Environ Monit Assess (2014) 186:3455–3476
DOI 10.1007/s10661-014-3630-z

The need for ecological monitoring of freshwaters in a changing world: a case study of Lakes Annecy, Bourget, and Geneva

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Received: 30 April 2013 / Accepted: 9 January 2014 / Published online: 23 January 2014

Abstract Lakes Annecy, Bourget, and Geneva are large, deep carbonated peri-alpine lakes in eastern France. They are located in the same ecoregion but have been subject to differing degrees of anthropogenic pressure over the past decades. A comparative analysis of these ecosystems can therefore provide valuable information on how the lakes have responded to changes in phosphorus runoff, fish management practices, and global warming. Each of these lakes has undergone a restoration process, and changes in water quality and trophic state, as measured using parameters like transparency, chlorophyll *a*, nutrient concentrations, and phytoplankton biomass and structure, can be used to evaluate efforts made to preserve these ecosystems. Our results reveal that (1) peri-alpine lakes are exemplary cases of restoration in the world where freshwater eutrophication is on the increase, and (2) efforts must be maintained because of the new context of climate change, the effects of which on the quality and the ecological functioning of lakes are still poorly understood.

Keywords Lake · Monitoring · Eutrophication · Restoration · Reoligotrophication · Phosphorus · Phytoplankton · Zooplankton · Fish · Transparency · Temperature

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Introduction

Long-term time-series studies of selected aquatic and terrestrial habitats were mainly started during the middle part of the last century. They yielded significant contributions to earth and ocean sciences, leading, for instance, to the recognition of acid rain (Likens et al. 1972) and the documentation of increasing carbon dioxide in the earth's atmosphere and global warming (Keeling et al. 1976). Although carrying out monitoring studies takes considerable time and effort, data accumulated over a long period of time remain the best and, sometimes, the only way to fully understand ecosystem changes and the reasons behind these changes (natural versus anthropogenic). When considering aquatic ecosystems, it is impossible not to cite the HOT (Hawaii Ocean Time-series) and BATS (Bermuda Atlantic Time-series), both of which were established with support from the US National Science Foundation (NSF). Since 1988 (plus additional data for BATS since 1954 from the neighboring Hydrostation S), these studies have collected measurements on such variables as water column temperature and chemistry, currents, optical properties, primary production, plankton community diversity, and structure and rates of particle export in key regions of the Atlantic and Pacific Oceans (Michaels and Knap 1996; Karl and Lukas 1996). The importance, problems, approaches, and outcomes of long-term monitoring studies of marine ecosystems have been highlighted in special reviews (Ducklow et al. 2009; Katsanevakis et al. 2012).

For freshwaters (i.e., rivers, lakes, and groundwater), many chemical, biological, and microbiological parameters can be measured to assess ecosystem status and how it evolves in response to local, regional, and global changes, such as pollution, species invasion, watershed use, and global warming (Jeppesen et al. 2005). Lakes are a good example of a sensitive environment that needs to be monitored and managed; this is why they have recently been called sentinels, integrators, and regulators of climate change (Williamson et al. 2009). The recognition that lakes provide goods and services and impact local economies has prompted the initiation of many monitoring studies. In Europe, for instance, the Water Framework Directive (WFD; Directive 2000/60/EC) was created in response to the increasing demand by citizens and environmental groups for cleaner rivers and lakes. Many lakes that underwent eutrophication during the twentieth century are now in the restoration phase. They therefore provide ideal case studies for elucidating the way in which deep, large lakes located close to relatively large towns react to anthropogenic pressures like pollution on their catchment areas. Nutrient enrichment is recognized as having some of the worst impacts on water quality (Smith et al. 2006), with phosphorus playing a determining role (Schindler et al. 2008). In recent decades, great efforts have been made by authorities to restore lake ecosystems suffering from eutrophication, chiefly by acting on the source of pollution and by reducing phosphorus inputs into the catchment area, typically by updating and/or replacing wastewater treatment plants that remove phosphate from wastewater. However, reconciling the various uses of ecosystems and returning the ecosystem to a more satisfactory state is never immediate. Rather, it requires a long-term perspective (Jeppesen et al. 2005; Anneville et al. 2004).

France's peri-alpine lakes have been monitored for decades under ecological monitoring programs funded by a number of collective lake management commissions and organizations: CIPEL (International Commission for the Protection of Lake Geneva), SILA (Inter-regional Association for Lake Annecy), and CISALB (Inter-regional Committee for the Clean-up of Lake Bourget). Today, the lake surveys are carried out collaboratively and constitute the SOERE GLACPE (System of Observation and Experimentation for Environmental Research in Large Peri-alpine Lakes). These data are being used to observe, understand, and model changing patterns in the status and ecological functioning of these lakes in response to changes in local and global anthropogenic pressures. SOERE GLACPE is part of a national and international observatory system whose goal is to consolidate scientific knowledge based on long-term data collection and to stabilize/optimize quality indicators used to assess ecosystem health and services (Maresca et al. 2011). The French government funds this observatory, recognizing that such monitoring needs special long-term funding, as is provided in the USA by the National Science Foundation Long-Term Ecological Research Network. Inevitably, the protection and management of large peri-alpine lakes must deal simultaneously with issues related to drinking water, fishing, tourism, and more recently, biodiversity. While nutrient pollution has generally been brought under control, continued vigilance is still required. Furthermore, peri-alpine lakes are not immune to new threats to their water quality and ecological functioning, such as (1) emerging pollutants like persistent organic micropollutants and pharmaceutical compounds, (2) colonization by invasive species (introduced or naturally colonizing), and (3) climate change.

In this paper, we examine annual and seasonal (winter/summer) changes in key limnological variables and biological parameters in three peri-alpine lakes in Western Europe: Lakes Annecy, Bourget, and Geneva. Our aim is to interpret times-series data for various parameters and indexes of water quality, trophic state, and functioning in relation to ecosystem changes like reoligotrophication and global warming. To the best of our knowledge, this is the first time that large deep lakes in the same ecoregion have been compared in this way. This paper clearly indicates the recent recognition that obtaining and analyzing long-term data series is valuable, even if it is not "sexy" science because the results are not immediate, nor the scientific gratification is "instant."

Materials and methods

The principal characteristics of Lakes Annecy, Bourget, and Geneva are summarized in Table 1. The environmental monitoring of the peri-alpine lakes is carried out at reference stations, which are located at the deepest part of the lakes and several kilometers from their main tributaries. These sampling stations are believed to be characteristic of the pelagic area and little influenced by terrestrial contributions and local disturbances related to

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	7,975
Water time residence (year)	8.5	3.5	11.5

certain human activities (e.g., harbors). They therefore provide a relatively reliable picture of the water mass and associated biota status as well as their response to disturbances. Sampling was initially carried out at intervals of 1 month, but since 1981, there has been bimonthly sampling in spring, summer, and autumn. The sampling has been carried out in accordance with standardized protocols that were established in the 1970s for Lake Geneva and in the 1990s for Lakes Annecy and Bourget. While the data do not allow for comparisons over the very long term, they do provide comparative data from at least the middle of the 1990s to the end of 2011.

Variables

Temperature

From 1974 to 1991, the temperature of the water column was measured at various depths between the surface and the bottom of Lake Geneva. Thereafter, the use of multiparametric probes in the three lakes (Ponselle, ME, Meeresch Technik, Sea & Sun Technology GMBH, SeaBird) made it possible to plot a continuous thermal profile as well as monitoring other parameters, such as conductivity, and concentrations of chlorophyll *a* and/or dissolved oxygen. For Lake Bourget, these probes have been in use since 1981. Intercalibration of the different probes is regularly carried out by our laboratory (INRA, Thonon-les-Bains). Temperature data can also be used to calculate the duration of stratification of the water column. We took measurements taken every meter and calculated the gradient between two consecutive depths. When this gradient was >1 °C, we considered this to represent the onset of the stratification, with stratification duration being the number of days until this gradient decreases to a value of <1.

Transparency

This is measured using a 30-cm-diameter white disc immersed in the water. Transparency is the depth at which the operator can no longer see this disc. We interested in both mean annual and summer transparency. We also reported what is referred to as the clear water phase when detected, i.e., the period associated with the maximum transparency measurement in spring.

Phosphorus

Concentrations of total phosphorus (Ptot) and dissolved phosphorus (PO_4) are measured in samples taken from a series of known depths between the surface and bottom of the lakes. Ptot is measured after mineralizing the sample by adding ammonium persulfate and sulfuric acid and then pressure sealing. The colorimetric analyses for Ptot and PO_4 involve adding a reagent (ammonium molybdate, sulfuric acid, ascorbic acid, antimony, and potassium) and running a spectrophotometric assay (Varian). These analyses are carried out according to a standardized protocol (AFNOR, http://www.afnor.org).

