

RESEARCH PAPER

Contrasting long-term trends and shifts in phytoplankton dynamics in two large rivers

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Knowledge about long-term dynamics of phytoplankton in river ecosystems as well as the physical and chemical drivers that potentially control the plankton is essential for predicting future developments, e.g. in response to global climate change. The present study analyzes long-term trends in phytoplankton biomass and shifts in the timing of phytoplankton spring blooms observed in the large rivers Rhine and Elbe from 1990–2009 and 1994–2009, respectively, and analyzes the factors potentially regulating phytoplankton biomass. While phytoplankton biomass in the Elbe was high (seasonal mean chlorophylla concentration: 62 µg/L) and showed an increasing tendency, it was much lower in the Rhine (seasonal mean chlorophylla concentration: 10 µg/L) where it decreased significantly during the study period. This decrease coincided with an earlier occurrence of the phytoplankton spring maximum. In the Elbe, the timing of low discharge conditions was crucial for the occurrence of the spring bloom, i.e. an earlier end of the discharge maximum was connected with an earlier spring bloom. In the Rhine, we found a positive correlation between the timing of the spring bloom and the end of winter flood flow. The maximum chlorophylla values during the bloom correlated with the timing of maximum light availability in the Rhine. The findings indicate that climate related factors, like discharge or light conditions, have a high potential to regulate phytoplankton spring bloom dynamics in large rivers. Such dependence could be relevant for predicting phytoplankton development under climate change.

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1 Introduction

Phytoplankton is a key component in large rivers, where it is often the dominant primary producer (Allan and Castillo, 2007). It has been demonstrated that native populations of phytoplankton can establish in large rivers, despite the loss of lotic phytoplankton downstream and

despite stronger light attenuation in turbid rivers (Reynolds, 1988; Dokulil, 1994; Rojo et al., 1994). While plankton dynamics have been studied extensively in lentic fresh waters such as lakes and reservoirs, comparatively little research has focused on factors that regulate phytoplankton biomass in lotic waters (Basu and Pick, 1995; Reynolds, 2000) and there is no general agreement concerning the factors that regulate phytoplankton dynamics in rivers (Thorp et al., 1994) compared with lakes (e.g. the PEG-model by Sommer et al., 1986). As phytoplankton responds quickly to local weather conditions and changes in discharge, it is probably sensitive to environmental change, including climate warming and might mediate climate-related changes in ecosystem functioning (Reynolds, 1998).

Possible factors regulating the plankton dynamics in rivers may be physical (temperature, light), hydrological

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Abbreviations: PAR, photosynthetically active radiation; RDA, redundancy analysis

(discharge, water residence time), chemical (nutrient concentrations), and biotic (grazing, competition) (Reynolds, 1988; Basu and Pick, 1997; Bukaveckas *et al.*, 2011). Sunlight is the most common limiting factor for primary production in streams (Basu and Pick, 1996). Hydrological conditions prevailing in rivers strongly influence phytoplankton dynamics, for instance short residence times (Soballe and Kimmel, 1987) or turbulence (Reynolds, 1994). Both, light climate (via turbidity and water depth) and water residence time in rivers are ultimately controlled by discharge. Changing discharge may be an indirect effect of climate change acting on phytoplankton dynamics via altered snow melt and altered precipitation, which may affect biomass dilution, particle input (and thus light climate) and nutrient input. Nutrient concentrations are mostly high in rivers affected by urbanization and agriculture and thus do rarely limit plankton growth in these systems (Reynolds and Descy, 1996). Among other anthropogenic factors that potentially alter phytoplankton are wastewater treatment effluents and the heat emission by cooling water (Friedrich and Pohlmann, 2009). Besides physical, hydrological, and chemical factors, biological factors like grazers can massively interfere with phytoplankton populations in rivers (Welker and Walz, 1998; Schöl *et al.*, 1999; Reckendorfer *et al.*, 2006). All these different physico-chemical and biotic factors are known to alter phytoplankton dynamics in rivers. However, it is insufficiently known how these individual factors act in concert, and how phytoplankton responds to changes in these factors. Furthermore, studies on the effect of climatic conditions on phytoplankton growth in rivers are still rare (Gomes and Miranda, 2001; Philips *et al.*, 2010; Desortová and Punčochář, 2011).

In temperate climates meteorological conditions are highly variable, particularly in spring and they are independent of developments during the preceding winter (Rocznik, 1995). Phytoplankton abundance in temperate rivers can be high during the complete vegetation period in spring and summer (Montesanto *et al.*, 2000; Philips *et al.*, 2000), while in other cases, low abundances prevail in summer, probably due to enhanced grazing (Weitere and Arndt, 2002). It is of major importance to identify the factors that provoke changes in the occurrence and the magnitude of the spring bloom in rivers, because phytoplankton mass developments have a huge impact on water quality and ecosystem functions (Gallegos and Jordan, 2000; Marques *et al.*, 2003). The temporal occurrence of phytoplankton spring blooms in rivers may be highly variable and is yet difficult to predict (Admiraal *et al.*, 1994). We assume that in spring, the biological variables strongly depend on the rapidly changing environmental factors. Thus, the analysis of long-term trends, including the appropriate detection of cardinal dates during spring blooms, is a useful tool to

identify relevant drivers of phytoplankton dynamics (Rolinski *et al.*, 2007).

