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REVIEW

A complete overview of algal blooms in Lake Geneva: shall the past shed light on the future?

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Abstract
Lake Geneva (Léman), the largest lake in Western Europe, is a vital freshwater ecosystem that supports a range of essential services, including water supply, fisheries, navigation, and recreational activities. However, like many other freshwater systems, it faces numerous threats that jeopardize its ecological integrity. These threats not only endanger the lake's biodiversity but also impact the ecosystem's overall functioning and the services it provides. One potential significant threat is the occurrence of algal blooms, particularly those involving toxic species such as pelagic cyanobacteria. These blooms can disrupt vital ecological processes and pose serious risks to animal and human health, local fisheries, and the regional economy. This article reviews the history of algal blooms in Lake Geneva over the last 70 years, aiming to identify the species involved and the services impacted, examine the common and unique factors driving these proliferations, and propose potential future scenarios in the context of both local and global changes. The ultimate goal is to inform effective management strategies to mitigate the impacts of these blooms.

Keywords Lake Geneva · Algal bloom · Ecosystem service · Algae · Cyanobacteria

Introduction

Algal blooms are characterized by the rapid and excessive growth of microalgae in aquatic environments. These events, which can have significant impacts on aquatic ecosystems and water quality, are becoming increasingly frequent worldwide, posing substantial ecological and socio-economic challenges (Ho et al. 2019; Hou et al. 2022). While elevated nutrient inputs—primarily phosphorus but also nitrogen—are well established as the main drivers of such proliferations in freshwater ecosystems, other mechanisms also play a role (Fig. 1). Altogether, this makes the prediction of these events increasingly complex and, in many cases, highly challenging or even impossible. However, the role of these mechanisms remains debated, as contrasting evidence has emerged in recent years. For instance, direct and/or indirect effects of rising temperatures are often cited as a key factor promoting algal blooms (Paerl and Huisman 2008). Nevertheless, growing evidence suggests that blooms, particularly those dominated by cyanobacteria, can also develop in cold waters or regions (Reinl et al. 2023; Shchapov et al. 2025). Similarly, eutrophication is no longer a prerequisite for the occurrence and expansion of algal species, as some proliferations have also been observed even in oligotrophic systems (Sterner et al. 2020; Zepernick et al. 2024). This diversity of potential drivers highlights the need for further case-specific studies, such as those focusing on Lake Geneva.

Located at the foothills of the Alps and forming a natural border between France and Switzerland, Lake Geneva (Léman) is classified as a large lake (Jenny et al. 2020). It plays a vital role in providing essential services to a growing lakeside population in both countries, including drinking water supply, aquatic and nautical recreation, fishing, thermal exploitation, and transportation. Other services, though less immediately visible or quantifiable, are equally crucial for both the environment and human well-being, such as biodiversity support and biogeochemical cycles (Baulaz 2020). Lake Geneva faces locally driven pressures, including pollution from increasing population density and economic activity (such as micropollutants, microplastics, local eutrophication), as well as broader challenges such as the arrival and settlement of exotic species and those linked to global change, particularly climate warming.

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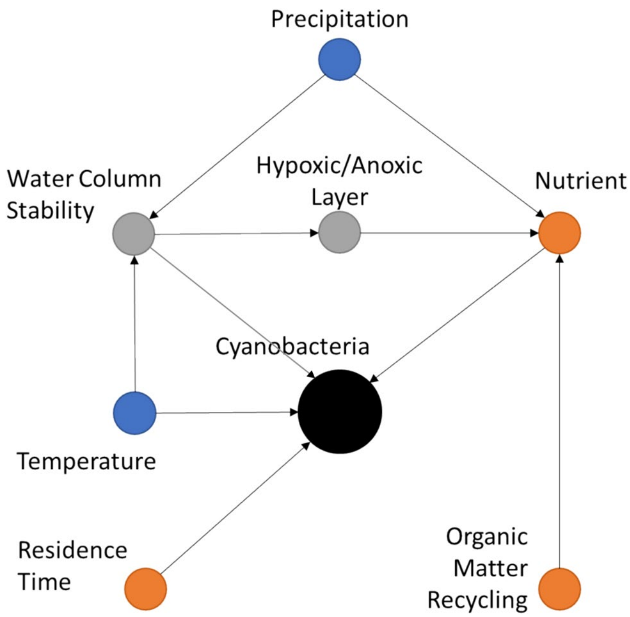

Fig. 1 Several mechanisms contribute to the occurrence and persistence of cyanobacterial blooms. Nutrients, particularly phosphorus and nitrogen, are essential for algal growth. Human activities, such as domestic, intensive agriculture, and industrial discharges, increase nutrient concentrations in water bodies, promoting algal proliferation. Environmental factors, including temperature, light availability, and water column stability, also play a crucial role. High temperatures and strong light intensity accelerate photosynthesis and algal growth, further encouraging blooms. In lakes, where water residence time is long, algae multiply more easily, with stagnant or slow-moving waters being particularly susceptible. Precipitation can wash nutrients from soils into water bodies, increasing their availability for algae. Conversely, droughts can concentrate nutrients in the remaining water, also stimulating proliferation. The breakdown of organic matter by bacteria releases additional nutrients, further fueling blooms—especially in waters rich in organic material. In deeper water layers, organic matter decomposition can create hypoxic or anoxic conditions, reducing biodiversity and favoring algal species that thrive in low-oxygen environments

This warming trend is leading to a rise in lake temperature (Desgué-Itier et al. 2023) and an increased frequency and duration of extreme weather events, such as heatwaves and storms (Tran-Khac et al. 2025). Lake Geneva hydrologic cycle is expected to experience a 5–15% reduction in direct water inflows, up to a 20% increase in evaporation, and a summer water level drop of over 25 cm under the RCP8.5 scenario by 2100, as regulation at the lake's outlet will no longer be sufficient to maintain water levels under extreme climate conditions (Michel and Soulignac, 2022). Given these challenges, it is clear why Lake Geneva and its watershed have been—and continue to be—the focus of extensive ecological monitoring, particularly by the International Commission for the Protection of the Waters of Lake Geneva (CIPEL, https://www.cipel.org/) in collaboration with the Lakes Observatory (OLA, https://www6.inrae.fr/soere-ola), a long-term mission of observation and experimentation on lacustrine ecosystems to generate high-quality scientific data and improve our understanding and modelling of ecological processes in lakes (Rimet et al. 2020). This monitoring is especially important, as further research is needed to better anticipate the effects of climate change and increasing local pressures on phenomena such as the occurrence, dynamics, and impacts of algal blooms.

Controlling eutrophication, primarily by reducing phosphorus inputs, has been and remains a central management objective for CIPEL. In the absence of algal blooms, microalgae (phytoplankton) are essential components of a healthy lake ecosystem. As primary producers, they form the foundation of the lake's trophic network and rely on nutrients for growth. Phosphorus is often the limiting factor and thus a key driver of their development. However, over the past century, major changes in nutrient loading, particularly phosphorus, have led to the eutrophication and subsequent re-oligotrophication of Lake Geneva, causing anoxia in its deep layers (Jenny et al. 2014; Soares et al. 2025) and significant shifts in phytoplankton communities (Anneville et al. 2002; Jacquet et al. 2014; Tadonléké et al. 2009). While phosphorus reduction should help mitigate future algal blooms, it is now evident that this strategy alone may be insufficient, as climate change, through rising temperatures and more frequent extreme weather events, also plays a major role in promoting blooms, particularly harmful cyanobacteria, an aspect not fully considered in early management efforts.