Phytoplankton

Raw water samples are taken in the 0–18 m layer using a patented integrating instrument developed by Pelletier and Orand (1978). For Lakes Annecy and Geneva, the depth integration was 0–10 m for Lake Annecy before 2001 and for Lake Geneva before 2002. For Lake Bourget, the depth integration was 2.5 times the transparency found using the white disc until 2005 and 0–20 m subsequently. After collecting, the water samples are immediately fixed with Lugol's solution. Then, 25 ml of each sample is tipped into an Utermöhl counting chamber (a cylinder over a blade with a sediment chamber; Utermöhl 1958) and left to form a deposit for at least 12 h, away from light and heat. The count is then carried out using reversed microscopy (Zeiss), providing a qualitative and quantitative examination of the phytoplankton. Abundance is converted into biomass (expressed in microgram per liter) based on the biovolume of each species (Druart and Rimet 2008). Species measuring less than 20 μm and with a biovolume of less than 10.000 μm^3 are assigned to the nanoplankton class. Those over 20 μm in length and/or with a biovolume of more than 10.000 μm^3 are classified as microphytoplankton. It should be noted that picophytoplankton are not taken into consideration, even though this compartment (mainly represented by picocyanobacteria) probably plays a key role at the bottom of the food web in these oligo- to mesotrophic lakes and could perhaps be used as a bioindicator of trophic or climatic change (Personnic et al. 2009). Several indices based on phytoplankton composition have been developed in recent years for evaluating the ecological state of lakes. These indices have been tested on the three large peri-alpine lakes presented in this study (Anneville and Kaiblinger 2009; Kaiblinger et al. 2009). The Brettum index (Brettum 1989) has yielded the best results in terms of determining trophic level, and so we use this index here. Brettum index (BI) is based on the probability of phytoplankton taxa occurrence along a gradient of total phosphorus divided into six trophic classes. For each class, we calculated the first index using the following equation:

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

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

We then calculated BI using the following equation:

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

where T_j is the weight of each index I ($T_1=6$, $T_2=5$, $T_3=4$, $T_4=3$, $T_5=2$, $T_6=1$).

We also used the Shannon index (Shannon 1948) to assess changes in diversity as follows:

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

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

Zooplankton

Zooplankton is sampled vertically using a net with mesh size of 212 μm, from a depth of 50 m to the surface. The samples are fixed with 5 % formol. In this study, we report microcrustacean count, which was determined using a standard microscope (Olympus BX40) on a counting blade. Abundances are given as number of individuals per square meter. No data are available for Lake Geneva for 2001 because the development of filamentous algae made it impossible to sample or observe the zooplankton properly. For the months when data are missing, we calculated means based on values for years $n-1$ and $n-2$.

Fish

Our fishing statistics are based on reported catches by commercial fishermen operating in the lakes. We consider only whitefish (*Coregonus lavaretus*) and perch (*Perca fluviatilis*), the two main commercially exploited fish species. The catches are expressed in units of weight caught per hectare. It is important to note here that this measurement cannot be used to compare ecosystems or fish species since fishing effort varies greatly between the lakes. For instance, in Lake Bourget, there were 120 commercial fishermen between 1970 and 1982, 42 between 1983 and 1986, 20–30 (half of whom were retrieved to be commercial fishermen) between 1987 and 1994, and 8–10 between 1995 and 2011 (CISALB). For Lake Geneva, between 1983 and 2011, the number of commercial fishing licenses granted varied between 130 and 150 (CIPEL). Lastly, for Lake Annecy, there were 35–40 licenses before 1971, but subsequently less than 10 due to a new law specifying that fishing had to be the sole source of income to qualify for a license. Between 1972 and 1990, the number fell steadily to 4, where it remained until 2011 (SILA).

Results and discussion

Time-series interpretation

A great variety of parameters have been measured for the peri-alpine Lakes Annecy, Geneva, and Bourget. We have selected a subset, the goal being to understand changes in the water quality, trophic state, and functioning of these ecosystems in response to management practices and/or global change. In particular we focus on (1) changes in ecosystem dynamics that may inform the development, testing, and validation of water quality and functional indexes; (2) changes in particular resources; and (3) the measuring restoration.

What can we learn from changes in transparency and phytoplankton dynamics?

On the basis of annual mean values, the transparency of Lake Geneva as measured in the pelagic zone has not improved since the end of 1960, shifting from approximately 9 m to less than 8 m (Fig. 1(a)). By contrast, there has been a significant increase in transparency in Lake Bourget since the beginning of the 1980s, increasing from around 4 m to more than 7.5 m today. Over the last 15 years, the transparency of Lake Annecy has oscillated between 6 and 8 m, reaching almost 9 m in 2011. Over the period during which the three ecosystems can be compared (i.e., since 1995), only the tendency in Lake Bourget is statistically significant ($r=0.83$, $p<0.01$), whereas the fluctuations recorded for the other two lakes make it impossible to identify any obvious tendency, either for annual or summer averages (Fig. 1(a, b)). The median values of transparency over the period 1995–2011 reveal that Lake Annecy is the clearest (7.2 m), followed by Lake Geneva (6.9 m) and then Lake Bourget (6.3 m). However, the disappearance of *Planktothrix rubescens* blooms in Lake Bourget since the end of 2009 (see below) has led to the highest mean annual (and summer) transparency in Lake Bourget since 2009. According to the OCDE classification (1982), the values reported above would classify all three lakes as being oligotrophic.

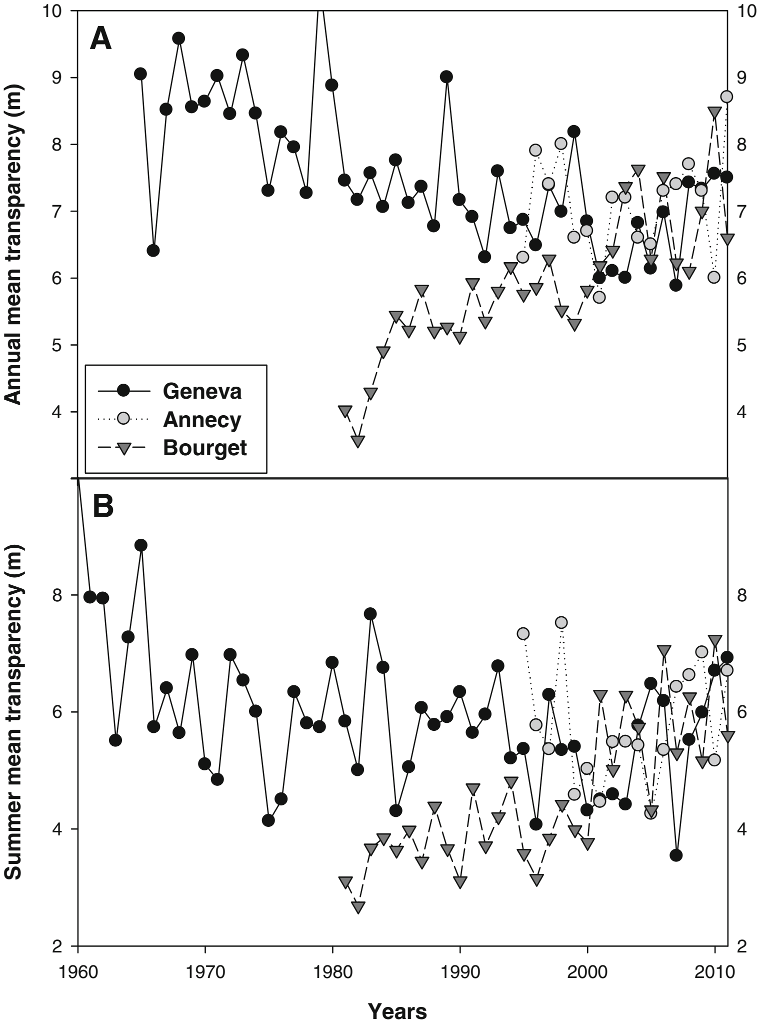


Fig. 1 Long-term changes in annual (*a*) and summer (*b*) mean transparency in Lakes Annecy, Bourget, and Geneva

Transparency is easy to measure and can be used to assess phytoplankton biomass in the pelagic zone of temperate large and deep lakes. However, the measure is integrative and may not be sensitive enough to indicate ecosystem changes related to, for instance, a decrease in P concentrations. In our case, this is exemplified by the fact that the trophic status indicated by transparency does not match that obtained using P concentrations or phytoplankton biomass (see below). Figures 2, 3, 4, and 5 show interannual variation in the biomass and proportions of the main phytoplankton classes, the relative proportions of nanoplankton (<20 μm) versus microplankton forms (>20 μm), and changes in BI and H. For Lake Annecy from 1995 to 2011, phytoplankton biomass was generally low, with the lowest value reported in 2010. The dominant phytoplankton classes in this lake were diatoms and Chrysophyceae. Mixotrophic species (e.g., *Dinobryon*), which are characteristic of oligotrophic ecosystems, were found in relatively high biomasses. These mixotrophic taxa use osmotrophy or phagotrophy to obtain nutritive elements when resources are limited. In oligotrophic systems and during periods of phosphorus limitation (for example, in the epilimnion in summer), mixotrophy offers a considerable competitive advantage to these photosynthetic microalgae, giving them two nutritive sources (Stickney et al. 2000; Domaizon et al. 2003). Contrary to these mixotrophic taxa, other taxa sensitive to grazing, such as the Chlorophyceae, regularly disappear, as do taxa indicative of richer environments (Domaizon et al. 2011). A high proportion of nanoplankton forms compared to larger forms (mean value on the time record, 67.3±16.6 %) corroborate the general conclusion that these lakes constitute an oligotrophic ecosystem.

