 125  
 71 dance has given rise to increasing concerns over 126  
 72 lake use and management because cyanobacteria 127  
 73 are known for their ability to form blooms (Rey- 128  
 74 nolds 2006) and produce toxins (Sivonen and 129  
 75 Jones 1999). In the past decade, the impact of cli- 130  
 76 mate change on cyanobacteria populations has 131  
 77 become a major concern in environmental sci- 132  
 78 ences, leading to a steadily increasing number of 133  
 79 studies on the topic. 134

80 It has been proposed that the impact of warming 135  
 81 on lakes is modulated by the amount of nutrient 136  
 82 resources (Winder and Sommer 2012), and hence 137  
 83 trophic status of the lake and/or climate-related 138  
 84 changes in nutrient loading (Elliott 2012; Arheimer 139  
 85 and others 2005). 140

86 Modelling studies generally predict increased 141  
 87 cyanobacteria biomass and/or dominance with 142  
 88 increasing water temperature and climate-induced 143  
 89 changes in the thermal regime (Jöhnk and others 144  
 90 2008; Trolle and others 2011; Elliott 2012). Al- 145  
 91 though several time series analyses of plankton 146  
 92 data have shown a tight link between climatic 147  
 93 forcing and variability in phenology (Scheffer and 148  
 94 others 2001; Edwards and Richardson 2004; 149  
 95 Winder and Schindler 2004; Adrian and others 150  
 96 2009), only a few studies based on field observa- 151  
 97 tions of phytoplankton communities have clearly 152  
 98 shown an increase in cyanobacteria abundance in 153  
 99 response to climate warming. Comparative and 154  
 100 long-term studies have shown that warmer condi- 155  
 101 tions are indeed associated with higher cyanobac- 156  
 102 teria abundance. For example, the percentage of 157  
 103 cyanobacteria in the phytoplankton community is 158  
 104 higher in warm than in cold shallow lakes (Kosten 159  
 105 and others 2012), warmer winters favor growth 160  
 106 and inoculum production in certain species 161  
 107 (Anneville and others 2004; Weyhenmeyer 2001; 162  
 108 Adrian and others 1995; Jacquet and others in 163  
 109 press). The above-mentioned field and modelling 164  
 110 studies, as well as the experimental work (De 165  
 111 Senerpont Domis and others 2007), provide some 166  
 112 evidence that climate warming likely favors 167  
 113 cyanobacterial forms. There is also the general 168  
 114 finding that cyanobacteria grow better at higher 169

temperatures and possess morphological, physio- 115  
 logical, and behavioral traits that confer advantages 116  
 in strongly stratified environments (Winder and 117  
 Sommer 2012). Distinct competitive advantages of 118  
 cyanobacteria over other taxa would principally 119  
 arise from the ability of cyanobacteria to efficiently 120  
 capture and utilize spatially segregated resources 121  
 (light and nutrients). Cyanobacteria should gain 122  
 advantage from their capacities to (1) regulate their 123  
 position through buoyancy, (2) capture light at low 124  
 intensities over a wide range of wavelengths thanks 125  
 to the accessory pigmentation and the structural 126  
 organization of their light-harvesting antenna, (3) 127  
 access organic phosphorus thanks to phosphatases, 128  
 and (4) to store luxury phosphorus (Carey and 129  
 others 2012). 130

In support of this hypothesis, recent comparative 131  
 studies show that water temperature is indeed a 132  
 predictor of cyanobacteria abundance. However, at 133  
 the same time, these studies emphasize the role 134  
 played by nutrients, trophic status (Beaulieu and 135  
 others 2013; Rigosi and others 2014) or even 136  
 mixing regime of the lake (Taranu and others 137  
 2012), and demonstrate that the response of cya- 138  
 nobacteria to climate change relies upon complex 139  
 interactions between nutrient availability and cli- 140  
 mate-related variables (Kosten and others 2012). 141  
 Some empirical evidence from long-term data point 142  
 to the impact of confounding factors, such as 143  
 phosphorus concentrations, that are stronger than, 144  
 or act in synergy with, meteorological fluctuations 145  
 and atmospheric modes of variability, to explain 146  
 observed changes in phytoplankton communities 147  
 (Jeppesen and others 2003; Anneville and others 148  
 2002, 2004; Shatwell and others 2008; Stich and 149  
 Brinker 2010; Salmaso and Cerasino 2012). 150

This is largely due to a lack of homogeneous 151  
 phytoplankton time-series that cover a time-period 152  
 long enough to include strong hydrological modi- 153  
 fications which might induce significant changes in 154  
 cyanobacteria abundances. Indeed, very few phy- 155  
 toplankton time-series extend back to before the 156  
 1960s, and phytoplankton time-series usually 157  
 cover a time-period that is long enough to capture 158  
 important changes in key environmental param- 159  
 eters, like phosphorus concentrations (Jeppesen and 160  
 others 2005), whose effects are often stronger or 161  
 combine with those induced by climate change (for 162  
 example, Stich and Brinker 2010; Pomati and 163  
 others 2012). 164

Paleolimnology has helped solve this problem by 165  
 broadening the time-period studied (for example, 166  
 Alric and others 2013; Berthon and others 2013). 167  
 Furthermore, cyanobacterial biomarkers like pig- 168  
 ments and DNA are starting to be included in pa- 169



170 leolimnological approaches, revealing the relative  
171 importance of nutrients and warming on cyano-  
172 bacteria dynamics (Domaizon and others 2013;  
173 Savichtcheva and others 2014).

174 An alternative way of studying the impact of  
175 climate warming on cyanobacteria abundance is to  
176 focus on extreme meteorological events (Gallina  
177 and others 2011; Huber and others 2012). Most of  
178 the global warming debate focuses on changes in  
179 global average temperature anomalies. However,  
180 climate change is characterized by important inter-  
181 annual variability and the occurrence of extreme  
182 conditions at certain periods of the year. As statisti-  
183 cal methods summarize patterns within data, such  
184 extremes are usually lost in temporal averages, and  
185 the impact of climate variability has long been  
186 neglected. Only recently have researchers started  
187 analyzing the impact of extreme weather events  
188 (Jentsch and others 2007). In fact, a number of  
189 studies have shown that extreme weather events  
190 strongly impact hydrodynamics and plankton  
191 communities (Jankowski and others 2006; Straile  
192 and others 2010; Anneville and others 2010; Gal-  
193 lina and others 2011). Research also suggests that  
194 the impact of climate extremes is different from the  
195 impacts of mean climate change such as the in-  
196 crease in mean water temperature for instance  
197 (Mearns and others 1997; Straile and others 2010).

198 It is crucial to assess the impact of warm extreme  
199 events because such events are expected to occur  
200 more frequently in the future and are characteristic  
201 of global warming (Beniston 2007). The present  
202 study addresses the impact of such events on cyano-  
203 bacteria abundance in deep peri-alpine lakes.  
204 Our objective is to test, using historical data, if  
205 cyanobacteria perform better and bloom during  
206 exceptional hot weather periods (EHWPs). To an-  
207 swer these questions, we analyzed long-term phy-  
208 toplankton data from Lakes Geneva, Annecy, and  
209 Bourget. These three lakes differ in trophic status  
210 and morphology (Jacquet and others 2014a, b). We  
211 examined data for a ten-year period to determine  
212 if: (i) the occurrence of an EHWP significantly im-  
213 pacts the seasonal dynamics of cyanobacteria, (ii)  
214 an EHWP increases the abundance of cyanobacteria  
215 and induces a change in the composition of the  
216 phytoplankton community, and (iii) at the inter-  
217 annual scale, cyanobacteria abundance is driven by  
218 air temperature.

