

Phytoplankton variability in Lake Bourget: Phytoplankton dynamics and meteorology

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Abstract

This paper presents the phytoplankton succession during two successive years in Lake Bourget, a deep subalpine lake recovering from eutrophication. A drastic reduction of the watershed phosphorus loading in 1980 stopped lake eutrophication. At present, the lake has nearly reached constant winter (January–February) nutrient concentrations. However, during the 2 years of the study, the phytoplankton data set shows a great interannual variability, which is analysed on the basis of the meteorological forcing variables.

Key words

lake restoration, meteorological forcing, phytoplankton succession, trophic state.

INTRODUCTION

In developed countries, many lakes are affected by eutrophication (European Environment Agency 1998; United States Environmental Protection Agency 1998). Since the early 1970s, it has been noted that phosphorus (P) is the key element that controls eutrophication in most lakes. Many actions have been implemented in lake watersheds to reduce P loading and to restore lake water quality. However, although many concordant results have been obtained to link watershed P loading to lake P concentration (Sas 1989; Tilzer *et al.* 1991; Davies & Blanc 1994), biological data showing the relationship between lake P concentration and algal response frequently leads to opposite outcomes, even in similar lake ecosystems (Polli & Simona 1992; Feuillade & Druart 1994; Häse *et al.* 1998; Anneville & Pelletier 2000). For example, Lake Bourget (Savoie, France), a deep, medium-sized alpine lake, was eutrophic at the end of the 1970s. In 1980, the diversion of the main sewers entering the lake reduced the watershed nitrogen (N) and P loading from 70% and 50%, respectively. On the one hand, some water quality indicators (e.g. winter overturn N and P concentrations and mean annual water transparency) have been improved. On the other hand, the algal biomass decrease is not significant and the hypolimnion bottom layers are deoxy-

genated from the end of summer (August) to the winter overturn (February). Since 1984, the lake's evolution has been continuously surveyed by regular monitoring including only physico-chemical and chlorophyll *a* measurements. During 1988–1989, a detailed field survey (increase of the sampling depths and frequency) was conducted in order to assess the first decade of lake restoration. During 1995–1996, a second detailed field survey with monthly measurements of phyto-, zoo- and bacterioplankton, was implemented (Centre d'Enseignement et de Recherche sur l'Eau, la Ville et l'Environnement 1998). According to all indicators based on these data, Lake Bourget lies between mesotrophic and eutrophic states.

Since 1993, the lake nutrient (N and P) concentrations have reached a constant value. According to many authors (Reynolds 1984; Sommer *et al.* 1986; Seip & Reynolds 1995; Ruggiu *et al.* 1998), the phytoplankton species assemblage is interannually rather stable in a given water-body when the nutrient concentration in the lake water is constant. Therefore, in Lake Bourget, it was expected that the 1995 and 1996 plankton data sets would be very similar and characteristic of the lake's trophic level. Conversely, the phytoplankton dynamics were vastly different between the two years. The trophic state of a lake, following the Organization for Economic Cooperation and Development (1982) project definition, is commonly assessed using the mean values of the parameters related to phytoplankton, for example, water transparency (Secchi depth) and chlorophyll concentration

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(Sas 1989; United Nations Educational Scientific and Cultural Organization 1989). These parameters lead to the same conclusion, that Lake Bourget's most probable trophic state, according to the OECD probabilistic trophic state curves, was eutrophic in 1996 and mesotrophic in 1995. Furthermore, a detailed analysis of the phytoplankton species assemblage provides different trophic assessments for the two years.

In this paper, phytoplankton data collected in the recovering Lake Bourget during two successive years (1995–1996) are presented. The main patterns of the phytoplankton succession differences are discussed in relation to the physical variable evolution that controls to a greater extent the algal light availability, that is, mixing depth and euphotic depth.

MATERIALS AND METHODS

Lake Bourget is a medium-sized lake (surface area: 42 km², maximum depth: 145 m, water residence time: ~7 years) located in the French Alps (Fig. 1). The lake watershed area

(~560 km²) encompasses two urban areas (Aix-les-Bains and Chambéry) with approximately 200 000 inhabitants.

The routine monitoring of Lake Bourget is based on monthly sampling at a single point (point B) located at the lake's maximum depth. The measurements have been regularly conducted since 1981 according to the same monitoring procedure (Centre du Machinisme Agricole, du Génie Rural, Des Eaux et des Forêts 1986). Therefore, long-term statistics are available for characterizing the lake's water quality trends.

The long-term evolution of Lake Bourget is assessed through classical numerical indicators based on the lake parameter measurements: (i) nutrients: concentration of P-PO₄ and N-NO₃ during the winter overturn period (generally in February); and (ii) algal production: summer average (1 April–30 September) values of chlorophyll *a* and summer average of water transparency (Secchi depth) including the data collected between 1 April and 1 October (1981–1996). This seasonal cut, which can be considered somewhat arbitrary, fits the thermal stratification period.