Changes in BI (e.g., mean value for 1995–2011, 4.40 ±0.16; oscillating between 4.16 and 4.70) indicate that the trophic quality of the lake has been very good since

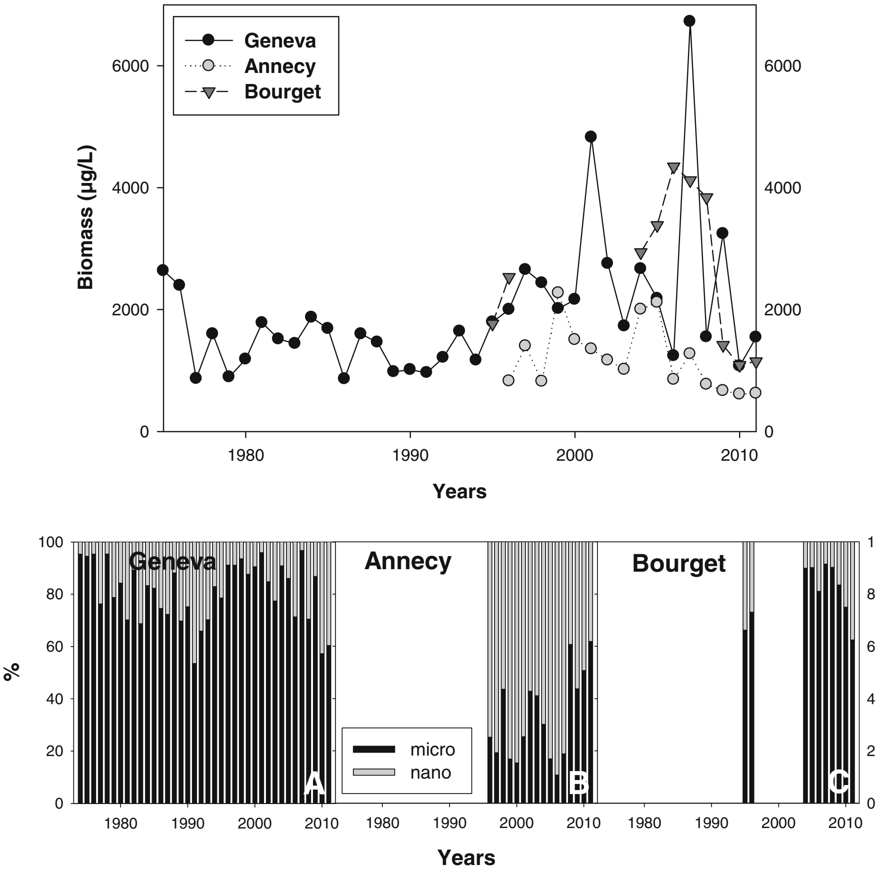


Fig. 2 Long-term changes in annual mean phytoplankton biomass and relative proportions of nanophytoplankton and microphytoplankton in Lakes Geneva (*a*), Annecy (*b*), and Bourget (*c*)

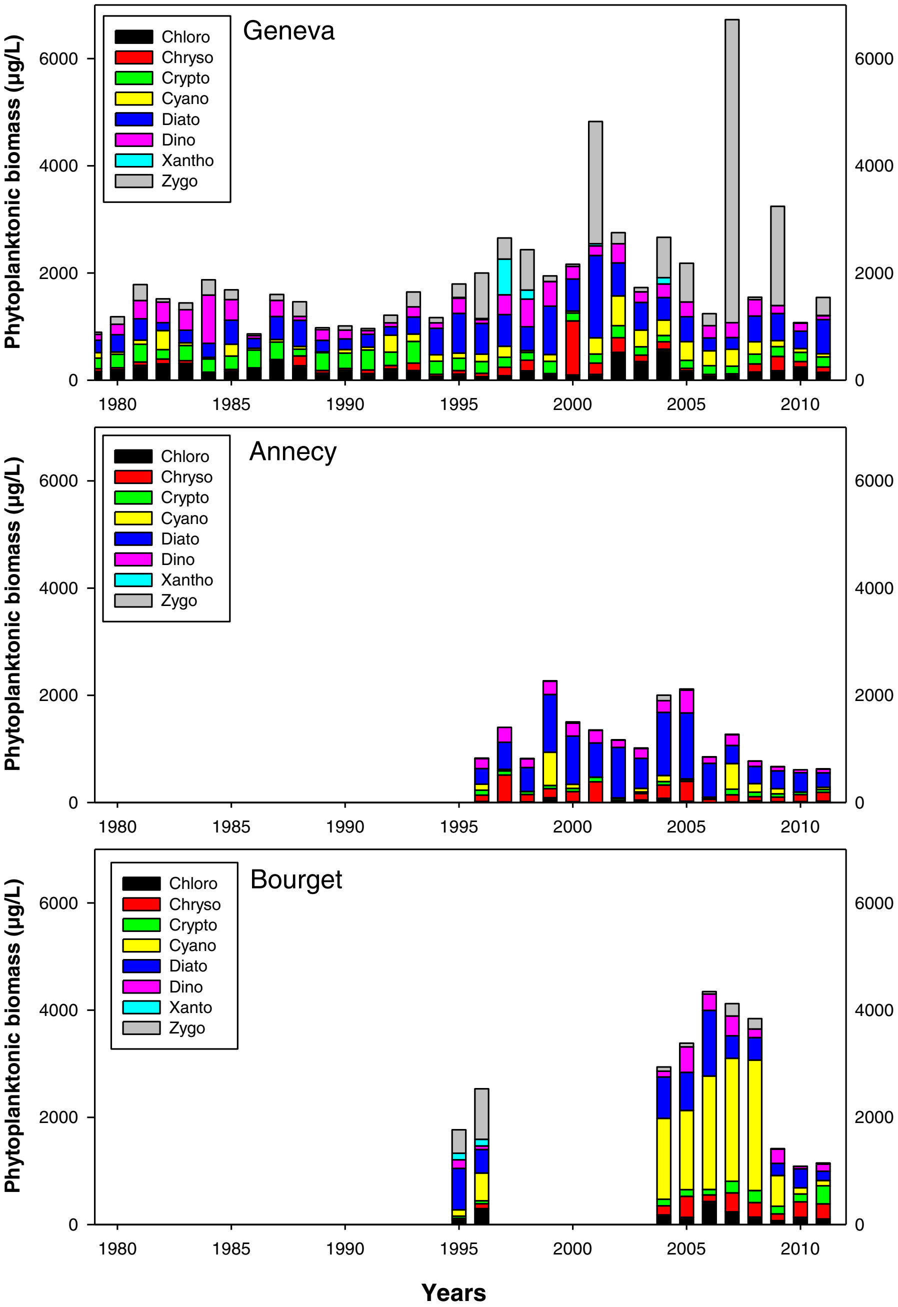
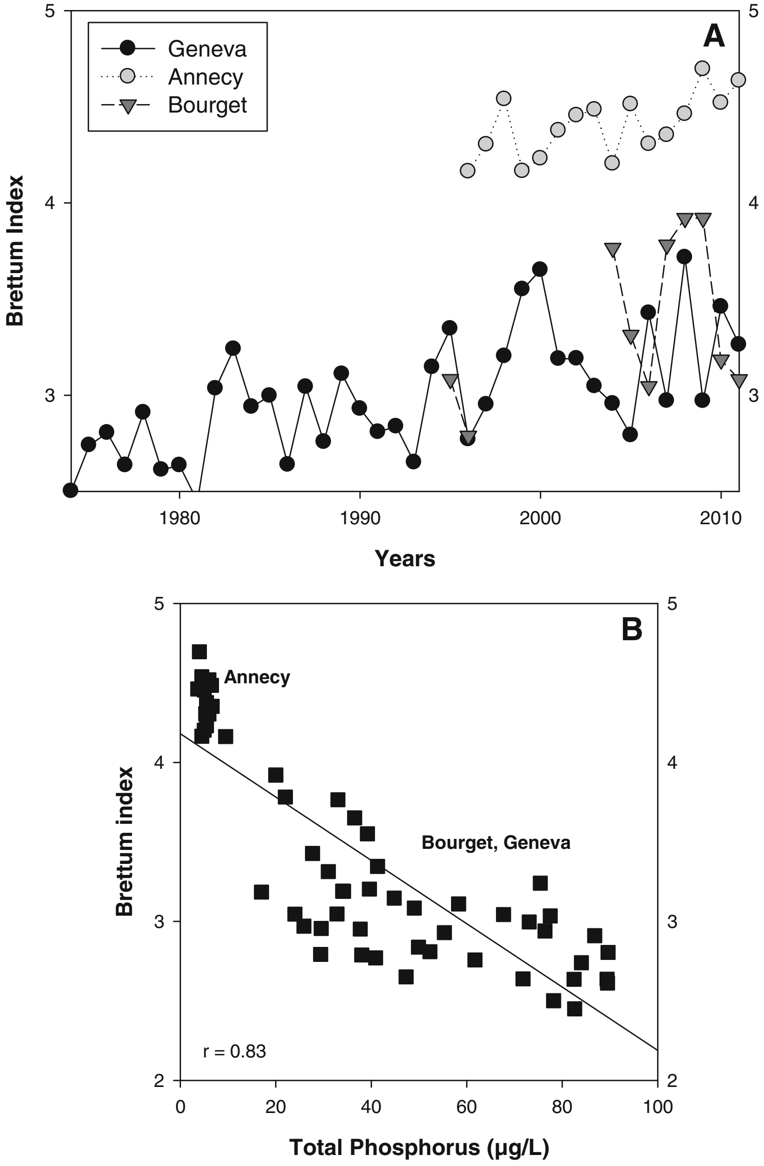


Fig. 3 Long-term changes in annual mean biomass of different phytoplankton classes in Lakes Annecy, Bourget, and Geneva. *Chloro* Chlorophyceae, *Chryso* Chrysophyceae, *Crypto* Cryptophyceae, *Cyano* Cyanobacteria, *Diato* diatoms, *Dino* Dinophyceae, *Xanto* Xanthophyceae, *Zygo* Zygophyceae

the end of 1990. In Lake Bourget, the phytoplankton biomass increased from 1995 to 2008, but 2009, 2010, and 2011 were marked by a definite reduction and the lowest biomasses measured during the monitoring period. If one compares 2006 to 2010 or 2011, for example, the estimated biomasses have decreased by a factor of 4. This pattern is explained in a large part by the disappearance of the cyanobacterium *P. rubescens*, which was present in large numbers until the end of the summer 2009 but then entirely disappeared (Jacquet et al. 2014).

