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Long-term impacts of nutrient control, climate change, and invasive clams on phytoplankton and cyanobacteria biomass in a large temperate river

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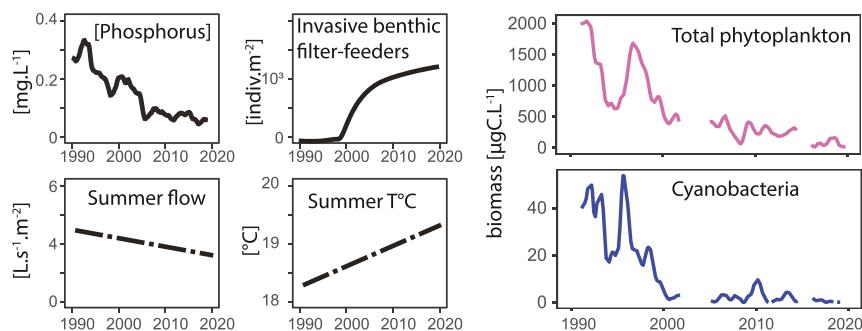
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HIGHLIGHTS

- Planktic algae and cyanobacteria may respond to alterations of rivers temperature and flow.
- The River Loire has been affected by P reduction, altered flow pattern, and Asian clam invasion.
- Algal and cyanobacterial biomasses have decreased ~10-fold over three decades.
- During this time, cyanobacterial contribution has remained low but community composition has changed.
- Phosphorus reduction may be an effective measure to mitigate climate change impacts.

GRAPHICAL ABSTRACT



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ABSTRACT

Recent studies suggest that climate change, with warmer water temperatures and lower and longer low flows, may enhance harmful planktic cyanobacterial growth in lakes and large rivers. Concomitantly, controlling nutrient loadings has proven effective in reducing phytoplankton biomass especially in North America and Western Europe. In addition, the impact of invasive benthic filter-feeder species such as *Corbicula* on phytoplankton has largely been overlooked in large rivers, leading to even more uncertainty in predicting future trajectories in river water quality.

To investigate how nutrient control, climate change and invasion of benthic filter-feeders may affect phytoplankton biomass and composition, we assembled a large database on the entire water course of the River Loire (France) over three decades (1991–2019). We focus on cyanobacteria to provide an in-depth analysis of the 30-year trend and insights on future possible trajectories. Since 1991, total phytoplankton and cyanobacteria biomasses have decreased 10-fold despite warmer water temperature ($+0.23\text{ }^{\circ}\text{C}\cdot\text{decade}^{-1}$) and lower summer flow ($-0.25\text{ L}\cdot\text{s}^{-1}\cdot\text{km}^{-2}\cdot\text{decade}^{-1}$). In the long-term, the contribution of planktic cyanobacteria to total biomass was on average 2.8%. The main factors driving total phytoplankton and cyanobacteria biomasses were total phosphorus (4-fold decrease), the abundance of *Corbicula* clams (from absence before 1998 to $250\text{--}1250\text{ individuals}\cdot\text{m}^{-2}$ after 2010), the duration of summer low flows and the intensity of summer heatwaves. The

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River Loire constitutes an example in Europe of how nutrient control can be an efficient mitigation strategy, counteracting already visible effects of climate change on the thermal regime and flow pattern of the river. This may hold true under future conditions, but further work is needed to account for the climate trajectory, land and water use scenarios, the risk of enhanced benthic biofilm and macrophyte proliferation, together with the spread of invasive filter-feeding bivalves.

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1. Introduction

There has been widespread concern that climate change, combined with eutrophication, would increase the occurrence of potentially toxic cyanobacteria blooms in freshwaters (O'Neil et al., 2012; Paerl and Huisman, 2009), threatening the water quality of inland waters (Brooks et al., 2016). Major underlying factors would be warmer water temperatures and enhanced thermal stratification in lacustrine environments (Kraemer et al., 2017; Woolway et al., 2020). In nutrient-rich lakes, longer periods of drought increase water residence times, allowing more time for slow-growing phytoplankton such as buoyant cyanobacteria to bloom (Reynolds, 2006).

Algal blooms are also a global environmental threat in rivers (Wurtsbaugh et al., 2019; Xia et al., 2019). However, while eutrophication is common in large rivers, planktic cyanobacteria blooms have rarely been reported, even in the most eutrophic conditions. In most rivers, short water residence time and turbulent and turbid flow constrain slow-growing phytoplankton (Reynolds et al., 1994). With a few exceptions, bloom-forming cyanobacteria usually thrive in nutrient-rich, warm, stratified water columns (Humbert and Fastner, 2017), conditions which are not commonly met in rivers. However, occurrences of cyanobacterial blooms, comprising potentially toxic strains, have long been reported in rivers, e.g. Potomac River, Maryland (Krogmann et al., 1986), the Ohio River (Wehr and Thorp, 1997), the Mississippi River (Reinhard, 1931), the lower Neuse River (Lung and Paerl, 1988), and the Rhine River (Ibelings et al., 1998). In some cases, these observations can be explained by an origin of blooms from lakes located upstream in the watershed. For instance, Ibelings et al. (1998) showed that the presence of *Planktothrix agardhii* and small Chroococcales in the River Rhine in the Netherlands originated from a bloom in Lake Untersee, Germany, located 800 km upstream. Cyanobacterial blooms may also appear in river impoundments (Lehman, 2007) or in the tidal section of rivers (Robson and Hamilton, 2004). In non-impounded rivers, dead zones may provide slow-growing cyanobacteria with opportunity to build populations that act as an inoculum to the main channel (Reynolds, 2000). Flow reduction, expected from water abstraction and climate change (Abbott et al., 2019), is also a key factor that may increase the risk of harmful bloom development in rivers by increasing water residence time (Oliver et al., 2012). It is then understandable that, in a context of climate change, there has been increasing concern that cyanobacteria and cyanotoxins might occur more frequently in large rivers, as shown by a recent study in large rivers of the USA (Graham et al., 2020). The authors emphasized that future changes in flow regime and temperature would result, in the most eutrophic rivers, in increased incidences of cyanotoxin-producing taxa. Another study in the Upper Mississippi River (Giblin and Gerrish, 2020) drew similar conclusions, insisting that management measures such as phosphorus control and reconnection of backwaters, providing more flushing of those water bodies, would be necessary to counteract the effect of climate change on water temperature and discharge.

The successful control of nutrient point sources over the decadal timescale has frequently been reported, especially in Western European rivers since the 1970s (Ibáñez et al., 2008; Ibáñez and Peñuelas, 2019; Le Moal et al., 2019). In most cases, the long-term decline in phosphorus concentration has also been followed by reductions in phytoplankton biomass (Abonyi et al., 2018; Floury et al., 2012; Hardenbicker et al., 2014; Ibáñez and Peñuelas, 2019; Istvánovics and Honti, 2012; Minaudo et al.,

2015; Romero et al., 2016). However, climate related factors, like discharge, light conditions and water temperature, may also control phytoplankton bloom dynamics in large rivers at the inter-annual scale (Garnier et al., 2018; Hardenbicker et al., 2014). The massive invasion of exotic benthic filter-feeder Asian clams, *Corbicula*, since the 1980s in European and American river networks may also be an important driver of phytoplankton over interannual to decadal timescales (Brancotte and Vincent, 2002; Pigneur et al., 2014). Asian clams have been reported in high density, up to several thousand individuals $\cdot m^{-2}$ with a filtration rate ~ 16 to $745 \text{ mL} \cdot \text{indiv}^{-1} \cdot \text{h}^{-1}$ (see e.g. Cohen et al., 1984; Vohmann et al., 2010). Consequently, they can exert an intense top-down control of phytoplankton biomass in large rivers and become a primary environmental driver (Floury et al., 2013; Pigneur et al., 2014). In addition, feeding selectivity may alter phytoplankton composition by preferential feeding on diatoms and avoidance of cyanobacteria (Bolam et al., 2019).

