High irradiation and low discharge promote the dominant role of phytoplankton in riverine nutrient dynamics

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Abstract

Rivers play a relevant role in the nutrient turnover during the transport from land to ocean. Here, highly dynamic planktonic processes are more important compared to streams making it necessary to link the dynamics of nutrient turnover to control mechanisms of phytoplankton. We investigated the basic conditions leading to high phytoplankton biomass and corresponding nutrient dynamics in eutrophic, 8th order River Elbe (Germany). In a first step, we performed six Lagrangian sampling campaigns in the lower river section at different hydrological conditions. While nutrient concentrations remained high at low algal densities in autumn and at moderate discharge in summer, high algal concentrations occurred at low discharge in summer. Under these conditions, concentrations of silica and nitrate decreased and rates of nitrate assimilation were high. Soluble reactive phosphorus was depleted and particulate phosphorus increased inversely. Rising molar C:P ratios of seston indicated a phosphorus limitation of phytoplankton, so far rarely observed in eutrophic large rivers. Global radiation combined with mixing depth had a strong predictive power to explain maximum chlorophyll concentration. In a second step, we estimated nutrient turnover exemplarily for N during the campaign with the lowest discharge based on mass balances and metabolism-based process measurements. Mass balance calculations revealed a total nitrate uptake of 423 mg N m$^{-2}$d$^{-1}$. Increasing phytoplankton density dominantly explained whole river gross primary production and related assimilatory nutrient uptake. In conclusion, riverine nutrient uptake strongly depends on the growth conditions for phytoplankton, which are favored at high irradiation and low discharge.

The uptake and transformation of matter is an essential ecological function of fluvial ecosystems (Seitzinger et al. 2002; Wollheim et al. 2006; Battin et al. 2008). It strongly affects not only the freshwater ecosystem itself but also the adjacent ecosystems by determining the load and form of terrestrial matter that reaches the coastal and marine systems (Alexander et al. 2000; Aufdenkampe et al. 2011). We assume removal as the sum of biotic uptake and dissimilatory processes, and nutrient removal in particular occurs by different mechanisms including denitrification (in case of N) as well as assimilatory uptake by either benthic or planktonic (micro-) organisms (both autotrophic and heterotrophic). It is generally believed that nutrient removal decreases with growing stream and river size and small streams emerge as N removal “hotspots” (Alexander et al. 2000; Peterson et al., 2001). Previous study suggests that nitrogen removal in streams can be dominated by assimilatory processes (Mullholland et al. 2008) but this uptake only temporarily retains nitrogen. However, denitrification is the only permanent N removal process in rivers (Seitzinger et al. 2002). Increasing stream size and hence mean depth provide less sources of labile organic matter, reducing denitrification opportunities. More recently, however, direct measurements (Tank et al. 2008), cross-site synthesis (Hall et al. 2013), and models (Wollheim et al. 2006) have suggested that larger rivers may retain high reactivity and thus provide important removal functions within river networks (Hensley et al. 2015). Nitrogen removal rates in large river networks depend on nitrogen loading and hydrological conditions. Findings from large rivers suggest that percentage N in-stream removal of the total load entering the river can vary in wide ranges between 8 and 30% (Howarth et al. 1996, Garnier et al. 2002, Bouwman et al. 2005). This removal is higher during dry conditions compared

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to wet conditions (Billen et al. 2007) and stream bottom area related removal by denitrification can be higher in larger rivers than in small streams (Billen et al. 2007).

Our understanding about the capacity for matter transformation of larger rivers still lags far behind smaller streams, largely for methodological reasons. However, emerging methods based on high frequency sensor measurements more readily applicable to large rivers (e.g., Heffernan and Cohen 2010; Kunz et al. 2017; Rode et al. 2016) hold promise for a better empirical basis from which to predict reactivity across river networks (Hensley et al. 2015; Yang et al. 2019a).