The large central-European rivers Rhine and Elbe provide good conditions for phytoplankton development due to the long residence time of the water in both rivers. In the downstream reaches of large rivers, the density of river plankton is generally highest (Vannote *et al.*, 1980), due to longer retention times. The rivers Rhine and Elbe are highly turbulent, fast flowing and were considered to be eutrophic, phytoplankton-rich rivers (river classification according to Behrendt and Opitz (2001)). Following measures against eutrophication, like banning of phosphorus in detergents and the tertiary treatment of wastewater or reducing the inputs from agriculture, the trophic state of rivers and freshwaters was generally improved (Bloch, 2001; Grizzetti *et al.*, 2012). More recently, however, the Rhine was reassigned to be a river with a low yield of chlorophylla per unit total phosphorus (TP), whereas the Elbe was still among the rivers with a high yield of chlorophylla per unit TP despite similar ranges of TP concentrations in both rivers (Mischke *et al.*, 2011). Both rivers experienced increases in the water temperature in recent years together with an overall increase in air temperatures in central Europe (Belz and Gratzki, 2009; Kysely, 2010). Furthermore, the discharge of the Rhine changed, as it is influenced by snowmelt in the Alps during spring and early summer. An analysis of the Pardé coefficients (i.e. the long-term mean monthly discharge divided by the long-term mean annual discharge; Pardé, 1947) during 1901–2000 indicated an increase in the winter half-year in the Rhine (Belz, 2010). An opposite trend was observed during the last two decades: at Koblenz (Rhine-km 590), the Pardé coefficients of mean monthly discharge from February to July during the last decade (2002–2011) decreased significantly compared to the preceding decade (1992–2001) (Federal Institute of Hydrology – BfG, unpublished data). By contrast, in the Elbe at Magdeburg the Pardé coefficients of mean monthly discharge from March to July decreased only slightly (no significant changes) during recent years (2002–2011) compared with the preceding decade (1992–2001) (BfG, unpublished data).

The present study analyzes long-term data for the development of phytoplankton biomass in the rivers Rhine and Elbe. The key question is how the chlorophylla content and the occurrence of the spring bloom have changed over time in response to changing environmental conditions. The aim of the study is to detect trends in the phytoplankton biomass and to identify the most important physico-chemical (meteorological, hydrological, or chemical) variables that potentially govern the timing of spring phytoplankton development in both rivers.

The following hypotheses on the regulation of river plankton and on the effects of climate change are tested:

(i) The long-term development of the phytoplankton biomass in both rivers shows distinct trends in response to changing environmental conditions. (ii) The timing of discharge decline is a prominent factor controlling the initiation and magnitude of the spring phytoplankton bloom in both rivers. (iii) The timing of the phytoplankton bloom correlates with climate-related factors in both large rivers regardless of their contrasting trophic state.

2 Methods

2.1 Study sites

The Rhine has its source in the Swiss Alps. It flows through Lake Constance (Rhine-km 0) and, further downstream, forms the border between France and Germany in the canalized part of the Upper Rhine. The Rhine drains 185 260 km² in total, has a total length of 1250 km and a long-term mean annual discharge of 2300 m³/s at the end of the Lower Rhine, close to Emmerich (Germany) at Rhine-km 852 (Uehlinger et al., 2009). The main tributaries, which are important sources of phytoplankton, are the rivers Neckar, Main, and Moselle (Bergfeld et al., 2009). The measuring station Koblenz, the sampling site of the present study, is located close upstream to the river mouth of the Moselle at navigation kilometer (Rhine-km) 590 in the Middle Rhine. The station is situated approximately in the middle of the free-flowing German river reach, from Rhine-km 336, at the weir of Iffezheim, to Rhine-km 891, the weir near Driel in the Netherlands.

Recent studies on the phytoplankton development describe a decrease of mean chlorophyll-*a* values at the station Bimmen (Rhine-km 865) during the vegetation period (March 1 to October 31) from 59 µg/L in 1979 to 21 µg/L in 2004, and a concurrent decrease of anthropogenic nutrient inputs (Friedrich and Pohlmann, 2009). Hence, concerning the chlorophyll development, trophic state was higher in the 1970s and the 1980s and decreased later on.

The Elbe originates in the Giant Mountains region in the north of the Czech Republic and has a catchment area of 148 268 km² and a total length of 1094 km (Pusch et al., 2009; IKSE, 2005). The free-flowing part of the Elbe begins 38 km upstream of the Czech-German border, situated 367 km from the source. This border marks the German navigation kilometer (Elbe-km) 0, from where the free flowing section extends to Elbe-km 586 at the weir of Geesthacht. The mean annual discharge at the Geesthacht Weir is 728 m³/s (IKSE, 2005). The most important tributaries along this reach are the rivers Mulde, Havel, and Saale. The water quality measuring station Magdeburg, the sampling site of the present study, is located at Elbe-km 312, approximately in the middle of the free-flowing

river stretch. Studies relying on results of the station Schnackenburg (Elbe-Km 475) revealed that despite reduced nutrient inputs in recent years, high phytoplankton concentrations can still be observed in the Elbe with maximum concentrations of more than 200 µg/L (Guhr et al., 2004; Quiel et al., 2011).

2.2 Data origin and acquisition

From the station Koblenz (Rhine), weekly measurements of chlorophyll-*a*, water temperature, TP content, and suspended substances (German Standard Methods, DEW, 2007) of the years 1990–2009 were used (data BfG). Daily data of discharge and water-levels were taken from the upstream gauging station Kaub (Rhine-km 546) and converted to the station Koblenz (data of the Federal Waterways and Shipping Administration). The daily global radiation data originated from the meteorological station Geisenheim, located 70 kilometers south of Koblenz (49° 98'N, 7°95'E) and were provided by the German Weather Service (DWD). From the station Magdeburg (Elbe) data of chlorophyll-*a*, water temperature, TP content, and suspended substances (German Standard Methods, DEW, 2007) from 1994 to 2009, measured at biweekly intervals were used (data provided by the River Basin Community Elbe). The hydrological data for discharge and water-level on a daily basis originated from the gauging station Magdeburg (data of the Federal Waterways and Shipping Administration). The daily data of global radiation were derived from the weather station Magdeburg (52°06'N, 11° 35'E) of the German Weather Service.