Accordingly, nutrient input reduction, climate change and the invasion of exotic benthic filter-feeders are three potential drivers of the long-term phytoplankton biomass and composition in European large rivers. They can act simultaneously and likely antagonistically across multiple timescales. However, their relative importance remains largely unclear, making the long-term effects of multiple anthropogenic pressures unpredictable on river ecosystems. Our knowledge is still elusive about basic questions such as: Can we safely expect the control of nutrient inputs in large rivers to counteract the effects of climate change on phytoplankton biomass and composition, like enhanced cyanobacteria growth? What exactly has been the role played by invasive clams and what can we expect in the coming decades?

In the 1980s and the 1990s, chlorophyll-a concentration in many European and North American rivers reached values well above the threshold needed to be classified as eutrophic (Dodds and Smith, 2016). The Loire River was, at that time, considered as the most eutrophic European river (e.g. Crouzet, 1983), with chlorophyll-a exceeding $300 \mu\text{g} \cdot \text{L}^{-1}$ in its middle river section (Minaudo et al., 2015). Since then, the river has undergone multiple changes: i) nutrient loads decrease with altered elemental ratios due to phosphorus load mitigation (Minaudo et al., 2015), resulting in P-limited conditions for phytoplankton growth (Descy et al., 2011; Floury et al., 2012; Garnier et al., 2018; Minaudo et al., 2018, 2015); ii) long-term increase in water temperature, together with extended low-flow conditions (Arevalo et al., 2020; Moatar and Gailhard, 2006); iii) substantial decrease of suspended matter concentration, especially during summer (Minaudo et al., 2016), and iv) massive invasion of the exotic benthic filter-feeders *Corbicula* in the river network (Floury et al., 2013), which, as expected also impacted phytoplankton biomass. Therefore, the River Loire is an excellent system to disentangle the long-term effects of all these environmental changes on phytoplankton and cyanobacteria biomass and composition.

In this study, we investigated the influence of these competing variables on phytoplankton and cyanobacteria biomass over multiple decades in the Loire River. To achieve this, we used time-series decomposition analysis and multivariate analysis on monthly data collected during the period 1991–2019. Furthermore, we detailed the short-term dynamics of cyanobacteria in the middle section of the Loire River by collecting and analysing plankton samples every three days during the summers 2012 to 2014. As a consequence of nutrient control and clam invasion, we expected the relative contribution of planktic cyanobacteria biomass to remain limited over the long-term.

2. Material and methods

2.1. Study sites

The River Loire, 1012 km long, is the longest river in France. It originates from the Hercynian Massif central (source at 1408 m a.s.l.), flows northwards until Orléans, where it turns west, flows over a sedimentary plain while receiving water from several large tributaries (Cher, Vienne, Maine), and then outflows into the Atlantic Ocean at Saint-Nazaire (Fig. 1). The Loire catchment covers $117 \cdot 10^3 \text{ km}^2$ ($\approx 20\%$ of France), with large influences from domestic, agricultural and industrial activities on its water quality (Minaudo et al., 2015) and can be separated in three sectors. The Upper Loire goes from the headwaters to Nevers (station S2), just before the confluence with the Allier River. The Middle Loire (downstream S2 to S5b) constitutes an elongated river corridor with minor tributary inputs (+140% increase in river length for only 30% increase in total catchment area). The Lower Loire, after S5b and the confluence with the River Cher, receives a series of major tributaries before entering its lowermost section from Montjean (S6). The annual mean water discharge at S6 is $843 \text{ m}^3/\text{s}$ (1863–2019, <http://www.hydro.eaufrance.fr>) considered as the lowermost river section without estuarine influence (Oudin et al., 2009).

2.2. Data collection

Here we present a long-term dataset (1991–2019) on 6 sampling stations covering the entire length of the Loire without the estuarine

influence (Fig. 1). Sampling was conducted by the Loire-Bretagne Water Authority at the following sites: Malvalette (S1, river km 150 from the source), Nevers (S2, rkm 451), Gien (S3, rkm 564), Orléans (S4, rkm 633), Chaumont (S5, rkm 712) and Montjean (S6, rkm 895). We also used a short-term phytoplankton dataset, based on samples collected every three days at stations S3, S5b (Cinq-Mars) and S6 over the period 2012–2014 within a research program led by University of Tours (Minaudo et al., 2018).

Long-term sampling on a regular basis for the monitoring of water quality was conducted by the Loire-Bretagne Water Authority (<http://osur.eau-loire-bretagne.fr/expertosur/Accueil>). For this study, we selected data covering the period 1991–2019. Water samples were collected monthly, from March to November except in stations S4 and S6, where the sampling frequency was twice monthly. Surface water was collected from the middle of the water course using buckets, from bridges crossing the river, and sent immediately to laboratories for chemical and phytoplankton analyses. For this study, we extracted time series for nitrates (NO_3^-), total and dissolved reactive phosphorus (TP and SRP, respectively), total suspended solids (TSS), silica (SiO_2) and chlorophyll-a (Chl-a). Some analytical techniques changed over time, in particular for phosphorus, with changing detection limits. Years when the lowest concentrations of SRP reached in summer were under the detection limit of $50 \mu\text{g P L}^{-1}$ were discarded for all subsequent analyses.

All phytoplankton samples (here forth phytoplankton refers to both algae and cyanobacteria) were analysed by the same laboratory (Bi-Eau Consultancy, Angers), during the entire study period 1991–2019