Fig. 4 Long-term changes in mean annual Brettum index (**a**) and the relationship between total phosphorus and Brettum index (**b**) in Lakes Annecy, Bourget, and Geneva



In parallel, the proportions of diatoms, Cryptophyceae and Chrysophyceae increased markedly, following the same pattern observed in Lake Annecy. However, BI remained lower and relatively stable compared to that for Lake Annecy (mean, 3.39±0.42; oscillating between 2.78 and 3.92), suggesting that the species in these two ecosystems are still very different and corroborating the predominance of microphytoplankton over nanophytoplankton in Lake Bourget (nanophytoplankton, 19.7±10.7 %; over the entire time series). In Lake Geneva, as in the other lakes, biomass was also lowest in 2010. There was a clear downward trend and BI; although lower on average than that in the other two lakes (mean, 3.00±0.31), it increased from about 25 in 1974 to 3.5 in 2010. The increase in the proportion of functional groups characteristic of low-nutrient ecosystems indicates an improvement in water quality (Jacquet et al. 2013). The relative proportion of nanoplankton forms is low in Lake Geneva and fairly similar to that in Lake Bourget (19.0±11.6 %).

Variation in H point to differences in phytoplankton biodiversity between the three lakes as well as temporal changes in this biodiversity was observed. The richness and relative proportion of taxa were initially similar in

Fig. 5 Long-term changes in mean annual Shannon index in Lakes Annecy, Bourget, and Geneva. *Inset* is a close-up for 2004–2011

Lakes Geneva and Bourget and were higher than those in Lake Annecy. However, the greater biodiversity in the first two lakes has decreased over the past decade, such that phytoplankton diversity was comparable in the three lakes in 2008. This convergence may be linked to the relative homogenization of the chemical characteristics of the three lakes (P concentrations in particular) but may also be attributable to a common effect of climatic changes on these lakes, which are located in the same ecoregion.

Our findings on ecosystem dynamics based on phytoplankton data can be very useful in developing, testing, and validating water quality indices. Due to high levels of competition between phytoplankton, the phytoplankton community responds rapidly to both external and internal forces, and shows compensatory dynamics (Jochimsen et al. 2013). Therefore, phytoplankton community composition appears to be a more sensitive indicator than integrative parameters like total biomass (this is well illustrated with Lake Geneva). Our data clearly indicate important changes in phytoplankton community composition, with an increase in the abundance of species better adapted to the new environmental conditions (e.g., Lake Bourget since 2009). Such low sensitivity of the measure, total phytoplankton biomass, when P concentrations decrease has led managers to seek improved water quality indices based on species. The European Water Framework council is now examining this issue, and we suggest that BI is a suitable candidate.

Is phosphorus the key parameter in determining phytoplankton community composition and dynamics?

Phosphorus is a key nutrient in lacustrine ecosystems. It is now recognized as the limiting factor controlling cell multiplication and, thus, a relatively faithful index of phytoplankton biomass and development. However, the relationship between phosphorus concentration and phytoplankton biomass is seldom linear (Watson et al. 1992). For example, our analysis shows a very marked fall in Ptot and PO_4 in recent decades for the three lakes studied (Fig. 6). Values for Lakes Geneva and Bourget fell from approximately 100 μg/L to approximately 20 μg/L (even lower for Lake Bourget). However, phytoplankton biomass displayed a different trend. In fact, it seems that phosphorus concentrations in Lake Geneva have remained too high for this parameter to be a limiting factor causing a significant decrease in phytoplankton abundance. On the basis of the literature and our experiments on the subject, we believe that phosphorus only begins to limit phytoplankton growth when the annual phosphorus concentration drops below 10–15 μg/L. However, phytoplankton communities are not completely insensitive to decreased phosphorus concentrations above this threshold. Rather, they reorganize, leading to a greater abundance of species better adapted to the environmental conditions (Anneville et al. 2002; Jacquet et al. 2014). In fact, there was a proliferation/appearance of species usually indicative of oligotrophic conditions in the lakes studied (Anneville

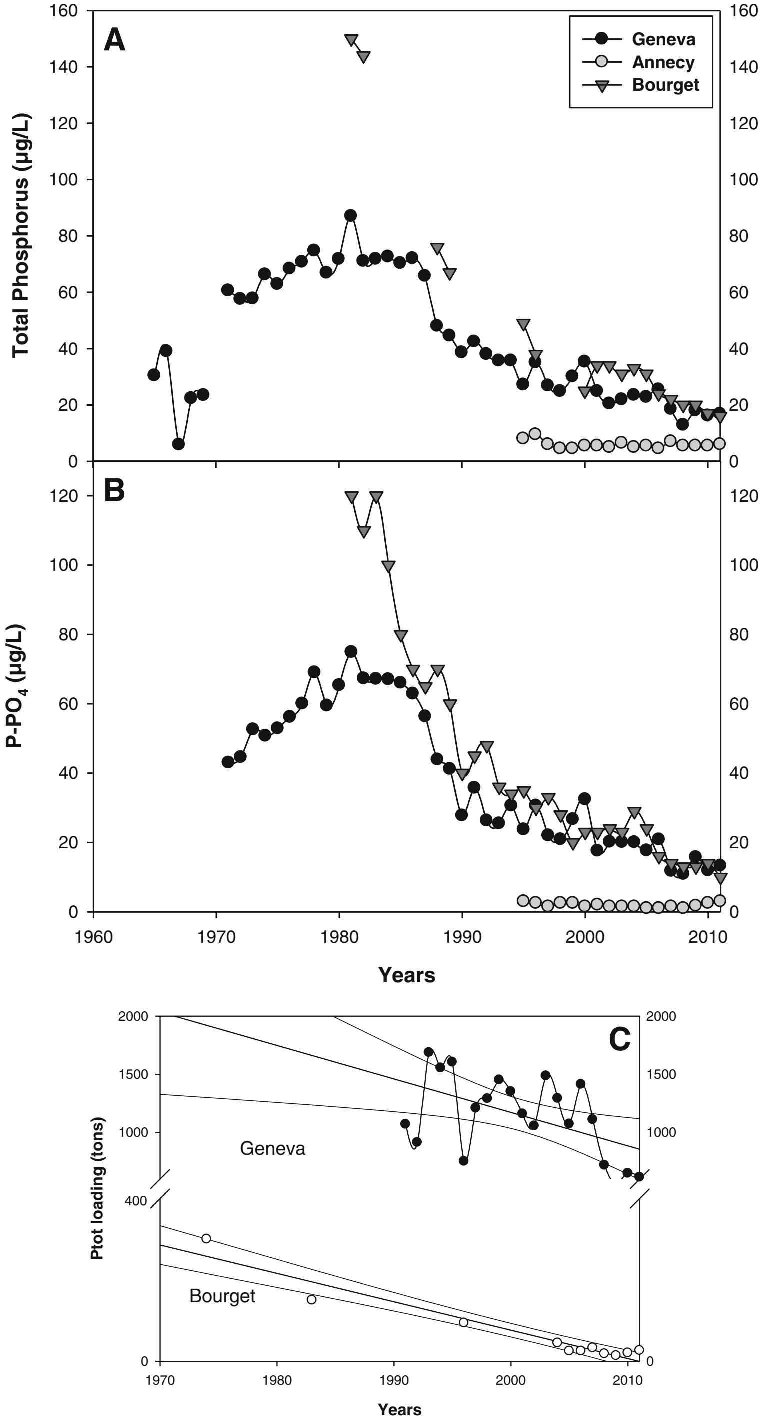
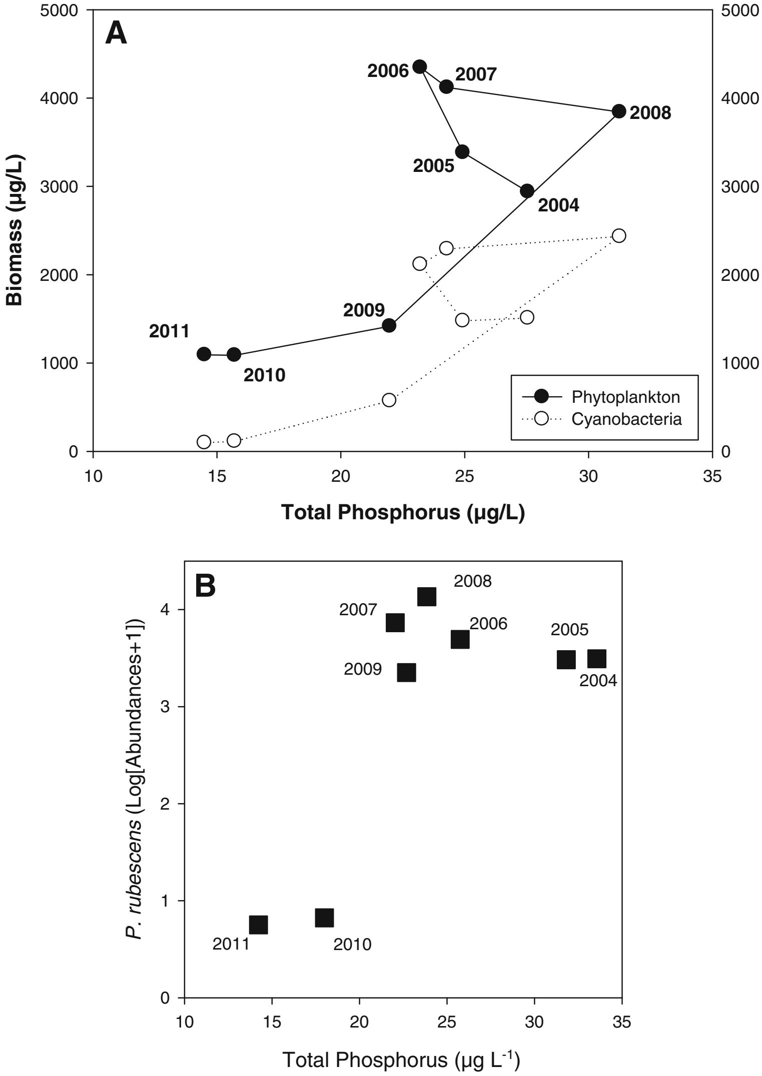


Fig. 6 Long-term changes in total phosphorus (*a*) and dissolved phosphorus (*b*) concentrations in winter in Lakes Annecy, Bourget, and Geneva and long-term changes in external loading (from the watershed) of total phosphorus for Lakes Geneva and Bourget (*c*)

et al. 2004; Jacquet et al. 2013). This is reflected in annual changes in BI and the significant correlation between BI and phosphorus concentration (Fig. 4). A clear example of the effect of the marked reduction in P in Lake Bourget is the disappearance of the cyanobacterium *P. rubescens* in 2009 (Fig. 7).