2.3 Trend and peak analysis

Trend analyses of the phytoplankton biomass (chlorophyll-*a*) were performed with different variables derived from a peak analysis and with mean chlorophyll concentrations (mean over the vegetation period from March to October). For peak analysis, so-called “cardinal dates” in the time series were identified using a method proposed by Rolinski et al. (2007). The “cardinal dates” describe the timing of the start point, the mid point, and the end point of a peak in days of the year, which are identified by means of fitting a Weibull-type function. The advantage of the method is the identification of characteristic peaks and the corresponding dates from a diffuse array of sampling data points in an objectified way. The Weibull function smoothes measuring errors, and neighboring values are taken into account. It is thus appropriate to use the described method instead of choosing a certain threshold level or defining the week when maximal abundances occur in spring, which is commonly applied to determine the timing of phytoplankton spring peaks (Gerten and Adrian, 2000). When more than one peak appears in the data set, the method serves

to accomplish a peak comparison relative to the baseline, and only one peak is identified (Rolinski *et al.*, 2007). By means of this peak analysis, the dates of the start point (S), the mid point (M), and the end point (E) of the spring phytoplankton peak of each year were identified. In the year 2009, no spring peak could be identified in the Rhine, because chlorophyll values were too low. The variables derived from the peak analysis as well as the mean chlorophyll concentrations (mean over the vegetation period) were then used for a trend analysis by means of the Mann–Kendall Test. This is a non-parametric, rank-based test for statistically significant trends in data series, wherein tests for significant monotonous trends over time, relying on Kendall's correlation coefficient, are performed (Yue and Wang, 2004).

2.4 Calculation of light availability

The light availability was calculated using the Lambert–Beer law connecting the absorption of light with the characteristics of the medium (Skoog *et al.*, 2003). The photosynthetically active radiation (PAR) prevailing in the water column was calculated under consideration of global radiation, suspended substances, chlorophyll-*a* concentration, and water depth (Eq. (1–3); V. Kirchesch, BfG, Personal Communication). As the water-level of a gauging station refers to a gauge zero point, each water-level value was corrected for the actual water depth identified in the profile.

The average PAR in the water column (I , $\mu\text{E}/\text{m}^2/\text{s}$) was calculated using the PAR at the water surface (I_0 , $\mu\text{E}/\text{m}^2/\text{s}$), the extinction coefficient (ε , 1/m) and the water depth (H , m) with the following equation:

$$I = \frac{I_0}{(\varepsilon \times H) \times (1 - \exp(-\varepsilon \times H))} \quad (1)$$

The water depth (H) was calculated using water-level data on each sampling day.

I_0 was calculated using available weather data of global radiation on each sampling day (GR, $\text{J}/\text{cm}^2/\text{day}$), the length of the day with sunlight (t_{light} , h/day) as well as a reflection factor (rf) of 0.97 and a conversion factor (cf) of 5.846 ($1 \text{ J}/\text{cm}^2/\text{h} = 5.846 \mu\text{E}/\text{m}^2/\text{s}$, Harris, 1978):

$$I_0 = \frac{\text{GR}}{t_{\text{light}}} \times \text{rf} \times \text{cf} \quad (2)$$

ε was calculated empirically using water quality data, i. e. the content of suspended substances (SS, mg/L) with a corresponding absorption coefficient of 0.13 (L/m/mg) and the chlorophyll-*a* concentration (Chla, $\mu\text{g}/\text{L}$) with the corresponding absorption coefficient of 0.012 (L/m/ μg) and a Chla:Biomass ratio of 21.5 ($\mu\text{gChla}/\text{mgBio}$) (Geider,

1987), as well as a constant value for humic substances (hs) of 0.48 (1/m):

$$\varepsilon = 0.13 \times \left(\text{SS} - \frac{\text{Chla}}{21.5} \right) + 0.012 \times \text{Chla} + \text{hs} \quad (3)$$

2.5 Multivariate analysis of data

To test the relationship between the variables related to the phytoplankton spring bloom with physical, climatic, and chemical variables, a multivariate analysis of the data was performed. A redundancy analysis (RDA) was used for the identification of important variables before testing these by ANOVA for significance.

The following dependent variables that describe the phytoplankton spring bloom were included (see section “Trend and peak analysis”): start (S), mid (M), and end (E) of the spring bloom peak in days of the year, the maximum value of the measured chlorophyll-*a* in $\mu\text{g}/\text{L}$ during the phytoplankton bloom (Max), the integral beneath the Weibull function as a proxy for total mass of the phytoplankton bloom in $\mu\text{g}/\text{L}$ (Int) and the total duration of the bloom in days calculated by subtracting the day of the start of the bloom from the day of the end of the bloom (Dur).

The independent variables encompassed the TP content, date of maximum light availability (Light_M) (see section “Calculation of light availability”), the day when water temperature exceeded 10°C (T10) and 12°C (T12), and the date of mid (Q_M) and end (Q_E) of the discharge peak. The TP content was calculated as a mean value of 2 weeks before the day of the beginning of the spring bloom. For the calculated light availability (Eq. 1) the peaks were determined according to Rolinski *et al.* (2007) as described for chlorophyll-*a*, and only the date of maximal light availability, i. e. the timing of light peak maximum was included in the following analysis. For the discharge data series, the peak determination was performed similarly and only the dates of the mid and the end of the peak were included, because particular attention was paid to the decline of the discharge with regard to spring bloom occurrence. As data for suspended substances, which were required for the calculation of the light availability, were not available from the years 1990 and 1991, the analysis of the Rhine dataset begins with the year 1992.

The RDA was performed to identify potentially important control factors. Subsequently, using the previous RDA result, the significance of environmental variables was assessed by the envfit function (Oksanen, 2011). In the following multiple linear regression analysis, the different independent physico-chemical variables, which potentially influence the phytoplankton development, were included. The variables were chosen using a stepwise backward

selection, and only the variables, which showed a significant effect were used in the subsequent analysis. By means of an ANOVA, the effects of the independent on the dependent variables were analyzed. The R software (R Development Core Team, 2010) was used for all computation and statistical analysis.