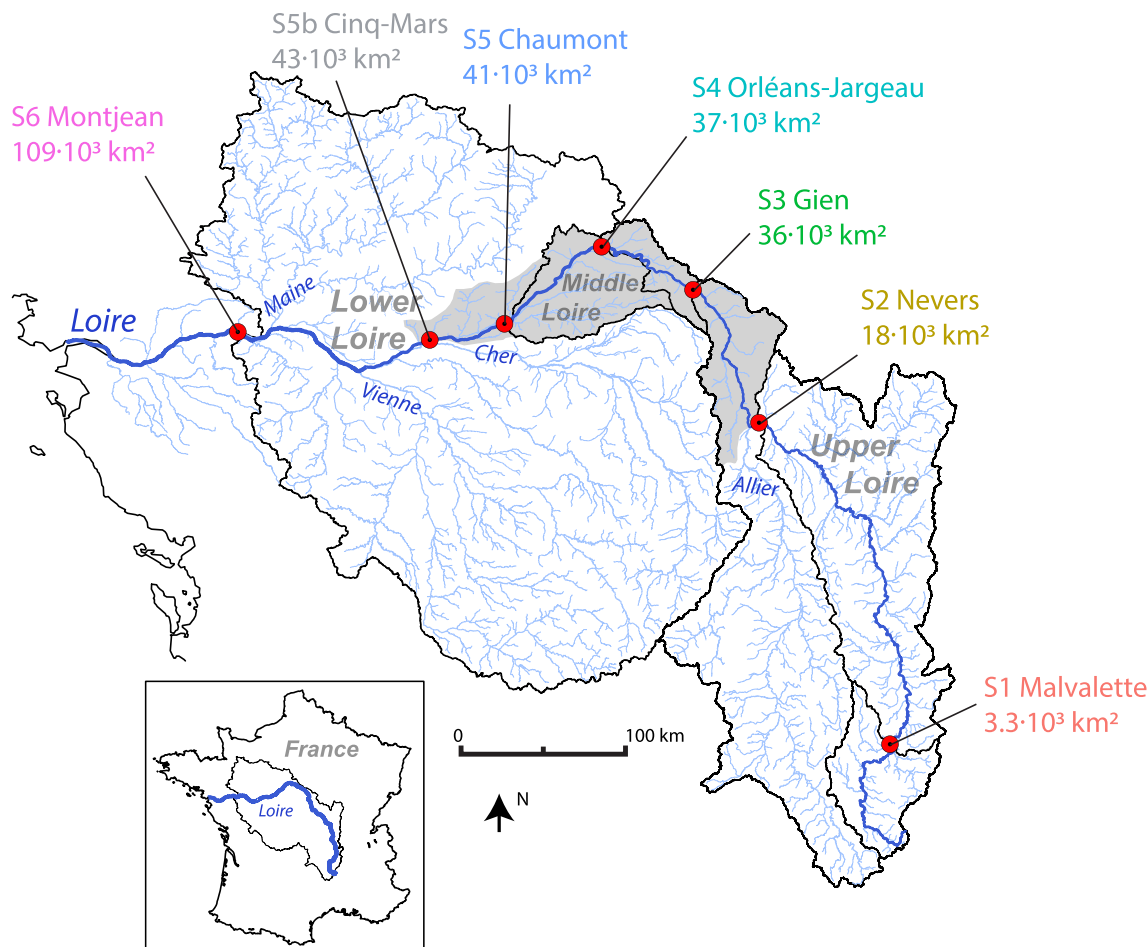


Fig. 1. Map of the Loire River basin, with the main tributaries and the location of the six sampling sites. Stations S1 (Malvalette) and S2 (Nevers) are representative of the Upper Loire, stations S3 (Gien) to S5b (Cinq-Mars) are part of the Middle Loire (shaded area), and Montjean (S6) is considered as representative of the Lower Loire. At each site, size of the drained area is indicated. All stations correspond to long-term monitoring sites (1991–2019) except S5b. A short-term (2012–2014) but intensive monitoring of the middle section of the Loire was carried out at stations S3 (Gien), S5b (Cinq-Mars) and S6 (Montjean).

(>1300 samples). Phytoplankton samples collected prior to 2001 were fixed in situ with formaldehyde, and with Lugol's iodine afterwards. Samples were sedimented in sedimentation chambers and taxa were counted as entities (cells, filaments, colonies) by the inverted microscope technique (Utermöhl, 1958). Before sedimentation, pressure was applied to the subsample to be counted, using a syringe, to collapse gas vesicles of buoyant cyanobacteria taxa. For each taxon, biovolume was estimated from dimensions of individuals of the Loire populations, using geometrical approximations according to Lund and Talling (1957), Hagmeier (1961) and Rott (1981). When diatoms were dominant, slides were prepared for their identification, after elimination of organic matter (treatment with hydrogen peroxide) and calcium carbonate (hydrochloric acid). The diatom slides were then mounted in Naphrax® for subsequent observations by phase contrast microscopy and diatoms were identified to the lowest possible taxonomic level. Phytoplankton biomass ($\mu\text{g C}\cdot\text{L}^{-1}$) was estimated from biovolumes using Eppley's equations (Smayda, 1978). Biomass was computed separately for each taxon present as >4 individuals \cdot sample $^{-1}$ during the counting phase. We considered a taxon to be significantly present in a single sample when its total biomass represented $>1\%$ of the total phytoplankton biomass. The short-term dataset consisted of 183 samples collected at stations S3, S5b and S6 over the summers 2012–2014 for phytoplankton and nutrients (not shown here, see Minaudo et al. (2018)) analyses. All measurements and analyses were conducted following the same protocol as mentioned above for the long-term monitoring.

Data on densities of the invasive Asian clams *Corbicula* originated from the company “Electricité de France” and were derived from benthic invertebrate samplings performed near three nuclear power plants located in the Middle Loire over the period 1991–2014. The sampling sites correspond to our study sites S3, S4 and S5, respectively. Invertebrates were sampled up to four times per year during the low-flow season, several kilometres upstream and downstream each power plant, following the protocol IQBG (‘Indice de Qualité Biologique Globale’; Verneaux et al., 1976) between 1991 and 1994 and then normalized to the IBGN field protocol (‘Indice Biologique Global Normalisé’; NFT 90–350, 2004) after 1995, (see Floury et al., 2013). *Corbicula* densities were then averaged by year at each station, resulting in an annual time series, considered representative of the Middle Loire (stations S3 to S5).

Daily river flow data at each site were available online from the French national database (<http://www.hydro.eaufrance.fr/>). Daily water temperature averages originated from the company “Electricité de France” and were measured upstream of two power plants in the Middle Loire. Daily averages of these two stations were considered as representative of the thermal regime of the entire Middle Loire (stations S3 to S5b), as in Moatar and Gailhard (2006).

2.3. Data processing and analysis

2.3.1. Long-term trends

Data analysis consisted first in the identification of long-term temporal trajectories in phytoplankton biomass and potential environmental predictors. Long-term trend components were first separated from seasonal variations using the seasonal decomposition approach by Loess-fitting (Cleveland et al., 1990; R Core Team, 2020) on averaged monthly data. Trend identification was computed for total phytoplankton and cyanobacterial biomass, nutrients (NO_3^- , TP, SRP, SiO_2 , TSS) and Chl-a concentrations, water discharge and water temperature data. Trends for *Corbicula* densities were computed directly on annual averages, disabling the extraction of any seasonal component for this variable. We conducted a systematic breakpoint detection analysis allowing two potential breakpoints in the long-term time series (R package BFAST, Verbesselt et al., 2010), and performed linear Sen's slope tests over the entire period of study (R package trend, Pohlert, 2020). A Sen's slope was considered significant when the associated p -value was below 0.05.

2.3.2. Hydrological and physical variables

A suite of indicators was defined to describe potential effects of climate change and changing water uses on river flow and water temperature over the most productive period (from April to October, named hereafter “summer” for the sake of simplicity in the text).

- P_{lowflow} was defined as the percentage of daily summer discharge below the long-term 10th percentile.
- P_{warm} corresponded to the percentage of daily summer water temperature exceeding the 90th long-term percentile. Therefore, P_{lowflow} P_{warm} could be computed on a yearly basis.
- Q_{summer} and T_{summer} corresponded to daily water discharge and water temperature averaged over the productive period.
- For each phytoplankton sample, we calculated specific water discharge and water temperature averages over 5 days preceding each sampling date. These two metrics were respectively noted $Q_{5\text{days}}$ and $T_{5\text{days}}$.

2.3.3. Multivariate statistical analysis

For the analysis of the relationships between total phytoplankton biomass and total cyanobacteria biomass and local environmental predictors, we focused on sites located in the Middle and Lower Loire (S3–S6). We analysed the fraction of variance in total phytoplankton and cyanobacteria biomass (as community matrix) explained by local environmental predictors using redundancy analysis (RDA) based on samples with no missing data in the *vegan* R package (Oksanen et al., 2019). All variables were ln-transformed except total cyanobacterial biomass and *Corbicula* density, which were both $\ln(x + 1)$ transformed. Environmental variables significantly affecting total phytoplankton and cyanobacterial biomass were first selected based on combined backward and forward selection (function *ordstep()* in *vegan*). The final significance of models was then tested by Monte Carlo permutation test (999 permutations) for each term in full models (*anova()* command by *terms* in *direct* models in *vegan*). We performed the RDA on the long-term dataset (stations S3–S6, 1991–2019, statistical population $n = 115$) based on annual averages of all parameters (or seasonal metrics derived on a yearly basis).