Given the intensification of both local pressures and global climate drivers, a retrospective and integrative understanding of algal bloom dynamics in Lake Geneva is important. In this article, we provide a comprehensive overview of algal blooms of cyanobacteria and microalgae that have occurred in the lake, considering and analyzing all documented events. Whenever available, we summarize not only their triggering factors but also their ecological and socio-economic impacts (drinking water, fishing and recreational activities), and we explore potential future occurrences and developments to support effective management strategies for mitigating their consequences. To compile this article, we drew on a diverse range of sources, including scientific literature, official reports, and regional press archives dating back to the 1950s. The sources consulted were predominantly in French, except for the scientific literature, which was mainly in English. All documents were photocopied or scanned and can be made available upon request. For regional press coverage, we consulted archives from various institutions, including the Musée du Léman (https://museeduleman.ch), the Association de Sauvegarde du Léman (ASL, https://asleman.org), and the Haute-Savoie departmental archives (https://archives.hautesavoie.fr). The scientific reports were obtained from CIPEL and ASL.

What are we talking about?

Lake Geneva

Lake Geneva is a deep, natural peri-alpine lake shared by Switzerland and France, consisting of two basins: the "Grand-Lac" to the east and the "Petit-Lac" to the west. Covering a surface area of 582 km^2, with a maximum depth of 309 m and a total volume of 89 km^3, the lake has a mean water residence time of approximately 11.4 years. Sometimes classified as warm and monomictic, the prevailing evidence suggests that it is more likely to be oligomictic, as complete mixing has become rare. Schwefel et al. (2016) reported that complete water mixing promoting deep reoxygenation occurs during very cold winters only once per 5–10 years on average since the 1950s. Complete mixing results in the thermal and chemical homogenisation of the entire water column and it is traditionally considered to be driven by vertical convective cooling. However, the last complete homogenization of the water column occurred in 2012 as a result of lateral advection caused by density currents that brought oxygen to the layers below 200 m (Peng et al. 2024). According to (Jenny et al. 2020), Lake Geneva ranks among the top 1709 largest lakes in the world (those with a surface area exceeding 100 km^2). The latest CIPEL report further classifies this ecosystem as oligo-mesotrophic (Jacquet et al. 2005).

The cyanobacteria

Cyanobacteria are a diverse group of photosynthetic prokaryotes whose life traits can vary greatly. The ecology of the most common species in freshwater is well documented in the literature (Huisman et al. 2005; Whitton and Potts 2002). In Lake Geneva, *Planktothrix rubescens* (a red-pigmented filamentous species strongly associated with eutrophication) and *Aphanizomenon flos-aquae* (capable of forming dense surface scums) can occasionally dominate the phytoplankton community. Similarly, the relationships between cyanobacterial biomass and nutrient concentrations (especially phosphorus) have often been described (Gobler 2020; Lürling et al. 2018). However, this knowledge is still insufficient to fully understand the emergence and maintenance of blooms, especially in the context of global change, which requires revisiting known relationships (Moiron et al. 2021). In the neighboring Lake Bourget (France), *P. rubescens* reappeared after several years of absence despite low surface phosphorus concentrations. Also, additional uncertainties arise from large-scale changes in the biological communities of phytoplankton grazers, for example in Lake Geneva with the reduction of zooplankton (Anneville et al. 2007; Balvay 1990) or the recent invasion by the quagga mussel (Haltiner et al. 2022). A reduced grazing pressure may favor the proliferation and persistence of cyanobacterial populations, while the quagga mussel can selectively remove certain phytoplankton taxa, potentially reshaping competitive interactions and indirectly promoting bloom-forming species (see below).

The issue of the determinism behind the appearance and biomass development of toxic cyanobacteria is typically both a scientific frontier and a significant societal challenge, locally as well as globally at the national and international levels (Benayache et al. 2019; Huisman et al. 2018; Jenny et al. 2020). Cyanobacterial blooms may pose numerous problems, often associated with trophic dysfunctions in ecosystems, a decline in fish productivity, and various nuisances that ultimately lead to economic, societal, and health impacts. A recent fully updated version of the World Health Organization's manual on toxic cyanobacteria in water highlights the causes, consequences, and risks of these proliferations (https://www.who.int/publications/m/item/toxic-cyanobacteria-in-water---second-edition). Indeed, the cyanobacteria in Lake Geneva, *P. rubescens* and *A. flos-aquae*, can both produce toxins that can affect all trophic levels and may lead to animal poisoning and sometimes human poisoning.

The cyanotoxins widely produced, such as microcystins, and increasingly neurotoxins, pose not only an acute risk to human health through activities, such as swimming or consuming fish (Briand et al. 2003; Ibelings et al. 2011; Ibelings and Chorus 2007), but they may also be involved in various types of cancer following chronic exposure to low doses in drinking water (Hernandez et al. 2022; Mrdjen et al. 2022). However, for Lake Geneva, precise data on the types and concentrations of cyanotoxins present are currently lacking. Additionally, cyanobacteria impact the production of drinking water for many lakes affected by these blooms (Steffen et al. 2017). These issues are closely related to global change, which affects phytoplankton communities by altering habitats and tends to favor cyanobacteria, particularly *P. rubescens* and *A. flos-aquae*, in environments experiencing significant environmental disturbances, such as extreme events including storms, heatwaves, and floods, whose frequency may increase (Anneville et al. 2015; Moiron et al. 2021; Paerl and Huisman 2008).

A globally under-researched risk, unlike pelagic blooms, is the proliferation of toxic benthic cyanobacterial mats (Quiblier et al. 2013). Studies on benthic cyanobacteria are at best anecdotal and generally linked to reports of animal poisonings in the media, such as the dead dogs in Lake Neuchâtel in 2020[1] and in Lake Geneva in 2024[2]! These

[1] https://lenews.ch/2020/07/31/beaches-closed-in-neuchatel-after-dogs-die-from-poisoning/
https://www.bluewin.ch/en/news/international/researchers-identify-blue-green-algae-responsible-for-dead-dogs-2379055.html

[2] https://www.20min.ch/fr/story/villeneuve-vd-chienne-morte-apres-la-baignade-analyses-en-cours-dans-le-leman-103160846
https://www.cipel.org/cyano2024/

mats observed in 2024 in Lake Geneva are composed of the toxic benthic cyanobacterium *Microcoleus anatoxicus* and primarily developed in a tributary of the lake during very low flow conditions. Then, these cyanobacteria detached and were carried into the littoral zone of the lake, where they were eventually consumed by dogs. It is believed that higher temperatures, long periods of calm conditions related to climate change, as well as increased water transparency linked to re-oligotrophication and/or the population development of the quagga mussel (an invasive filter feeder), can promote the conditions for the growth of benthic cyanobacteria (Sandrini et al. 2025; Tang et al. 2014). However, data on what controls growth and toxicity of benthic cyanobacteria blooms (hepatotoxins, neurotoxins, and dermatotoxins) are still largely lacking. This is particularly true for Lake Geneva. Currently, we have no fundamental understanding of the presence and dynamics of benthic cyanobacteria in the lake, and we also lack efficient predictive models to forecast their future development. Risk assessment protocols and risk management procedures for benthic cyanobacteria are also absent (Ibelings et al. 2021, 2011).