3 Results

The mean concentration of TP in the Rhine from 1990 to 2009 was 0.19 mg/L and the total amount decreased from 0.31 mg/L (average in 1990) to 0.12 mg/L (average in 2009). The TP concentration in the Elbe was in a similar range (mean of 1994–2009: 0.22 mg/L) and decreased from 0.28 mg/L (average in 1994) to 0.18 mg/L (average in 2009) (Fig. 1). In the Elbe, low ortho-phosphate concentrations coincided with high phytoplankton biomass. The seasonal (March–October) mean chlorophyll-*a* concentration in the Elbe was about sixfold higher compared to concentrations in the Rhine. The seasonal (March–October) mean chlorophyll-*a* content in the River Rhine at Koblenz was 10 $\mu\text{g/L}$ and maximum values reached 100 $\mu\text{g/L}$ in the observed time period, while seasonal mean concentration in the Elbe at Magdeburg was 62 $\mu\text{g/L}$ and maximal chlorophyll-*a* concentrations of 296 $\mu\text{g/L}$ were observed (Fig. 1). A trend analysis of the seasonal mean chlorophyll-*a* concentrations revealed a significant

decrease in the Rhine (Mann–Kendall Test, $m = -0.870$; $p < 0.001$) (Fig. 2a). At the same time, in the Elbe chlorophyll-*a* values tended to increase (Mann–Kendall Test, $m = 1.556$; $p = 0.096$) (Fig. 2b).

The maximum of the spring bloom in the Rhine occurred increasingly earlier in the year during the time series 1990–2008, as demonstrated by a significant effect in the Mann–Kendall Test ($m = -2.461$; $p = 0.009$) (Fig. 3a). At the beginning of the study period in 1990, it had occurred around day 132 (beginning of May) whereas the timing of the spring phytoplankton peak shifted towards end of March (day 83) in recent years. In contrast, the date of the maximum of the spring bloom showed no significant trend in the Elbe (Mann–Kendall Test, $m = 0.177$; $p = 0.343$) (Fig. 3b).

However, these recent early phytoplankton peaks in the Rhine were much smaller than the peaks recorded in the beginning of the study period. The chlorophyll-*a* content in the Rhine at the time of the peak maximum decreased strongly in the years from 1990 to 2008 (Mann–Kendall Test, $m = -2.913$; $p = 0.001$) (Fig. 4a). In the Elbe, there was a non-significant increase in chlorophyll-*a* concentration at the time of peak maximum (Mann–Kendall Test: $m = 3.499$; $p = 0.112$) (Fig. 4b). This matches the observed trends in mean chlorophyll-*a* concentration during the vegetation period (March–October), which also showed a strong and significant decline in the Rhine and tended to increase in the Elbe (Fig. 2).

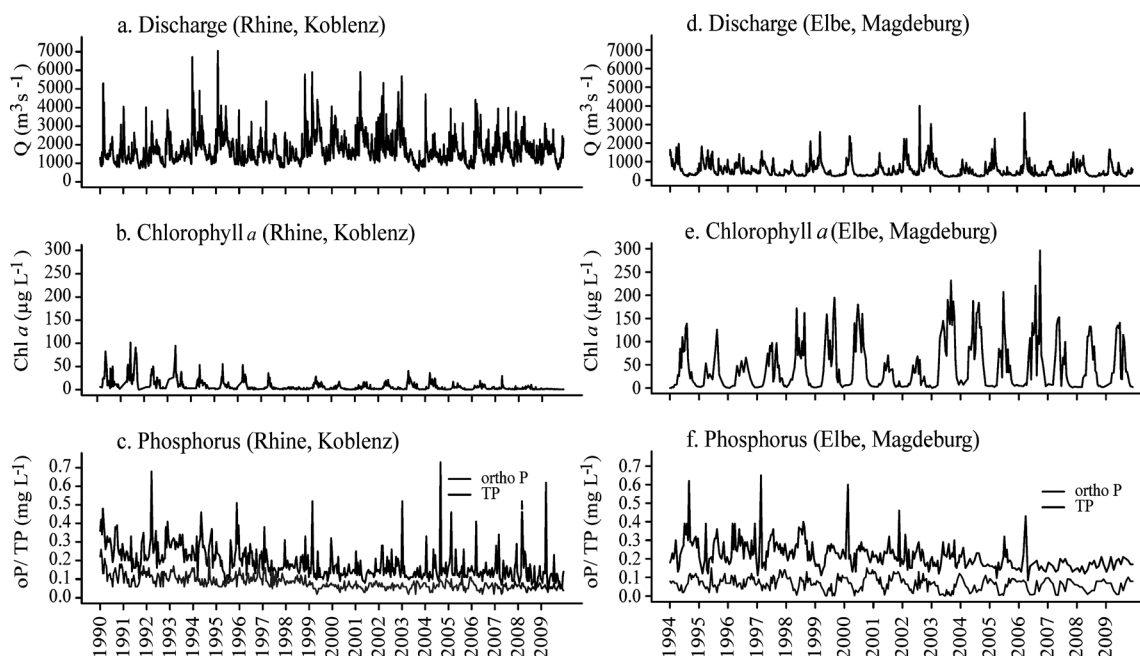


Figure 1. Data for (a, b, and c) the Rhine at Koblenz from 1990 to 2009 and (d, e and f) the Elbe at Magdeburg from 1994 to 2009: (a and d) discharge, (b and e) chlorophyll-*a* concentration and (c and f) TP (=total phosphorus, upper lines) and ortho P (=ortho $\text{PO}_4\text{-P}$, lower lines) concentration.