3. Results

3.1. Long-term trends of phytoplankton biomass and abiotic drivers

Total phytoplankton biomass (annual mean) reached a peak of $2200 \mu\text{g C}\cdot\text{L}^{-1}$ in the Middle Loire in the early 1990s (Fig. 2) and decreased 10-fold to approximately $200 \mu\text{g C}\cdot\text{L}^{-1}$ in the 2010s. Over the entire period considered here, Sen's slopes were significant for total phytoplankton biomass at all sites and presented a longitudinal increase in the magnitude of biomass decrease, from $-10 \mu\text{g C}\cdot\text{L}^{-1}\cdot\text{decade}^{-1}$ at S1 to $-280 \mu\text{g C}\cdot\text{L}^{-1}\cdot\text{decade}^{-1}$ at S6. Breakpoint analysis on long-term phytoplankton biomass trends evidenced 2005 as a major tipping point (Fig. S1). More precisely, the main breakpoints identified occurred in the years 2005, 2004, 2000, 2005, 2005, 2004 from station S1 to S6, moving downstream. Year 2005 also represented the middle point in the long-term time series being used here, therefore, we chose 2005 as a long-term cut off for subsequent statistical analyses (see Sections 3.2 and 3.3).

Cyanobacteria biomass also presented a clear decreasing trend, with significant and negative Sen's slopes from $-0.1 \mu\text{g C}\cdot\text{L}^{-1}\cdot\text{decade}^{-1}$ at S1 to $-3.1 \mu\text{g C}\cdot\text{L}^{-1}\cdot\text{decade}^{-1}$ at S6. Chlorophyll-a presented a similar trend, decreasing progressively in the 2000s at a rate of $-0.5 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{decade}^{-1}$ at S1 to $-1.9 \mu\text{g}\cdot\text{L}^{-1}\cdot\text{decade}^{-1}$ at S6, in parallel with a 4-fold decrease of both TP and SRP concentrations (Fig. 2, -0.06 and $-0.01 \text{mgP}\cdot\text{L}^{-1}\cdot\text{decade}^{-1}$ on average for TP and SRP, respectively). Simultaneously, there was a 3-fold decrease in TSS concentration at all sites except S1. Concentrations of NO_3^- presented no significant trend, despite substantial changes in agricultural practices in the 1990s; this has been linked to long hydrological time-lags existing in the Loire basin

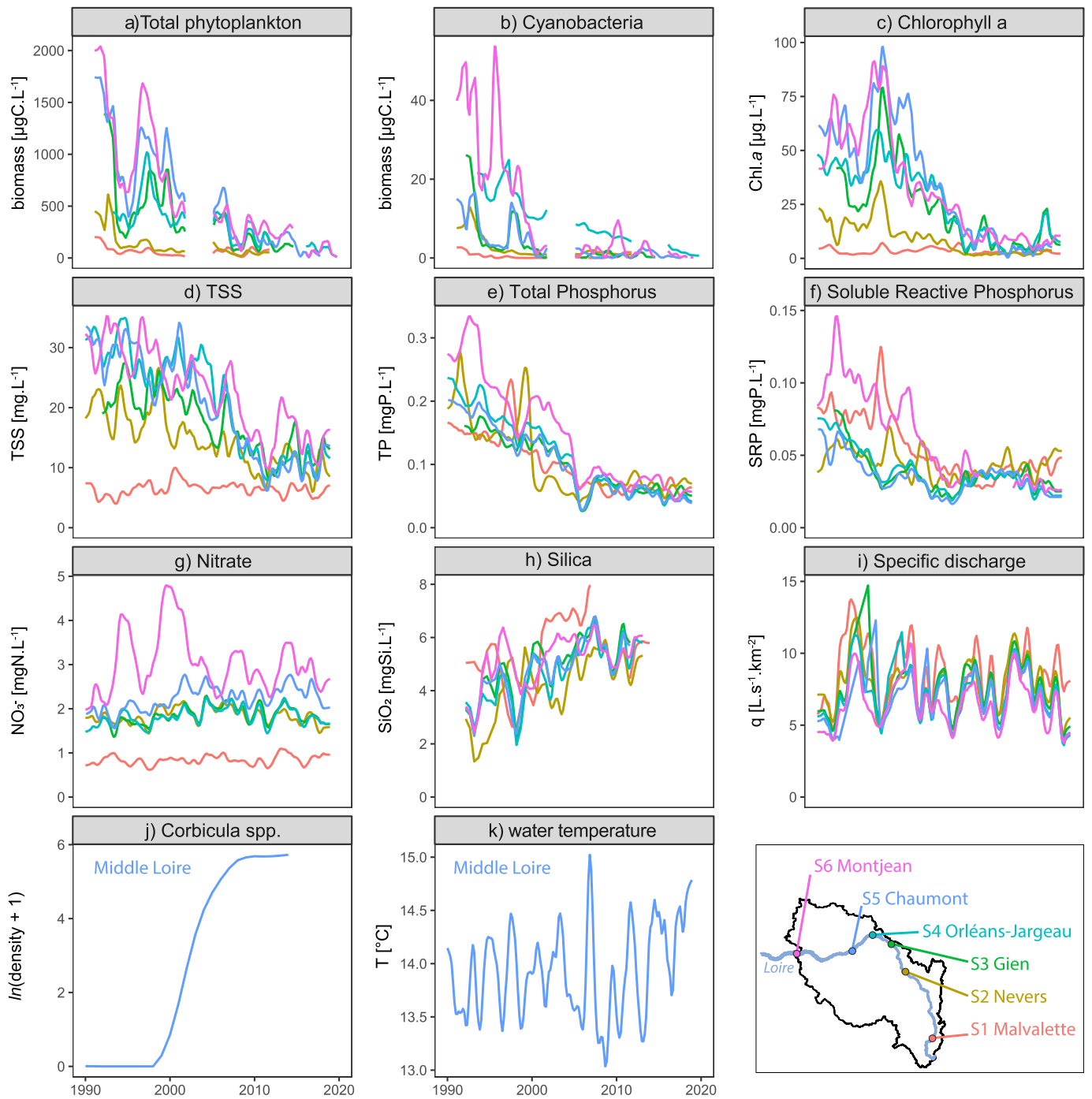


Fig. 2. Long-term trends components at the River Loire sampling sites over 1991–2019 of a) total phytoplankton biomass, b) cyanobacterial biomass, c) Chl-a concentration, d) TSS, e) total P, f) soluble reactive P, g) nitrate concentration, h) silica concentration, i) specific discharge. j) density of *Corbicula* ($\ln(X + 1)$ transformed, average values for all samples in Middle Loire), and k) water temperature near station S5 (Chaumont), which was considered representative of the whole Middle Loire. Bottom-right panel indicates the location of all 6 stations (see Fig. 1 for more details) and serves as figure legend for the other panels.

(Poisvert et al., 2017). Time series of SiO_2 concentration unfortunately did not cover the entire period of study and stopped in 2013, but the trend component indicated a gradual increase during the 1990s and 2000s, suggesting a reduced phytoplankton uptake due to decreasing diatom biomass (Minaudo et al., 2016). *Corbicula* density increased massively from strict absence of any individuals prior 1998 and reaching 250–1250 individuals $\cdot \text{m}^{-2}$ from 2010 on. It is worth highlighting that both total phytoplankton and cyanobacteria biomasses started to decline before the first occurrences of *Corbicula*, although the decline of Chl-a appeared synchronous with rising *Corbicula* densities. Finally, total phytoplankton biomass and Chl-a

presented a local maximum in the 1990s at all sites downstream of S1, concomitant with a drop in specific discharge.