Unfortunately, no phytoplankton quantitative data are available between 1982 and 1994. The long-term evolution of the algal production has been regularly assessed over the whole recovery period only through chlorophyll *a* and water transparency measurements.

A major difficulty in studying phytoplankton dynamics comes from the difference in field sampling scales between regular monitoring and the time-scale of algal blooms. Contrary to regular monitoring based on large space and time scales and aimed at assessing a seasonal global evolution of the lake, small-time scale campaigns are necessary in order to follow the phytoplankton pulses and to identify which environmental variables drive them to a greater extent. During 1995–1996, in order to obtain the most complete data set, we followed a methodological approach based on both field surveys including different space and time scales and numerical modelling (Centre d'Enseignement et de Recherche sur l'Eau, la Ville et l'Environnement 1998).

Integrated samples aimed at measuring algal biomass and chlorophyll *a* were collected at point B from the 0–10 m water layer (Fig. 1). Weekly measurements of Secchi depth and chlorophyll concentrations were done from the beginning of April to the end of September. Outside this period, they were undertaken monthly. The phytoplankton cells were counted by the sedimentation method using an inverted microscope, and the monthly estimation of the biomass (expressed as mg fresh weight/m³) was based on the mean cell volume of each species, assuming a mean density of 1 g/mL.

A one-dimensional vertical thermal model gives the water temperature evolution, the onset of stratification

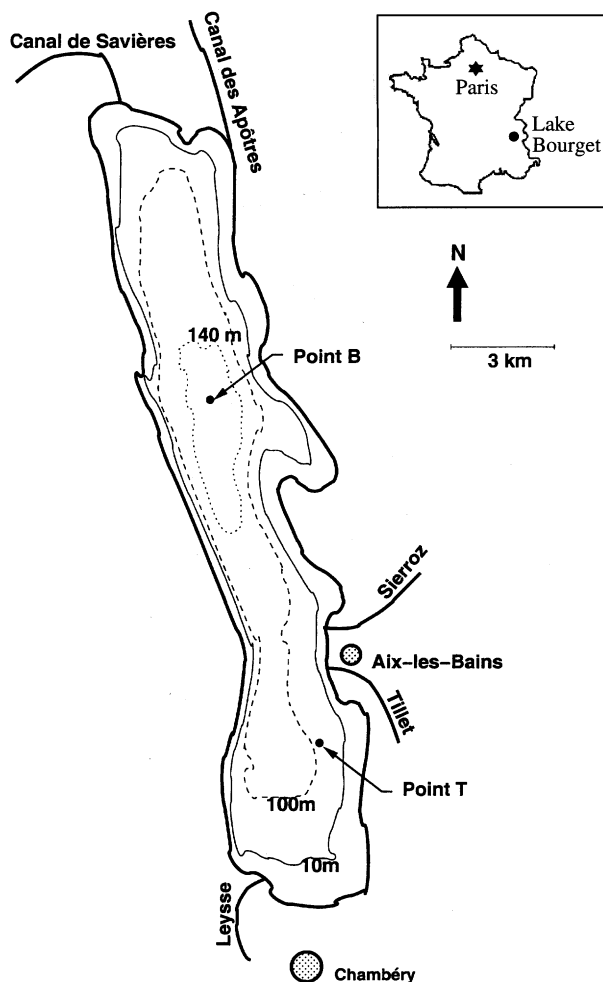


Fig. 1. Map of Lake Bourget.

and the occurrence of mixing in the water column (Vinçon-Leite *et al.* 1989; Tassin & Vinçon-Leite 1998). The time and space steps of the model are 1 day and 1 m, respectively. The meteorological data are supplied by the Météo France station located at the south end of the lake (Voglans).

RESULTS

Long-term lake evolution

The P winter overturn concentrations (January/February) and the mean summer values (1 April–30 September) of chlorophyll and water transparency from 1981 to 1996 are

presented in Fig. 2. During this period, the P concentration decreased significantly until 1993. Afterwards, it reached a steady state but still relatively high concentration of 30 $\mu\text{g/L}$. The summer water transparency followed a slightly increasing trend until 1991. Thereafter, it fluctuated around 4.5 m. The summer chlorophyll *a* did not show any trend over the whole period. It oscillated between 5 $\mu\text{g/L}$ and 9 $\mu\text{g/L}$, with a mean value of 7.5 $\mu\text{g/L}$.

The 1995 Secchi depth and chlorophyll indicators belong to the best values of the period whereas the 1996 values are very close to those of the beginning of the restoration process.