The microalgae

Unlike cyanobacteria, microalgae are eukaryotic phytoplankton. While they generally do not pose the same risks, certain species can form dense blooms when nutrients are abundant and environmental conditions are favorable. As will be discussed, Lake Geneva has experienced issues with the proliferation of some very different species such as *Rhodomonas minuta*, *Mougeotia gracillima* (a filamentous green alga of the zygophytes) or *Uroglena* sp. Similar to cyanobacterial blooms, microalgae blooms—indicated by high concentrations of pigments, biovolumes, or cell counts—can negatively affect water supply, professional fishing, tourism and recreational activities, such as swimming and water sports. This is often due to water discoloration or unpleasant odours. Additionally, visible fish mortality, which is likely caused by oxygen depletion or toxins (such as those produced by *Prymnesium parvum*), can further discourage recreational activities, as people may avoid swimming, snorkeling, or diving (Soulignac et al., in revision).

Results and discussion

Global overview of the eutrophication and restoration of Lake Geneva

The changes in phosphorus concentration and water transparency presented here were derived from monitoring data collected at the SHL2 station, i.e., the reference station located in the middle of the lake, between Evian and Lausanne. Similarly, the changes in phytoplankton composition and abundance were also obtained from measurements at SHL2, but only from 1974 onward. Prior to 1974, information on phytoplankton composition was reconstructed from a variety of sources, including scientific literature, official reports, and regional press archives compiled in the present study.

Changes in phosphorus concentration and water transparency

Like many freshwater ecosystems across Europe and beyond, Lake Geneva experienced eutrophication during the twentieth century before undergoing partial restoration (Loizeau and Dominik 2005; Soares et al. 2025). The eutrophication process began in the 1940–1950's, with a period of significant degradation between 1960 and 1980. During this time, total phosphorus concentrations measured at SHL2, which had typically ranged between 10 and 12 μg L^{-1} before 1960, surged to about 90 μg L^{-1} between 1976 and 1979. This increase was primarily driven by human activities, including the discharge of untreated or poorly treated municipal and industrial wastewater, the intensive use of phosphorus-rich fertilizers in agriculture, and urban runoff carrying nutrients into the lake. Dissolved oxygen concentrations in the deepest waters also dropped drastically during these two decades (mainly as a result of low and incomplete mixing), reaching levels below 2 mg L^{-1}, accompanied by frequent episodes of anoxia. Water transparency using a Secchi disk was similarly impacted, with annual and summer values measured at SHL2 decreasing from approximately 10 m and 7 m (1957–1960) to around 8 m and 5.5 m (1981–2002), respectively.

The re-oligotrophication process began in the early 1980's, following a consistent decline in phosphorus concentrations. This decline was largely driven by the implementation of coordinated monitoring and research programs initiated in 1971 under the guidance of CIPEL, which progressively recommended measures to the governments for reducing and preventing eutrophication (Rapin 2013). On the basis of these recommendations, both France and Switzerland inaugurated new wastewater treatment plants and significantly improved phosphorus removal efficiencies. Regulatory measures were also adopted to target detergent-derived phosphorus. Switzerland promulgated a ban on phosphates in laundry detergents through the Ordinance on Environmentally Hazardous Substances (Osubst, RS 814.013) on 9 June 1986, while France later implemented restrictions under the REACH Regulation (EC No. 1907/2006) of 18 December 2006. In response to the remediation measures, from 1990 to 2024, total phosphorus concentration decreased from ~ 55 μg L^{-1} to ~ 17 μg L^{-1} while the mean annual and summer water transparency by Secchi disk remained relatively stable, varying from ~ 8 and ~ 6 m to ~ 8 and ~ 5 m, respectively, at SHL2 (Jacquet et al. 2005, Fig. 2).

Changes in phytoplankton composition and abundance

In parallel with the changes in phosphorus concentrations and the successive phases of eutrophication and re-oligotrophication, profound modifications also occurred in the composition of the phytoplankton community. Prior to the 1960’s, diatom species were dominant, with typical oligotrophic species such as *Cyclotella* spp. and *Tabellaria fenestrata* (Balvay et al., 1984). Notably, this last species was the first to be reported by local fishermen in 1950 as forming an unusual phytoplankton bloom in the littoral zone, as a possible reason of the negative impacts of wastewater discharges into surface waters and the subsequent deterioration of water quality at that time. However, significant changes really occurred in the phytoplankton community between 1963 and 1966. Zygophytes, particularly *Mougeotia gracillima*, saw a sharp concentration increase, surpassing the abundance of chrysophytes species. This trend may reflect the comparatively higher tolerance of *M. gracillima* to nutrient enrichment and reduced water transparency, conditions under which many chrysophytes are less competitive. By 1967, the proportion of diatoms (silica-shelled algae) in the phytoplankton community dropped to less than 50% of the total biomass, and Cyanobacteria, specifically *P. rubescens*, a strong indicator of severe eutrophication, showed substantial increases. These temporal comparisons should nevertheless be interpreted with caution, as the sampling strategy evolved over time: until 1974 phytoplankton was collected with a 64-µm pore-size net, after which closing bottles were used; moreover, integrated sampling was carried out from 0–10 m depth before 2000–2001, and from 0–20 m thereafter (Jacquet et al. 2014; Jacquet and Anneville 2012).

Later, from 1968 to 1980, the phytoplankton community became more diverse. In addition to diatoms, the community also included dinoflagellates such as *Ceratium hirundinella* (a large dinoflagellate), *M. gracillima*, and several cyanobacteria, notably *P. rubescens*, *Oscillatoria bourrellyi*, and *A. flos-aquae*. In contrast, other algal groups such as