The proportion of summer discharge below the long-term 10th percentile, p_{lowflow} , presented large variations synchronous across all sites, but there was no significant trend (Fig. 3a). The most recent years showed, however, an increase in summer low flow duration, with up to 40–50% of daily summer discharge below the long-term 10th percentile threshold. Annual median discharge over the productive period April–October, q_{summer} , presented slightly decreasing values over the 1990–2019 period (Fig. 3b). Sen's slope was negative ($-0.25 \text{ L} \cdot \text{s}^{-1} \cdot \text{km}^{-2} \cdot \text{decade}^{-1}$) but was non-significant (p -value =

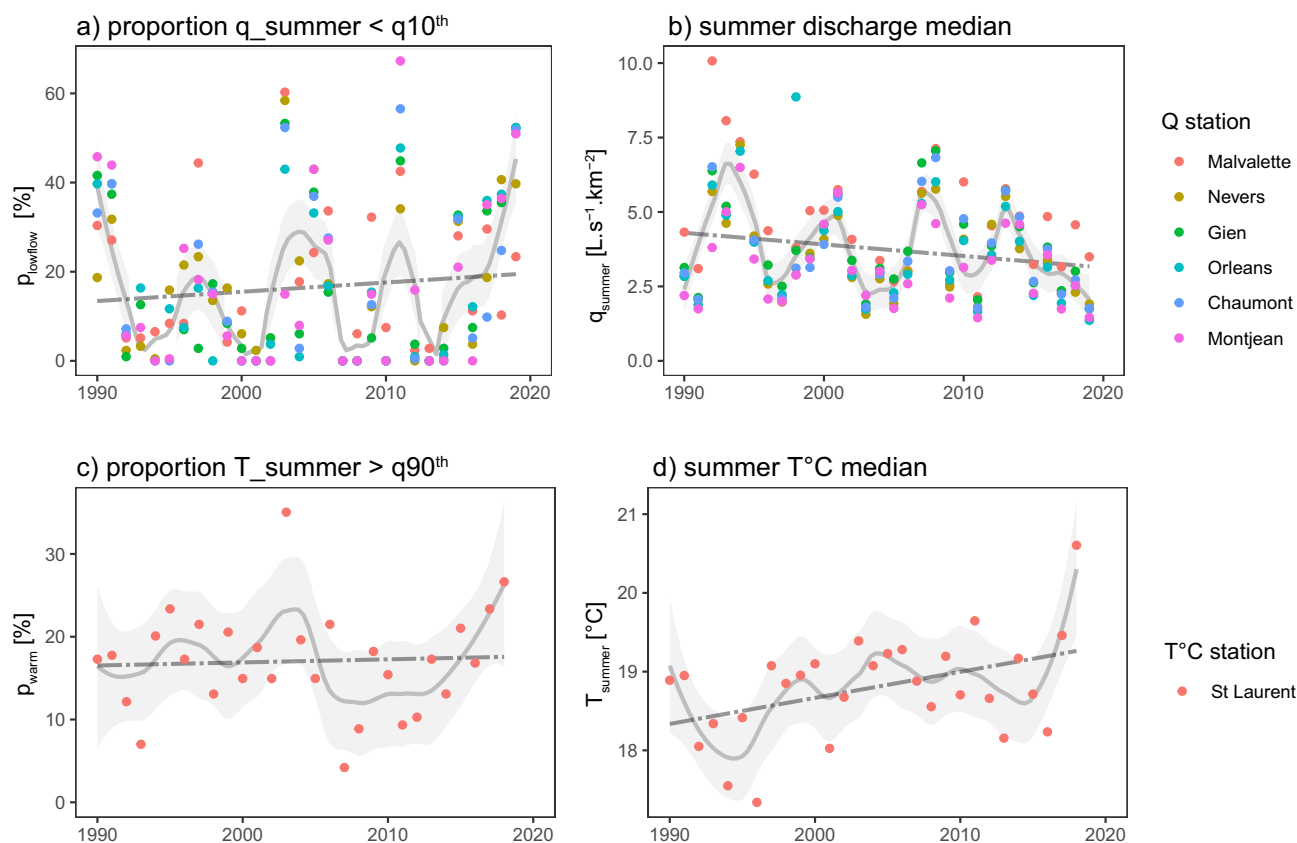


Fig. 3. Long-term evolution of hydrological and thermal metrics assumed to be sensitive to climate change. a) p_{lowflow} , proportion of daily flow in summer below the long-term 10th percentile, b) q_{summer} , summer median of specific discharge, c) p_{warm} , proportion of daily water temperature in summer above the long-term 90th percentile, d) T_{summer} , summer median water temperature.

0.39). The proportion of summer water temperature in the Middle Loire exceeding the long term 90th percentile, p_{warm} , was on average 17% (Fig. 3c). No significant Sen's slope was found over the entire period, but a recent rising trend has been observed over the 2010s from $\approx 9\%$ in 2011 to 27% in 2018. The year 2003 clearly was an extreme year with 35% of daily summer temperature exceeding the long-term 90th percentile. Annual summer water temperature median, T_{summer} , presented a significant positive trend (Sen's slope was $+0.23 \text{ } ^\circ\text{C}\cdot\text{decade}^{-1}$, p -value = 0.05) and highlighted a recent sharp increase since 2015 (Fig. 3d). The most prominent long-term water temperature increases appeared in April, June and July, and the water of the Loire is now $1.5 \pm 0.2 \text{ } ^\circ\text{C}$ warmer than in the 1990s.

3.2. Temporal and longitudinal trends in cyanobacteria biomass

Cyanobacteria biomass exceeded 1% of total phytoplankton biomass in 39% of the samples and on average accounted for 2.8% of the total phytoplankton biomass. Cyanobacterial biomass remained very low across all stations although data showed a longitudinal increase, particularly in the 1990s (Fig. 4). The highest annual average was $322 \mu\text{g C}\cdot\text{L}^{-1}$ at station S6 in 2006, i.e., 3.4% of the total annual phytoplankton biomass. June 2006 at S6 showed the highest concentration, up to $2121 \mu\text{g C}\cdot\text{L}^{-1}$, i.e., 64% of the total phytoplankton biomass, but this type of event remained extremely rare. This 2006 peak was found to originate from the Vienne River, a slow-flowing tributary meeting the Loire between S5 and S6 (data not shown). Although cyanobacteria biomass presented a significant long-term decrease, its contribution to the total biomass did not present any trend. In a floristic list of >700 taxa observed during the 1991–2019 study period, 96 cyanobacteria taxa were identified. Among these, 10 cyanobacteria genera reached a total annual biomass exceeding $10 \mu\text{g C}\cdot\text{L}^{-1}$ (Fig. 4). Filamentous forms reached 44% of the total cyanobacteria biomass, some of them being primarily of benthic origin (*Phormidium*),

and observed mainly in the Middle Loire stations. Coccoid forms (e.g. *Merismopedia*) represented up to 51% of the total cyanobacteria biomass. They were observed often, but in low biomasses.

We identified two major groups among cyanobacteria taxa. One group reached a maximum in the 1990s, and declined or disappeared after 2005: these were in particular filamentous or coccoid taxa with gas vesicles: *Anabaena* (now *Dolichospermum*), *Aphanizomenon*, *Microcystis*, *Oscillatoria* and *Planktothrix*, all these genera contain potentially toxic species. The second group of cyanobacteria was found during the entire period of study (1991–2019), with marginal or no biomass change. This second group included mostly filamentous forms from the genera *Limnothrix*, *Phormidium*, *Pseudanabaena* and one colonial coccoid cyanobacterium, *Merismopedia*. Among these taxa, only *Limnothrix* (essentially *L. redekei*) has gas vesicles.