Table 1. Main indicators of algal production

	1995	1996
Mean annual Secchi depth (m)	6.3	7.1
Mean summer Secchi depth (m)	5.1	4.2
Minimum Secchi depth (μm)	2 (3 August)	1.8 (30 July)
Mean annual chlorophyll ($\mu\text{g/L}$)	6.1	5.6
Mean summer chlorophyll ($\mu\text{g/L}$)	6.5	8.4
Maximum chlorophyll ($\mu\text{g/L}$)	15.4 (19 April)	13.9 (29 August)
Mean annual biomass ($\mu\text{g/L}$)	1823	2280
Mean summer biomass ($\mu\text{g/L}$)	2475	3863
Maximum biomass ($\mu\text{g/L}$)	7844 (25 August)	7296 (6 August)

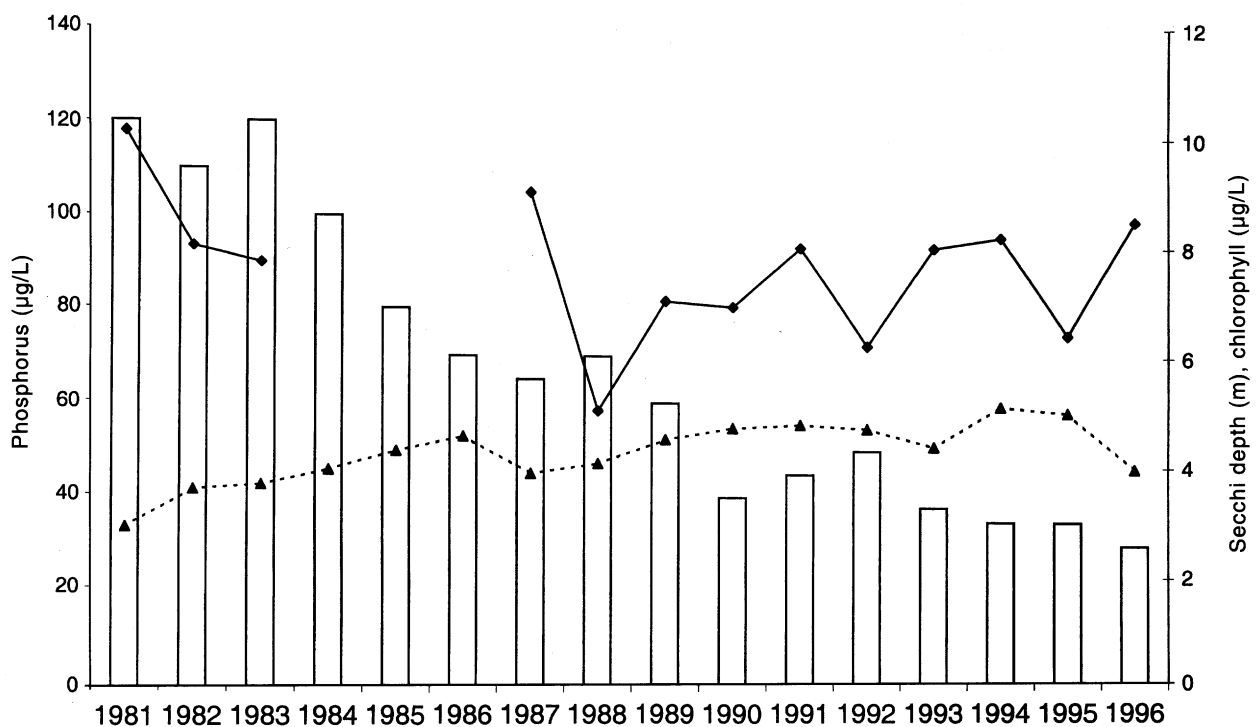


Fig. 2. Long-term evolution of winter phosphorus concentrations and mean summer values of chlorophyll and water transparency (1981–1996). (□) Winter phosphorus, (—▲) Secchi depth, (—◆) chlorophyll.

The main indicators of algal production during the two years are reported in Table 1. According to the summer indicators, it can be inferred that the global summer algal production is higher in 1996 than in 1995. The two year summer indicators are significantly different. The amplitude of

the differences is very high, approximately 50% of the indicator range over the whole restoration period, which impairs a clear assessment of the lake's trophic state evolution.

