Chapter

COMPOSITION AND DYNAMICS OF PHYTOPLANKTONIC COMMUNITIES IN 3 LARGE AND DEEP WESTERN EUROPEAN LAKES: AN OUTLINE OF THE EVOLUTION FROM 2004 TO 2012

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ABSTRACT

This chapter details the evolution over the last decade of the phytoplanktonic community biomass and diversity for three large natural lakes in Western Europe (e.g. Lakes Annecy, Bourget and Geneva). Such a comparison has never been proposed before for these major ecosystems. It is shown that these lakes which have been restored or are still in a process of re-oligotrophication, display different phytoplanktonic populations, structure and succession while species (Shannon) diversity recently reached the same level. The last 9 years of the lake survey (2004-2012) has been particularly interesting since the phytoplanktonic structure changed abruptly, especially for Lake Bourget and both its biomass and (class) diversity tend to mimic what is now observed in Lake Annecy. However, the Brettum trophic state index based on phytoplankton composition or the proportion of nano- vs. microphytoplankton forms still classify Lake Bourget as mesotrophic (like Lake Geneva) whereas all parameters define Lake Annecy as oligotrophic. This is explained by species assemblages that remain very different between each ecosystem with typically a larger proportion of small cells and mixotrophs in the latter but also, probably to index pitfall. One of the main drivers for such differences between the 3 lakes, situated in a same ecoregion, seems to be the phosphorus concentration although it is also likely that many other factors intervene (e.g. other nutrients, grazing and parasitism, light availability, etc).

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INTRODUCTION

Phytoplankton is represented by small free-floating autotrophic organisms, composed either by individual cells, colonies or filaments. They play a key role in the functioning of aquatic ecosystems as primary producers (i.e. through their photosynthetic activity that produce oxygen and use carbon dioxide) and food for higher trophic levels including zooplankton, fish or mollusk larvae, and benthic macro-invertebrates (Wetzel 2001, Reynolds 2002).

A variety of factors intervene in the regulation of the dynamics and diversity of the phytoplankton as recently highlighted by the revised Plankton Ecology Group (PEG) model (Sommer et al. 2012). Both the phytoplankton biomass and seasonal succession are a complex function of many factors including inorganic nutrient availability, lake morphology and physical conditions encountered in the upper lit layers, and biotic interactions such as zooplankton grazing, viral lysis, eukaryotic or bacterial parasitism (Banse 1994, Reynolds 2002, Brussaard 2004, Mayali & Azam 2004, Chambouvet et al. 2008).

Studying phytoplankton in lakes is very informative to have a better insight on the ecosystem functioning but also because algal species or assemblages may provide a useful indicator of the trophic state of the ecosystem (which nowadays corresponds to a strong societal demand) and of its response (rapid or delayed) to environmental fluctuations (Reynolds et al. 2002, Padisak et al. 2009). For instance, when lakes suffer from eutrophication (i.e. an excess of nutrients like phosphorus), an important biomass of phytoplankton is generally recorded and some harmful species such as toxic cyanobacteria can bloom (Smayda 1997, Chorus & Batram 1999, Reynolds 2006). Also, it has recently been shown that phytoplankton constitutes a very sensitive indicator of climate variability so that both this biological compartment and lakes in general provide some of the most compelling evidence that species and ecosystems are being influenced by global environmental change and can in turn be considered as sentinels of these changes (Straile 2002, Winder & Schindler 2004, Wagner & Adrian 2009, Williamson et al. 2009, Gallina et al. 2011).

Despite of the existence of studies that have been carried out about the phytoplankton in Lake Geneva (Anneville & Pelletier 2000, Anneville & Leboulanger 2001, Anneville et al. 2002, 2004, Rimet et al. 2009), Lake Bourget (Vinçon-Leite et al. 2002, Jacquet et al. 2005, submitted) and Lake Annecy (Domaizon et al. 2003), there is not yet any reference that aimed at comparing these three ecosystems except for Jacquet et al. (2012). The present chapter attempts to compare the inter-annual dynamics over the period between 2004 and 2012 of the different phytoplankton classes, functional groups and diverse indexes in these three lakes located in the same eco-region (Savoie and Haute-Savoie), in order to highlight the existence of a link between community structure and lake trophic status.

MATERIALS AND METHODS

The principal characteristics of Lakes Annecy, Bourget, and Geneva are summarized in Table 1 and Figure 1 provides to the reader a geographic situation and map of the study area.

Table 1. Main characteristics of Lakes Bourget, Annecy, and Geneva

	BOURGET	ANNECY	GENEVA
Maximum length (km)	18	14.6	72.3
Maximum width (km)	3.4	3.1	13.8
Surface, Area (km^2)	44.5	26.5	580.1
Altitude (m)	231.5	447	372
Maximum depth (m)	147	65	309
Mean depth (m)	80	42	152.7
Total volume (km^3)	3.6	1.13	89
Watershed area (km^2)	560	278	7975
Water time residence (year)	8.5	3.5	11.5

The environmental monitoring of the peri-alpine lakes is carried out at reference stations, which are located where the lakes are at their deepest, and several kilometers away from their main tributaries. These sampling stations are regarded as being characteristic of the pelagic area and little influenced by terrestrial contributions and local disturbances related to certain human activities. They therefore provide a relatively reliable picture of the water mass and associated biota status, as well as their response to more global disturbances. Samplings were carried once each month during winter and twice-monthly in spring, summer, and autumn. Between 15 and 22 campaigns are realized each year.

Concentrations of nutrients are measured in samples taken from a series of known depths between the surface and the bottom of the lakes. Among these nutrients, phosphorus is a key element and its concentration is measured after mineralizing the sample by adding ammonium persulfate and sulfuric acid and pressure-sealing. Colorimetric analyses involved adding a reagent (molybdate of ammonium, sulfuric acid, ascorbic acid, antimony, and potassium) and assaying spectrophotometrically (VARIAN). These analyses are carried out according to French standardized protocols (AFNOR).