219 What is today considered an extreme meteoro-  
220 logical condition may become the norm in a future  
221 warmer climate (Beniston 2007). It has therefore  
222 been suggested that an EHWP may be a useful tool  
223 for predicting the impact of climate warming  
224 (Jankowski and others 2006; Huber and others

2010; Gallina and others 2011). However, the  
225 general applicability of an EHWP is unclear; for  
226 example, we know that it cannot be used for all  
227 variables and it is inappropriate for predicting  
228 changes in water temperature (Straile and others  
229 2010). Drawing on our results for Lakes Geneva,  
230 Annecy, and Bourget, we discuss two main ques-  
231 tions regarding the use of EHWPs: can they serve to  
232 analyze the impact of climate change and, can they  
233 be used to empirically test models and conceptual  
234 predictions about the impact of climate warming on  
235 cyanobacteria. 236

## MATERIALS AND METHODS 237

### Lakes 238

239 Lakes Geneva, Annecy, and Bourget are located in  
240 the western part of the Alps (Figure 1). They are  
241 large, never freeze over, and are thermally strati-  
242 fied during much of the year (Table 1). These three  
243 lakes differ in mixing regime and trophic status.  
244 Although Lake Geneva does not undergo complete  
245 mixing every year, Lakes Annecy and Bourget  
246 regularly undergo winter mixing over the entire  
247 water column. Finally, in contrast to Lake Annecy,  
248 which has not suffered from large increases in  
249 phosphorus concentrations over the past 40 years,  
250 Lakes Geneva and Bourget have been eutrophic for  
251 several years (Jacquet and others 2014a, b). In all  
252 three lakes, measures to reduce phosphorus load-  
253 ing in the watersheds were implemented in the  
254 1970s, leading to a decrease in phosphorus con-  
255 centrations starting in the early 1980s. In Lake  
256 Geneva, annual average total phosphorus concen-  
257 tration dropped from 89.5 to 21.6  $\mu\text{g P l}^{-1}$  (Laz-  
258 zarotto and others 2013), in Lake Bourget winter  
259 average total phosphorus concentration dropped  
260 from 150 to 14 between 1980 and 2012 (Jacquet  
261 and others 2013). In Lake Annecy, the annual  
262 concentrations of total phosphorus remained rather  
263 stable over the last 30 years with an average of  
264  $6 \pm 1.9 \mu\text{g P l}^{-1}$  (Domaizon and others 2014).  
265 Lakes Annecy, Bourget, and Geneva are now  
266 respectively oligotrophic, oligo-mesotrophic, and  
267 mesotrophic (Jacquet and others 2014a, b).

### Sampling 268

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



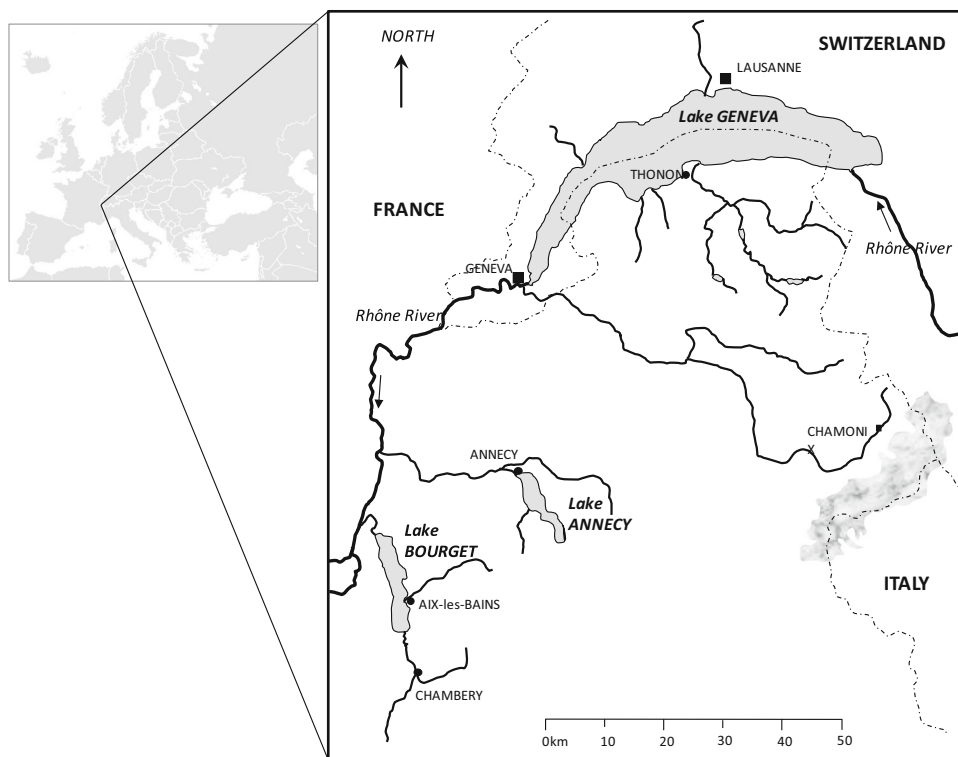


Figure 1. A map showing the location of the studied lakes in the western range of the Alps (from north to south: L. Geneva, Annecy and Bourget).

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

Lake	Latitude	Longitude	Elevation (m)	Mean depth (m)	Max. depth (m)	Surface area (km <sup>2</sup> )	Watershed area (km <sup>2</sup> )
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

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

278 The lakes were sampled at a single station located  
 279 at the deepest point in the lake basin. Sampling was  
 280 carried out once a month in winter and twice a  
 281 month in spring, summer, and autumn. Water  
 282 temperature was measured using a multiparameter  
 283 probe. Water for nutrient concentration measure-  
 284 ments was sampled at a series of discrete depths  
 285 between the surface and bottom of the lake. The  
 286 analytical methods used are detailed in a CIPEL  
 287 annual report (Monod and others 1984) and on the  
 288 website dedicated to the observatory of alpine lakes  
 289 ("<http://www6.inra.fr/soere-ola>").

290 The water samples for identification and estima-  
 291 tion of phytoplankton abundance and composition  
 292 were collected using a custom-made integrating bell  
 293 sampler (Pelletier and Orand 1978). The samples  
 294 were taken in the upper 18 and 20 m in Lakes  
 295 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, b). Phy-  
 toplankton 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 bio-  
 volumes for each species, assuming a fresh weight of  
 1 g cm<sup>-3</sup>. 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 EHWP

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



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

## 329 Analyses

330 We used principal component analysis (PCA) to  
331 examine the impact of EHWPs on the annual  
332 dynamics of cyanobacteria. The PCA was run on  
333 the abundance of phytoplankton groups (PPG) as  
334 identified based on Bourelly's classification  
335 (Bourelly 1972, 1981, 1985) which relies on  
336 morphology and pigment content. We have iden-  
337 tified nine PPG in the studied lakes: Zygo-  
338 phyceae, Chlorophyceae, Diatomophyceae, Xantho-  
339 phyceae, Chrysophyceae, Euglenophyceae, Crypto-  
340 phyceae, and Cyanobacteria. Values for PPG  
341 biomass were ln-transformed and centred. We ran  
342 a PCA for each year and each lake to identify an-  
343 nual variability in cyanobacteria compared to other  
344 phytoplankton taxa. If an EHWP favors cyanobac-  
345 teria, there should be higher variability in cyano-  
346 bacteria abundance during a year with an EHWP  
347 versus other years. In terms of the PCA, if an EHWP  
348 favors a cyanobacterial bloom, the relative contri-  
349 bution of cyanobacteria to the formation of the  
350 PCA axis should be higher during years with an  
351 EHWP.

352 Inter-annual changes in phytoplankton compo-  
353 sition were analyzed using between-groups PCA.  
354 The goal of the method is to describe between-  
355 group variability (Dolédéc and Chessel 1989). The  
356 method consists of running a PCA on the group-  
357 weighted mean values of the variables. The weight  
358 of each group is computed during the analysis and  
359 is proportional to the number of samples in the  
360 group. In our study, the years constituted the  
361 groups, and PPG biomass the variables. We per-  
362 formed the analysis for each season and each lake  
363 separately. Taxa biomass was ln-transformed and  
364 centered before being entered in the analyses. We  
365 chose to use between-group PCA because this  
366 method effectively removes any background noise

related to phytoplankton variability over the sea- 367  
son and focuses, instead, on inter-annual changes. 368

## RESULTS 369

### Identification of Seasonal EHWPs 370

371 Although air temperature showed pronounced 371  
seasonal changes, no long-term increase in annual 372  
mean air temperature could be observed between 373  
2000 and 2011 (Figure 2A). Within this time peri- 374  
od there was, however, strong inter-annual vari- 375  
ability (Figure 2B). The identified EHWPs were: 376  
winter 2007, spring and summer 2003, and au- 377  
tumn 2006. Air temperature anomalies were rather 378  
similar during these EHWPs: +1.9, +1.5, +1.9 and 379  
+1.8°C in winter, spring, summer, and autumn, 380  
respectively (Figure 2B). 381

### Cyanobacteria Community Structure 382

383 In total, 97% of the cyanobacterial biomass was 383  
made up of three species in Lake Bourget, four 384  
species in Lake Annecy, and seven species in Lake 385  
Geneva (Table 2). In both Lakes Geneva and 386  
Bourget, the three dominant genera were *Plankto-* 387  
*thrix*, *Aphanizomenon*, and *Aphanocapsa*. The cy- 388  
anobacteria community was strongly dominated by 389  
*Planktothrix* and, more specifically *P. rubescens*. This 390  
species also dominated in Lakes Bourget and Gene- 391  
va during the four identified EHWPs. In Lake 392  
Annecy, the composition was different: *Aphano-* 393  
*capsa* along with *Chroococcus* dominated the com- 394  
munity, that is, they were more abundant than the 395  
other species during the EHWPs. It is noteworthy 396  
that the picocyanobacteria were an abundant 397  
group in all three lakes (Personnic and others 2009; 398  
Jacquet and others 2013). However, this group, 399  
merely represented by small-sized phycoerythrin- 400  
rich *Synechococcus* spp. (Personnic and others 2009), 401  
were not considered in this study. 402