However, the indicators based on the annual mean values provide a different statement. The two year algal productions

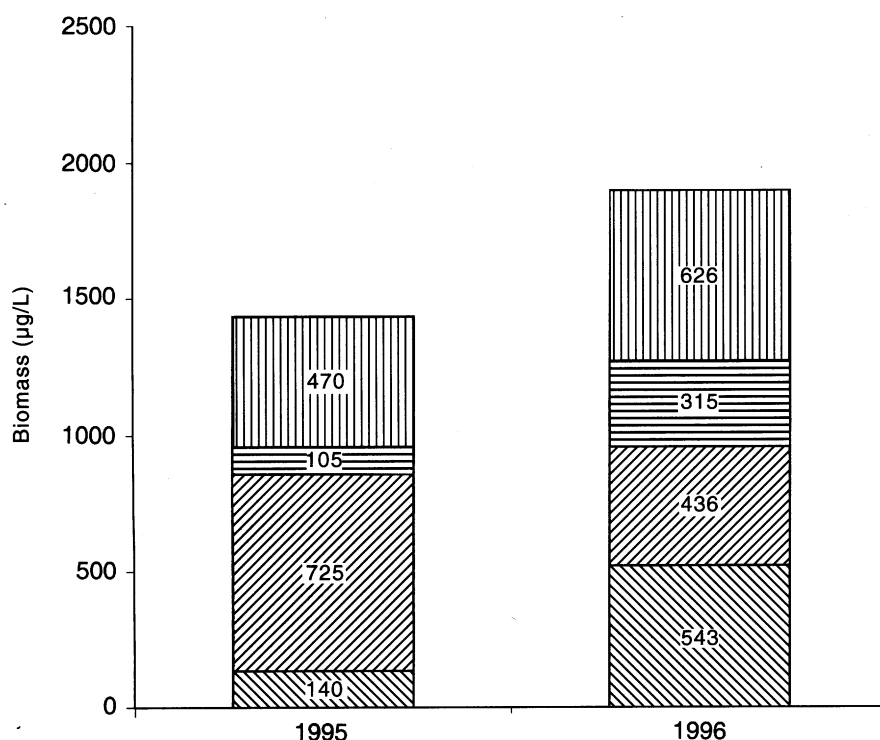


Fig. 3. Distribution of main algal groups expressed in biomass (µg/L). (||||) Conjugates, (|||) Chlorophytes, (\\) Diatoms, (⊞) Cyanophytes.

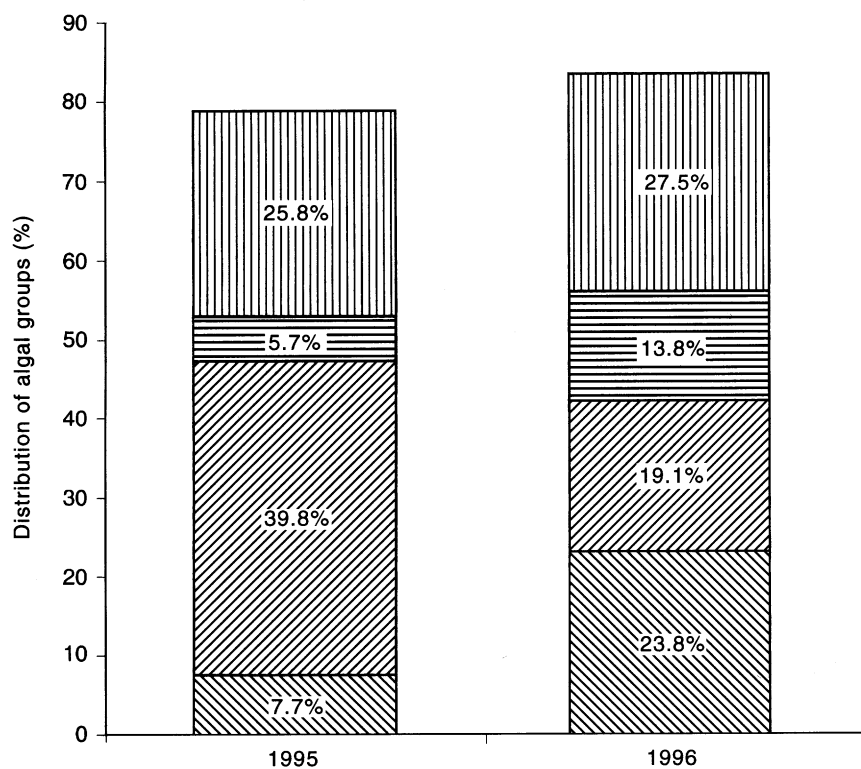


Fig. 4. Distribution of main algal groups (%). (||||) Conjugates, (|||) Chlorophytes, (\\) Diatoms, (⊞) Cyanophytes.