Raw water samples were taken in the 0-18 m layer using an integrating water sampler developed by Pelletier & Orand (1978). After collection, the water samples used for phytoplankton analysis were immediately fixed with Lugol's solution. 25 mL of each sample were tipped into an Utermöhl (1931) counting chamber and left form a deposit for at least 12 hours, away from light and heat. The count was then carried out using reversed microscopy (Zeiss) to perform a qualitative and quantitative examination of the phytoplankton. The abundances found were converted into biomass (expressed in µg/L) starting from the biovolumes of each species (Druart & Rimet 2008). Species measuring less than 20 µm and with a biovolume of less than 10.000 μm^3 were assigned to the nanoplanktonic class. Those over 20 µm in length and/or with a biovolume of more than 10.000 μm^3 were classified as microphytoplankton.

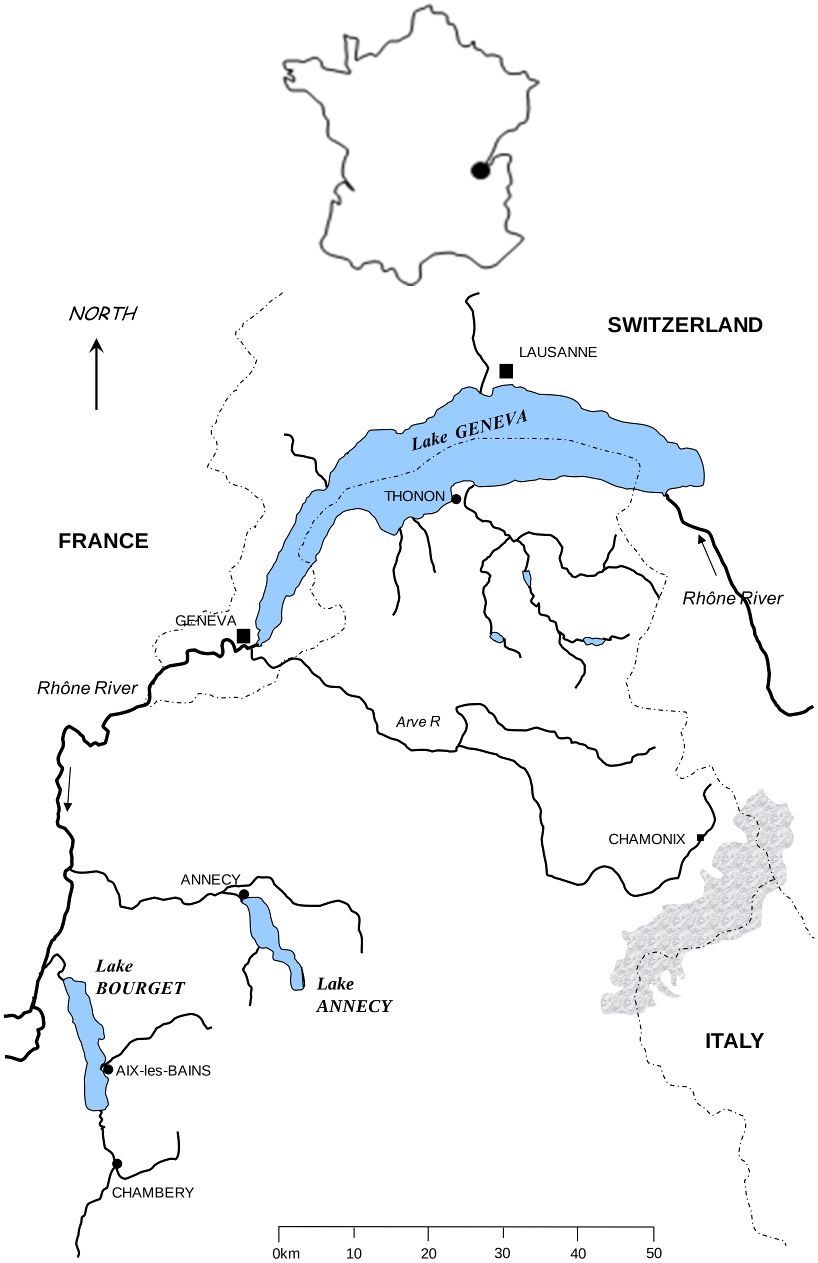

Figure 1. Geographical location in France and map of the 3 peri-alpine lakes situated in Région Rhones-Alpes.

Different biotic indexes based on the phytoplanktonic composition are reported. The Brettum index is related to the trophic level and it has been tested on the three lakes presented in this chapter (Anneville & Kaiblinger 2009, Kaiblinger et al. 2009). It is based on the probability of phytoplankton taxa occurrence along a gradient of total phosphorus divided in 6 trophic classes. For each class, a first index is calculated as follows:

$$I_j = \frac{\sum_{i=1}^{n} v_i x_{ij}}{\sum_{i=1}^{n} v_i}$$

where v_i is the biovolume of the taxon i and x_{ij} is the score of this taxon in the trophic class j

At last, BI is calculated as:

$$BI = \frac{\sum_{j=1}^{6} I_j T_j}{\sum_{j=1}^{6} I_j}$$

where T_j is the weight of each index I, (T1 = 6, T2=5, T3=4, T4=3, T5=2, T6=1).

The Shannon index (1948, H) is also used to assess the change in diversity, according to the following formula:

$$H = -\sum \frac{n_i}{n} \ln\left(\frac{n_i}{n}\right)$$

where n_i and n are the biomass of the taxon i and of the total phytoplankton.

We also used the functional groups as defined by Reynolds et al. (2002) where phytoplanktonic traits such as rapid or low growth rates, high or low requirement of nutrients, light or water column stratification, etc. allow to regroup species, define tolerance to environmental factors and typical habitats.

RESULTS AND DISCUSSION

Evolution of the Biomass and Phytoplankton Classes

Figures 2 and 3 reveal the inter-annual changes (from yearly averaged values) in the biomass and the proportions of the main phytoplankton classes between 2004 and 2012 in the three lakes.