At a finer temporal scale in the short-term dataset with intensive sampling, cyanobacteria biomass remained very low and accounted on average for 1.3% of the total phytoplankton biomass (Fig. 5). Among the most common genera, the benthic *Merismopedia* was a regular contributor; among the planktonic taxa, *Limnothrix* was mostly observed in 2013 at S5b, and *Chroococcus* showed limited occurrence in 2013 and 2014 at S5b (Fig. S2). In only three samples did cyanobacteria biomass contribute $>20\%$ to the total phytoplankton biomass, one observed in November 2014 at S3, and two in May and July 2013 at S5b (respectively samples a, b, c depicted in Fig. 5). In these three instances, cyanobacteria composition was largely dominated by one single taxon, *Planktothrix agardhii*, *Jaaginema*, and *Phormidium*, respectively.

3.3. Driving factors of phytoplankton and cyanobacteria

Environmental variables that affected total phytoplankton and cyanobacteria biomass significantly at the inter annual scale (Fig. 6) were p_{lowflow} , summer TP and p_{warm} ($p < 0.001$, in all cases),

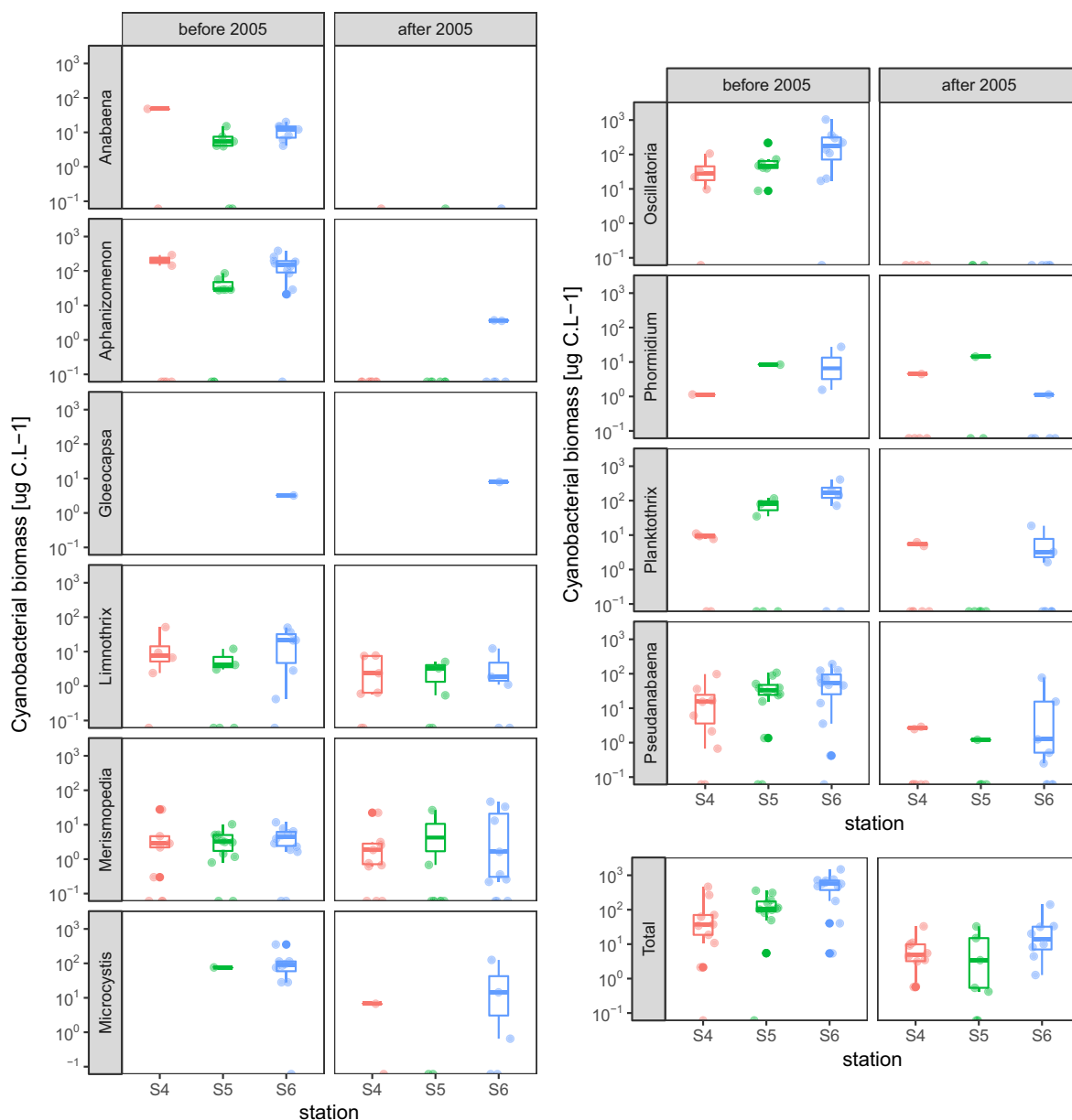


Fig. 4. Longitudinal change in the mean annual biomass ($\mu\text{g C L}^{-1}$) of the main cyanobacterial genera (total annual biomass $>10 \mu\text{g C L}^{-1}$) along the Middle and Lower Loire before and after 2005, identified as a major breakpoint in long-term total phytoplankton biomass.

and the density of *Corbicula* ($p < 0.01$). The variance in total phytoplankton and total cyanobacteria biomass explained by local environmental predictors was 73.45%. The most significant explanatory variables responsible for the distribution of years in the RDA ordination space were summer TP concentration (50% of the total variance explained), p_{lowflow} (13%), p_{warm} (6%), and *Corbicula* density (3%). The distribution of samples (years) on the RDA plot showed two contrasting periods in community composition: before and after 2005 (<2005 and >2005).

4. Discussion

In this study, we show that over a period spanning almost 3 decades (1991–2019), phytoplankton biomass has drastically decreased in the River Loire, in agreement with previous studies based on Chl-a concentration (e.g. Minaudo et al., 2015). Total phytoplankton and cyanobacteria biomass decreased at all sites since at least 1991, simultaneously with P decrease, and before any massive invasion by *Corbicula*, which developed

during the 2000s (Fig. 2). Minimum phosphorus concentrations were reached later, around the year 2005, when both Chl-a and total phytoplankton biomass had already decreased sharply.