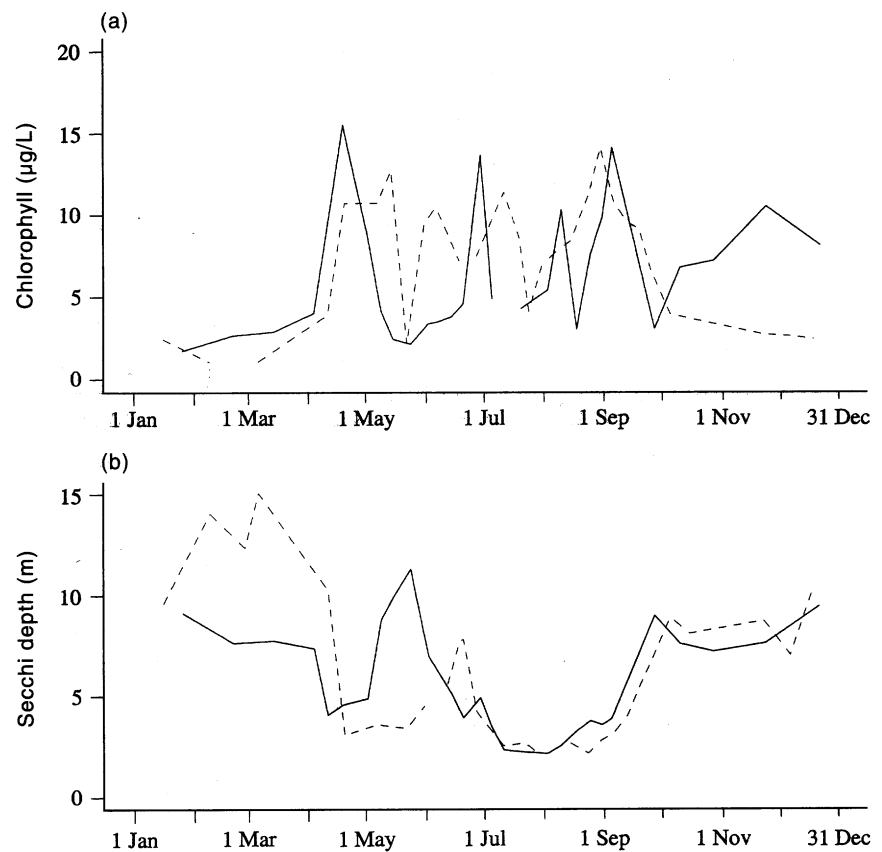


Fig. 5. Chlorophyll concentration and water transparency. (—) 1995, (---) 1996.

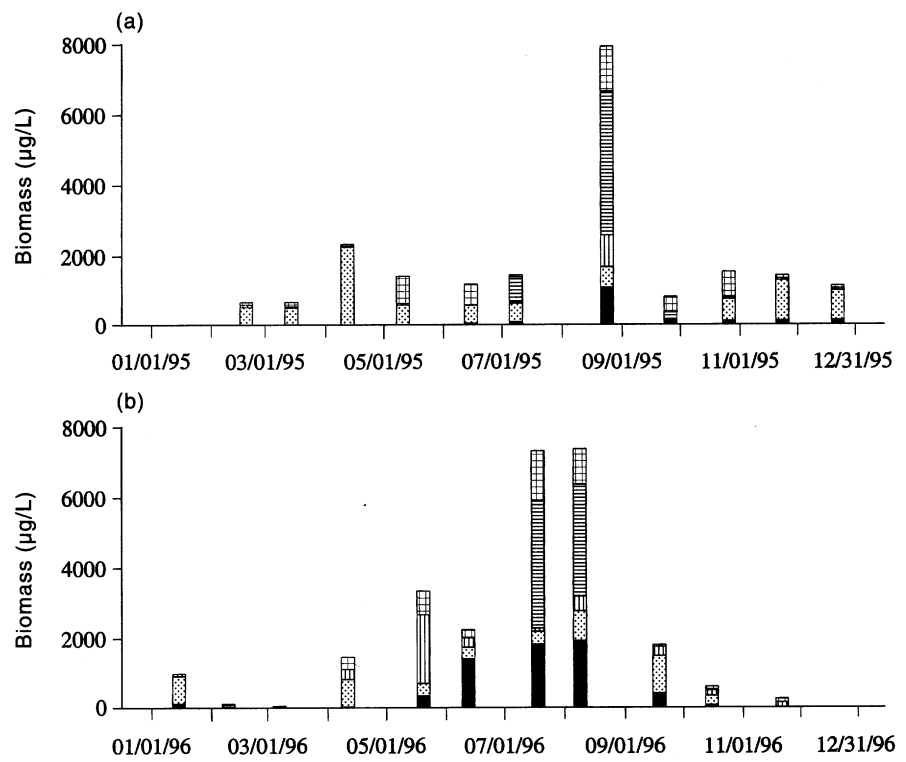


Fig. 6. Algal biomass (1995 and 1996). (■) Cyanophytes, (▨) Diatoms, (▩) Chlorophytes, (▧) Conjugates, (▦) Others.

appear to be very similar. Nevertheless, the annual mean contribution of the main algal groups, expressed in biomass and percentages, is different (Figs 3,4). In 1995, the diatom proportion was high and the cyanobacteria proportion was low, while in 1996, the opposite proportions were found.