For the 3 lakes, it appears that annual phytoplankton biomass decreased during the last decade and became relatively comparable during the last years. For Lake Annecy, the values of phytoplankton biomass were relatively low (<2 mg/L) throughout the period examined. During the last 4 to 5 years, the biomass remained at relatively constant values of about 1 mg/L and the lowest value was reported in 2010. The dominant phytoplanktonic classes in this lake are the diatoms and Chrysophyceae. For this last group, mixotrophic species (e.g. *Dinobryon* spp), which are characteristic of oligotrophic ecosystems, can display relatively high biomasses (up to 200-300 µg/L in 2004-2005). These mixotrophic taxa use osmotrophy or phagotrophy to obtain nutritive elements under conditions in which resources are limited, and this trait has been suggested recently to be a more common strategy than previously imagined (Hansen 2011). In oligotrophic systems or periods of phosphorus limitation (for example in the epilimnion in summer), mixotrophy offers a considerable competitive advantage to these photosynthetic microalgae, giving them a two-fold system of nutrition (Stickney et al. 2000, Domaizon et al. 2003). Contrary to these mixotrophic taxa, other taxa sensitive to grazing, such as the Chlorophyceae, show a disappearing trend over years, as do the taxa indicating richer environments (Domaizon et al. 2011).

In Lake Bourget the annual phytoplanktonic biomass increased from 2004 to 2006, reaching 4.3 mg/L, and then the biomass reduced only slightly until 2008. Since 2009, a marked reduction has been recorded, and the lowest biomasses have been indeed measured during these last years. If one compares 2006 to 2010 or 2011 for example, the estimated biomasses have been reduced by a factor of 4. This pattern is explained very largely by the disappearance of the cyanobacterium *P. rubescens,* which was present in large numbers until the end of the summer 2009, but which then entirely disappeared in response to a conjunction of factors, including significant phosphorus reduction (Jacquet et al. 2012, submitted). In parallel, the proportions of diatoms, Cryptophyceae and Chrysophyceae increased markedly, which followed the same pattern as was observed in Lake Annecy. The increase of the mixotrophs observed during the last years in Lake Bourget confirmed this lake constitute a changing environment where the community adapts with successions of strictly autotrophic to mixotrophic groups and with increasing proportions of species that do not rely on just one resource but can bring the gap between periods of high resources and periods where resources are scarce.

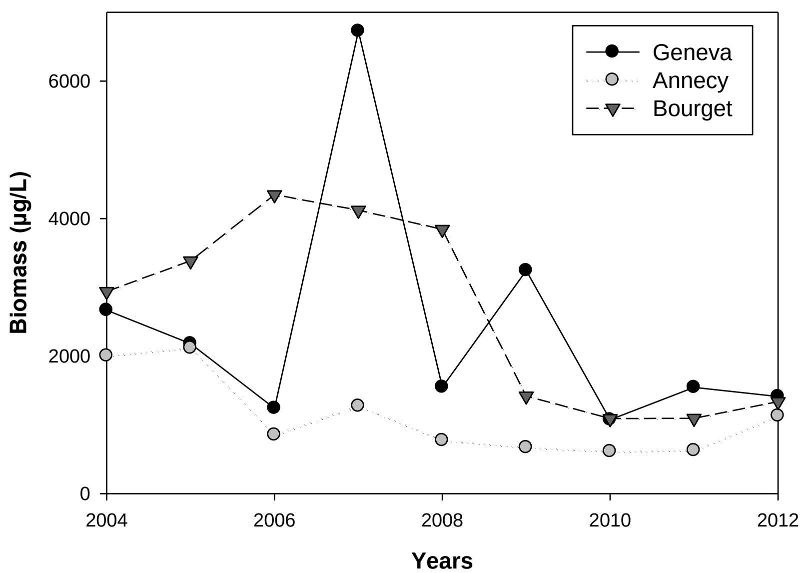

Figure 2. Inter-annual changes in the average phytoplankton biomass between 2004 and 2012.