Phosphorus concentrations have changed very little in Lake Annecy over the past 15 years, oscillating

Fig. 7 Relationship between total phosphorus and annual mean biomass of phytoplankton and cyanobacteria (**a**) and between *P. rubescens* abundance and total phosphorus (**b**) in Lake Bourget for 2004–2011



between 4.5 and 9.5 µg/L for Ptot and between 1 and 3 µg/L for PO_4, making this lake highly oligotrophic. This is due to a wastewater collection system that was built all around the lake during the 1970s (Druart and Balvay 2009). By contrast, in 2011, Lakes Geneva and Bourget displayed concentrations of 26 and 16 µg/L, which meant that they were still mesotrophic according to the OCDE (1982). This phosphorus originates in the catchment area and has various sources, including agriculture, industry, and domestic. The main culprit behind the eutrophication observed in 1970–1980 was found to be a domestic pollution. The results of efforts to reduce the contributions of the catchment can be seen in Fig. 6. The contributions are from the principal tributaries of these lakes: the Leysse and Sierroz Rivers for Lake Bourget and the Rhone, Dranse, Aubonne, and Venoge Rivers plus secondary rivers for Lake Geneva. To our knowledge, no data of this type are available for Lake Annecy. There are clear differences in Ptot contributions for these ecosystems, but note that the slope of the regression line, which represents abatement, is very similar for these two lakes. This shows that the similar efforts made to manage the contributions of phosphorus influx into these two lakes have led to quite similar reductions of the external load over the same period of time. In 2011, the input was approximately 26 metric tons for Lake Bourget and 615 metric tons for Lake Geneva. The approximately 30-fold difference between the inputs into the two lakes must surely be explained by the relationship between water volumes (25) and

catchment area (15) for these ecosystems. It is also interesting to note that the relationship between surface catchment area and lake area is roughly similar (11.5 versus 12.5) for these two lakes, which no doubt accounts for the very similar kinetics of Ptot and PO_4 since the end of 1980 plus comparable efforts to reduce P loading from the watershed. It is also important to remember that the rainfall deficit recorded in recent years has had a major effect on phosphorus entering the lakes, which makes it important to remain vigilant and continue abatement efforts in anticipation of a return to "normal" rainfall or even an expected increase in extreme events involving heavy rain (Anneville et al. 2013; OCDE 2012).

Are zooplankton an indicator of lake functioning?

Zooplankton constitute a key component in the functioning of lake ecosystems. They tell us about the organization of the food web, which itself is closely related to the trophic state of the lake ecosystem (Fig. 8). Although there is no standardized water quality index based on zooplankton communities, studying this compartment can provide valuable indications about changes in pelagic systems. Zooplankton community structure is shaped by complex regulation pressures, including the quantity and quality of phytoplankton resources, predation from zooplanktonophages, and by both direct and indirect effects of thermal conditions (Masson et al. 2004; Korosi et al. 2013). In the case of Lake Geneva, the abundance of microcrustacea has decreased since 1984, mainly due to changes in the abundance of cladocerans (daphnids) and cyclopoids. In Lake Bourget, there has been an increase in the mean annual number of cyclopoids and, especially, of cladocerans (daphnids), since 2009, as well as a decrease in the mean abundance of calanoids (in particular of *Eudiaptomus gracilis*). Mean annual abundances of microcrustacea in Lake Annecy fluctuated moderately in 1995–2011, but there was no obvious trend. There was a very clear increase in calanoid abundance between 2003 and 2009; this group was barely present in the zooplankton community before 2004 but accounted for 34–36 % of microcrustacea in 2008–2009.

Over the period during which the three ecosystems can be compared (2004–2011), the mean total abundance of microcrustacea was not significantly different: approx. 376,000 individuals (ind)/m^2 in Lake Geneva, 370,000 ind/m^2 in Lake Bourget, and 326,000 ind/m^2 in Lake Annecy, which is a difference of less than 15 %. However, we found a marked difference in abundance for the various crustacean groups: calanoids dominated in Lake Geneva (167,000 versus 59,500 ind/m^2 in Annecy and 117,000 in Bourget), cyclopoids in Lake Annecy (184,000 versus 123,000 ind/m^2 in Lake Bourget and 128,000 in Lake Geneva), and cladocerans in Lake Bourget (130,000 versus 81,000 ind/m^2 in Lake Geneva and 82,000 in Lake Annecy).

As already pointed out, dynamic patterns in zooplankton community structure result from a combination of factors related to physiology, food, and predation. However, the general fall in crustacean biomass seen in Lake Geneva is what we would expect in the context of reoligotrophication. However, we could not detect any simple linear relationship between phytoplankton and total zooplankton abundance, for either individual lakes or all lakes taken together. In Lake Geneva, there was no significant reduction in the total phytoplankton biomass, and so the reduction in crustacean biomass must be due to other factors. Possible reasons are a change in phytoplankton community structure, such as available size classes and their nutritional quality (CIPEL 2011), and/or an increase in the abundance of zooplanktivorous fish like whitefish. Indeed, we found a marked positive correlation between the abundance of calanoids (herbivores with a narrow range of particle sizes and particularly selective for the quality of algae) and Cryptophyceae (a class of small algae of good nutritional quality) and also between the abundance of calanoids and Chlorophyceae ($r=0.54$ and 0.62, $n=49$, $p<0.01$). We also found an inverse (but weaker) relationship between cyclopoid and Chlorophyceae abundance ($r=0.34$, $n=49$, $p<0.05$) and between calanoid and diatom abundance ($r=0.36$, $n=49$, $p<0.05$), perhaps because these algal classes include many large algae. It is clear that the size and/or nutritional quality of phytoplankton is an important factor in structuring plankton food webs, as has been reported by others (e.g., Hulot et al. 2000; Perhar and Arhonditsis 2009).

Analyzing seasonal variation in zooplankton community for each lake would make it possible to refine our interpretations and highlight differences between the lakes at the species scale. For example, in the calanoid group, only one species was found to be present in each lake: *E. gracilis* in Lakes Geneva and Bourget and *Mixodiaptomus laciniatus* in Lake Annecy. However, all three lakes contained several species of cyclopoids.

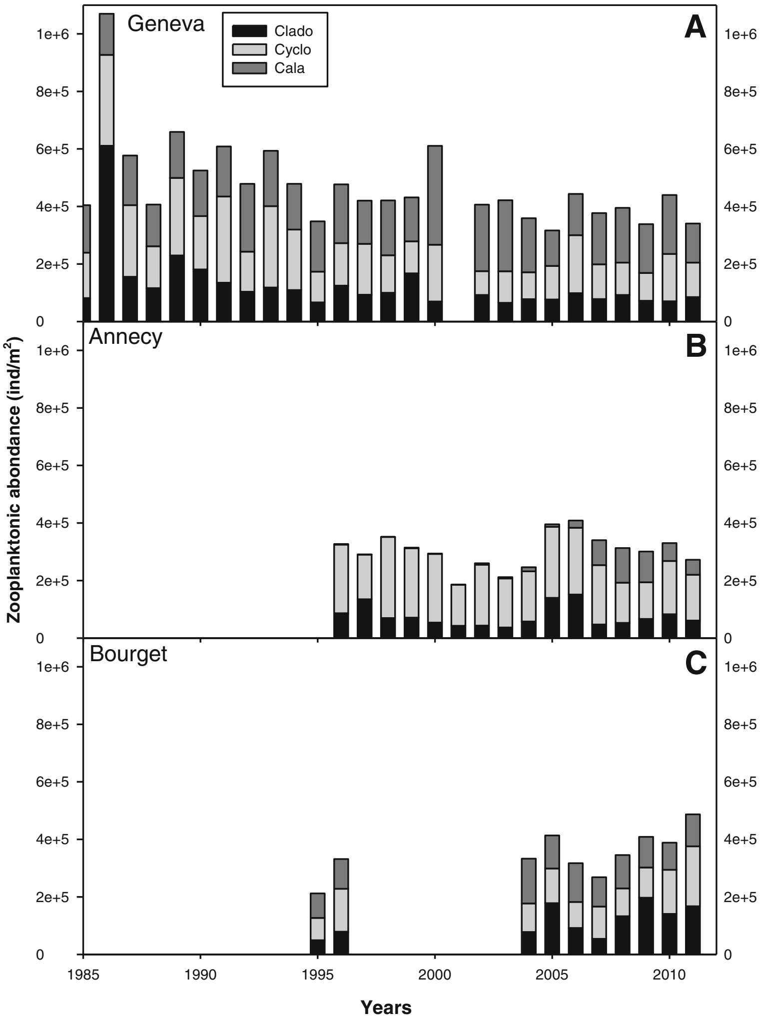


Fig. 8 Long-term changes in the annual mean concentration of the main microcrustacean groups (cladocerans, cyclopoids, and calanoids) in Lakes Annecy, Bourget, and Geneva

Another example is our finding that in Lake Bourget, there was an inverse relationship between *P. rubescens* (a toxic species characterized by long filaments) and daphnids. This suggests that future analyses would benefit by discriminating between edible and nonedible species and also, of course, discriminating between herbivorous zooplankton and carnivorous species. Indeed, our analysis has already revealed some relationships between the Cryptophyceae and calanoids, thereby corroborating the findings of Perga and Lainé (2010) in CIPEL and SILA reports and supporting the assertion that other factors affect the zooplankton dynamics of this compartment. Perga et al. (2009) suggested that the important role played by the microbial loop may explain the lack of any relationship between phytoplankton and zooplankton in Lake Annecy. Particularly important may be the input of organic matter of terrestrial origin, microbes and fish (Perga et al. 2010).