Even though the whole system nutrient removal capacity as well as the contribution of different compartments to the total nutrient removal is poorly understood for large rivers, it is well accepted that maximum planktonic production occurs in mid-sized rivers (Reynolds and Descy 1996), suggesting that phytoplankton plays a dominant role in nutrient uptake under such condition. However, phytoplankton density is often highly dynamic showing very strong seasonal and spatial variations (e.g., Friedrich and Pohlmann 2009; Hardenbicker et al. 2016). Assuming a dominant role of phytoplankton, it is thus likely, that nutrient uptake in plankton dominated large rivers is highly variable and dependent on the major control factors for phytoplankton. In order to predict nutrient uptake in rivers, it is thus important to link nutrient uptake to mechanisms that control plankton dynamics.

Given sufficient input of plankton from headwaters or tributaries, water residence time, nutrient availability and light exposure are important factors which determine phytoplankton density in rivers (e.g., Reynolds et al. 1994). In addition, different mechanisms for phytoplankton loss occur, including sedimentation under reduced flow conditions (e.g., Reynolds and Descy 1996, Caraco et al. 2006, Köhler et al., 2002) and grazing by benthic filter feeders. However, the importance of such loss factors varies strongly between river systems. While some systems show rapid plankton losses due to high densities of benthic filter feeders (e.g., Welker and Walz 1998) others (such as the focus river of the present study, the Elbe; Hardenbicker et al. 2014) are hardly affected by this process. Most of the controlling factors mentioned above are superimposed by discharge. Low discharge during summer droughts enhances residence time and increase light exposure of the algae and thus improves growth conditions unless discharge-related loss processes occur (e.g., Weitere and Arndt 2002; Houser et al. 2015).

Once phytoplankton achieves high biomasses, its growth is mostly limited by light or nutrients. The proportions of light and nutrient limitations are often unclear in rivers. Light availability is determined externally by seasonally variable global radiation, and within the water by mixing depth. In a large river, internal light was dominantly controlled by discharge and corresponding water depth (Julian et al. 2008). Regarding nutrients, Bowes et al. (2012) observed a phosphorus and also a silicon depletion in the River Thames at high algal biomass. For estimating whether or not phytoplankton and microphytobenthos in streams and rivers is mainly limited by phosphorus or nitrogen, the calculation of the molar ratio of dissolved inorganic nitrogen to soluble reactive phosphorus was suggested (Keck and Lepori 2012; Minaudo et al. 2015). The direct measurement of phytoplankton stoichiometry may provide information on the limiting nutrient and depends on cell quota, growth rate, light regime, and algal species (Klausmeier et al. 2008; Hillebrand et al. 2013). The Redfield ratio describes the elemental composition for optimal growth (C:N:P = 106:16:1) which was shown to vary only slightly (e.g., 117:17:1, Hillebrand and Sommer 1999; 125:16:1, Quigg et al. 2003). Phosphorus limitation was suggested to start from a C:P ratio of around > 130 (Hillebrand and Sommer 1999; Tittel et al. 2012).

In the present study, we analyzed the nutrient dynamics in relation to phytoplankton development in the water column of the large River Elbe (Germany), a eutrophic 8th order river with negligible densities of benthic grazers (Hardenbicker et al. 2016, Yang et al. 2019b). In contrast to other rivers where re-oligotrophication led to a dominance of macrophytes (Ibanez and Penuelas 2019), the contribution of macrophytes to primary production is neglectable in the Elbe River (Deutsch et al. 2009). In a first step, we performed six Lagrangian sampling campaigns in different seasons and at different hydrological conditions in order to identity the conditions for phytoplankton development and corresponding nutrient dynamics. Maximum chlorophyll concentration was related to measures of external (global radiation) and internal (mixing depth) light availability whereas high light attenuation is a consequence of high phytoplankton chlorophyll itself. In a second step, we focussed on a sampling campaign with strong phytoplankton growth (2018) and additionally estimated assimilatory nitrate uptake and dissimilatory nitrate removal via denitrification by metabolism measurements and mass balance calculations.