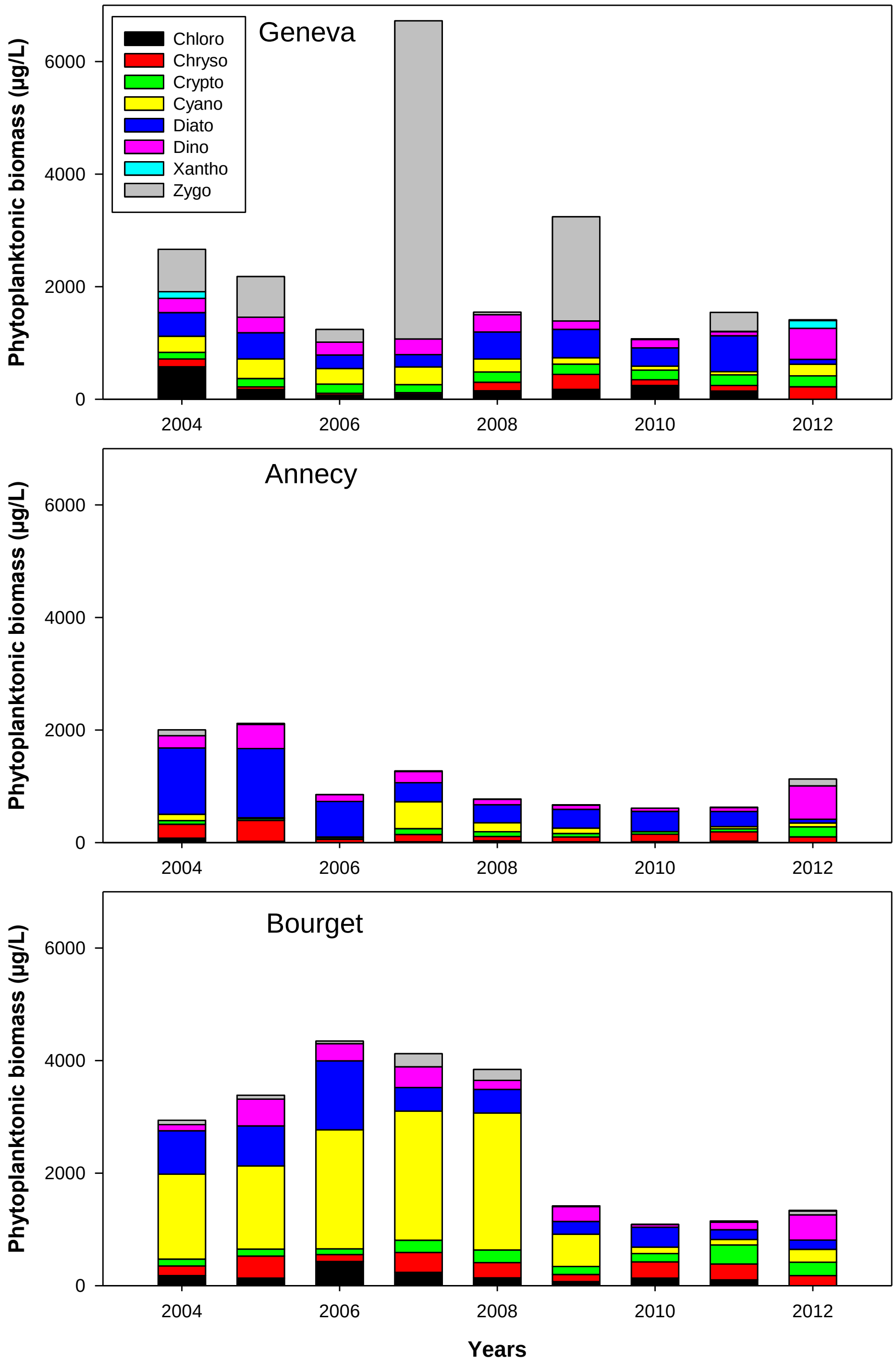

Figure 3. Inter-annual changes in the proportions of the phytoplankton class biomass between 2004 and 2012.

In Lake Geneva, patterns recorded for the phytoplankton biomass appear more chaotic and there is not a clear trend as compared to the other two ecosystems. 2007 was marked by an important phytoplankton peak that was only due to one particular Zygophyceae species, i.e. *Mougeotia gracillima.* The peak observed in 2009 was also due to the development of this species (see below). As for the two other lakes, annual biomass remained below 2 mg/L since 2010.

Evolution of Different Indexes Based on Phytoplankton Biomass or Species

The size of phytoplankton cells constrains many of their physiological rates (e.g. nutrient uptake, growth rate), biotic interactions (e.g. grazing) and behavior (e.g. sinking speed) so that cell size plays a key role in determining the diversity and relative abundance of competing phytoplankton species as well as their transfer to higher trophic levels (Raven 1998).

The high proportion of nanoplanktonic forms in Lake Annecy compared to the larger forms (63.3 ± 20.3%; average value on the time record) corroborates the general view of an oligotrophic ecosystem (Figure 4). Indeed, larger cells are more common under high nutrient supply (Ward et al. 2012) what was confirmed when considering the two other lakes (see below). Changes in the Brettum index for Lake Annecy (e.g. IB = 4.46 ± 0.17; average value over the period 2004-2012 and oscillating between 4.20 and 4.70) indicates that the trophic quality of the lake has been very good since the end of 1990 (Figure 5). It is noteworthy, however, that if between 2004 and 2008, the proportion of the nanophytoplanktonic biomass was indeed dominant in Lake Annecy, after 2008 the proportion of the microphytoplankton increased. In 2012 for instance, the nanophytoplankton represented only 32% of the annual biomass and this percentage was the lowest ever recorded. Moreover, the Brettum index of Lake Annecy decreased markedly in 2012, typically because of the increase of species such as *Scenedesmus* spp, more related to eutrophic environments.

Despite the biomass in Lake Bourget was considerably reduced during the last 4 years, the Brettum index remained low and relatively stable (average IB = 3.50 ± 0.38, oscillating between 3.05 and 3.92) compared to that observed for Lake Annecy, showing that the species in these two ecosystems are still very different. This is also corroborated by the predominance of micro- over nanophytoplankton in Lake Bourget (nanophytoplankton = 17.1±10.1% over the entire chronicle). It is noteworthy, however, that the nanophytoplankton size proportion increased to app 40% since 2009 in this lake. In 2011 and 2012, the relative proportions of these forms in Lakes Annecy and Bourget were in fact comparable.

In Lake Geneva as in the other lakes the biomass was also the lowest in 2010. In this lake, there was a clear downward trend and the Brettum index, although lower on average than in the other two lakes (IB = 3.19 ± 0.32) increased regularly. This indicates an improvement of the water quality, as revealed by the increase in the proportion of the functional groups characteristic of low-nutrient ecosystems (see below). The value in 2012 for the Brettum index in Lake Geneva was even the highest ever recorded but still classified the lake as meso- to moderately eutrophic. The relative proportion of the nanoplanktonic forms is low in Lake Geneva, and fairly similar to that in Lake Bourget (22.5 ± 14.6%).

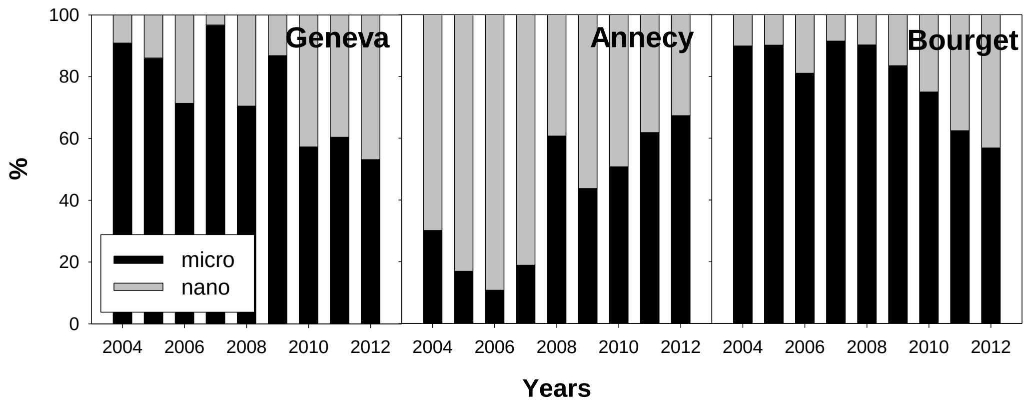

Figure 4. Inter-annual changes in the proportions of the micro- (in black) vs nano- (in grey) size classes.

The difference still observed between Lake Annecy Brettum index and the other lakes is clearly associated to differences in the specific composition. In Lake Annecy, species such as *Kephyrion* spp. or *Chrysolykos planktonicus* which are typical of oligotrophic conditions are still nearly absent from the other two ecosystems. Moreover, some species such as *Scenedesmus* spp, *Aphanothece* spp or *Aphanocapsa* spp still observed in Lakes Bourget and Geneva (especially in 2012 for the former) indicate that these lakes are still higher nutrient-rich ecosystems compared to Lake Annecy.