### Impact of EHWPs on Annual Variability 403 in Cyanobacteria Abundance 404

405 In Lake Annecy, cyanobacteria tended to show an 405  
annual dynamic characterized by higher abun- 406  
dances at the end of the year. However, no clear 407  
recurrent and characteristic annual pattern could 408  
be identified because differences between months 409  
were not significant (Figure 3). In Lake Geneva 410  
and Bourget, where cyanobacteria were more 411  
abundant, their biomass showed a pronounced 412  
annual pattern with significant differences between 413  
some months (Figure 3). In these lakes, cyano- 414  
bacteria demonstrate clear seasonal patterns char- 415



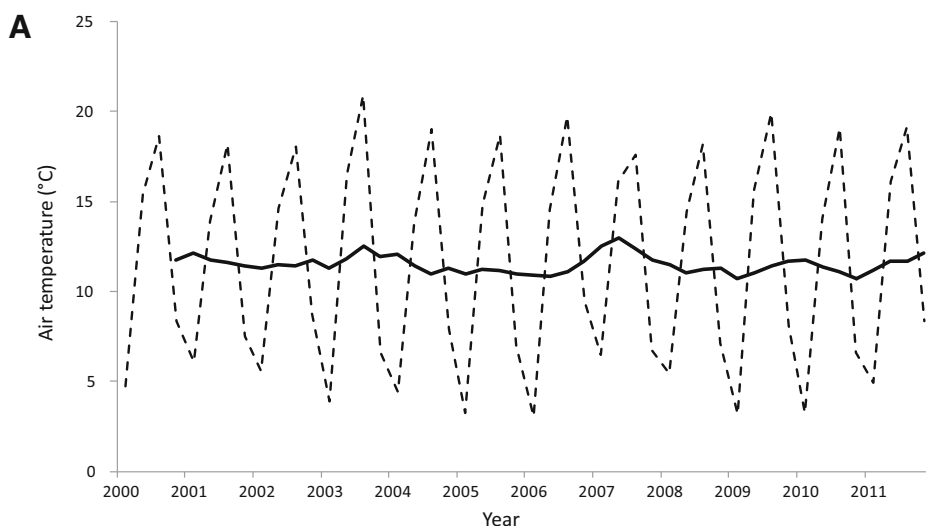
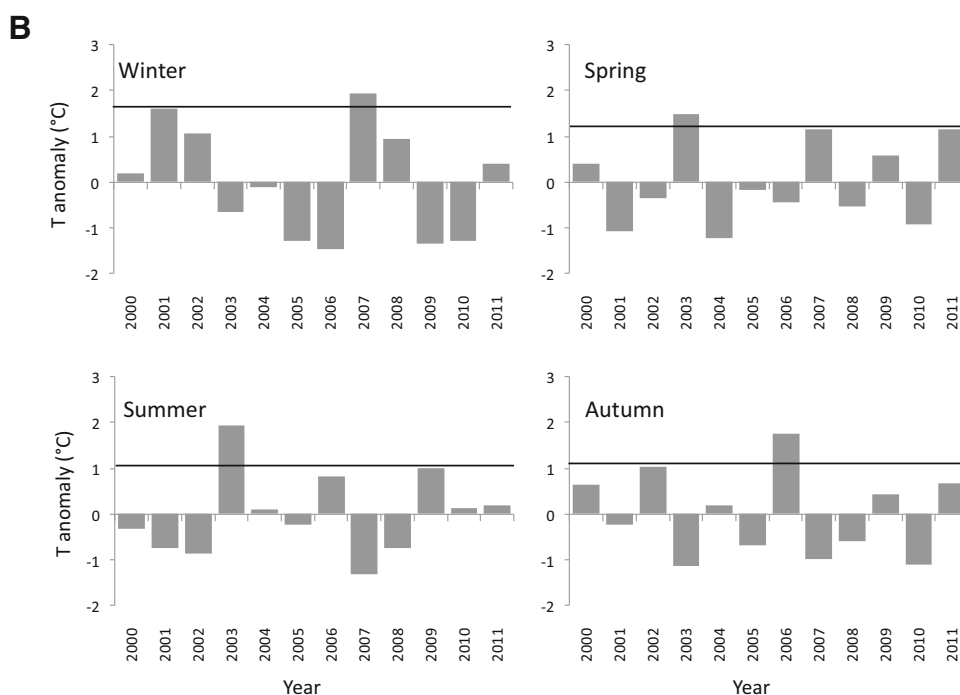


Figure 2. **A** Long-term changes in seasonal mean air temperature (*dotted line*) and 4-year moving average air temperature (*solid line*). **B** Long-term changes in seasonal air temperature anomalies measured at the INRA meteorological station from 2000 to 2011. The horizontal line indicates the 99th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



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

418 The relative contributions of cyanobacteria to the  
419 formation of the first, second, and third PCA axes  
420 are proportional to the size of the circles shown in  
421 Figure 4A. The relative contribution of cyanobac-  
422 teria to the formation of the first three axes was not  
423 exceptionally high during years of an EHWP.  
424 Rather, the contributions were generally low, ex-  
425 cept in 2006 (Figure 4A). In 2003 and 2007, low  
426 contributions indicated low annual variability in  
427 cyanobacteria abundance and, thus, no occasional  
428 blooms during the EHWP associated with these  
429 years. Indeed, in 2003, cyanobacteria were

430 abundant in winter and spring in Lake Geneva but  
431 then decreased during the summer, even though  
432 an EHWP occurred during the summer. In Lake  
433 Annecy, a decrease in cyanobacteria abundance  
434 was also observed during the warm summer of  
435 2003. During the 2007 winter EHWP, an excep-  
436 tionally high biomass of cyanobacteria was ob-  
437 served in all three lakes (Figure 4B). Cyanobacteria  
438 maintained a high abundance throughout the year,  
439 resulting in a low contribution to the formation of  
440 the PCA axes (Figure 4A). In 2006, cyanobacteria  
441 abundance exhibited high annual variability; the  
442 2006 autumn EHWP was associated with a strong  
443 increase in cyanobacteria abundance in autumn in

Author Proof

**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
Annecy	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).

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

#### 450 Influence of EHWP on Seasonal 451 Phytoplankton Composition

452 During the warm winter 2007, cyanobacteria  
453 showed high abundances in all three lakes and  
454 contributed substantially to total phytoplankton  
455 abundance in Lakes Geneva and Annecy (Fig-  
456 ure 5). The results of the between-group PCA  
457 underscored the peculiarity of 2007 that was seg-  
458 regated on axis I during winter in both Lakes  
459 Geneva and Bourget (Figure 6A). Cyanobacteria  
460 and Zygothryx had a strong contribution to that  
461 axis. In Lake Annecy, 2007 was also associated with  
462 cyanobacteria, although this year was close to 2004  
463 in the first plane (Figure 6A).

464 In spring, 2007 remained different from the  
465 other years and was still associated with cyano-  
466 bacteria in Lake Annecy and with cyanobacteria  
467 and conjugates (Figure 6B) in the other lakes. In-  
468 deed, after the 2007 winter EHWP, cyanobacteria  
469 remained abundant and contributed greatly to  
470 phytoplankton biomass in all three lakes, but  
471 especially in Lakes Bourget and Annecy, where  
472 cyanobacteria biomass was exceptionally high  
473 (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 phyto-  
plankton 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 abun-  
dance in summer.