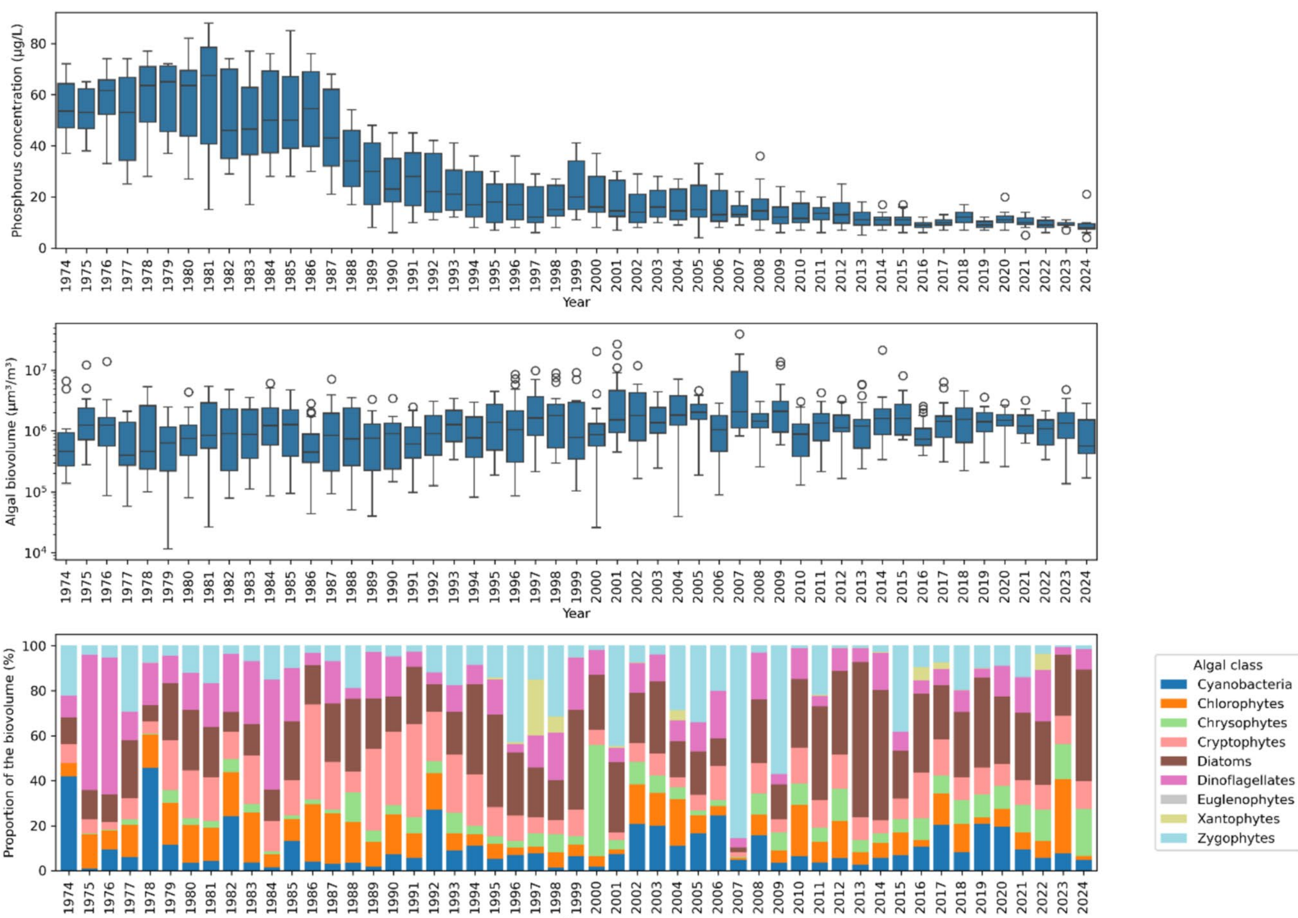

Fig. 2 Annual boxplots of total phosphorus concentration (0–30 m depth) in the top graph, annual boxplots of phytoplankton biovolume in the middle graph, and annual phytoplankton composition from 1974 to 2024 in the bottom graph

green algae (chlorophytes), golden algae (chrysophytes), and yellow-green algae (xanthophytes) were present but in smaller abundance. From 1981 to 1985, summer communities remained dominated by *C. hirundinella*, although cyanobacteria declined noticeably during this period. At the same time, golden algae such as *Dinobryon sociale* (a colonial species) and cryptophytes (nanoplankton-sized flagellates, important food for zooplankton) began to re-emerge (Anneville et al. 2002; Anneville and Pelletier 1998). These taxonomic shifts were reflected in the overall biomass dynamics at the lake's central station. While *C. hirundinella* was responsible for algal blooms in 1975 and 1976, its subsequent decline coincided with the moderate but steady reduction in phytoplankton biomass observed between 1976 and 1990.

However, since 1992, despite the continued reduction in phosphorus concentrations, the mean annual algal biomass has maintained or started to rise again. Concurrently, the contribution of oligotrophic species to total phytoplankton biomass has diminished, though their biomass has shown an irregular but steady increase. It is important to note that these species represent only a small fraction ($<1\%$) of the total phytoplankton biomass, based on observations made at point SHL2. Anneville et al. (2002) suggested that the increase in phytoplankton biomass observed in the 1990s might have been owing to a combination of at least two factors interacting with the expansion of the phosphorus-depleted stratum: (1) global warming, which led to milder winters and summer conditions suited for algal growth and development in the late 1990s, and (2) the physiological tolerance of some taxa such as the "autumnal species." Summer communities were characterized by an increase in Chrysophycea, Zygophycea, and Xanthophycea, along with massive growth of *Diatoma tenuis*, *M. gracillima*, and *Dynobryon divergens*.

Over the past two decades, phytoplankton structure and biomass have continued to change significantly. An exceptional bloom occurred in 2007, dominated by *M. gracillima*, which alone accounted for 79% of annual biomass and significantly disrupted fisheries. The algae attached to fishing nets, making them visible to fish, which then avoided them and resulted in reduced catches. On the basis of observations made at point SHL2, phytoplankton diversity has fluctuated between a minimum of 89 taxa in 2007 and a maximum of 140 in 2003. Since the mid-2000s, a trend toward re-oligotrophication has emerged. Functional group analysis and the Brettum trophic index consistently indicate a shift toward oligotrophic or mesotrophic taxa, such as the chrysophyte *Dinobryon sp*. and the dinoflagellate *Peridinium sp*., particularly since 2008. In 2012, a complete winter mixing of the water column redistributed nutrients to the upper part of the lake, temporarily increasing the dominance of chlorophytes and triggering an autumn bloom of the potentially toxic cyanobacterium *A. flos-aquae*, which exceeded the World Health Organization (WHO) alert threshold 1 (https://www.who.int/publications/m/item/toxic-cyanobacteria-in-water--second-edition). The bloom occurred in November, and concentrations decreased in December. However, its impact and toxicity have not been reported. Since 2012, the trend toward re-oligotrophication has continued, with a further reduction in nutrient concentrations and the maintenance of the dominance of taxa adapted to low nutrient and clear water conditions. On the basis of observations made at SHL2, diatoms remain important in spring, but often give way to smaller, flagellated taxa such as cryptophytes, chrysophytes, and dinoflagellates during the summer. Dinoflagellates, particularly *Peridinium* species, have become increasingly important, probably due to warmer and more stratified conditions. The diversity of the phytoplankton community remains high. Cyanobacteria development remains sporadic, with no persistent dominance, but with occasional blooms under favorable thermal and nutrient conditions. Functional indicators and trophic indices have consistently indicated a mesotrophic to oligotrophic state.

The different algal blooms in Lake Geneva

To the best of our knowledge, the earliest recorded algal bloom in Lake Geneva dates back to the 1950's, while the most recent occurrence was in 2021. In complement to what could be observed from shore by anyone, the first whistle-blowers were very often the fishermen who observed unusual algal blooms from the middle of the last century and warned the journalists, the sanitary authorities or the scientific community about such phenomena and negative impact on their activity. Although algal proliferations have concerned a variety of species/taxa, only a few of them (e.g., *R. minuta*, *P. rubescens*, *M. gracillima* and *Uroglena* sp.) have been particularly mentioned in the press or scientifically studied, and their specific impacts on ecosystem services have also been reported (Fig. 3) (Irani Rahaghi et al. 2024; Tapolczai et al. 2015, 2013).