Our final finding is that zooplankton populations have started to develop earlier in the year than in past decades, as shown by an advancement in maximum transparency value during the spring clear water phase over the past 20–30 years in Lake Geneva (Fig. 9, $r=0.43$, $n=48$, $p<0.01$) and Lake Bourget (Fig. 9, $r=0.41$, $n=33$, $p<0.05$). These changes have occurred in parallel to global climate changes (see below).

Are fish able to adapt to long-term changes?

As they are at the top of the food chain, fishes provide us with an interesting biological model for changes taking place at lower trophic levels. The relatively long lifespan

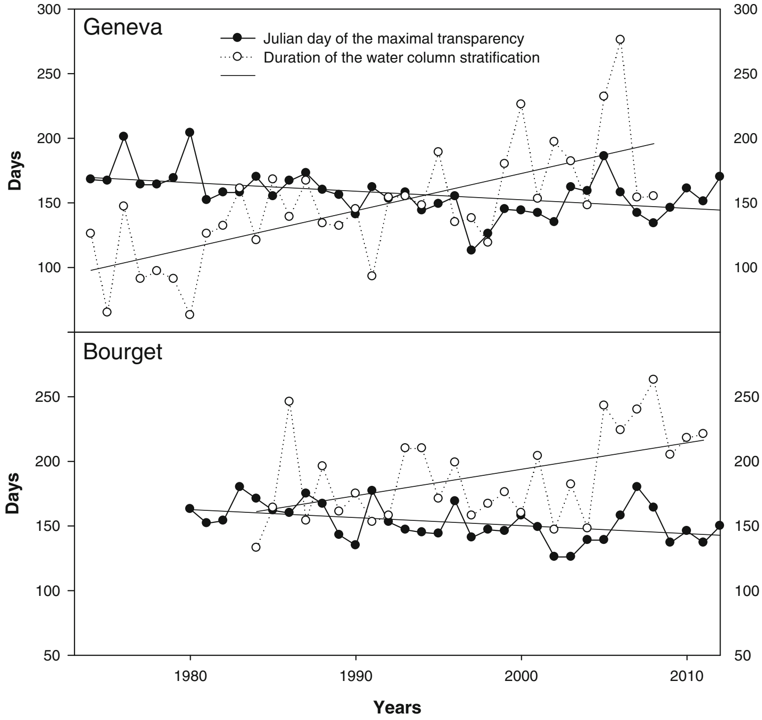


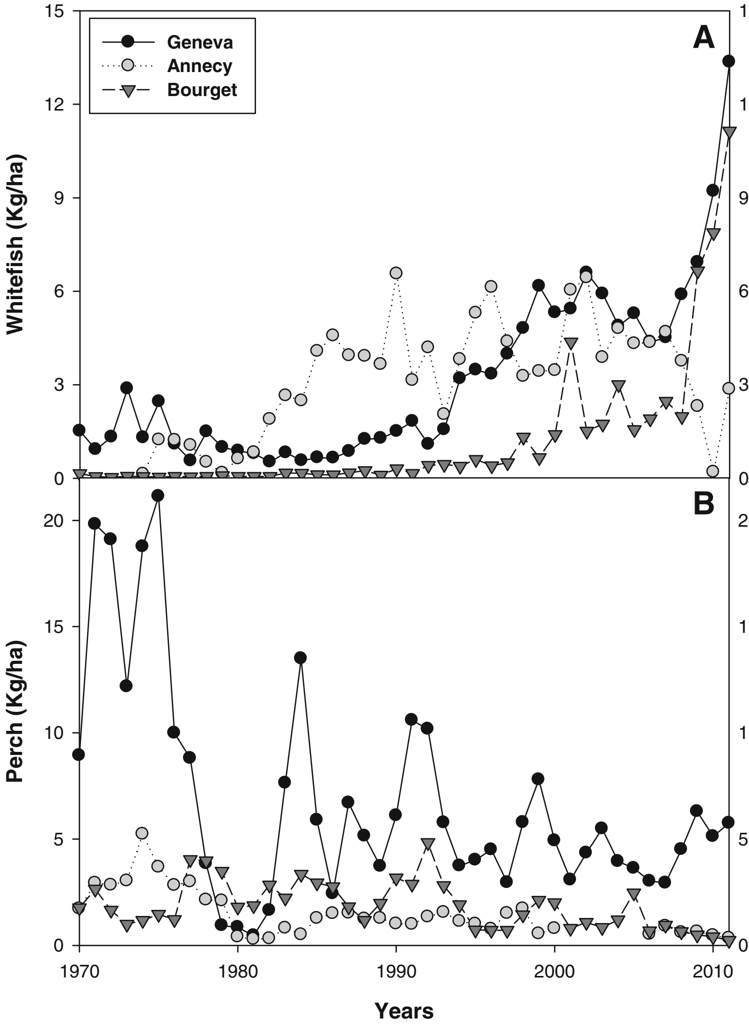
Fig. 9 Long-term changes in the duration of water column stratification and date of maximum transparency in Lake Geneva

of fish compared to the other biological compartments also makes it possible to track changes over time. Here, we will only report data for two fish species of commercial interest: whitefish (*C. lavaretus*) and perch (*P. fluviatilis*). These fish reflect trophic evolution of the three lakes (Fig. 10). While these data must be interpreted with caution because fishing pressure varies over time, the common unit (kilos of fish caught per hectare) does make it possible to identify specific trends in each lake. Note that these data include only reported catches by commercial fishermen but not anglers, which may be quite considerable in these lakes.

The production of whitefish seems to peak at between 20 and 30 μg/L of Ptot in peri-alpine lakes (Gerdeaux and Perga 2006). However, Ptot has fallen below 30 μg/L since the end of 1990. In Lake Bourget, since 2000, the catch of young whitefish has increased and the breeding stock has been rather weak (CISALB). To mitigate this fishing pressure on young cohorts, in 2007, authorities increased the minimum size of fish that can be caught and adapted allowable net mesh size. Following a moratorium on fishing in 2008 due to "a threat associated to PCB" and an improvement in water quality that restored natural recruitment, the whitefish catch increased markedly, especially in 2009, 2010, and 2011, as Fig. 9 clearly shows. A similar pattern has been reported for Lake Geneva.

The findings of several studies enable us to conclude that decreasing phosphorus concentrations and improving the quality and area of spawning grounds (Gillet and Dubois 2007) increases the larval population through natural reproduction. Since late 1980, larvae have benefited from more clement environmental conditions in winter and early spring, including higher temperatures and phenological shifts in the zooplankton as a result of the global climate change. This enables them to grow more quickly and thus escape predation by larger fish. Now that one of the main factors adversely affecting the whitefish population has been addressed, and the rate of recruitment is now proportional to the abundance of parents, thus ensuring a population increase (Anneville et al. 2009). While Gerdeaux and Perga (2006) showed a link between trophic level and whitefish catch in peri-alpine lakes, in the specific case of Lake Bourget, the increase in whitefish is most probably due to an improvement in trophic state and, as proposed by Anneville et al. (2009) for Lake Geneva, the recent increase in surface temperature, which means better feeding conditions and initial growth rates. The co-occurrence of all these changes has improved the

Fig. 10 Long-term changes in whitefish *C. lavaretus* (*a*) and perch *P. fluviatilis* (*b*) catches by commercial fishermen



survival of both eggs and larvae, thereby leading to higher fish catches.

Managers of the fish farming industry on Lake Annecy are taking note of the lake's oligotrophic status and the fact that it has been maintained in recent years. This status, combined with excessive fishing pressure, is likely to weaken populations subject to preferential fishing (e.g., whitefish). There has been a marked reduction in the number of commercial fishermen since 1971, and only four commercial fishermen were working on the lake from 1990 to 2011, during which time the catch taken by commercial fishing fluctuated without any clear overall trend. However, these data provide only a partial picture of fish stock dynamics, and an overall policy for fishery management, for both commercial and amateur fishing, is needed for Lake Annecy. We also need studies that will increase our understanding of the trophic network that supports fish farming (Janjua et al. 2008).

Perch are less sensitive to a deterioration in the quality of water and/or sediments. For example, they are less sensitive to high rates of sedimentation related to phytoplankton development. This partly explains why perch dominated throughout the eutrophication period in Lakes Geneva and Bourget. The size of perch stocks is directly related to the quantity of food present (Dubois et al. 2008; Gillet and Dubois 2007). In fact, with the reduced abundance of zooplankton and increased abundance of whitefish (zooplanktivores), interspecies competition for food probably increases, which explains why the perch stock has declined over time, especially in Lake Geneva. However, Gillet (2001) showed that perch populations undergo marked interannual fluctuations linked to a sensitivity at the recruitment stage, which is strongly impacted by unfavorable weather conditions (i.e., low temperatures). Therefore, the tendencies observed must be interpreted with caution.