In 2006, autumn biomass of cyanobacteria  
reached the highest values recorded during the  
studied period in Lakes Geneva and Bourget (Fig-  
ure 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 phytoplank-  
ton 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



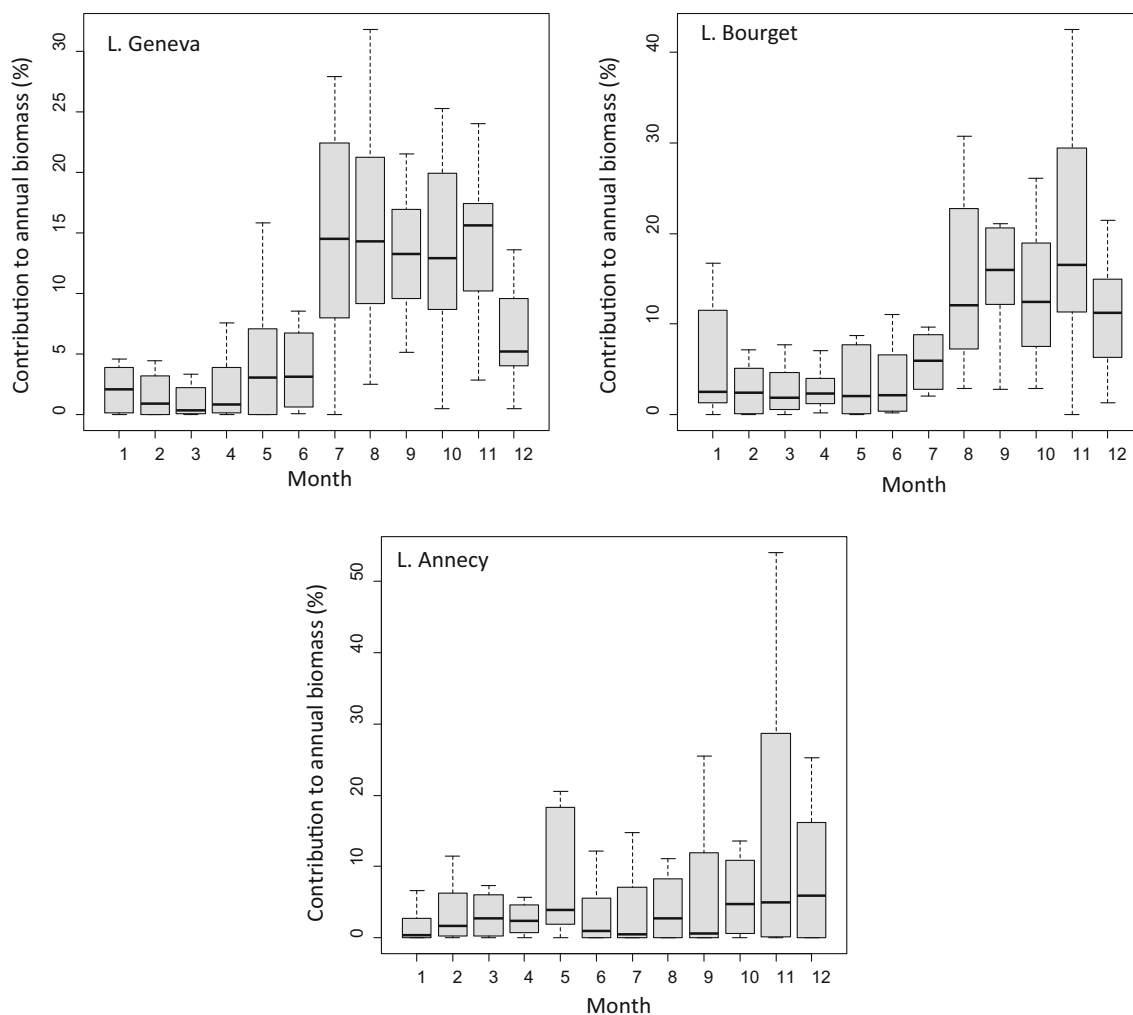


Figure 3. Monthly percentage contributions to the annual cumulative cyanobacteria biomasses in Lakes Geneva, Bourget, and Annecy. Boxes and whiskers, respectively, represent the 25th–75th and 5th–95th percentiles.

504 phosphorus concentrations, measured in February  
 505 during the winter mixing. A second order polyno-  
 506 mial model fitted the data most closely, indicating a  
 507 hump-shaped relationship between phosphorus  
 508 concentration and cyanobacteria abundance in  
 509 Lakes Geneva and Bourget (Figure 8). Significant  
 510 relationships between the residual and winter air  
 511 temperatures were observed for these two lakes  
 512 ( $P$  value < 0.05; Spearman coefficient, Lake Bour-  
 513 get:  $\rho = 0.809$ ; Lake Geneva:  $\rho = 0.608$ ). Both  
 514 in Lake Geneva and Bourget, warm winters were  
 515 associated with high annual cyanobacteria biomass.

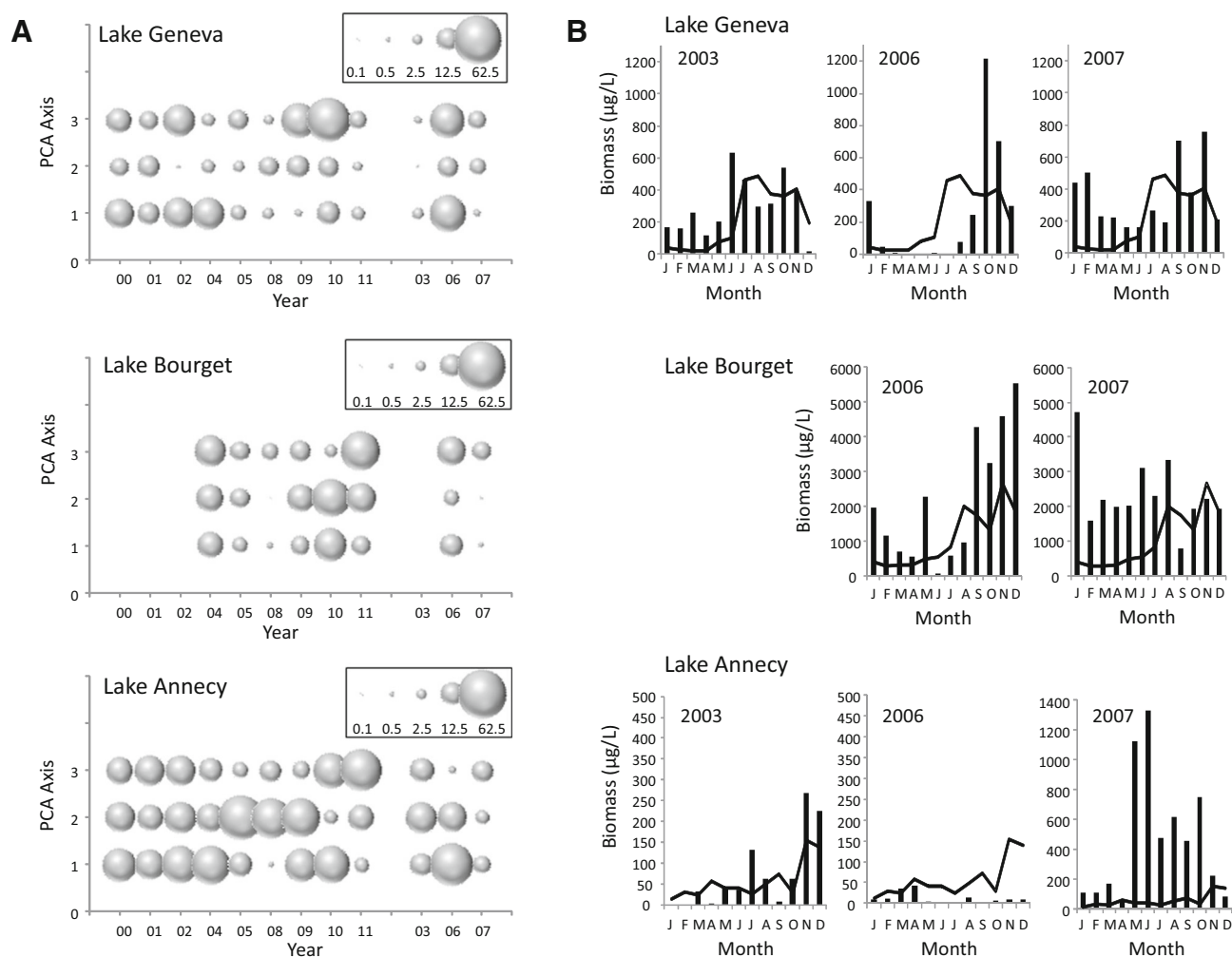
## 516 DISCUSSION

517 No significant increase was detected in the 2000–  
 518 2011 temperature measurements considered in this  
 519 study. This stability in air temperature was also  
 520 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 asso-  
 ciated with the La Nina phase of the El Nino phe-  
 nomenon (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 iden-  
 tification of the extreme meteorological conditions  
 support the relevance of the EHWP identified in  
 our study and which resulted in the warmest sea-  
 sons ever observed in central Europe in the past  
 30 years.