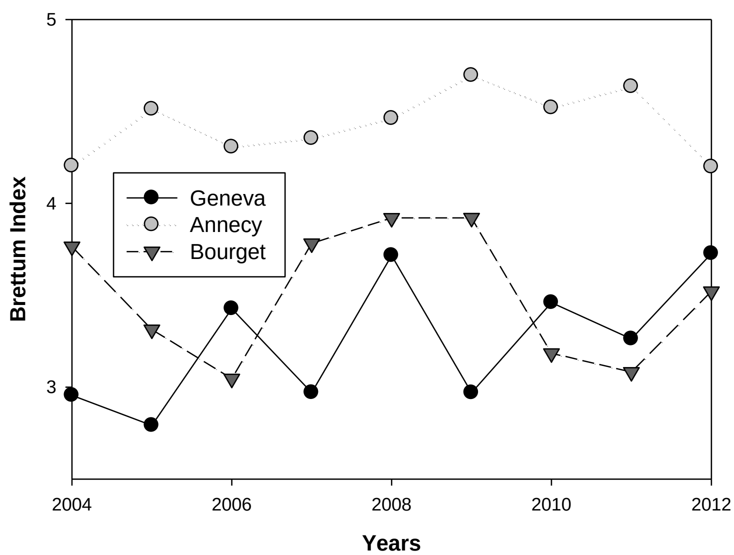

Figure 5. Inter-annual changes in the Brettum index between 2004 and 2012.

Diversity can indicate nutrient level and/or quality of aquatic ecosystems and some relationships have already been reported (Russel-Hunter 1970, Schelske & Stoermer 1971, Reynolds et al. 2002, Padisak et al. 2009). The Shannon diversity index was used to observe the differences in phytoplanktonic biodiversity and changes over time in the 3 lakes (Figure

6). It also reports the richness and the relative proportion of taxa and appears to be comparable in Lakes Geneva and Bourget, which have higher values than Lake Annecy. However, this diversity seems to have fallen during the last decade in the first two lakes and since 2008, phytoplanktonic diversity has been comparable in all 3 ecosystems. This similarity may be linked to the relative homogenization of the chemical characteristics of these 3 lakes (their P contents in particular), but may also be attributable to the same impacts of climate in these lakes, which are located in the same ecoregion. In 2012, the Shannon index calculated for Lake Geneva was quite similar to the previous 5 years and it was lower than that observed before 2007. The significant decrease recorded in 2007 and 2009 could be directly associated to *Mougeotia gracillima* blooms.

Because of strong competition within the phytoplankton community, quick response of this community to external and internal forcing but also compensatory dynamic (Jochimsen et al. 2013), the composition appears to be a more sensitive indicator than integrative parameters such as total biomass (this is well exemplified with Lake Geneva). However, our data clearly indicate important changes in the composition, and the increase in the abundance of better adapted species to new environmental conditions (e.g. phosphorus depletion in Lake Bourget since 2009).

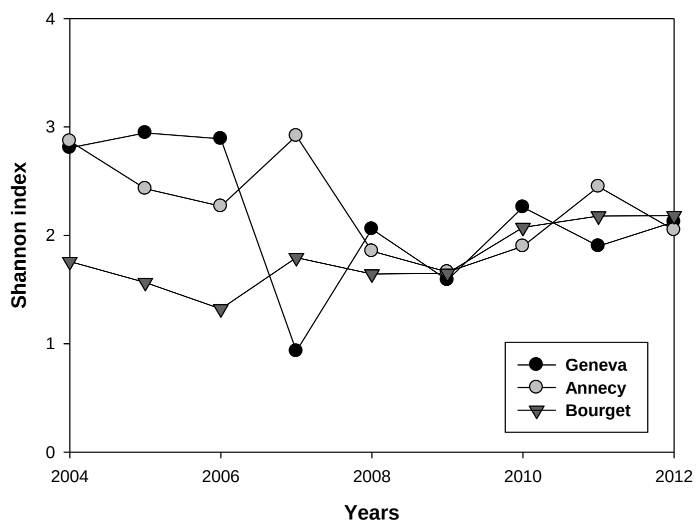

Figure 6. Inter-annual changes in the Shannon index between 2004 and 2012.

From the structure of freshwater phytoplankton assemblages, Reynolds et al. (2002) grouped the various species according to their particular ecological characteristics. Thus, a functional group corresponds to a whole of species having the same ecology. These groups gather taxa living for example in the same trophic levels, same turbulence conditions or the same limnetic and make it possible to better appreciate the factors influencing the phytoplankton and the quality of the lake. Figure 7 presents the annual dynamics of the functional groups of Reynolds.

For Lake Bourget, two main periods could be discriminated. Between 2004 and 2009, the group R was dominant and corresponded to species living in the metalimnion of stratified lake, enable to growth in low light conditions and relatively rich environments (e.g.

Planktothrix rubescens). From 2010, the group R decreased and the biomass was largely represented by the group E, corresponding to mixotrophic taxa (e.g. *Dinobryon* spp.), typical of oligotrophic conditions. It is noteworthy, however, that 2012 was quite different from 2010-2011 since groups J and K became important and are indicators of relatively nutrient-rich environments. A possible explanation here was that winter 2012 was particularly cold and nutrients from the bottom could reach up the upper lit layers, resulting in the development of taxa characteristics of eutrophic ecosystems (e.g. *Scenedesmus acutus*).