Can we observe the effects of global warming?

Environmental questions relating to the effects of global climate change are very critical in water ecology studies. Research has shown that water temperature in lakes has increased significantly over the past 20–30 years. The extent of the increase depends to a large extent on lake depth and season. Gillet and Quétin (2006) and Tadonléké (2010) have already shown that in Lake Geneva, water temperature rose between 0.5 and 2 °C between 1983 and 2000 or an increase of +0.5 to 1 °C per decade. Figure 11a shows that an increase in temperature of the whole water column at the end of the winter is indeed perceptible in all three lakes, but it seems likely that there are marked differences between the lakes and major fluctuations from year to year. The same trend is seen for surface water temperature; in Lake Bourget (at 2 m) and Lake Geneva (at 5 m), the temperature increased significantly, although there were differences between the lakes (Fig. 11b).

We now know that forcing is of atmospheric origin and that it involves the Northern Atlantic Oscillation (NAO), a weather phenomenon characterized by an atmospheric pressure difference between the anticyclone over the Azores and the depression over Iceland. This phenomenon strongly influences local weather conditions, including air temperature and rainfall, which in turn determine energy exchanges between the atmosphere and lakes situated in Western Europe (Straile et al. 2003). In total, for Lakes Geneva and Annecy, the increase in temperature between 1970 and 2011 was between 0.4 and 0.5 °C or approximately 0.1 to 0.2 °C per decade. Over the period for which data are available for Lake Bourget (1984–2011), a similar increase was recorded, and this pattern seems to be common to all Western European lakes (Dokulill et al. 2006). This warming of peri-alpine lakes has multiple consequences. First, it affects the onset and duration of water column stratification, as shown in Fig. 9. For example, in Lake Geneva, since 1974, the onset of stratification has advanced by almost 1 month, and stratification duration increased by approximately 80 days (r=0.58, n=38, p>0.99). For Lake Bourget, we observed the same trend (r=0.48, n=18, p>0.95). This has resulted in significant modifications to (1) phytoplankton dynamics and production (Anneville et al. 2002; Tadonléké 2010), (2) growth and predation of zooplankton (Anneville et al. 2009, 2010), and (3) larval recruitment and regulation in some fish populations (Gillet and Quétin 2006; Anneville et al. 2009). It is also possible that warming could lead to a deterioration in water quality by stimulating phytoplankton growth, in particular undesirable species like certain cyanobacteria (Paerl and Huisman 2008; Shatwell et al. 2008; Gallina et al. 2011). This would surely hamper efforts aimed at ecosystem recovery. Note that the increase in water temperature has not been so great during the past decade, which underscores the importance of having long-term data.

Global considerations

Long-term monitoring observations have proven useful for acquiring knowledge on complex seasonal and interannual patterns and processes taking place in aquatic ecosystems (e.g., Suthokin and Berger 2013). When establishing a long-term time-series measurement program, a number of scientific and logistical considerations need to be taken into consideration, including site selection, variables to measure, and sampling design (type and frequency). While the primary objective of such programs is to document and understand weekly, monthly, seasonal, and interannual variability in physical, chemical, and biological parameters that may constitute their primary objectives, they can also provide site and logistical support for numerous complementary research programs. In short, these data are invaluable in the field of environmental sciences because they produce data that can help us better understand the local and global changes operating within reference ecosystems and validate or improve existing biogeochemical models.

Whereas a single instantaneous observation is often of limited value because it is like looking at a single snapshot taken at time T, obtaining thousands of measurements and analyses over a long period of time makes it possible to study changes in biodiversity, the impact of anthropogenic pressures on the ecosystem, and the response of the ecosystems to environmental changes. Long-term data can improve our understanding of ecological mechanisms and, consequently, enable us to make correct interpretations and informed decisions in the future when faced with

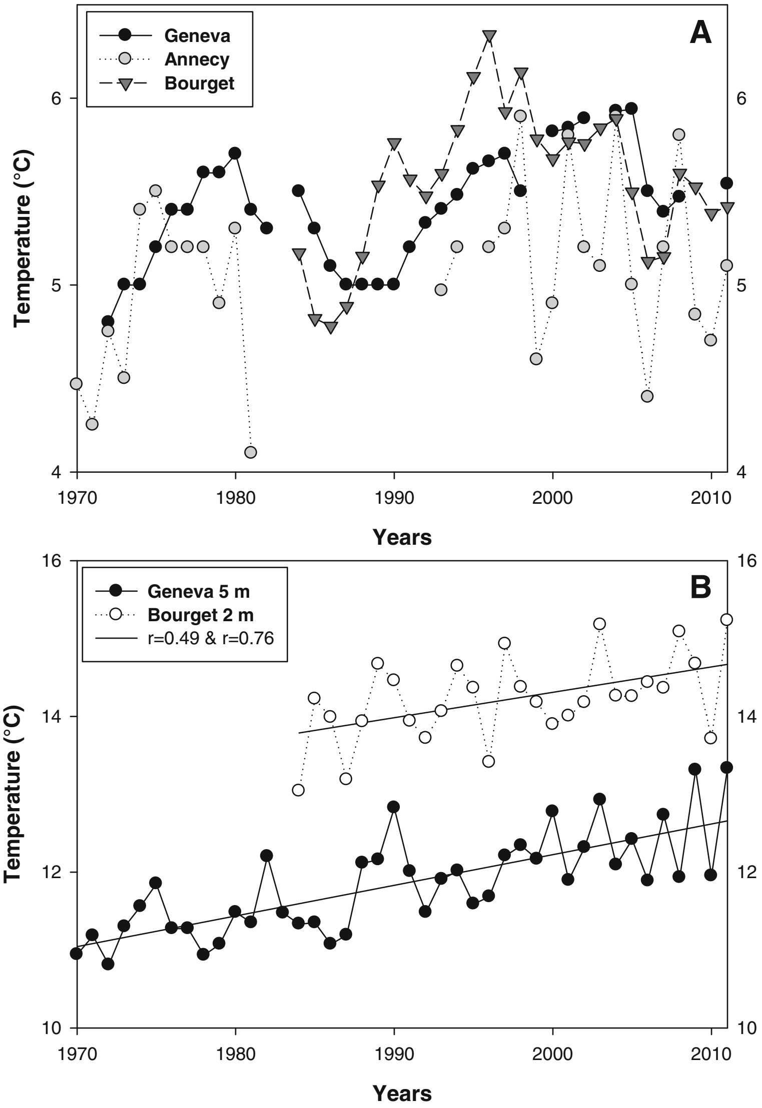


Fig. 11 Long-term changes in end-of-winter temperature (when the lake temperature is the same throughout the water column) in Lakes Annecy, Bourget, and Geneva (**a**) and long-term changes in mean surface water temperature in Lakes Bourget and Geneva (**b**)

completely unexpected, and even catastrophic, environmental disturbances like pollution and anthropogenic pressures.

As has been shown for other ecosystems, a fall in phosphorus concentrations in the lakes we studied did not always immediately lead to the predicted effects, such as a fall in phytoplankton biomass or an increase in transparency. In fact, given that there is often a time lag between a cause and its effect, a phenomenon known as hysteresis, it is not so surprising that phosphorus concentrations would have to fall below a certain threshold value before effects on other variables are visible (Jacquet et al. 2014).

The fall in phosphorus concentrations is, however, an important factor in explaining various dynamic changes observed during recent decades in these lakes. In the case of Lake Geneva, the fall in phosphorus concentrations has been accompanied by an increase in whitefish abundance and a shift in the seasonal dynamics and species composition of the phytoplankton community. By a cascade effect (top-down and/or bottom-up), these changes have impacted the zooplankton community, modifying both its composition and abundance. For Lake Bourget, the fall in phosphorus concentrations and the persistence of intermediate concentrations permitted the development and blooms of the cyanobacterium *P. rubescens* between 1995 and 2009. Since 2009, in response to a fall in phosphorus concentrations to 10–15 μg P/L, this phenomenon seems to have disappeared (Jacquet et al. 2014).

For reasons that may be related to fishing management practices, improved trophic state, and warming, the whitefish population has also recently displayed an improvement in Lake Bourget. By contrast, in Lake Annecy, where phosphorus concentrations have oscillated but remained within a range of values indicative of an oligotrophic state, the community composition does indeed reflect an oligotrophic ecosystem. But can this lake sustain relatively high fish production? The answer will depend on (1) inputs of terrestrial origin, which benefit the zooplankton community (Perga et al. 2009) via effects on microbial communities; (2) mixotrophic species in the phytoplankton, which are able to optimize their development, even in a situation of phosphorus depletion (Domaizon et al. 2003); and (3) a reduction of interspecies competition as a result of severe fishing pressure (Janjua and Gerdeaux 2009).

As we pointed out in our "Introduction," the threats facing peri-alpine ecosystems include an increase in temperature and the presence of synthetic micropollutants. These factors are currently arousing a considerable interest among regulators. To date, a few studies have modeled future trends in water temperature for Lake Geneva (Perroud et al. 2009), Lake Bourget (Bryhn et al. 2010), and Lake Annecy (Danis et al. 2004). Between now and 2100, the increase in temperature is likely to be between +2 and +4 °C in the surface layers. Moreover, the difference in temperature between the different layers will be more marked, intensifying temperature variation in the metalimnion and tending to increase the stability of the water column, with stratification occurring earlier and lasting longer. This has already been recorded for Lake Geneva since 1974.