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





**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).

540 and wind storms, have a great impact on both  
 541 ecosystems and human society. For example, heat  
 542 waves, whose frequency and intensity are likely to  
 543 increase through the twenty-first century (Benis-  
 544 ton and others 2007; Kirtman and others 2013), are  
 545 now being carefully considered in the framework  
 546 of global warming (Cubasch and others 2013). In  
 547 general, extreme weather events are emerging as  
 548 one of the most important facets of climate change.  
 549 Consequently, analyzing the effect of EHWP might  
 550 be used to investigate past impacts of climate  
 551 warming on ecosystems. However, despite the  
 552 growing interest in the impact of extreme events  
 553 (Jentsch and others 2007), few studies have ana-  
 554 lyzed their impacts on cyanobacteria abundance, a  
 555 taxonomic group which is expected to be favored  
 556 by global warming (Pearl and Huisman 2008).

557 This research aims to address this lack by focus-  
 558 ing on the annual dynamics and inter-annual  
 559 variability of cyanobacteria in response to EHWP.  
 560 We have chosen to sequence the years into sea-  
 561 sonal periods to examine the variability in the  
 562 ecological response to EHWP (Huber and others  
 563 2010). Finally, contrary to Gallina and others  
 564 (2011), who analyzed the impact of extreme  
 565 weather events on cyanobacteria at the larger scale  
 566 of European alpine lakes, we focused on a few lakes  
 567 located in the same ecoregion (Jacquet and others  
 568 2012). Although our results may be less powerful  
 569 in terms of generalizability, our approach in which  
 570 each lake is analyzed separately, means the results  
 571 can be synthesized and interpreted based on the  
 572 biotic and abiotic properties specific to each lake.  
 573 This approach enables us to better formulate

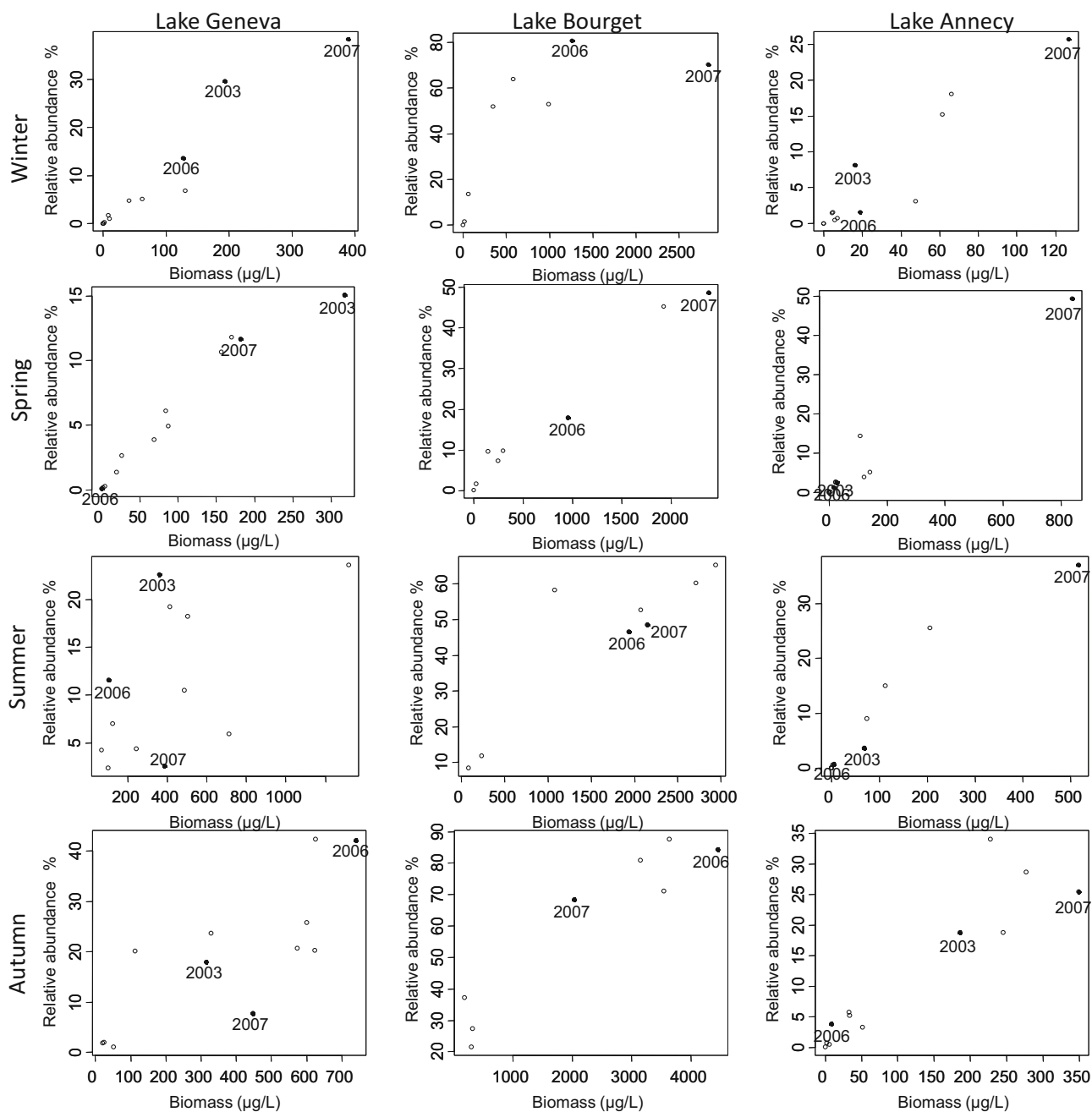


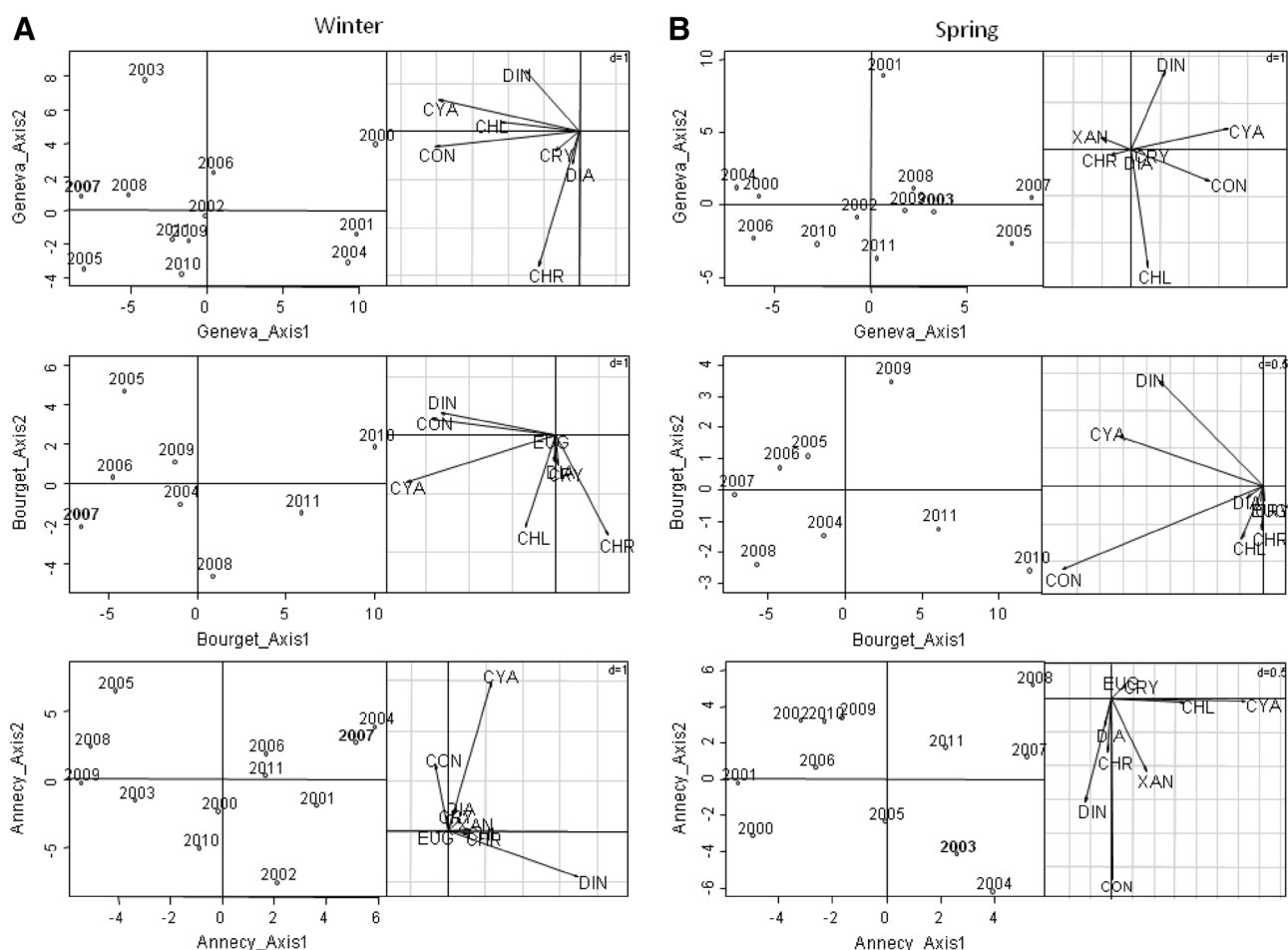
Figure 5. Interannual comparisons of the contribution of cyanobacteria to total phytoplankton biomass (as a percentage) versus absolute biomass of cyanobacteria in Lakes Geneva, Bourget, and Annecy by season.