The first mention of an algal bloom we found was in 1957 in "*La Croix Rouge Suisse*" where a former scientist from the French Research Institute for Agriculture, Food, and the Environment (INRAE), i.e., Bernard Dussart, reported the massive development of *Tabellaria fenestrata* off the coast of Thonon-les-bains (France). It is noteworthy to mention here that this species could have been misidentified with *Tabellaria floculosa* (Druart et al., 2001). Interestingly, it was also reported a few years later, during the winter of 2000–2001 (Druart and Balvay, 2007). That winter, *Tabellaria floculosa* produced a very high biomass from November 2000 to March 2001. Water quality checks revealed an unusual taste in the water supply. This unpleasant taste was due to the presence of this proliferation in Lake Geneva. The

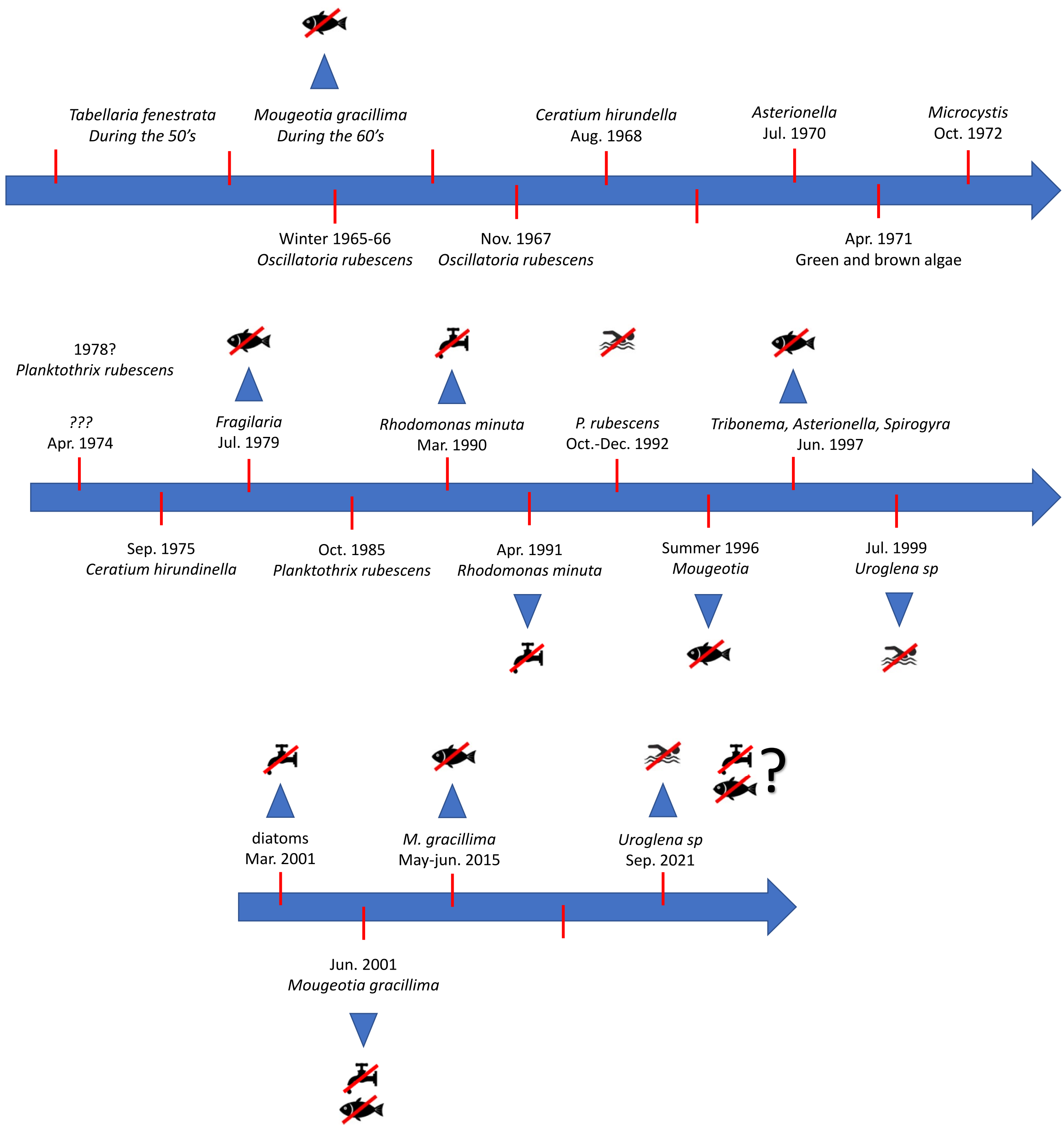

Fig. 3 Timeline of all recorded algal blooms in Lake Geneva. In all cases, except for the *Uroglena* bloom that occurred in 2021, the proliferations were relatively localised. This figure also highlights the impacted ecosystem services (e.g., fishing, drinking water or recreational activities here symbolized by the small drawings) when and if they were reported. *Oscillatoria rubescens* changed to *Planktothrix rubescens* in 1988 after the name revision made by Anagnostidis and Komarek

lake water pumping station in Geneva was closed to prevent the phenomenon from spreading (article dated March 22, 2001, in "GHI"). Winter blooms of diatoms are favored by mild winters with temperatures above seasonal norms, and *Tabellaria floculosa* can proliferate in various trophic states.

During the following three to four decades, different species were reported to bloom occasionally, typically the red-colored, filamentous cyanobacterium *P. rubescens*. This species formerly named *Oscillatoria rubescens* and reported as such before the 1980s is known to form deep water maxima in the stratified lakes of temperate latitudes (Bright and Walsby 2000; Feuillade 1994; Jacquet et al. 2005; Micheletti et al. 1998). It is able to adjust its buoyancy and thus its position in the water column through gas vesicles to obtain an optimum in terms of light and nutrient availability (and possibly also in response to other factors). If *P. rubescens* blooms are not visible at the lake surface during spring and summer, mixing events and water column destratification in fall and winter result in the rising of the species in surface waters at these periods of the year. There have been several episodes of *P. rubescens* blooms in Lake Geneva during the second half of the twentieth century, preventing ecosystem services such as recreational activities. The first reports date back to the fall/winter 1967/68 where newspaper relayed that "the blood of the Burgundians" (referred to as *O. rubescens* at that time) invaded Lake Geneva (probably since 1965) and represented more than 10% of the phytoplankton. The journalist wrote "Where the algae settle, there is a noticeable darkening of the water color, a decrease in oxygen, a change in the biological regime, and the disappearance of certain species of fish. The alarm call is therefore fully justified". Interestingly, while we know this is not true, he also wrote: "*Oscillatoria rubescens* is neither toxic nor dangerous to health, and its presence does not mean that the water will be less drinkable." The end of the article is nearest from the reality when the journalist concludes: "But it indicates that the condition of a lake has suddenly worsened and will continue to deteriorate". (article dated 7 September 1975, in "Tribune de Genève"). New episodes of proliferations occurred in 1979 and during the autumns 1985 and 1992. *P. rubescens* has been studied at different occasions in Lake Geneva (Anneville et al. 2015; Carratalà et al. 2023; Derot et al. 2020; Gallina et al. 2017). All these studies revealed that *P. rubescens* has long been the dominant species among the cyanobacteria and is likely to bloom again in the future (see below). *P. rubescens* often proliferates under comparable environmental conditions: after a mild winter, when the water column remains stratified, *P. rubescens* can survive and even thrive thanks to its tolerance to low light intensities. This species has a high survival rate in cold, dark conditions; however, cells transported more than 80 m during winter mixing generally do not survive (Selmeczy et al. 2025). The early presence of *P. rubescens* suggests that winter stratification had been maintained. Furthermore, its maximum abundance generally occurs at temperatures close to 14 °C, highlighting its preference for specific thermal conditions within the stratified water column, typically in the metalimnion (Derot et al. 2020).