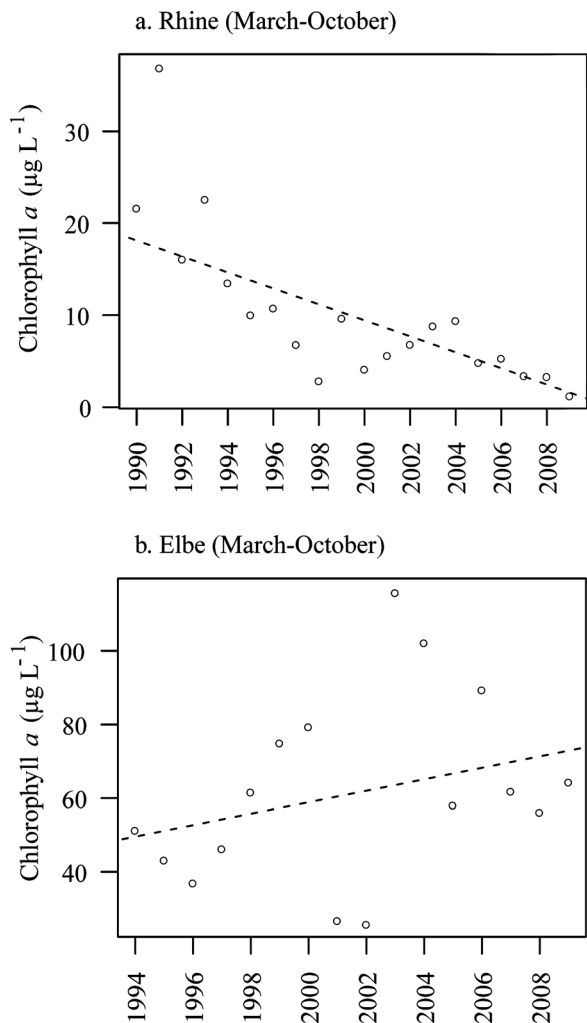


Figure 2. Mean chlorophyll-*a* concentration during the vegetation period March to October in (a) the Rhine at the station Koblenz from 1990 to 2009 and (b) the Elbe at Magdeburg from 1994 to 2009. Lines represent trends according to the Mann–Kendall Test with a slope of -0.870 ($p < 0.001$) for the Rhine and of 1.556 ($p = 0.096$) for the Elbe.

The RDA included all dependent variables concerning the phytoplankton bloom and all independent, i.e. physical and chemical variables (Fig. 5a). The subsequent environmental factor analysis performed with all variables indicated for the Rhine that the phytoplankton development (biomass and peak) was significantly related to the timing of maximum light availability (Light_M) and that the timing of discharge peak (Q_M) was also important. By contrast, the variables temperature and nutrient concentration had no effect. The multiple linear regression was performed to select the variables for the ANOVA. The timing of maximum light availability (Light_M) had a significant effect on the maximum (Max) of the chlorophyll-*a* content during the bloom (ANOVA: $p = 0.001$; $R^2 = 0.54$;

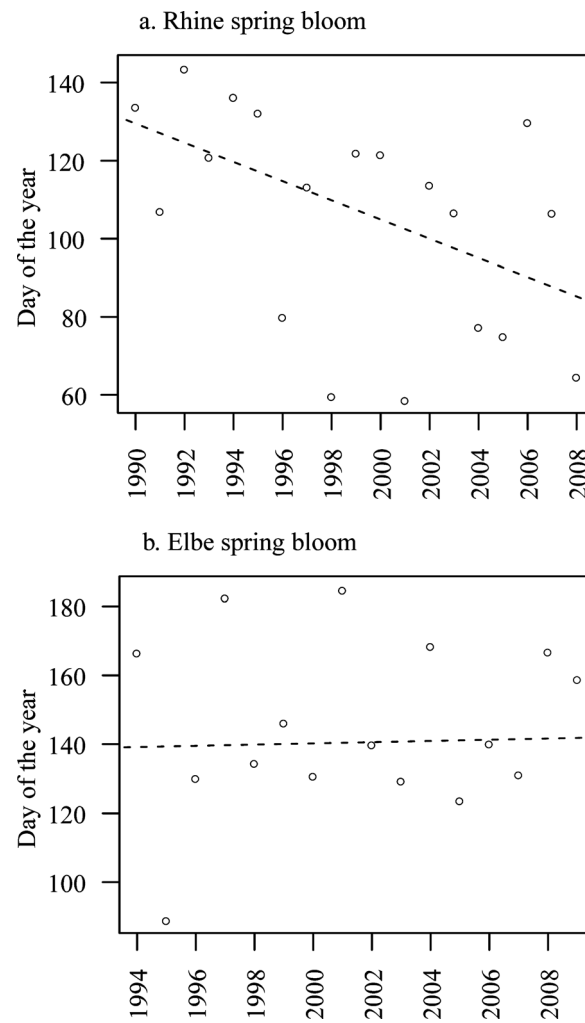


Figure 3. Mid of the spring bloom peak in (a) the Rhine at Koblenz from 1990 to 2008 and (b) the Elbe at Magdeburg from 1994 to 2009. Lines represent trends according to the Mann–Kendall Test with a slope of -2.461 ($p = 0.009$) for the Rhine and of 0.177 ($p = 0.343$) for the Elbe.

Table 1). The end of the discharge peak (Q_E) instead of mid discharge peak (Q_M) as revealed by the environmental factor analysis, was significantly related to the timing of the spring bloom peak (M) in the ANOVA (Q_E; $p = 0.029$), but the relationship was rather weak (adjusted $R^2 = 0.32$) (Table 1). Like in the previous analyses, all other variables concerning water temperature and nutrient concentration had no effect on the phytoplankton spring bloom peak.

Likewise, in the Elbe, the RDA and environmental factor analysis identified the end of the discharge peak (Q_E) to be important for the timing of the phytoplankton peak (Fig. 5b). This was confirmed by the ANOVA that showed that the end of the discharge peak (Q_E) significantly