574 hypotheses to explain variability between sites that  
 575 differ in morphology, trophic status, and composi-  
 576 tion of the cyanobacterial community.

577 **Importance of Nutrients and Trophic**  
 578 **State**

579 Based on the criteria of the European Water  
 580 Framework Directive, according to the Austrian BI

and German PSI indices, the species composition of 581  
 the phytoplankton community indicates that Lake 582  
 Annecy, an ultra-oligotrophic lake, is of good eco- 583  
 logical quality (Kaiblinger and others 2009). Its 584  
 cyanobacteria abundance was low compared to 585  
 that of Lakes Geneva or Bourget, and in terms of 586  
 cyanobacteria assemblages' composition, Lake 587  
 Annecy is mainly characterized by the presence of 588  
 Chroococcales, whereas the cyanobacteria com- 589

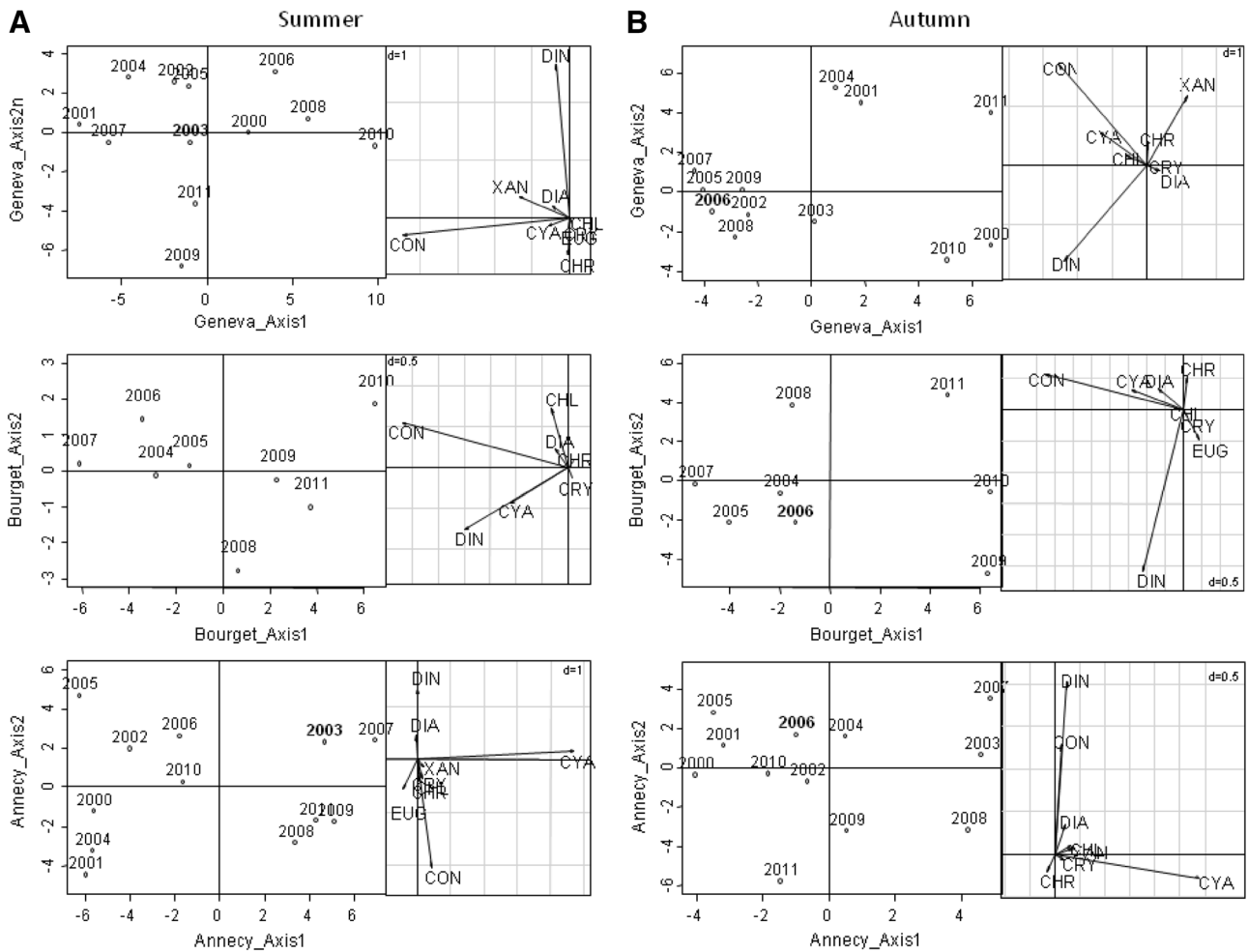


**Figure 6.** Distribution of the center of gravity of years for winter (**A**) and spring (**B**) within the first plane (defined by axes I and II) from the between-group PCA run separately on data from Lakes Geneva, Bourget, and Annecy. Warm years are indicated in *bold text*. *Right hand side* of 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* Zygothryx, *CHL* Chlorophyceae, *DIA* Diatomophyceae, *XAN* Xanthophyceae, *CHR* Chrysophyceae, *EUG* Euglenophyceae, *CRY* Cryptophyceae, *DIN* Dinophyceae, *CYA* Cyanobacteria.

590 community in Lakes Bourget and Geneva, is comprised  
 591 mainly of Oscillatoriales and Nostocales. Although  
 592 for the mesotrophic Lakes Bourget and Geneva, we  
 593 observed a relationship between cyanobacteria and  
 594 phosphorus concentrations, no such relationship  
 595 was found for Lake Annecy. This may be explained  
 596 by the fact that in Lake Annecy, phosphorus con-  
 597 centrations were low and did not change substan-  
 598 tially during the study period (Jacquet and others  
 599 2014a, b). In Lake Geneva and Bourget, the rela-  
 600 tionship between phosphorus and cyanobacteria  
 601 was hump-shaped. In these lakes, the cyanobacteria  
 602 community was dominated by *P. rubescens*. Such a  
 603 relationship supports the finding that the prolifera-  
 604 tion of *P. rubescens* is greatest in meso to moder-  
 605 ately eutrophic conditions (Dokulil and Teubner 2012;  
 606 Jacquet and others in press). Indeed, this species is

used in the European Water Framework Directive as 607  
 an indicator of medium quality state (Brettum 608  
 1989), as opposed to other species like *Microcystis* or 609  
*Limnithrix redeckei*, which are associated with very 610  
 rich nutrient habitats (Brettum 1989). Such a habi- 611  
 tat preference may explain the long-term dynamics 612  
 of *P. rubescens* in Lake Bourget. *P. rubescens* appeared 613  
 in the middle of the last century when phosphorus 614  
 concentrations started to increase (Laurent 1970), 615  
 then decreased strongly at the height of eutrophica- 616  
 tion, formed blooms again in the late 1990s, and 617  
 finally collapsed in recent years (Jacquet and others 618  
 in press). Finally, in the lakes where phosphorus 619  
 concentrations were high enough to support a *P.* 620  
*rubescens* population, winter air temperature was the 621  
 second driver of its abundance. This relationship 622  
 between *P. rubescens* and winter air temperatures 623

Author Proof



**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* Zygothryx, *CHL* Chlorophyta, *DIA* Diatoms, *XAN* Xanthophyceae, *CHR* Chrysophyta, *EUG* Euglenophyta, *CRY* Cryptophyta, *DIN* Dinophyta, *CYA* Cyanobacteria.