Therefore, it is useful to analyse the algal production at a seasonal time-step in order to better understand the origin of the variability between the two years.

Phytoplankton succession (1995–1996)

The data set used to assess algal production during 1995–1996 is presented through the evolution of chlorophyll concentrations and Secchi depth and main algal species biomass shown in Figs 5 and 6.

Three periods describe the algal development in Lake Bourget. Taking into account the definition of trophic state indicators, these periods are defined according to the following dates: (i) winter, 1 January–31 March; (ii) spring–summer, 1 April–30 September; and (iii) autumn, 1 October–31 December. The spring–summer period includes the first spring algal pulse, generally occurring in April, and the clear water phase, which is characterized by a rapid decline of the phytoplankton population, an increase in water transparency and a decrease in chlorophyll concentration.

1995

Winter

Winter algal biomass (January–March) remained at a relatively high level ($\sim 700 \mu\text{g/L}$), the mean winter Secchi depth was 8.1 m and the mean chlorophyll *a* concentration was $2.4 \mu\text{g/L}$.

Spring–summer

The first algal peak appeared between 4 and 11 April. It was relatively high (approximately $2500 \mu\text{g/L}$). The algal population was dominated by diatoms (96%), mainly large-sized diatoms (*Fragilaria*, *Asterionella*, *Tabellaria*). The clear water phase appeared rapidly at the beginning of May and lasted until mid-June (43 days). The maximum water transparency was 11 m. During the summer algal succession, only one biomass peak ($\sim 8000 \mu\text{g/L}$) was observed in August. This peak contained mainly conjugates (52%). Cyanobacteria were present (mainly *Aphanizomenon flos-aquae*) but they represented only 13% of the total biomass. Two other groups represent more than 10% of the total biomass: Xanthophytes (14%) and Chlorophytes (11%).

Autumn

The autumn algal production continued at a relatively high level. From October to December, the mean biomass was

approximately $1275 \mu\text{g/L}$, the mean Secchi depth was 7.7 m and the mean chlorophyll *a* was $7.8 \mu\text{g/L}$.

1996

Winter

Algal biomass nearly disappeared ($\sim 60 \mu\text{g/L}$ in March). The mean winter Secchi depth was 12.7 m and the mean chlorophyll *a* concentration was $1.5 \mu\text{g/L}$.

Spring–summer

The first bloom appeared between 10 and 19 April, but was lower ($1400 \mu\text{g/L}$) than in 1995. Three main algal groups composed the population: diatoms (50%), dinoflagellates (22%) and chlorophytes (20%). The diatoms were small centric species (*Cyclotella* and *Stephanodiscus*). The spring algal peak was reached in May ($3200 \mu\text{g/L}$), mainly composed of chlorophytes (59%). The clear water phase appeared one month later than in 1995 at the beginning of June and lasted until the beginning of July. It was much shorter, 25 days, and the water transparency did not exceed 7.7 m. Two biomass peaks ($\sim 8000 \mu\text{g/L}$) were measured in July and August. The conjugates were again dominant (40–50%) but the proportion of cyanobacteria ($\sim 25\%$) was higher than in 1995. In 1996, the cyanobacteria appeared in June where they were the dominant group (62%), and comprised of only one species, *Planktothrix rubescens*.

Autumn

The autumn algal growth decreased quickly. The November algal biomass was only $200 \mu\text{g/L}$. From October to December, the mean Secchi depth was 8.5 m and the mean chlorophyll *a* concentration was $2.8 \mu\text{g/L}$.

Summary of 1995–1996 algal growth

The following provides the variations in the two year algal growth.

During the winter, the algal population remained the same in 1995, but disappeared in February and March 1996.

The spring first bloom happened earlier (April) in 1995 but it was rapidly interrupted by the clear water phase, and was dominated by large-sized diatoms while in 1996, the small-sized diatoms prevailed in the early spring biomass with the spring biomass peak, composed mainly of chlorophytes, occurring later (21 May).

The clear water phase occurred early and had a long duration (43 days) in 1995, but a late occurrence and short duration (25 days) in 1996. The water transparency remains relatively low and the chlorophyll concentrations high during the 1996 clear water period.

The species assemblages were rather different during the summer algal successions. In 1995, the cyanobacteria presence was moderate and restricted to the August peak (13% of the total biomass) while in 1996, the cyanobacteria rep-

resent, during the whole year, an important fraction of the biomass (24% of the annual mean biomass). The cyanobacteria biomass (*Planktothrix rubescens*) was particularly high from June to August in 1996.