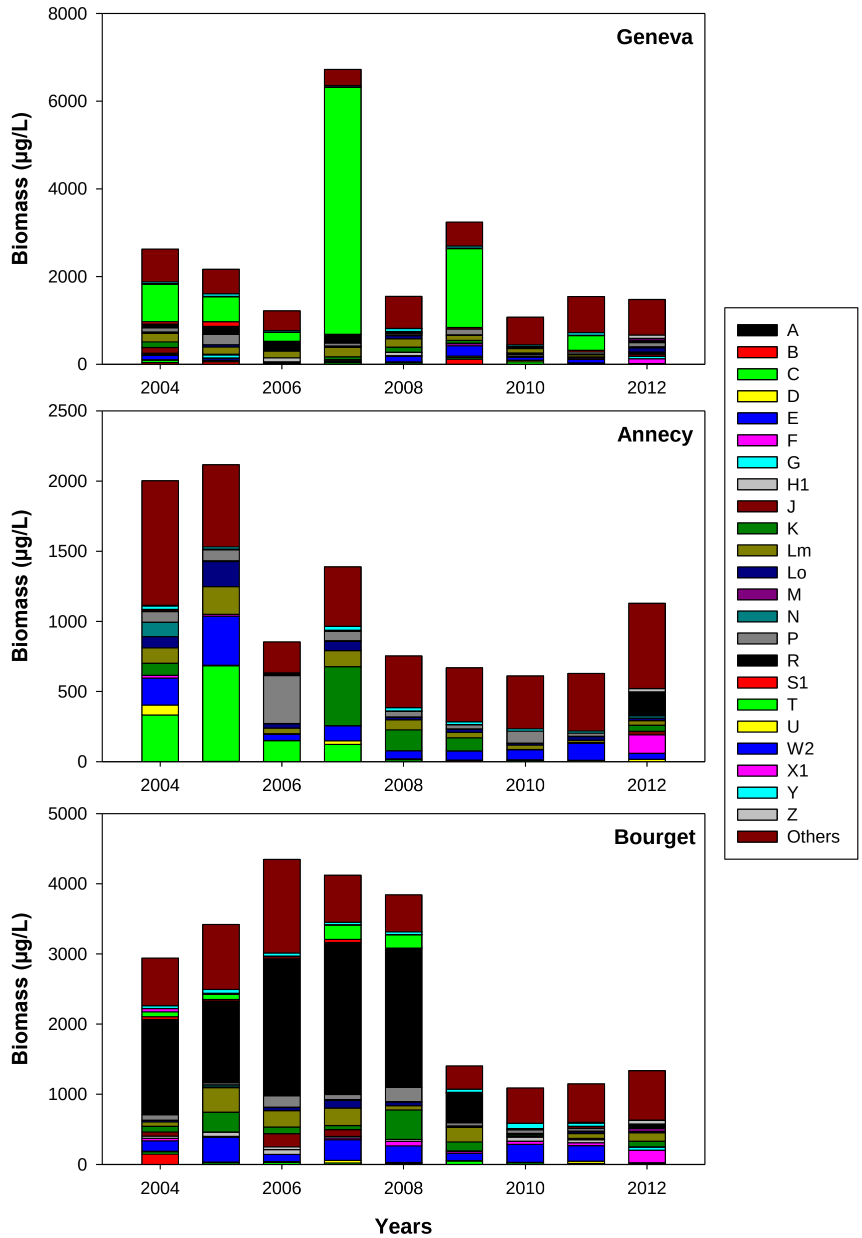

Figure 7. Inter-annual changes in the functional groups between 2004 and 2012.

In Lake Geneva, with the exception of the years when *Mougeottia gracillima* bloomed, all years during the last decade displayed relatively similar biomass. The proportions of the different algal classes varied only slightly despite species composition could change dramatically. In 2012, large quantities of A*chnanthidium catenatum, Tabellaria flocculosa*, *Aphanizomenon flos-aquae*, and of Chlorophyceae such as *Chlamydomonas* spp., *Pandoriona morum* were measured. During recent years the group E, regrouping taxa characteristics of oligotrophic environments, increased, while eutrophic species became rarer, indicating the process of re-oligotrophication.

For Lake Annecy, the group E (regrouping mixotrophic taxa) increased significantly between 2006 and 2011. In 2012, however, the proportion of this group was lower while the group J with species like *Scenedesmus spp.* and *Pediastrum spp.* (i.e. chlorophyceae more characteristics or eutrophic conditions) increased. The presence of these "eutrophic" species and higher biomass observed in 2012 compared to previous years were likely due to the strong mixing event recorded during winter (February) 2012 that resulted in higher nutrient levels in surface waters that favored the development of the phytoplankton.

Clearly, the high proportion of the group E now observed in both lakes Annecy and Bourget may suggest that these (and other) functionally similar morphotypes exhibit similar dynamics. This has been recently highlighted in another temperate deep and large lake, e.g. Lake Constance (Rocha et al. 2011).

Relationships between Variables

Among key factors likely to explain both biomass and diversity of the phytoplankton, phosphorus is known as determinant in freshwaters. Figures 8 and 9 show the relationship between the annual biomass or the Brettum index with this nutrient.

As expected, these figures reveal a positive relationship between total phosphorus and phytoplankton biomass ($r=0.56$, $n=27$, $p<0.05$) while a negative relationship is observed between total phosphorus and the Brettum index ($r=-0.72$, $n=27$, $p<0.01$). They translate that long-term changes in both the abundance and composition of the phytoplanktonic communities are strongly associated to changes in this resource supply. It is noteworthy however that biomass decline in response to P reduction is not immediate and the ecosystem must reach a relatively low P level before phytoplankton biomass reduces significantly. This was clearly observed for Lake Bourget for which phytoplanktonic biomass was reduced by a factor 3 to 4 before and after 2009 when total phosphorus and phosphates winter concentrations) reached and maintained below 17 and 14 µg/L, respectively (Jacquet et al. submitted).

This phosphorus originates in the catchment area and has various sources (agriculture, industry, domestic); however domestic pollution was identified as having made a major contribution to the phenomenon of eutrophication observed in the years 1970-80. The efforts which have been made to reduce the contributions of the catchment area have been important and relatively similar between Lake Geneva and Bourget, leading to quite similar reductions of the external load in these two ecosystems over the last two decades (Jacquet et al. 2012).

Although our result highlights the critical role of phosphorus availability, this does not exclude the importance of other environmental factors such as the physical structure of the water column, other nutrients and biotic interactions including grazing by zooplankton, infection and lysis by viruses or fungi (Anneville et al. 2004, Sommer et al. 2012). Anneville et al. (2005) or Thackerey et al. (2008) showed indeed that the long-term changes observed in a variety of lakes in the biomass and phenology of the phytoplankton are the result of both nutrient enrichment/limitation and climatic variability.