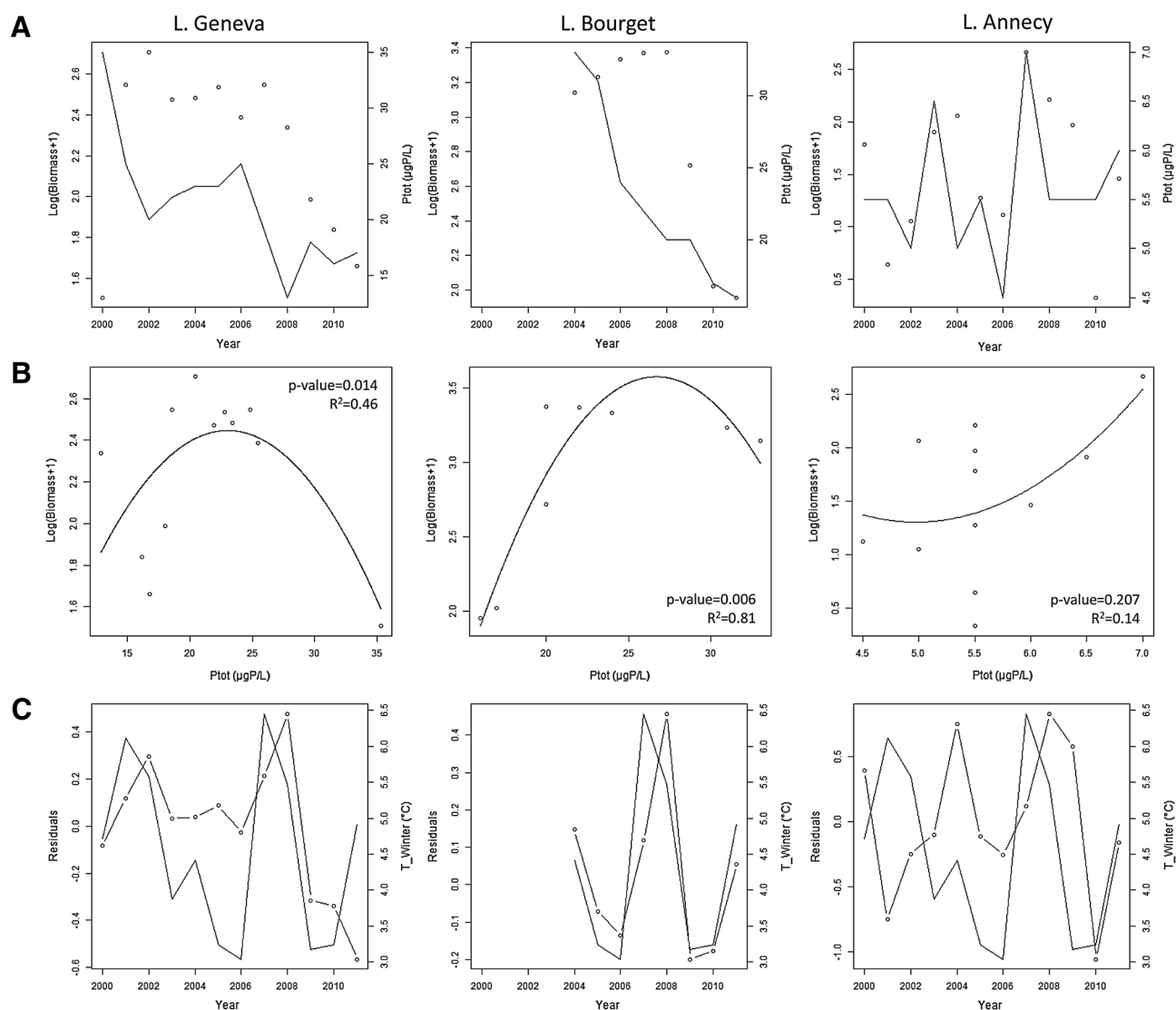
624 suggests that mild winters and winter EHWPs have a  
 625 positive impact on this population (Anneville and  
 626 others 2004; Jacquet and others 2005; Dokulil and  
 627 Teubner 2012; Jacquet and others in press).

628 **The Impacts of Exceptionally Hot**  
 629 **Meteorological Conditions are Season**  
 630 **Dependant**

631 The importance in the timing of meteorological  
 632 events has already been underlined (Huber and  
 633 others 2010), and our observations support this  
 634 assertion: according to our findings, the impact of  
 635 an EHWP depends on the season in which it occurs.  
 636 Our results show that phytoplankton composition  
 637 is particularly sensitive to the winter EHWP. In our  
 638 analysis, a year characterized by an extreme warm

winter was associated with a high cyanobacteria 639  
 biomass and high proportion of cyanobacteria 640  
 in the phytoplankton community during winter 641  
 (Table 3). In short, a winter EHWP favored cyanobacteria 642  
 abundance during winter in the three 643  
 lakes studied. In Lakes Geneva and Bourget, 644  
 according to the priority effects (Louette and De 645  
 Meester 2007) and the idea that past events play 646  
 an important role in structuring communities (Drake 647  
 1991), the high abundance of cyanobacteria prob- 648  
 ably resulted from the extremely high biomass that 649  
 occurred during the warm autumn 2006. The fol- 650  
 lowing mild winter may have served to maintain this 651  
 population. Furthermore, our results show that 652  
 favorable conditions during the winter can impact 653  
 cyanobacteria abundance right through into spring. 654  
 Indeed, the literature suggests that warm winters 655





**Figure 8.** **A** Long-term changes in cyanobacteria abundance (*dots*) and total phosphorus concentration measured 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 EHWP on Cyanobacteria (Summary of Results Presented in Figures 4, 5, 6, 7)

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



656 favor *P. rubescens* (Anneville and others 2004; Jacquet  
 657 and others 2005; Dokulil and Teubner 2012; Jacquet  
 658 and others in press) because this organism's success  
 659 is related to the timing of the onset of stratification  
 660 (Dokulil and Teubner 2012) and the depth of winter  
 661 mixing, which in turn influences spring inoculum  
 662 abundance (Walsby and others 1998). Inoculum is  
 663 known to play an important role in structuring the  
 664 community; the species already present in largest  
 665 numbers because they had the largest residual  
 666 population from the previous episode, or were re-  
 667 cruited by germination of the greatest number of  
 668 resting propagules, are likely to become prominent  
 669 after stabilization of a deep-mixed water column  
 670 (Reynolds 1999). Our result strongly supports the  
 671 concept of ecological memory (Padisak 1992), de-  
 672 fined as the capacity of the ecosystem or its experi-  
 673 ences from past states to influence present or future  
 674 responses of the community. Ecological memory  
 675 can involve various mechanisms and it can be the  
 676 manifestation of priority effects, according to which  
 677 temporal priority of a species may confer a com-  
 678 petitive advantage over other taxa (Hodge and  
 679 others 1996). To resume, our results put forward  
 680 that the successions of events may have consider-  
 681 able implications for the abundance of phytoplank-  
 682 ton taxa and they suggest that phytoplankton  
 683 communities appear as historically derived struc-  
 684 tures. In Lake Annecy, cyanobacteria were  
 685 not abundant in autumn 2006. However, they  
 686 reached a high biomass in winter 2007, when the  
 687 cyanobacteria community was dominated by  
 688 *Aphanocapsa*, *Aphanothece*, and *Chroococcus*. *Aphano-*  
 689 *capsa* abundance increased and managed to domi-  
 690 nate throughout the year. *Aphanocapsa* is quite  
 691 ubiquitous and some papers have reported its ability  
 692 to use organic compounds (Beauclerk and Smith  
 693 1978). Thus, the mixotrophic capacities of these taxa  
 694 may explain their presence in Lake Annecy, a  
 695 strongly phosphorus-limited ecosystem. We have  
 696 shown that a warm spring had a positive effect on  
 697 cyanobacteria in Lake Geneva; unfortunately, we  
 698 have no data comparable to the data from the other  
 699 years for Lake Bourget. In Lakes Geneva and Ann-  
 700 ecy, the summer EHWP did not promote blooms and  
 701 did not favor cyanobacteria over other taxa. During  
 702 the monitoring of Lake Bourget, a very low biomass  
 703 of cyanobacteria was reported for summer 2003  
 704 (Jacquet and others 2013; Vinçon-Leite 2014).  
 705 These results differ from that of Jöhnk and others  
 706 (2008); they showed that the 2003 summer heat  
 707 wave had a strong influence on water temperature  
 708 and hydrodynamics, boosting the growth of cyano-  
 709 bacteria and shifting the competitive balance in fa-  
 710 vor of buoyant cyanobacteria. Such contrasting