The algal seasonal dynamics were different and opposite: (i) the winter and the autumn algal production was relatively high in 1995 and low in 1996; and (ii) the summer algal production was lower in 1995 than in 1996. At an annual step, as the winter–autumn data balance the opposite summer data, the algal production cannot be considered significantly different, but at a seasonal level, it appeared to be substantially different. Variable weather conditions are assumed to cause fluctuating algal production and to hamper a clear assessment of the lake's trophic state evolution. In the following section, a qualitative analysis of the physical forcing upon the algal growth will be proposed.

LINKS BETWEEN PHYTOPLANKTON DYNAMICS AND METEOROLOGICAL VARIABLES

Depending on the season, the dominant factors (e.g. nutrient limitation, meteorological forcing, zooplankton grazing) driving the algal production vary. In winter and early spring, the meteorological conditions are normally considered to be the uppermost driving forces (Reynolds 1984; Tilzer & Beese 1988; Sommer 1989), mainly because they determine the

mixed layer depth and the light-energy input that controls the balance of algal growth and losses.

The euphotic layer and the mixed layer have been studied in 1995 and 1996 in order to infer the links between the winter–spring phytoplankton dynamics and the forcing meteorological variables. The mixing depth was computed by the one-dimensional thermal model. The euphotic depth (Z_{eu}), where the light intensity is 1% of the surface intensity, was estimated from the Secchi depth (Z_{SD}) using an empirical relationship (Equation 1) that links the attenuation of light with depth according to a Beer–Lambert law and the assumption that, at the Secchi depth, the light intensity is 16% of the incident light intensity (Lemmin 1995):

$$Z_{eu} = 2.5 Z_{SD} \quad (1)$$

The 1995 and 1996 mixing and euphotic depths are presented in Fig. 7.

Winter

During February and March 1995, the mixed surface layer was thinner than the euphotic layer. Therefore, the algal losses were balanced by algal production and the winter algal species were able to hold on. They were promoted by the moderate mixing and the milder water temperature (the mean surface temperature was approximately 0.3°C higher in February 1995 than in February 1996).

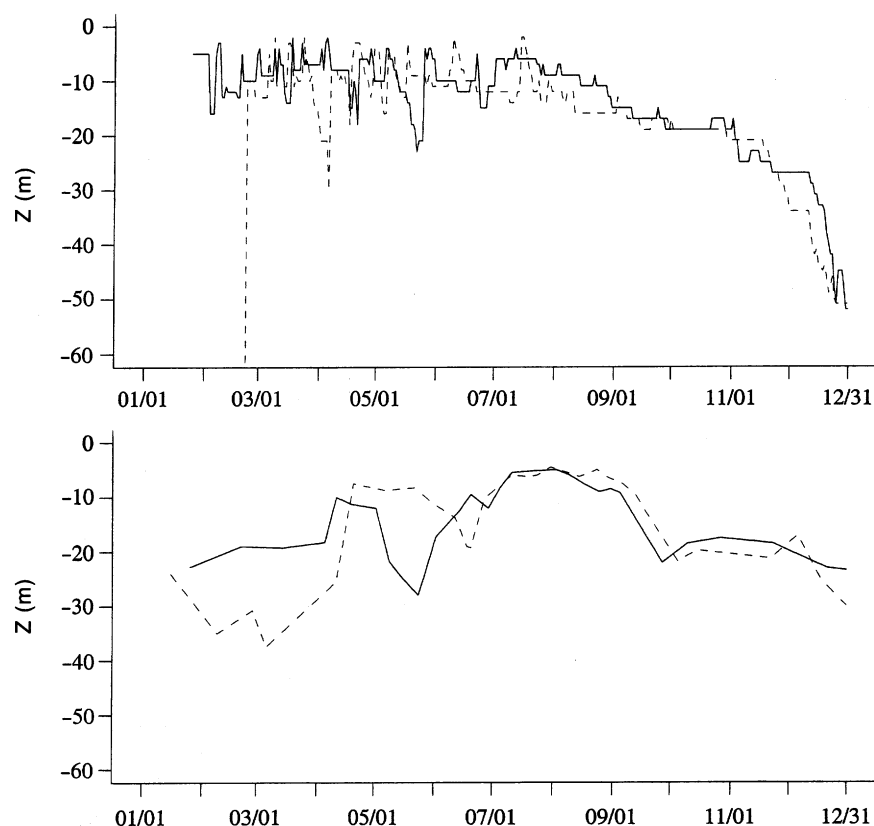


Fig. 7. Mixing depth and euphotic depth. (—) 1995, (---) 1996.

During January and February 1996, a deep mixing period occurred. The mixing depth was much deeper than the euphotic layer and the algal losses prevailed. The algal biomass decreased drastically in February and nearly disappeared in March 1996.