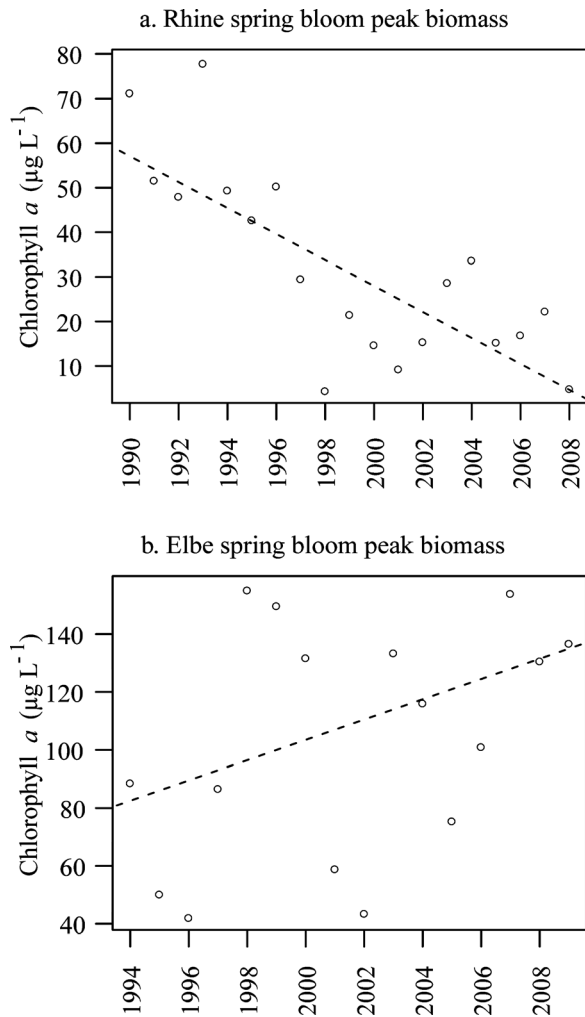


Figure 4. Maximum chlorophyll-*a* concentration during the spring bloom (a) in the Rhine at Koblenz (1990–2008) and (b) the Elbe at Magdeburg (1994–2009). Lines represent trends according to the Mann–Kendall Test with a slope of -2.913 ($p=0.001$) for the Rhine and of 3.499 ($p=0.112$) for the Elbe.

influenced the timing of the spring bloom peak (M) (ANOVA: Q_E; $p=0.012$; $F^2=0.40$; Table 2). Like for the Rhine, the variables concerning nutrient concentration, and water temperature had no significant effect in any of the performed analyses in the Elbe. Regarding the maximum value of the chlorophyll-*a* content (Max), no significant effect of any factor could be identified.

4 Discussion

Our analyses showed that the timing of discharge was a dominant factor being related to the timing of the spring bloom in both rivers, with other factors modifying this basic

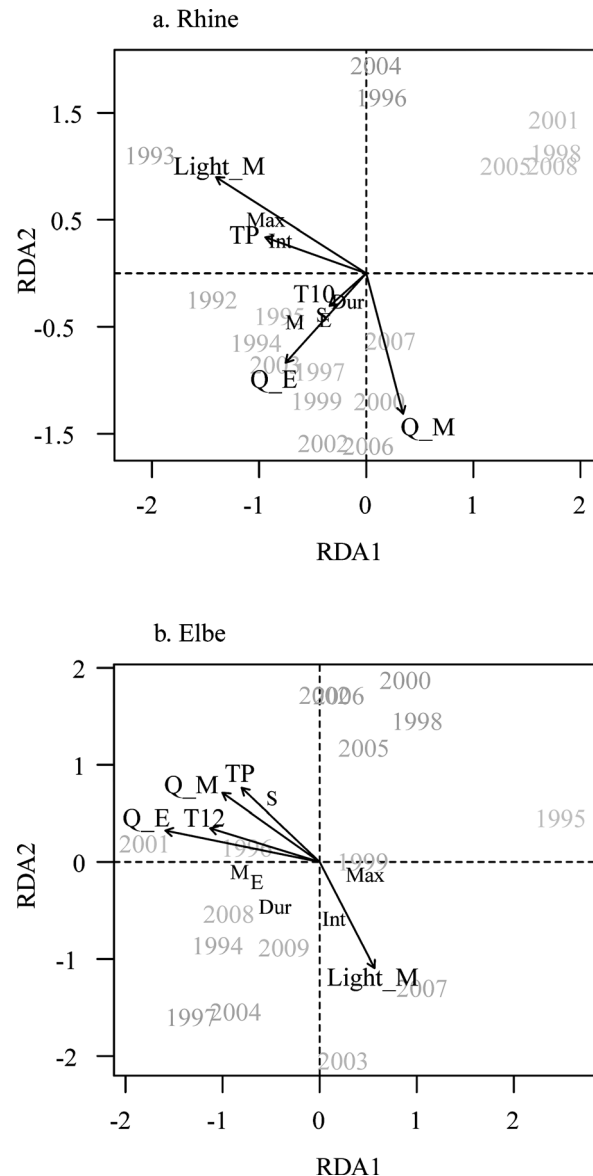


Figure 5. First two axes of RDA with “environmental factor analysis” of all dependent variables (small letters): start (S), mid (M), end (E), maximum value (Max), total mass (Int) and duration (Dur) of the spring bloom in (a) the Rhine at Koblenz from 1992–2008 and (b) the Elbe at Magdeburg from 1994 to 2009. Results of environmental factor analysis for the Rhine: maximum light availability (Light_M) $p=0.009$; mid of the discharge peak (Q_M) $p=0.063$; end of the discharge peak (Q_E) $p=0.132$; water temperature exceeding 10°C (T10) $p=0.752$ and total phosphorus (TP) $p=0.198$. Results of environmental factor analysis for the Elbe: maximum light availability (Light_M) $p=0.105$; mid of the discharge peak (Q_M) $p=0.112$; end of the discharge peak (Q_E) $p=0.016$; water temperature exceeding 12°C (T12) $p=0.164$ and total phosphorus (TP) $p=0.184$.

Table 1. Results of the ANOVA and the multiple linear regression analysis for the Rhine (Koblenz) for the response variables mid of the spring peak (M) and maximum chlorophyll-*a* value during the spring peak (Max). The results of the ANOVA for each in dependent variable are presented and the results of the multiple linear regression including all independent variables (cf. Methods: *Multivariate analysis of data*).