4.1. Phosphorus input management and *Corbicula* invasion together control the long-term trends of phytoplankton and cyanobacteria biomasses

The most obvious reason behind the total phytoplankton and cyanobacteria biomass decline is a response to P reduction at all river sites. It is no surprise that cyanobacteria responded to the P reduction: cyanobacterial blooms tend to occur in lakes and ponds with relatively high total phosphorus $>50 \mu\text{g L}^{-1}$ (Humbert and Fastner, 2017). Correspondingly, common bloom-forming taxa (*Dolichospermum*, *Microcystis*, *Planktothrix*), have relatively high half-saturation constants for P (Kohl and Nicklisch, 1988; Riegman and Mur, 1984) when compared to other phytoplankton groups. Our data on the changes of cyanobacteria over time in the River Loire are in line with the fact that bloom-forming cyanobacteria depend on high concentrations of bioavailable

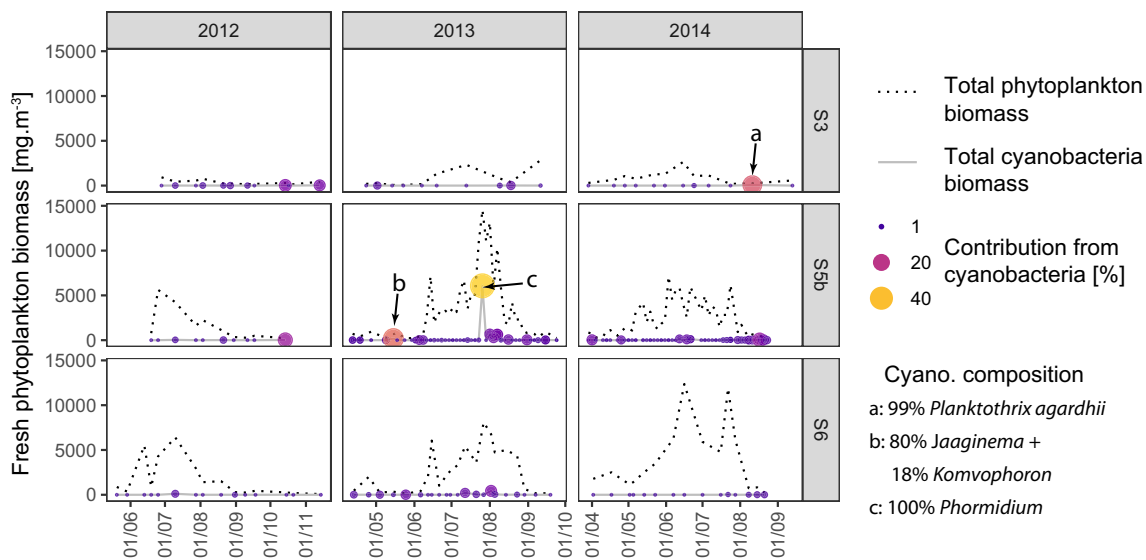


Fig. 5. Total phytoplankton (dotted lines) and total cyanobacteria (grey line and coloured dots) fresh weight biomasses observed in the Loire River at station S3, S5b, and S6 over a short-term extensive sampling (summers 2012–2014). Colour scale and size of the dots indicate the contribution of cyanobacteria to total biomass for each sample. Cyanobacteria exceeded 20% of the total biomass in three samples, indicated with arrows a, b, c. For these samples, the dominant cyanobacteria genera are given in the legend.

phosphorus. There is evidence that other phytoplankton groups in the river also became P-limited, albeit to a lesser extent. Accordingly, Descy et al. (2011) showed on the River Loire that both diatoms and green algae experienced some degree of P limitation during the year 2005. It is likely that P-limitation has become even stronger nowadays, given further reduction of P inputs after 2010.

Surveys of *Corbicula* biomass in the River Loire showed that the invasive clams can reach densities between 200 and 1200 individuals/m², depending on substrate, water velocity and season, but with a great spatial heterogeneity. Such *Corbicula* densities, however, may have a significant impact on phytoplankton abundance when the river is invaded

along hundreds of kms (Pigneur et al., 2014). The maximal impact is expected under summer low-flow conditions, when the adult clam population peaks, potentially resulting in a dramatic decrease in phytoplankton biomass after a spring maximum. The RDA analysis (Fig. 6) presented *Corbicula* density as a minor predictor of the total variance in phytoplankton biomass (3%). The interannual variability of benthic filter-feeders density is difficult to assess reliably due to large spatiotemporal variability (e.g. Pigneur et al., 2014). Therefore, we attempted to account for this by averaging the surveys conducted on several sites on an annual basis. While this confidently reproduces the long-term trends, the inter-annual variability remains uncertain, and therefore this variable can hardly be the most important explanatory variable in front of reliable seasonal estimates of phosphorus concentrations. Based on our reasoning on the temporal trends, given the order of magnitude of the densities reached after 2010, and considering previous works on the role played by *Corbicula* (Descy et al., 2011; Latli et al., 2017; Pigneur et al., 2014), it is likely that the impact of the massive invasion of *Corbicula* on the long-term phytoplankton biomass remains underestimated by multivariate analysis. Beyond this gradual increase in clam densities already observed over the 2000–2010 period (Floury et al., 2013), the longer time series used in the present study highlighted a plateau after 2010 which could indicate resource limitations. Recent publications (e.g. Marescaux et al., 2016) demonstrated that a combination of several exotic filter-feeding bivalves (*Corbicula* and *Dreissena*) may have an even greater impact on river phytoplankton, as these species present different feeding behaviours, influenced by seasonal activity and food concentration. Studies of long-term data from the River Meuse (Latli et al., 2017) have identified exotic predators as the main drivers of changes in macrobenthic and fish communities. Conversely, in the River Loire, changes in the macrobenthic assemblage, including the return of pollution-sensitive taxa, have been related to water quality improvements (Floury et al., 2013) brought about by successful phosphorus reduction.

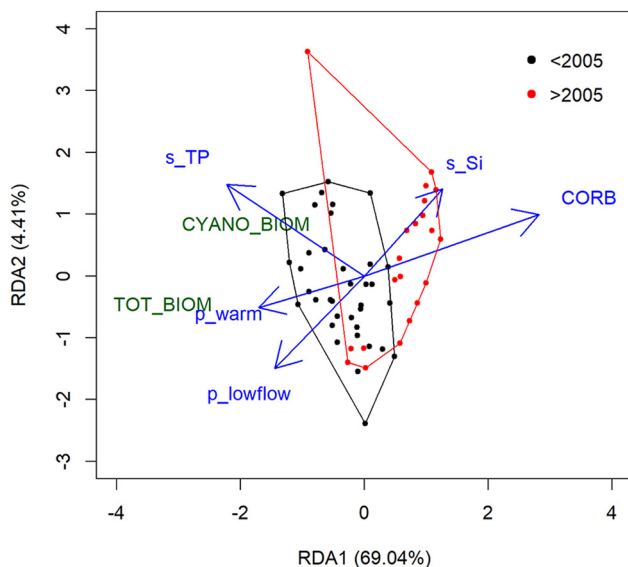


Fig. 6. Redundancy analysis (RDA) predicting interannual variation of total phytoplankton biomass (TOT_BIOM) and total cyanobacteria biomass (CYANO_BIOM) by local environmental variables in the middle section of the River Loire (France) in the study period (1991–2019). CORB: *Corbicula* density, s_TP: summer TP concentration, s_Si: summer SiO₂ concentration, p_lowflow: proportion of daily summer discharge below the long-term 10th percentile, p_warm proportion of daily summer river temperature above the long-term 90th percentile. Observations before 2005 are represented by black dots and after 2005 by red dots, separated by coloured polygons; the 2005 threshold was determined from a breakpoint analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Lotic or limnetic: where do cyanobacteria in the Loire River originate from?

Cyanobacterial biomass generally remained very low throughout the whole period of study, but showed a persistent longitudinal increase in the River Loire. The maxima were reached at the lowermost sampling station, Montjean (S6), likely favoured by longer water residence time and higher water temperatures. Both in the long-term data and in our intensive phytoplankton survey, cyanobacteria only rarely reached

relatively high abundances in the river. It is likely that cyanobacteria during these “events” actually originated from eutrophic reservoirs located upstream in the Upper basin (Jugnia et al., 2004; Misson et al., 2012; Sabart et al., 2009), and were transported downstream into the main river. In fact, reports of *Microcystis* blooms in rivers can often be linked to the presence of impoundments or of eutrophic reservoirs in the watershed. For instance, *Microcystis* colonies and associated toxins were observed over hundreds of km downstream a major reservoir of the Paraná River (Forastier et al., 2016). Similarly, the genetic structure of the populations of *Microcystis aeruginosa* in the Grangent reservoir, located in the Upper Loire basin, suggested that the colonies found in downstream sections of the river originated from the reservoir (Sabart et al., 2009).