Spring-summer

The first spring algal pulse is generally considered to be triggered by the light conditions in the surface layer (Reynolds 1984; Sommer 1996; Bleiker & Schanz 1997). In 1995 and 1996, the available light threshold was reached in mid-March and triggered the spring algal production. However, in 1995, the algal biomass concentration was high in March (680 $\mu\text{g/L}$). An early biomass peak (2500 $\mu\text{g/L}$) occurred in mid-April. In 1996, the spring growth grew from a very low initial condition (60 $\mu\text{g/L}$). The algal biomass increased in April (1427 $\mu\text{g/L}$) with a very high growth rate but it reached a maximum value only in mid-May (3200 $\mu\text{g/L}$).

At the beginning of May 1995, the algal biomass, mainly composed of large size diatoms, broke down. The following clear water period lasted until mid-June (~43 days). Generally, zooplankton grazing is the dominant factor triggering the clear water period but other factors, for example, nutrient depletion (e.g. diatom silica limitation), sedimentation losses and meteorological forcing, can superimpose. In May 1995, the zooplankton population was at its maximum and it gave rise to the clear water period. However, a strong mixing episode (high wind velocity and low air temperature) occurred in mid-May, and contributed to the decrease in phytoplankton population.

In 1996, the spring algal succession was only slightly affected by a clear water period. The zooplankton population reached a high level but the different species of the diversified algal association were differently consumed and therefore the grazing pressure was buffered. The cyanobacteria population appeared in May.

The summer peak biomass was similar in 1995 and 1996, ~8000 $\mu\text{g/L}$ in July 1995 and ~7000 $\mu\text{g/L}$ in July and August 1996. The algal association was similar with conjugates (*Mougeotia gracillima*) comprising approximately 50%, cyanobacteria comprising approximately 10% in July 1995 and 24% in July and August 1996. However, in summer 1995, the main species was a nitrogen-fixing cyanobacteria, *Aphanizomenon flos aquae*, while in summer 1996, the dominant species was *Planktothrix rubescens*. In 1995, the cyanobacteria constituted a significant part of the algal biomass only during July whereas in 1996, their biomass was noticeable from May to September. Their growth rate was high in June, probably owing to the strong stratification prevailing during this period.

Autumn

The autumn decrease in algal production occurred in September in both years. In autumn, the algal production was again mainly driven by the physical conditions, for example, cooling of water, deepening of mixing layer and decrease of the light climate.

In 1995, the biomass collapse was drastic from August to September (8000 $\mu\text{g/L}$ to 1000 $\mu\text{g/L}$). Thereafter, the algal biomass, mainly composed of diatoms, remained steady (~1200 $\mu\text{g/L}$) until December. The meteorological conditions remained rather mild from September to October.

In 1996, the August–September decrease was very strong but the biomass decrease continued (170 $\mu\text{g/L}$ in November 1996).

It is generally assumed that meteorological conditions have a major effect on algal production in winter and early spring. In summer, biological interactions and nutrient limitations are the deciding factors. In fact, meteorological variables act in many different ways and produce different effects depending on the season.

In Lake Bourget, the different algal start-up dates in 1995 and 1996 can be qualitatively correlated to the winter weather conditions, particularly the mixing depth and the light climate. The spring first algal pulse is conditioned by the initial algal assemblage. In summer, the physical forcing is not the main driving factor of the algal production but some short episodes can trigger the emergence of specific algal species and lead the algal succession in a different way. For example, a spring mixing episode enhanced the clear water phase in 1995, the summer light and water temperature conditions helped the installation of *Planktothrix rubescens* in June 1996, and an early autumn weather worsening in autumn 1996 led to a marked algal decline.

CONCLUSIONS

In a recovering lake, even with constant nutrient concentrations, the interannual phytoplankton dynamics might vary greatly from one year to another. The interannual variation can be of the same order as the amplitude of the recovering long-term trend.

During the two years of the study, the meteorological variables were clearly controlling biomass during the winter and driving the following spring species' successions. The spring algal production was determined by the algal species able to overcome the winter conditions, which provided the initial biomass for the commencement of spring algal growth. The clear water phase was jointly controlled by zooplankton grazing and meteorological forcing. In summer and autumn, the dominant role of the meteorological variables appeared again during some short episodes. It seems that brief extreme meteorological episodes that differ greatly

from the mean interannual values controlled algal evolution throughout the year.

The key factors that influence the phytoplankton succession in a lake of a given trophic status cannot be easily identified. Therefore, interpretation of the data aimed at characterizing the trophic level of the water-body must be very cautious. Aggregated indicators are frequently used to summarize the water quality assessment but, depending on the aggregation level, the conclusions might differ. For example, in Lake Bourget in 1995 and 1996, summer and annual biological indicators led to opposite conclusions about the lake's trophic state evolution. Furthermore, pluriannual monitoring is essential to obtain a conclusive statement. However, our insights remain mainly qualitative. Further studies are necessary in order to find a reliable quantitative description of the interannual variability of the phytoplankton assemblage and to incorporate them into ecological models.

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