M (peak mid)					
ANOVA	Df	Sum sq.	Mean sq.	<i>F</i> -value	<i>p</i> -value
Q_E	1	3792.7	3792.7	6.0307	0.029
Light_M	1	318.1	318.1	0.5059	0.490
Q_E:Light_M	1	609.9	609.9	0.9698	0.343
Residuals	13	8175.7	628.9		
Regression	Df	Standard error	<i>R</i> -squared	<i>F</i> -statistic	<i>p</i> -value
	15	14.12	0.324	8.661	0.010
Max					
ANOVA	Df	Sum sq.	Mean sq.	<i>F</i> -value	<i>p</i> -value
Light_M	1	2991.50	2991.50	15.7377	0.001
T10	1	559.07	559.07	2.9411	0.108
Residuals	14	2661.20	190.09		
Regression	Df	Standard error	<i>R</i> -squared	<i>F</i> -statistic	<i>p</i> -value
	15	10.07	0.543	20.01	<0.001

relationship to some degree. The maximum biomass was related to the timing of maximum light availability in the Rhine but not in the Elbe. It was confirmed that the controlling factors for phytoplankton growth in rivers clearly differ from the common regulation mechanisms for lacustrine plankton.

4.1 Long-term trends in phytoplankton biomass

Mean chlorophyll-*a* concentration in the Rhine (station Koblenz) decreased significantly from 1990 to 2009,

whereas in the Elbe (station Magdeburg) an increasing tendency in mean chlorophyll-*a* concentration could be detected (hypothesis 1). The strong decrease in chlorophyll-*a* concentrations in the Rhine has been mainly attributed to decreasing nutrient concentrations and a subsequent re-oligotrophication of Lake Constance, the source of the Rhine (Friedrich and Pohlmann, 2009). Other potential factors were seen in a slight increasing tendency of the annual means of discharge and the presence of filter feeding bivalves, which are propagating in the River Rhine since the 1990s (Friedrich and Pohlmann, 2009). In the Rhine catchment, wastewater treatment has been

Table 2. Results of the ANOVA and the multiple linear regression analysis for the Elbe (Magdeburg) for the response variables mid of the spring peak (M) and maximum chlorophyll-*a* value during the spring peak (Max). The results of the ANOVA for each in dependent variable are presented and the results of the multiple linear regression including all independent variables (cf. Methods: *Multivariate analysis of data*).

M (peak mid)					
ANOVA	Df	Sum sq.	Mean sq.	<i>F</i> -value	<i>p</i> -value
Q_E	1	3337.6	3337.6	8.4099	0.012
T12	1	762.0	762.0	1.9200	0.189
Residuals	13	5159.3	396.9		
Regression	Df	Standard error	<i>R</i> -squared	<i>F</i> -statistic	<i>p</i> -value
	14	12.77	0.40	11.12	0.005
Max					
ANOVA	Df	Sum sq.	Mean sq.	<i>F</i> -value	<i>p</i> -value
TP	1	2193.5	2193.5	1.3801	0.260
Residuals	14	22252.2	1589.4		
Regression	Df	Standard error	<i>R</i> -squared	<i>F</i> -statistic	<i>p</i> -value
	14	11.94	0.025	1.38	0.260

improved since 1970 (Friedrich and Pohlmann, 2009) and in the Elbe, wastewater treatment improved and industrial effluents were reduced after the German reunification in 1989 (Adams et al., 1996). In the Elbe, ortho-phosphate levels decreased from 0.26 mg PO₄-P/L in 1990 to 0.07 mg PO₄-P/L in 2000 (Guhr and Schwartz, 2006). In the Rhine, phosphorus was reduced from 0.65 mg PO₄-P/L in 1970 to 0.11 mg PO₄-P/L in 2004 (Friedrich and Pohlmann, 2009). Thus, after these improvements, ortho-phosphate concentrations in both rivers were still distinctly above the level, which limits phytoplankton growth. Growth limiting concentrations are approximately in the range of 0.02 mg/L for ortho-phosphate and nitrate (Lampert and Sommer, 1999), thus challenging the conclusion that the observed decline in mean chlorophyll-*a* concentrations in the Rhine was mainly a consequence of lower P concentrations. In the Elbe, where total P concentrations were in the same range, chlorophyll-*a* concentrations were considerably higher (Fig. 1). Macrophytes, which might also alter the P-dynamics, are almost absent in the middle and downstream sections in both rivers and occur only in floodplain areas or sporadically in groyne fields (ICPR, 2009a, b; River Basin Community Elbe).

Also, an increasing tendency of discharge conditions could not be confirmed for the observed time period, because Pardé coefficients were significantly decreasing from February to July in the decade 2002–2011 compared to 1992–2001. In the free-flowing part of the Rhine, phytoplankton densities are additionally influenced by the import from the major tributaries Neckar and Main (both being upstream our study site) as well as the Moselle (downstream our study site), which are characterized by numerous impoundments and high plankton concentrations (Uehlinger et al., 2009). Likewise, during recent sampling campaigns tributaries carried high loads of phytoplankton compared to the Rhine itself (Bergfeld et al., 2009; ICPR, 2009a, b). A contrasting situation is found in the Elbe and its tributaries. Here, the tributaries have mostly lower phytoplankton concentrations than the Elbe, while a constant inoculation of phytoplankton is provided from the impoundments in the Czech section, the upper part of the Elbe (Guhr et al., 2004).

Taking the comparable situations in both rivers with respect to nutrient load and plankton import from tributaries, the long-term decline in mean chlorophyll-*a* concentrations in the Rhine is probably not explained by “bottom-up effects”, i.e. growth and import. As phytoplankton concentrations were distinctly higher in the past (see also Friedrich and Pohlmann, 2009), it is also unlikely that phytoplankton growth is not possible in the Rhine in general, e.g. due to the morphology-related light regime or residence time. It is thus possible that the recent decline in the phytoplankton concentrations in the Rhine evolved due to increasing loss rates. Losses to zooplankton are