Another filamentous species whose dynamics have been partly described in Lake Geneva (Tapolczai et al. 2015) and regularly reported as problematic on several occasions (i.e., with significant impacts for professional fishing) has been *M. gracillima*. Indeed, Fishermen have been forced to temporarily stop their activities because their nets were clogged by this filamentous algae (Fig. 4). The proliferation of *M. gracillima* has not been quantified economically. We found that such proliferations of this algae, accumulating on the nets and making them visible to the fish and thus ineffective, occurred in 1966, 1972, 1976, 1992, 1996, 1997, 2001, and 2012. It is noteworthy that the producers of drinking water have also been impacted by this algae at different occasions due to the clogging of the filters in the pumping stations (person. com.). Like *P. rubescens*, this species could develop again in the future (see below). The appearance, location, duration, and intensity of *M. gracillima* blooms in Lake Geneva are still poorly understood. However, its proliferation is favored under meso-oligotrophic conditions and tends to become dominant when the annual mean concentrations of total phosphorus in the epilimnion fall below 20 µg L^{-1} (Tapolczai et al. 2015). Higher annual peaks have been observed when population growth begins earlier in the season. Key environmental drivers of *M. gracillima* blooms include the depth and strength of the thermocline, as well as early summer wind speeds, which can influence nutrient replenishment and mixing of the epilimnion (Tapolczai et al. 2015).

Some species have been reported one or two times during the period examined to bloom and impact either the functioning of the lake or a specific service. This was the case for *Fragilaria* in summer 1979, and *Tribonema* in the summer 1997 and 1998 which, like *M. gracillima*, impacted fishing activity. In contrast, *Asterionella* in 1970 and *Microcystis* in 1972 also reported as very abundant in the lake were not associated to problems. A very interesting case came from *Rhodomonas minuta* (Fig. 5), which proliferated for two consecutive years near the city of Geneva. In March 1990 and April 1991, this species proliferated spectacularly in the small lake, colouring the surface waters a reddish-brown and reducing transparency to 1 or 2 m. Following a north wind (the "bise"), the organisms were carried to the pump strainers and decomposed in the filtration chambers, which transferred a strong, unpleasant odor and taste to the drinking water of the city of Geneva. In the newspapers, one could read: "Geneva drinks red" or "the tap water smells like sewage" (article dated March 28, 1990, in "La Suisse"). This species probably multiplied due to increased availability of nutrients and optimal light and temperature conditions at the beginning of the year, which may have triggered rapid population growth.

More recently, in the summer of 2021, Lake Geneva experienced a large input of terrestrial material owing to a combination of several factors: a very rainy summer, an unprecedented rise in the lake level, and a strong northeast wind episode (named "la bise") that eroded the southern French shoreline of the lake (Irani Rahaghi et al. 2024). Organic matter, particularly organic carbon from

Fig. 4 Impacts of the filamentous green algae *Mougeotia gracillima*. On the left, nets heavily clogged by algal biomass during a proliferation episode hindering professional fishing activities. On the right, seaweed fillets drying after fishing activities. These blooms considerably reduce the efficiency of fishing and illustrate the disruption of this ecosystem service. © *INRAE CARRTEL* © Druart & Balvay, 2007

Fig. 5 The bloom of *Rhodomonas minuta* and its impact include not only ecological disruptions but also a significant deterioration in water quality, resulting in a bad taste and odour in tap water. This affects the overall usability of water for consumption and other domestic purposes. On the left, the Geneva water jet colored by the presence of R. minuta. © *La Suisse.* On the right, a newspaper cover showing a person drinking tap water contaminated with *R. minuta.* © *Lémaniques*

the watershed, "fed" the lake's littoral zone in a sustained manner. This organic matter most likely led to the development of heterotrophic bacteria capable of degrading this partly refractory (humic) organic matter, making it more labile and available, while also participating in nutrient regeneration. Various bacterial populations with different functions probably succeeded each other during this period. By early September 2021, mild temperatures, strong sunlight, and calm waters added to the favorable conditions for the development of mixotrophic species (i.e., species capable of photosynthesis but also able to use organic matter, including bacterial biomass). *Uroglena sp.* benefited from these conditions and provoked a huge bloom as in 1999 (Fig. 6). Such an event serves as a reminder of how much the functioning of the lake depends on its watershed. Strong links exist between littoral and pelagic zones, suggesting that implementing scientific monitoring of the littoral zone would likely be relevant (Irani Rahaghi et al. 2024).

A little outside of the pelagic blooms mentioned above, there has been a new threat occurring during the summer 2024 with the possible danger represented by benthic cyanobacteria. A dog passed away after swimming and drinking water in Lake Geneva, where it was likely poisoned by some neurotoxins (e.g., anatoxins) produced by cyanobacteria. The analysis revealed that the cyanobacteria concerned were probably *Tychonema* and/or *Microcoleus* and probably issued, not directly from the lake but from a nearby river. In Lake Geneva, there are several dozens of tributaries likely to be a source for such benthic cyanobacteria and they could also develop in many parts of the littoral zone.

In the future, the same species and some others?

Although *P. rubescens* is the best-known harmful organism in Lake Geneva, recent studies on this species in other Swiss lakes indicate significant knowledge gaps. Suarez et al. (2023), in their study of long-term changes in Lake Hallwil, demonstrated that the depth of the maximum biomass of *P. rubescens* has deepened by an average of 35 cm per year between 1998 and 2020. The decrease in phosphorus, the increase in water transparency, and the deepening of the euphotic zone can explain the deepening of *P. rubescens*. This toxic cyanobacterium now develops about 2–3 m below the lower layer of the metalimnion, where it has direct access to nutrients that can be relatively elevated in the hypolimnion of the lake. With autumn cooling and water mixing, the significant bloom that occurs in the upper hypolimnion is then transported to the surface, resulting in red coloration and potentially dangerous toxin concentrations (e.g., microcystins) at the surface of the lake and along the shoreline. With the ongoing re-oligotrophication, the euphotic zone is expanding and favoring species whose pigment composition allows them to use green wavelengths and low light intensities at depth, which is typically the case for *P. rubescens*. Additionally, with stronger and longer stratification, the hypolimnion will increasingly become a zone where nutrients remain available throughout the growing season. The exact location and extent of *P. rubescens* development, in response to environmental gradients of temperature, light, and phosphorus, therefore need to be studied in more detail.

While *P. rubescens* is indeed the dominant cyanobacterium in autumn/winter, its abundance drops in the spring, and the picocyanobacteria cluster takes over in the summer, with concentrations reaching more than 10^5 cells mL^{-1} (Jacquet, 2025). This finding regarding the quantitative importance of these picocyanobacteria during the summer has been described (Parvathi et al. 2014, 2012; Personnic et al.