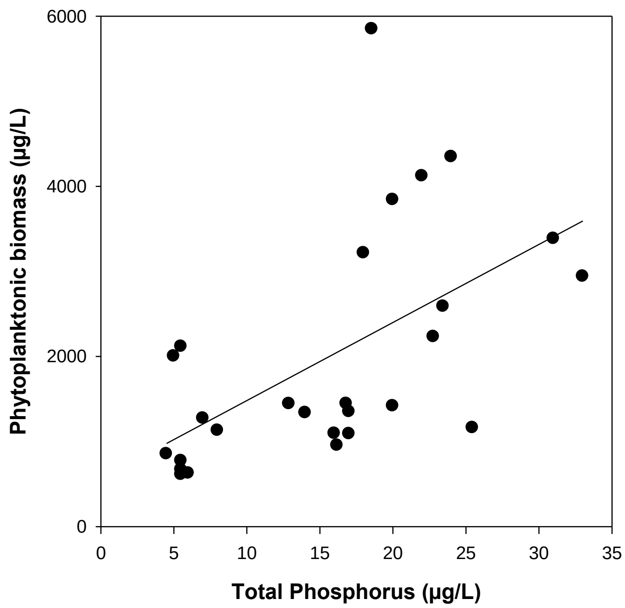

Figure 8. Relationship between total phosphorus and total biomass.

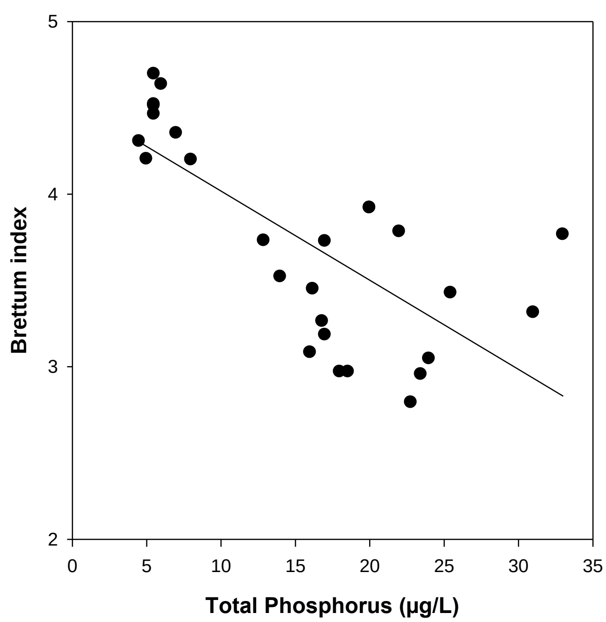

Figure 9. Relationship between total phosphorus and the Brettum index.

CONCLUSION

In recovering ecosystems such as Lakes Bourget and Geneva, even with constant nutrient concentrations, the inter-annual phytoplankton dynamics may still vary greatly from one year to another suggesting that many other factors (including typically meteorological forcing, grazing, parasitism, etc) can be of importance to explain patterns and diversity evolution. However, for Lake Bourget, it was clear that important reduction of phosphorus observed during recent years led to the disappearance of the cyanobacterium *P. rubescens* and that a new phytoplanktonic assemblage is settling. The pluri-annual monitoring study proposed here was mainly qualitative and highlighted either the absence of important changes or dramatic modifications in phytoplankton biomass and groups that could be at least related to P evolution in the different ecosystems. Further studies are now necessary in order to find a reliable quantitative description of the inter-annual variability of the phytoplankton assemblage and to incorporate them into ecological models. A first step could be to detail inter-annual dynamics of the whole community, main population and various species or morphotypes and compare such dynamics between the 3 lakes and the PEG (Plankton Ecology Group) model.

This is critical when one knows that aquatic ecosystems are expected to change markedly over the next century in response to anthropogenic stressors. It is expected indeed that the increase of air temperature will probably impact dramatically surface waters where phytoplankton develops. Water will become warmer (and this will be more marked in winter), the column stratification will increase and this will lead to enhanced light exposure. All together, such changes will thus result in a longer phytoplankton growing season but in another way, stronger stratification will also limit the vertical supply from deep waters of nutrients. Obtaining long-term series of phytoplankton abundances and diversity in conjunction with a large set of environmental parameters constitute an important step to be able to predict and assess plankton shifts and their consequences in food webs and biogeochemical cycles. Indeed, models will need to capture the ecology of diverse phytoplankton communities and assess how community structure varies under various environments to make in fine accurate predictions of the consequences of any anthropogenic change.

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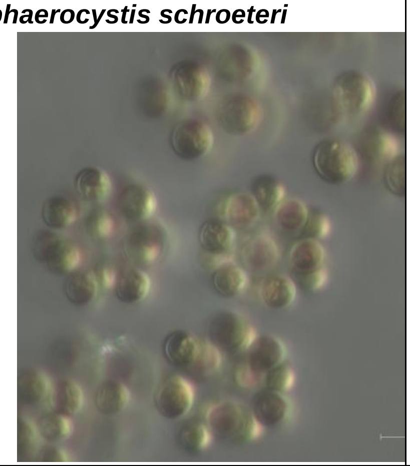
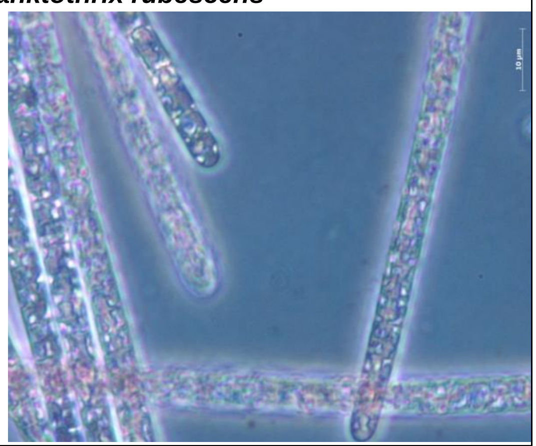
ANNEX