In our study, we show that several potentially toxic cyanobacteria taxa, typical of eutrophic shallow lakes, were found in the phytoplankton of the Loire River in the 1990s, and that their biomass declined or they even disappeared after the 1990s. *Limnothrix redekei* is currently the only species that can be found at relatively high abundance in the Lower Loire. The fact that this species, which has gas vesicles and typically develops in eutrophic shallow lakes (e.g. Rücker et al., 1997), was found in the Loire River further suggests that the bloom started in a lentic environment connected to the Loire river network. As this species is adapted to turbid and turbulent conditions, and has relatively low P requirement, it has often been reported that they can maintain large populations in the main channels of large rivers (e.g. Köhler and Hoeg, 2000; Piirsoo et al., 2008). In contrast with such allochthonous species, the taxa found throughout the study period (e.g. *Merismopedia*) most likely developed in the main river channel. They have regularly been recorded in other large rivers of Western Europe (Reynolds and Descy, 1996), and are hardly bloom-forming harmful cyanobacteria.

Larroudé et al. (2013) reported a long-term increase of the cyanobacteria contribution to total phytoplankton biomass (particularly *Microcystis*) in the River Loire. It is quite possible that *Microcystis* colonies were transported from large eutrophic reservoirs in the upstream section of the river basin, and were eventually concentrated in samples taken with plankton nets in downstream river reaches. The increasing trend in cyanobacteria contribution observed in these measurements would actually result from an increasing severity of cyanobacterial blooms in these reservoirs. To the best of our knowledge, there are unfortunately no studies on the long-term evolution of eutrophication in these reservoirs to help us confirm this assumption.

In our study, the biomass of planktic cyanobacteria decreased over time, especially during the last decade, and the majority of observed taxa were not potentially toxic. From a public health point of view, the risk of adverse health effects by cyanotoxins should then remain very limited. Contemporarily, the decrease in phytoplankton biomass and summer TSS (Minaudo et al., 2016) likely resulted in increased water transparency. This may be favouring benthic biofilms, inducing a shift from planktic to benthic production, as already hypothesised for the River Danube phytoplankton (Abonyi et al., 2018), and in the Loire River (Floury et al., 2017). Such a shift may also have affected benthic cyanobacteria, as suggested by the *Phormidium* dominance presented in Fig. 5. These benthic cyanobacteria can develop under oligotrophic conditions, with low phosphorus concentration ($< 0.05 \text{ mgP}\cdot\text{L}^{-1}$, McAllister et al., 2018). Hence, the possible production of cyanotoxins remains a potential public health risk (Wood et al., 2020), regardless of the origin of cyanobacteria (planktic or benthic habitats), raising justified concerns from the water basin authorities.

4.3. What to expect in the coming decades?

The River Loire provides an excellent example showing that nutrient control has been an efficient mitigation strategy. This strategy can counteract the already visible effects of climate change and water use on the river thermal regime and its discharge pattern, both major drivers of river phytoplankton biomass and composition. Climate models predict

a 40% decrease in summer discharge in the River Loire for the period 2081–2100 (Moatar et al., 2010; Moatar and Gailhard, 2006) and an increase of +2 to 3.5 °C in water temperature (Bustillo et al., 2014) compared to the current period. Models predict even more severe warming (+3 to 5 °C) for extreme events (at the 90th and 99th percentiles), possibly due to more frequent and severe droughts with warmer air temperatures. Based on the most pessimistic climate scenario SRES A2, nutrient fluxes discharged into the Atlantic could decrease by approximately 50% by the end of the 21st century due to lower river discharge, reducing the risk of coastal eutrophication, but likely increasing in-stream nutrient concentrations due to a lower dilution capacity of point sources (Garnier et al., 2018). In turn, this would lead to a higher risk of phytoplankton blooms in the river network. In this case, some additional efforts on nutrient control would become the only option to constrain excess phytoplankton biomass production.

The present study covering three decades shows that controlling phosphorus inputs reduced the risk of cyanobacterial blooms notwithstanding higher water temperatures and lower discharge in the Loire River. Therefore, we believe that the general decreasing trend of bioavailable phosphorus in most European large rivers (Le Moal et al., 2019) due to improved waste water treatment and other nutrient management measures – most notably in agriculture – should result in the reduction of cyanobacterial blooms, or render them less likely to occur. Also, the potential impact from the invasive *Corbicula* bivalves on phytoplankton should not be forgotten. In fact, filtration activity in *Corbicula* appears to be temperature-dependent (e.g. Lim et al., 2005) and the rates at which phytoplankton is being ingested increases under lower discharge (Pigneur et al., 2014). Also, these organisms exhibit plasticity in their feeding activity influenced by physiological and environmental factors (Viergutz et al., 2012). Yet, the relative importance of filter-feeding clams in controlling the Loire phytoplankton biomass remains uncertain.

The potential increase in water transparency due to a decrease in suspended solids' concentration, nutrient control and proliferation of filter-feeding bivalves may not only favour benthic biofilms (see Section 4.2), but also enhance macrophyte growth. In fact, the effects of nutrient control on water transparency, producing a shift from phytoplankton to macrophytes dominance, have been reported in multiple occasions in shallow lakes (e.g. Scheffer et al., 1993). In large rivers, despite data scarcity on macrophytes cover, nutrient control may produce a similar regime shift, impacting the entire ecosystem and fundamentally challenging environmental management strategies (Hilt et al., 2011; Ibáñez and Peñuelas, 2019). In the Middle Loire River, recent observations of macrophyte proliferation have also been documented (Greulich et al., 2016), and may indicate that a regime shift has already occurred. This possible shift, together with a switch from planktic to benthic producers in a more transparent river needs to be further quantified by field studies.

5. Conclusion

The analysis of three decades of phytoplankton data from the Loire River shows that the reduction of P inputs together with the invasion by *Corbicula* clams were involved in the decline of phytoplankton, counteracting the potential effect of observed summer flow decrease and warmer water temperature related to climate and water use changes. Total phytoplankton and cyanobacteria biomass decreased 10-fold over the period 1991–2019. Cyanobacteria were found in very low abundance, contributing on average to 2.8% of the total phytoplankton biomass. Their biomass contribution presented no significant trend over the long-term, discarding immediate concerns on potentially increasing risk of harmful algae blooms in the Loire River. On some rare occasions, cyanobacteria biomass was higher, but careful analysis of the phytoplankton records showed that these were most probably transported from slow-flowing tributaries, impoundments or reservoirs located upstream the sampling sites.

Our results demonstrate that nutrient control in large rivers, in our case by reducing P inputs, can be an efficient mitigation strategy to counteract the expected effects of climate change on potamoplankton biomass and composition, reducing the risk of cyanobacteria blooms. This trend is likely to hold true under future conditions, but further work is needed to account for the climate trajectory, potential effects of land and water use scenarios, the potential risk of enhanced development of benthic biofilms, potential amelioration effects tied to proliferation of macrophytes, together with the spread of invasive filter-feeding bivalves.

CRedit authorship contribution statement

ML, AML and AA collected the data and conducted all phytoplankton analysis; CM and AA performed the data analyses and visualisation. FM performed trend analyses on water temperature and relationships with phytoplankton. MF provided long-term data and elements for the discussion on *Corbicula*. CM and JPD wrote the manuscript, with substantial contributions from all authors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.144074>.

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