Fig. 6 Bloom of *Uroglena* sp. in Lake Geneva visible across the entire lake and from space. At the top, false-color image, obtained from one of the European Space Agency's Sentinel-2 Earth observation satellites developed under the Copernicus program, on September 6, 2021 (©Copernicus). At the bottom, photographs (©sjacquet) taken in Thonon-les-Bains, in front of INRAE CARRTEL, on the same day. Each milliliter of surface water contained several hundred to thousands of *Uroglena* sp. cells

2009), but the novelty lies in the detection of genes coding for microcystin, particularly the *mcyA* gene (Carratala et al., person. com.). This gene was measured throughout the year 2024, while microcystin itself peaked at the end of the summer (with, however, concentrations to date below the values recommended by the WHO, i.e., around 1 and 10 μg/L for drinking water and recreational activity purposes, respectively). A major concern is that this group of cyanobacteria could increase in the future, with both re-oligotrophication and temperature increase in surface water of the Lake. Therefore, we have a still unidentified toxin-producing cyanobacterium that seems to dominate the cyanobacterial community in the summer, during the peak recreational use of the lake, and we know almost nothing about it. Unlike *P. rubescens*, the *Cyanobium-Synechococcus* cluster is found in the upper part of the lake, the epilimnion, where recreational activities take place (Fig. 7). A better understanding of abundance (cell count and biovolume over time and space) is now necessary, and this should be done year-round. Further studies on the toxins produced—types and concentrations—would also be necessary as a basis for risk assessment during the summer.

In a more recent case (2015), *M. gracillima* developed rather unexpectedly in response to the re-oligotrophication of the lake. This species typically thrives under phosphorus levels between 5 and 15 μg L^{-1}, while its seasonal dynamics are strongly influenced by water stratification. This filamentous taxon, resistant to sedimentation, is clearly at risk of being competitively "selected" over other algae in a lake that is becoming increasingly stable (Tapolczai et al. 2013). If phosphorus concentrations do not drop below 5 to 10 μg L^{-1} in the 0 to 20 m layer, and if warm weather and stable hydrological conditions occur more frequently in the coming years (as expected), blooms in the lake will likely reappear. As with its competitor *P. rubescens*, a more in-depth study is now required.

As mentioned above, at the end of summer 2021 (September) *Uroglena* sp. bloomed in Lake Geneva because it benefited from very specific conditions, following a succession of events (climatic, hydrologic and biogeochemistry), that explained its proliferation for several days (Irani Rahaghi et al. 2024). This scenario is likely to repeat in the future with the increase in extreme weather events and their consequences on watershed-lake relations. Indeed, the summer 2021 episode reminded us of how much the functioning of the lake is strongly dependent on its watershed. There are close links between littoral and pelagic zones, so

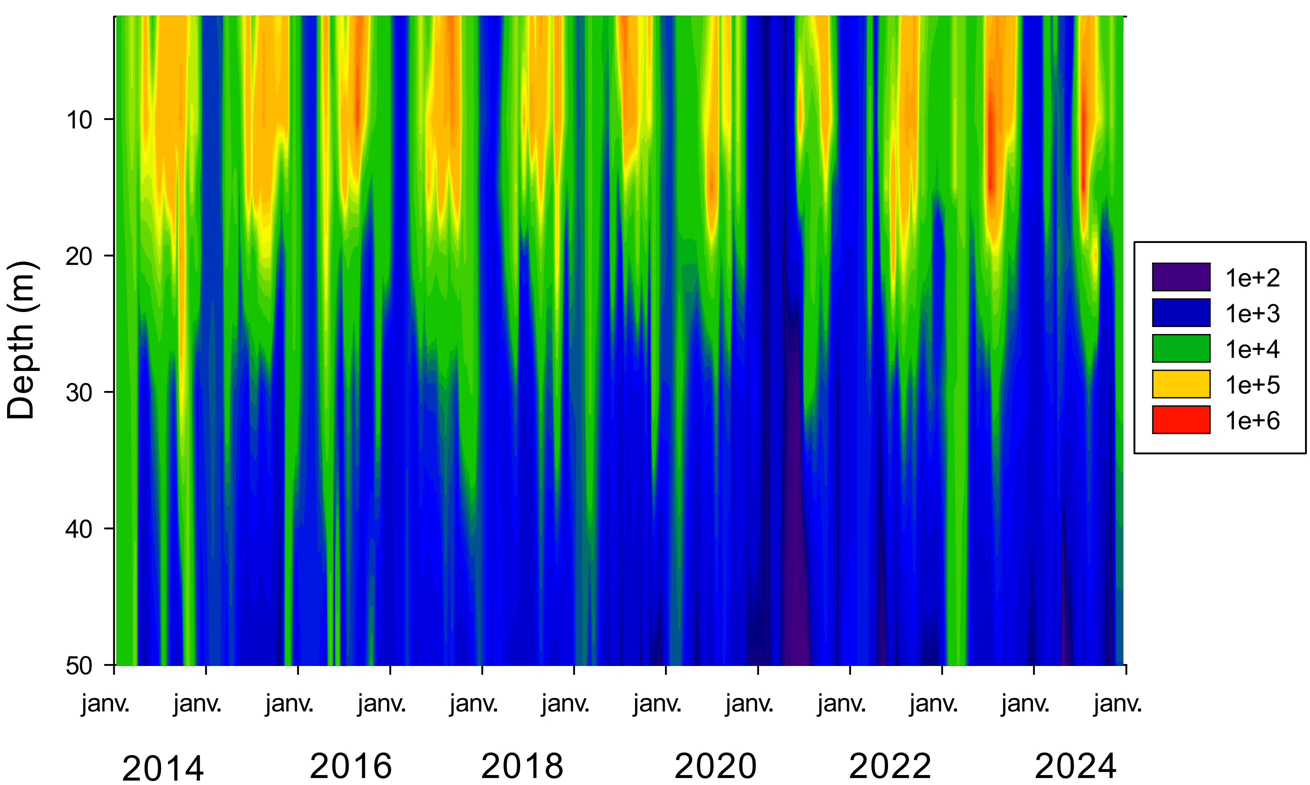

Fig. 7 Spatio-temporal dynamics of phycoerythrin-rich picocyanobacteria in surface waters of Lake Geneva at SHL2 between 2014 and 2024. Cell concentrations (cells mL^{-1}) were measured at 2, 10, 15, 20, 30, and 50 m by flow cytometry. Concentrations are maximal in the 0–15 m layer especially in summer

the implementation of scientific monitoring of the littoral zone, which is currently lacking, would certainly be relevant.

Compared with pelagic species, benthic cyanobacteria became a new threat that emerged recently. The risks associated with benthic cyanobacterial mats in the western alpine region became evident with the death of several dogs in Lake Neuchâtel in August 2020 and another dog in Lake Geneva in 2024. Benthic cyanobacteria remain under-studied compared with pelagic species. More broadly, studies on the development of mats are fragmented, incomplete, and generally only related to dramatic and visible incidents, such as the death of domestic animals (Quiblier et al. 2013). In Lake Geneva, we have almost no knowledge about the presence of toxin-producing cyanobacterial mats. In addition to the need for effective monitoring of these benthic cyanobacteria, genetic analysis on species and toxin-producing genes is crucial. A public awareness campaign on the possibility of canine intoxications could be suggested to local veterinarians, and in case of poisoning, information on the conditions surrounding these events would be important. This work is ongoing (Tromas et al., unpublished).