Annex: A Few Taxa from Peri-Alpine Lakes

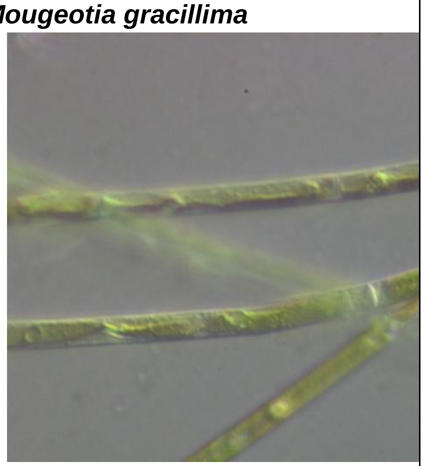
Sphaerocystis schroeteri



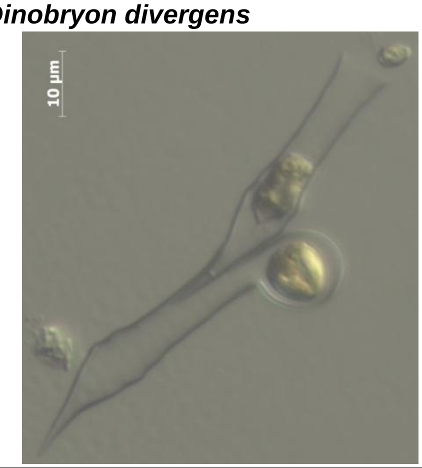
Planktothrix rubescens



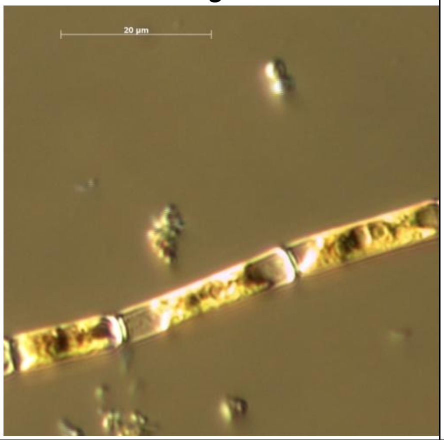
Mougeotia gracillima



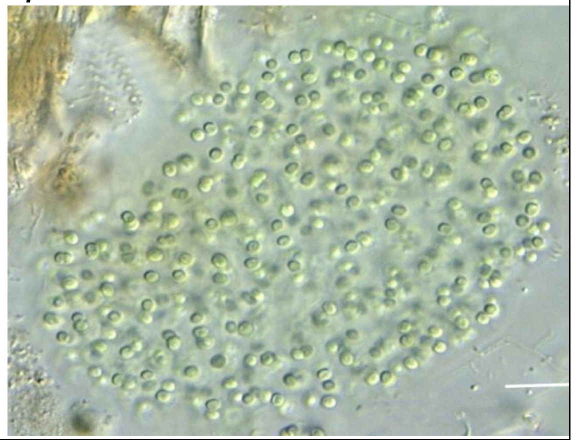
Dinobryon divergens



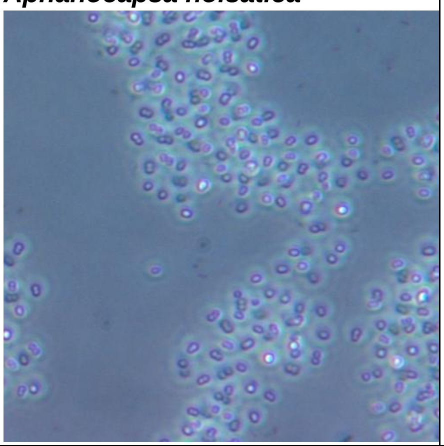
Tribonema ambiguum



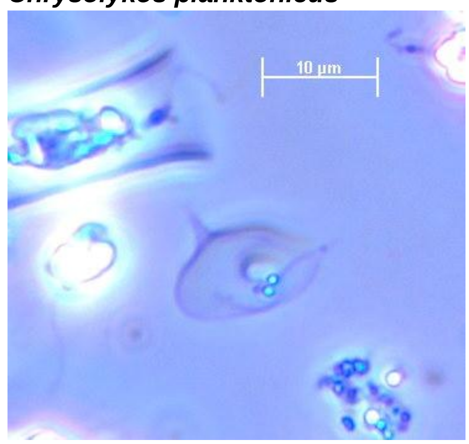
Aphanothece delicatissima



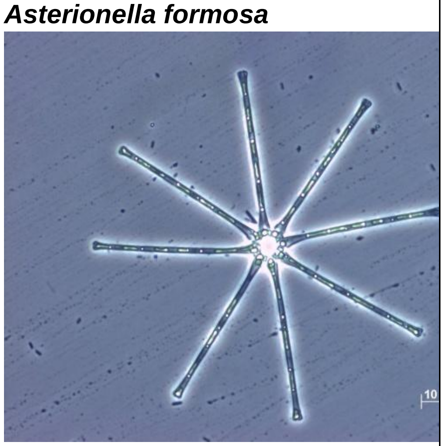
Aphanocapsa holsatica



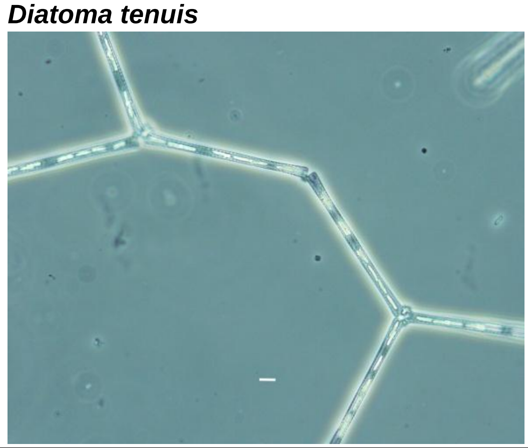
Chrysolykos planktonicus

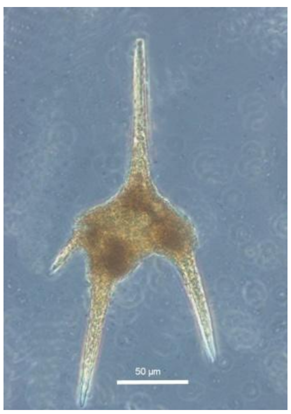


Asterionella formosa



Diatoma tenuis



Chlorella vulgaris 	***Rodomonas minuta*** 
Ceratium hirundella 	***Aphanizomenon flos aquae*** 

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