generally low in the Rhine due to very low abundances of both metazooplankton and algivorous protozoans (Weitere et al., 2005). In contrast, losses caused by benthic herbivores might be high due to high densities and filtration activities of benthic filter feeders including the invasive bivalves *Dreissena polymorpha* and *Corbicula fluminea* (Viergutz et al., 2007; Friedrich and Pohlmann, 2009; Kathol et al., 2011). Losses of plankton are generally high in the Rhine and most probably related to benthic filter feeders (Weitere and Arndt, 2002). By contrast, significant plankton reduction via benthic filter feeding is probably low in the Elbe due to generally low abundances of bivalves (Schöll and Balzer, 1998). Reasons for the different filter feeder abundances in both rivers are not fully understood and probably complex. With respect to the invasive filter feeder *C. fluminea* (the dominant filter feeder in the Rhine, which also has suitable habitats in the Elbe), Weitere et al. (2009) recently demonstrated that its reproduction success is strongly reduced during cold compared to warm winters. As the water temperature of the Rhine is enhanced by numerous thermal discharges (ICPR, 2006; BUND, 2009), winter water temperatures rarely drop below 2°C. By contrast, in the Elbe water temperature regularly drops below 2°C, which is considered to be the critical temperature for the survival of *C. fluminea* (McMahon, 1983). Losses of phytoplankton to the zooplankton can temporarily play a prominent role in the Elbe (Holst et al., 2002). However, this appears particularly in reaches below our sampling site. Thus, the increasing success of (invasive) filter feeders in the Rhine in contrast to the low success in the Elbe is one possible explanation for the negative trend of the phytoplankton in the Rhine.

4.2 Control of phytoplankton spring bloom dynamics

In hypothesis 2, we proposed discharge reduction to be the most important regulating factor for phytoplankton spring bloom dynamics. Our data show that discharge decrease was partly related to the spring increase in phytoplankton in the Rhine, whereas light availability was a stronger predictor for the maximum value of chlorophyll-*a* during the bloom. In the Elbe, the occurrence of the maximum of the phytoplankton spring bloom was significantly correlated to the timing of the end of high winter flow rates. Hence, the timing of discharge reduction explained the timing of maximum spring biomass in the Elbe. Increasing retention times generally improve the conditions for the development of planktonic organisms (Reynolds, 1995; Zwolsman and Van Bokhoven, 2007; Lucas et al., 2009). Likewise, as discharge increases, the dilution effect, the worsened light climate and the shorter residence time of the water lowers phytoplankton concentrations (Everbecq et al., 2001). A negative correlation between discharge and chlorophyll-*a*

has therefore been reported concerning seasonal short-term development of phytoplankton in rivers of eastern England (Neal *et al.*, 2006). Our results reveal that this also applies to long-term phytoplankton spring developments.

Besides discharge, river phytoplankton biomass may strongly be correlated with prevailing nutrient concentrations (Basu and Pick, 1996; Van Nieuwenhuysse and Jones, 1996). In our study, total phosphorus concentration had no significant influence concerning the timing or the magnitude of phytoplankton mass development (see section “Long-term trends in phytoplankton biomass”). As diatoms are dominating phytoplankton communities in both the Rhine and the Elbe, dissolved silicate concentrations could temporarily limit phytoplankton growth as was reported by Karrasch *et al.* (2003) for the Elbe and by Ruyter van Steveninck *et al.* (1992) for the Rhine. Nevertheless, in contrast to stratified lakes, where nutrient concentrations are of central importance for the regulation of phytoplankton, they are of less importance in rivers as they are constantly replenished from upstream regions and therefore present in sufficient amounts. In our study, light was an important predictor for the phytoplankton in the Rhine: the occurrence of favorable light conditions in spring was related to maximum chlorophyll values of the phytoplankton peak. By contrast, in the Elbe the factor light availability had a minor impact on the spring bloom development. Light limitation may exert a considerable influence on river phytoplankton development, because of turbid conditions in many large rivers, like the River Ohio, the Mississippi or the Tennessee Rivers (Koch *et al.*, 2004; Ochs *et al.*, 2013). Measurements of under water light climate in relation to discharge in the Great Ouse River showed that the onset of the spring bloom was determined by the discharge pattern (Marker and Collett, 1997) and in the River Seine, phytoplankton development in spring was initiated by the decrease of flow (Garnier *et al.*, 1995). The Rhine and the Elbe are characterized by a similar mean water depth in the range between 3 and 4 meter and similar seston concentrations of 24 mg/L (mean seston content 1992–2009, data International Commission for the Protection of the Rhine/BfG) and 26 mg/L (mean seston content 1994–2009, data River Basin Community Elbe), respectively, in the considered time period. In our study, water temperature in spring had no significant effect on phytoplankton development, neither in the Rhine, nor in the Elbe. That means that the direct effect of temperature on phytoplankton is of less importance and the main focus concerning plankton regulation in lotic waters has to be set on discharge conditions and light availability. This is in line with the general conclusion that temperature has a minor effect on autotrophic processes in contrast to pronounced temperature effects on heterotrophic processes (Müren *et al.*, 2005; Sommer and Lengfellner, 2008).

Our data show that flow conditions regulate phytoplankton in both rivers, thus a change in spring flow should lead to a temporal displacement of the phytoplankton bloom (hypothesis 3). Accordingly, we found that the maximum of the spring bloom in the Rhine appeared earlier and was connected with a change in the discharge conditions, whereas the timing of the spring bloom showed no significant trend in the Elbe. The flow regime of the Rhine, which is influenced by the snow melt from the alpine catchment of this river, was subject to temporal trends. In the Elbe, where most of the catchment is situated at lower altitudes, there was not such a trend. Several studies predict changes in the discharge regimes of rivers according to climate change (Weiland *et al.*, 2012). For the Rhine, in the far future (2071–2100) a reduction of discharge conditions in summer is projected (Nilson *et al.*, 2010). For the Elbe, it was shown that climate change could lead to longitudinal shifts in primary production and respiration as a result of decreasing discharge conditions (Quiel *et al.*, 2011).

While the overall decreasing long-term trend in phytoplankton biomass in the Rhine might involve stronger loss processes by benthic filter feeders compared to the Elbe, spring bloom dynamics were mainly regulated by abiotic, climate-related factors. It can be concluded that despite the interaction of complex regulation mechanisms in the Rhine and practically in any other large river, the timing of the spring bloom was related to the timing of winter/spring discharge decline in both the Rhine and the Elbe. In spite of this similarity, the occurrence of the spring bloom showed contrasting long-term changes in the two large rivers, highlighting the importance of assessing the ecosystem responses towards climatic regulation factors.

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