711 results may be due to differences between the lakes  
 712 in morphology, nutrient availability, and dominant  
 713 cyanobacterial taxa. The three lakes we studied have  
 714 much lower phosphorus concentrations, different  
 715 stratification dynamics due to their greater depth  
 716 ( $Z_{\max} = 30$  m in Jöhnk and others vs.  $Z_{\max} = 65$  m  
 717 in Lake Annecy, the shallowest of our three lakes)  
 718 and different morpho-functional properties of the  
 719 dominant cyanobacterial forms. An increase in air  
 720 temperature intensifies stratification (Livingstone  
 721 2003; Kerimoglu and Rinke 2013), which, in deep  
 722 water bodies, can result in a substantial reduction in  
 723 nutrient replenishment in the surface layer and lead  
 724 to a decrease in primary production, especially if the  
 725 intensified stratification leads to incomplete mixing  
 726 during winter (Straile and others 2010). Historical  
 727 and paleolimnological data suggest that climate  
 728 change has contributed to diminished productivity  
 729 (O'Reilly and others 2003). Furthermore, the cya-  
 730 nobacteria consist of many different species exhib-  
 731 iting a great diversity of traits and physiological  
 732 characteristics. Different cyanobacteria species  
 733 would be expected to respond in different ways to  
 734 changes in environmental conditions (Rigosi and  
 735 others 2014). In Lakes Bourget and Geneva, where  
 736 the cyanobacterial community was dominated by *P.*  
 737 *rubescens* (Table 2), our findings are in agreement  
 738 with other authors who have observed a decline of  
 739 the *P. rubescens* population in Lake Zurich (Posch  
 740 and others 2012) and low *P. rubescens* biomasses in  
 741 Muggelsee (Huber and others 2012) during the ex-  
 742 tremely hot 2003 summer. Finally, our results  
 743 illustrate that an autumn EHWP can promote  
 744 cyanobacterial growth in mesotrophic lakes (Table 3).  
 745 It impacts cyanobacteria biomass but not the com-  
 746 position of the phytoplankton community. This  
 747 would suggest that milder autumn temperatures  
 748 benefit the entire phytoplankton community rather  
 749 than just cyanobacteria. Gallina and others (2011)  
 750 found similar results, and they hypothesized that lake  
 751 temperature must reach a critical threshold to induce  
 752 a change in phytoplankton composition. An autumn  
 753 EHWP has no effect on oligotrophic lakes, probably  
 754 because phosphorus concentrations are not high  
 755 enough to support high phytoplankton biomass in  
 756 this type of lake.

## 757 Impacts of Exceptional Hot Weather 758 Periods are Informative But Unlikely to 759 be Used to Forecast Future Changes in 760 Cyanobacteria Abundances 760

761 Model projections for the temperate climatic zone  
 762 point to higher air temperatures, increased stability  
 763 of the water column, increased duration of the 763



764 stratified period, and a reduction in vertical tur-  
 765 bulent mixing. In such a habitat, the eco-physio-  
 766 logical properties of some cyanobacteria species  
 767 should enable them to maintain and out-compete  
 768 other phytoplankton taxa (Carey and others 2012).  
 769 Indeed, at relatively high temperatures, the growth  
 770 rate of cyanobacteria typically reaches an optimum  
 771 where other groups are severely inhibited (But-  
 772 terwick and others 2005; Jöhnk and others 2008),  
 773 and many cyanobacteria can regulate their position  
 774 in the water column and so resist intensified  
 775 stratification and exploit nutrients reaching meta-  
 776 limnic layers. Finally cyanobacteria may benefit  
 777 from an increase in the duration of their optimal  
 778 growth period. All in all, global warming is anti-  
 779 cipated to favor cyanobacteria. However, there are a  
 780 few caveats to keep in mind. First, it is unlikely that  
 781 all cyanobacteria will respond in the same way to  
 782 global warming, and taking the cyanobacteria as a  
 783 group rather than considering species individually  
 784 may bias our interpretation. Second, phosphorus  
 785 runoff and availability may act in combination with  
 786 internal loading and lake morphology to mediate  
 787 the effect of EHWP on cyanobacteria.

788 Our results suggest that EHWP can be used to  
 789 study past impacts of global warming. Extreme  
 790 meteorological conditions are a way to track the  
 791 consequences of warming during a period in which  
 792 there is no increase in air temperature. They can be  
 793 used at a large scale to identify exceptional years for  
 794 inter-lake comparisons. Our results provide evi-  
 795 dence that air temperature has an impact on cya-  
 796 nobacteria biomass in deep peri-alpine lakes  
 797 (Gallina and others 2011) and supports the claim  
 798 that climate change favors some phytoplankton  
 799 taxa over others. But we have also showed that the  
 800 timing of the EHWP is crucial and so it may not  
 801 always favor cyanobacteria. Furthermore the im-  
 802 pact of an EHWP can extend through several sea-  
 803 sons and thereby influence the annual succession  
 804 of communities. Such a constraint from historical  
 805 states supports the concept of ecological memory,  
 806 which has been shown to be important in shaping  
 807 phytoplankton dynamics in aquatic ecosystems  
 808 (Padisak 1992).

809 As recent record temperatures have been com-  
 810 parable to temperatures in a greenhouse climate  
 811 (Beniston 2007), various authors have suggested  
 812 using EHWP as a tool for forecasting future impacts  
 813 (Jankowski and others 2006; Gallina and others  
 814 2011) but Straile and others (2010) showed that  
 815 direct extrapolations can be misleading, as the se-  
 816 quence of meteorological events are also relevant.  
 817 Furthermore, ecological memory and sensitivity to  
 818 nutrient concentrations are two properties of

819 aquatic ecosystems that are crucial constraints on  
 820 this approach. Furthermore, in deep aquatic eco-  
 821 systems, reduced winter mixing reduces euphotic  
 822 layer fertilization with deep water (O'Reilly and  
 823 others 2003). Consequently, extreme events that  
 824 occur today cannot be expected to occur under the  
 825 same conditions in the future, nor have the same  
 826 impacts on a phytoplankton community whose  
 827 structure has been shown to be influenced by past  
 828 events. Thus, extreme events are not suitable for  
 829 predicting the future abundance of cyanobacteria;  
 830 nor can they be used as proxy for forecasting future  
 831 effects on the phytoplankton community.

### 832 What is the Future for Cyanobacteria in a 833 Warmer World?

834 Our study did not provide any evidence that higher  
 835 summer air temperatures promote cyanobacterial  
 836 growth (Table 3). However, this does not mean  
 837 that some cyanobacteria taxa will not in fact pro-  
 838 liferate more than others in such a situation. To  
 839 better address this issue, future research should (i)  
 840 take into account changes in the watershed that  
 841 could potentially impact runoff and future phos-  
 842 phorus availability, and (ii) consider individual  
 843 cyanobacteria species rather than the cyanobacteria  
 844 as one homogeneous group. For example, one  
 845 could distinguish among cyanobacteria based on  
 846 shape and/or size, or focus on picocyanobacteria,  
 847 which are expected to be favored by a temperature  
 848 increase and nutrient decrease (Callieri 2008,  
 849 2010). In general, nutrient limiting conditions are  
 850 expected to favor picocyanobacteria over larger  
 851 phytoplankters (Agawin and others 2000). Indeed,  
 852 the relative contribution of picocyanobacteria to  
 853 total phytoplankton abundance has been shown to  
 854 increase with decreasing trophic state (Agawin and  
 855 others 2000). In addition, increased summer tem-  
 856 peratures, combined with lowered soluble reactive  
 857 phosphorus levels, could provide picocyanobacteria  
 858 with an ecological advantage over other phyto-  
 859 plankton classes in various aquatic systems,  
 860 including lakes (Agawin and others 2000; Collos  
 861 and others 2009; Fu and others 2007). However, it  
 862 is still difficult to disentangle the effects of reoli-  
 863 gotrophication and concomitant global warming in  
 864 the response of lacustrine picocyanobacteria, partly  
 865 due to the lack of long-term monitoring data  
 866 (Jacquet and others 2013). A recent study based on  
 867 a DNA-paleolimnological approach suggested a  
 868 significant effect of summer temperature on pico-  
 869 cyanobacteria dynamics in Lake Bourget (Domai-  
 870 zon and others 2013). In light of this result, we  
 871 emphasize the need to analyze picocyanobacteria,



872 which is not regularly monitored and often ex-  
 873 cluded from the majority of long-term monitoring  
 874 programs. Finally, there is still a great challenge in  
 875 understanding how the combined effects of the  
 876 drivers (nutrient supply rates, light, temperature,  
 877 oxidative stressors, interactions with other biota)  
 878 impact cyanobacteria blooms and cyanotoxin pro-  
 879 duction (Pearl and Otten 2013), and the diversity of  
 880 responses of native and invasive cyanobacteria  
 881 species to local and global drivers has to be taken  
 882 into account to better understand the impact of  
 883 climate change on these communities.

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