The simultaneous effects, synergistic and antagonistic, of reoligotrophication and climate change lie at the heart of current problems in the management of these lakes. The impact of these two forcing factors is the outcome of complex biogeochemical processes and requires multidisciplinary approaches. Interactions with other stress factors must also be considered in parallel. For example, studies currently underway show that pesticides in Lake Geneva are affecting the structuring of its phytoplankton community. This suggests that we need to consider changes to plankton populations and the trajectories of recovery of eutrophicated ecosystems in relation to changes in other stress factors (e.g., organic pollutants).

The changes that researchers have observed in Lake Annecy, along with its current state, can be used as a frame of reference and indicator for what is likely to happen in the other two lakes. Based on existing data, we predict that Lake Geneva and Lake Bourget will change between now and 2020 in a number of ways. First, the drop in phosphorus will continue, reaching concentrations that are limiting for phytoplankton production and the development of large microalgae. In short, 2011 data for primary production in the three lakes showed that Lake Annecy is clearly less productive than its two neighbors, but also that primary production clearly decreased in Lake Bourget between 2005 and 2011 (Jacquet et al. 2012). Second, the structure of the phytoplankton community will also change (something that is already observable), leading to an increase in the proportion of smaller forms like mixotrophic species, which are of better nutritional quality for zooplankton. Picophytoplankton may play an increasingly important role in Lakes Bourget and Geneva, as Fig. 12 suggests. If small forms dominate, this will occur alongside a reduction in nutrient contributions linked to an increased thermal stratification that will likely block the vertical transfer of food. Less phytoplankton will probably lead to a fall in zooplankton biomass and an increase in the relative proportion of the Copepoda cyclopoids among the microcrustacea. Finally, there may be changes to the fish compartment, although these are more difficult to predict because of the effect of variation in food resources (plus potential competition), and also changes in fishing pressure and parameters related to the breeding conditions.

It is difficult to predict how an increase in temperature will modify this overall picture. Climate change may produce a possible cascade of multiple consequences on the quality and functioning of these ecosystems. Climate change interacts with other changes and pressures on the ecosystem, such as increases in atmospheric concentrations of CO_2 and ozone, atmospheric deposits of nitrogen, and species introductions. Changes in biodiversity and attempts to adapt will surely play an important role. Few studies have investigated how lakes like these are adapting to climate change, despite the potential for enormous socioeconomic ramifications. We urgently need to forecast scenarios of the regional impacts of climate change on peri-alpine ecosystems. To do this, we need to investigate and model the key

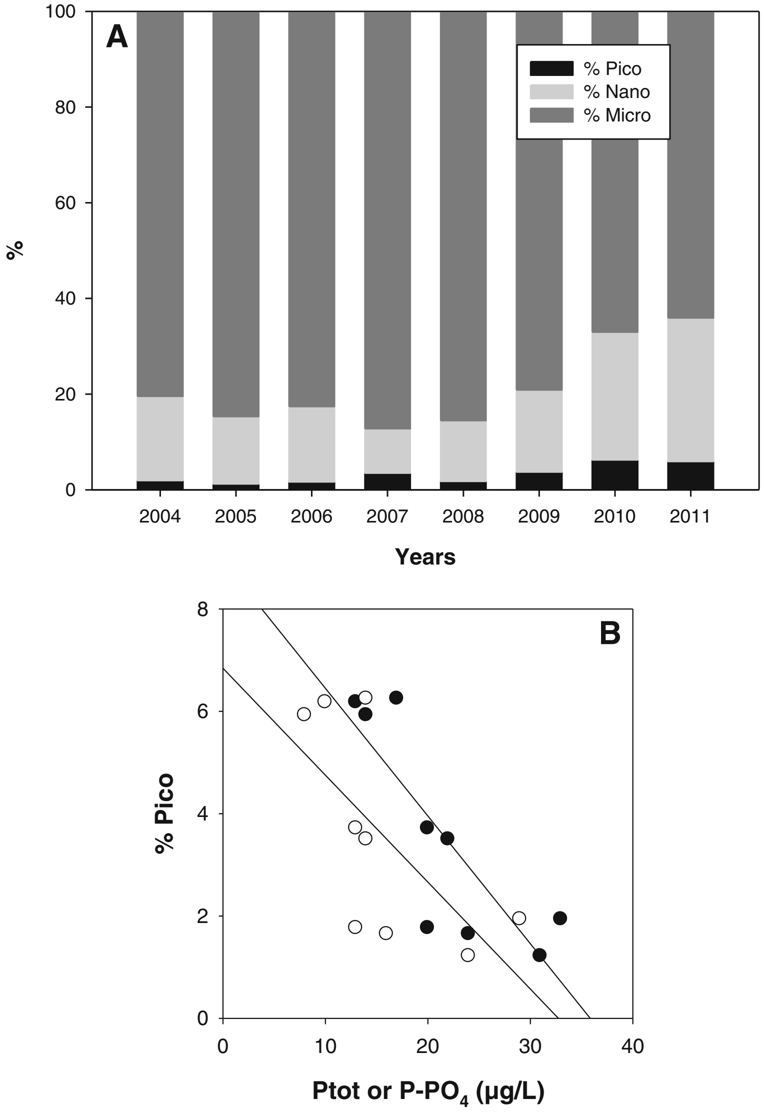


Fig. 12 Changes in the proportion of pico-, nano-, and microphytoplankton in Lake Bourget for 2004–2011 (**a**) and the relationship between the proportion of picophytoplankton (represented by picocyanobacteria) and total phosphorus (r=0.83, *black symbols*) and dissolved phosphorus (r=0.67, *white symbols*) concentrations in Lake Bourget (**b**)

processes involved in short- and medium-term responses as well as adaptations to the predicted climate variability and extremes. Such work is best achieved through scientific cooperation, which is now facilitated by increased data sharing in international working groups, such as the Global Lake Ecological Observatory Network.

Conclusions

Using peri-alpine lakes as case studies, we have provided evidence for the importance of long-term time series in documenting variation, from seasonal to decennial, in key biogeochemical, physical, and ecological parameters in pelagic freshwaters. Such ecosystem monitoring serves both science and management. The water quality of lakes is of great importance not only to human health but also to tourism and the economy. We now have a combination of tools that we can use to increase our understanding of system behavior and inform management decisions: relatively short-term, high-resolution contemporary data; long-term, low-resolution paleoenvironmental data; and fine-scale modeling (Barr et al. 2013).

Our study shows that long-term time series are required to monitor local and global changes and to help develop quality and/or functional indexes. Without the use of such data, we would not have been able to identify specific composition changes in phytoplankton in Lakes Annecy, Bourget, and Geneva, such as an increase in small-sized forms following reoligotrophication and a concomitant increase in mixotrophs, which have always been characteristics of the oligotrophic Lake Annecy, in the past 2 years in Lake Bourget following an important decrease in phosphorus concentrations and the disappearance of the *P. rubescens* bloom (Jacquet et al. 2014). Due to strong interspecific competition, species with the most advantageous traits, such as small cryptophytes, chrysophytes, and diatoms, have become dominant. Overall, the phytoplankton community has responded quite rapidly to environmental changes. Clearly, phytoplankton composition is an excellent indicator for highlighting regime shifts, being more sensitive and reactive than older, but still used, global indexes like chlorophyll *a*, which tend to smooth out compensatory dynamics. Perhaps it is time to gradually replace the OCDE global indexes with new indexes based on community composition, like BI for instance.

Another advantage of using long-term series is the ability to highlight changes that occur in response to more global forcing processes, in particular the worldwide increase in temperature associated with global warming. Considerable data have been collected from both terrestrial and aquatic ecosystems in recent years, and a number of specialized journals on the topic have emerged, including Global Change Biology and Nature Climate Change. Our study showed phonological shifts in the peri-alpine lakes, with zooplankton developing earlier in the year, leading to an advance in the clear water phase and an environment favoring the development of a *P. rubescens* bloom (especially in conjunction with higher winter temperatures).

Long-term time series can help us better understand resource changes. In our case, it provided considerable insights into whitefish and perch populations, along with the seeming paradoxical development of harmful species like *P. rubescens* or *Mougeotia gracillima* during the reoligotrophication process. Finally, long-term time series can be useful when evaluating restoration decisions and the success of restoration programs, as we showed for the case of phosphorus in Lakes Annecy, Geneva, and Bourget. Our data showed that phosphorus concentrations have decreased, noxious species like filamentous toxic cyanobacteria have disappeared, and the water transparency has increased.

Acknowledgments This article is a contribution to SOERE GLACPE. The authors would like to thank the many technicians (Pascal Chifflet, Jean-Christophe Hustache, Pascal Perney, Jean-Paul Moille, Michel Colon, Leslie Lainé, and Aurélie Hébert), engineers (Jean-Claude Druart, Frédéric Rimet, Ghislaine Monet, Jérome Lazzarotto, Philippe Quétin, and Jean Guillard), and researchers (Gérard Balvay, Christian Gillet, Jean-Marcel Dorioz, Marie-Elodie Perga, and Daniel Gerdeaux) at the research laboratory of Thonon-les-Bains (UMR CARRTEL), without forgetting Gérard Paolini (Engineer at the CISALB), who have all contributed to research and continue to work alongside lake managers (CIPEL, SILA, CISALB) in the environmental monitoring of Lakes Annecy. CIPEL (Commission Internationale pour la Protection des Eaux du lac Léman) is the international commission for the protection of Lake Geneva, SILA (Syndicat mixte du Lac d'Annecy) is the inter-syndic protecting Lake Annecy waters, and CISALB (Comité InterSyndical pour l'Assainissement du Lac du Bourget) is the inter-syndical commission protecting Lake Bourget. Monika Ghosh and Susan Lampriere are acknowledged for correcting the English.

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