Two other cyanobacteria of interest, never observed so far in Lake Geneva, *Raphidiopsis raciborskii* (formely named *Cylindrospermopsis raciborskii*) and *Dolichospermum flos-aquae*, could deserve attention. We mention them because they have been described in other western European lakes and because, in some situations or places, Lake Geneva could sustain eutrophic conditions that seem to be important here. *D. flos-aquae* (formerly *Anabaena flos-aquae*) is a species of cyanobacteria commonly found in freshwater environments. It is known for its potential to form harmful algal blooms (HABs) that can negatively impact water quality and ecosystem health. These blooms are often associated with eutrophic conditions, where an excess of nutrients, particularly nitrogen and phosphorus, promotes rapid cyanobacterial growth. In lakes and reservoirs, *Dolichospermum flos-aquae* can form dense blooms, especially during warm summer months. The species thrives in calm, nutrient-rich waters and can dominate the phytoplankton community under favorable conditions. These blooms can pose serious ecological and public health risks, as *Dolichospermum flos-aquae* produces toxins, including microcystins, which are harmful to aquatic life, animals, and humans. One of the challenges of managing blooms of *Dolichospermum flos-aquae* is their unpredictability. They can occur suddenly and be difficult to detect until the bloom reaches a large scale. During such events, the toxins produced by the cyanobacteria can contaminate drinking water sources, making them unsafe for human consumption. Additionally, these toxins can accumulate in fish, affecting local fisheries and wildlife. In some cases, *Dolichospermum flos-aquae* blooms may lead to oxygen depletion in the water, which can result in fish kills and further disrupt the aquatic ecosystem. The occurrence of *Dolichospermum flos-aquae* blooms has been linked to global climate change, with warmer temperatures, altered rainfall patterns, and increased frequency of extreme weather events favoring their development (Pham et al. 2017; Kapkov et al. 2019). Effective management strategies for *Dolichospermum flos-aquae* blooms require comprehensive monitoring of water quality, including the presence of cyanotoxins, as well as the identification of nutrient sources and the implementation of measures to reduce nutrient loading in water bodies. Understanding the factors that trigger and sustain blooms of *Dolichospermum flos-aquae* is crucial for developing long-term strategies to protect freshwater ecosystems and public health from the harmful effects of these blooms (Salmaso et al. 2015). Recent research has focused on the bloom-forming potential of *R. raciborskii* due to its toxicity and the impacts it has on public and environmental health (Antunes et al. 2015). This planktonic species is native to tropical lakes and has rapidly spread across various freshwater habitats worldwide (Padisák, 1997). It appears to thrive in eutrophic waters, particularly in conditions of high-water temperatures and low light, though its growth is not heavily influenced by lower trophic levels. *R. raciborskii* can also dominate under diverse environmental conditions, such as waters with high dissolved mineral concentrations or fluctuating salinity levels (Maileht et al. 2013). The species' success in lakes around the world can be attributed to several factors, including its excellent buoyancy for daily migration, tolerance to shading, efficient ammonia uptake, ability to fix atmospheric nitrogen, high phosphorus uptake capacity, and resilience to grazing pressures.

Conclusions and perspectives

Throughout its recent history, Lake Geneva has faced a phase of eutrophication followed by a period, still ongoing, of re-oligotrophication, resulting in numerous occurrences of phytoplankton proliferation. It appears that episodes of blooms, which were relatively frequent in the 1970s, have significantly decreased, going through an intermediate period marked by proliferations of *M. gracillima* and, more rarely, *P. rubescens*. Since then, except for the two notable events of *Uroglena* in 1999 and 2021 related to heavy rainfall and a high lake level, blooms are now rarer. However, the risk remains because, from the perspective of phosphorus concentrations, the stock in the Grand Lac, estimated from the SHL2 profiles, has remained relatively constant since 2019 (around 17 µg/L for total phosphorus and 13 µg/L for orthophosphate, Tran Khac et al., 2024). It is observed that the Petit lac and the shoreline have often been impacted, and SHL2 is therefore not a good reference for algal proliferations. As evidence, the *Uroglena* bloom in 2021 was

Table 1 Management recommendations for algal bloom control in Lake Geneva

Factor or driver	Management recommendation	Expected outcome
High phosphorus and nutrient loading	Continue phosphorus reduction policies, improve wastewater treatment and control agricultural runoff	Limits eutrophication and prevents nutrient-enriched conditions that promote blooms
Water temperatures increase	Integrate climate adaptation into lake management	Limits warming-induced HAB risk, particularly cyanobacteria dominance
Extreme weather (storms, runoff)	Integrate climate adaptation into watershed management	Limits sudden nutrient influxes that can be an important trigger for bloom
Calm/low-flow conditions in tributaries	Monitor tributary flow regimes; implement flow regulations where feasible	Limits the development of benthic cyanobacteria mats that could detached and go to the lake Reduces animal/human health risks
Knowledge gaps in cyanotoxins and benthic cyanobacteria	Invest in research on bloom ecology	Provides scientific foundation for management
Ecosystem services and public health	Continue transborder governance (CIPEL); integrate water security and health risk management into bloom strategies	Protects ecosystem services and public health

scarcely "seen" at SHL2, even though almost the entire lake was affected.

The observed and expected increase in the frequency, duration, and biomass of harmful algal blooms (HABs) or toxic cyanobacteria suggests that environmental conditions are becoming increasingly favorable for their presence and development. Eutrophication remains the most straightforward explanation, with increased nutrients fertilizing phytoplankton and allowing cyanobacteria, in many cases, to "win the race" (Table 1). However, in some situations, the growing incidence of HABs seems disconnected from nutrient inputs, with blooms occurring at unexpected times (e.g., in winter) and in unpredictable places (e.g., oligotrophic lakes). Cyanobacteria, to name just one example, can grow or even form blooms even when concentrations of dissolved mineral phosphorus and/or nitrogen are below the limits of analytical detection. Furthermore, weak correlations have been reported between traditional water quality parameters and (cyano)toxin concentrations (Tran Khac et al., 2024, Chorus and Welker, 2021). It is therefore essential to better understand the strategies of these microorganisms in overcoming phosphorus and/or nitrogen limitations to propose control and mitigation solutions for blooms. Moreover, the unpredictable behavior of cyanobacteria calls for not only new considerations on the best ways to control these water blooms but also the adaptation of our risk assessment and management mechanisms to prevent exposure of the population around Lake Geneva to toxins. This highlights the need to implement real-time monitoring and use remote sensing to be more responsive (as observations are more frequent, Table 1).

Climate change is expected to cause significant alterations in lake ecosystems by affecting their thermal regimes, physical structure, biogeochemical processes, and biotic interactions, ultimately reshaping their overall dynamics. Additionally, societal demand for water will evolve both qualitatively and quantitatively, necessitating the development of strategies and adaptive management plans to address the consequences of these changes on various lake ecosystem services. In this context, Lake Geneva, as a model transboundary ecosystem, provides an ideal setting for developing future governance strategies (Table 1).

Harmful algal blooms can have significant impacts on Lake Geneva. In addition to local and global stressors that may influence their occurrence, invasive species could also play a crucial role. For instance, the proliferation of quagga mussels in the lake over the past decade could be linked to increased phosphorus cycling, which, in turn, may exacerbate harmful algal blooms in areas where these mussels are present (Tang et al. 2014; Beisel 2021).

At last, combined with increased development and the impacts of climate change—such as rising air temperatures, droughts, and more frequent storm events—sediment-derived nutrients, particularly phosphorus (along with nitrogen), may contribute to the proliferation of cyanobacteria during critical periods. Although recent research has highlighted the role of legacy nutrients in lake sediments in fueling the growth of cyanobacteria, studies dedicated to this remain scarce.

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Data availability No datasets were generated or analyzed during the current study.

Declarations

Conflict of interests The authors declare no competing interests.

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