Materials and methods

The River Elbe in Central Europe is 1094 km long and drains a catchment of 148.268 km². After passing several dams in the Czech Republic, it is a free-flowing river for 585 km from the Czech-German border until the weir Geesthacht near Hamburg before the tidal zone, oxbow lakes are not connected at low and medium discharge, and groyne fields do not affect chlorophyll concentration (Ockenfeld and Guhr 2003). Sampling was performed using the research vessel Albis applying a Lagrangian approach, i.e., a sampling of nearly the same water body along the way downstream according to its travel time. Investigations were done in the lowland part between Magdeburg-Westerhüsen (km 318 according to German river kilometration) and Geesthacht (km 585; Fig. 1a). Six cruises were performed in total (Table 1, Fig. S2): three of them at low discharge around mean low discharge at Magdeburg (231 m³ s⁻¹) in summer (2007, 2008, and 2018). The other
three cruises were done at low discharge in autumn (2017) and at moderate discharge around mean medium discharge at Magdeburg (554 m$^3$/s) in summer (2009) and autumn (2013). Sampling was conducted at the left and right bank of each site (2007, 2008, 2009, and 2013) or at three to five points along cross sections (2017 and 2018).

Standard methods were applied for surface water samplings, sample preparations and analytics as described in Baborowski et al. (2018).
et al. (2011) and Kamjunke et al. (2013) including all instructions of German standards. Quality control was done using blanks, validations, and certified interlaboratory comparisons. Surface water samples were taken with a bailed polypropylene sampler. All filtrations were conducted immediately after sampling on board of the vessel using quartz fiber filters (MN QR10, Macherey-Nagel) or glass fiber filters (GF-F, Whatman). Filters were frozen, and samples were stored at 4°C until further analyses. Nitrite (NO$_2^-$), nitrate (NO$_3^-$), and silicon (Si) were photometrically determined using the segmented flow technique. Total (TP) and soluble reactive phosphorus (SRP) were measured after persulfate digestion using the ammonium molybdate spectrometric method. Inorganic (IC), organic (OC) and total (TC) carbon concentrations in the filtered and unfiltered original water samples as well as particulate nitrogen were analyzed based on high temperature oxidation using Non-Dispersive InfraRed sensor detection. Chlorophyll a was measured by High Performance Liquid Chromatography calibrated with commercial standards. For each longitudinal sampling, maximum chlorophyll a concentration was regarded as measure for eutrophication and the minimum SRP concentration for nutrient depletion. Global radiation was measured by the German Weather Service (Deutscher Wetterdienst, DWD) in Seehausen close to the middle of the sampling stretch in Wittenberge at km 455.

In 2018, high frequency sensors were installed at ferries in Westerhüsen (km 318) and Werben (km 422) in a river stretch not affected by tributaries. We measured cross section concentration profiles using GPS data (Fig. S1) as concentration can vary in the profile due to incomplete mixing of tributaries, e.g., the Saale River. Temperature, dissolved oxygen, pH, and electric conductivity were measured with a YSI 610 multi-parameter probe at the ferries from 25 June to 2 July 2018. Furthermore, YSI 610 measurements at both abovementioned stations continued from 21 July to 15 November 2018 for calculating autotrophic respiration (see below). High frequency nitrate measurements were conducted using a TRIOS ProPS-UV sensor with an optical path length of 10 mm. Maintenance of all sensors including manual cleaning and calibration was done before the measurement campaign. Self-cleaning of the TRIOS sensor was done with air pressure prior to every measurement. For the TRIOS sensors, a regression of grab samples of NO$_3^-$ concentrations and sensor NO$_3^-$ concentrations showed that both values were strongly correlated ($R^2 = 0.93; \gamma = 0.98x$) with a bias of only 0.01 mg NO$_3^-$ N. Discharge data (15 min interval) were obtained for Magdeburg (km 326.5) and Werben (km 422). High frequency measurements were taken at 15 min time step. Installation of the sensors on the ferries ensured cross sectional concentration measurements during the day (13–28 per day at Westerhüsen). Flow velocity profile measurements were conducted at Westerhüsen and Werben stations on 26 June 2018 using an Acoustic Doppler Current Profiler (ADCP, RD Instruments). For nitrate load calculations, eight cross sectional flow segments were used and mean nitrate concentrations were multiplied with segment flows. At station Werben, cross sectional measurements show that the water column was well mixed within the cross section. Therefore, nitrate load was calculated by multiplying mean discharge with mean cross sectional nitrate concentration. We evaluated the nitrate-N balance between Elbe stations Westerhüsen and Werben considering a flow time of 52 h which was determined using cross correlation analysis of electric conductivity at both stations. Daily mean total areal nitrate removal was determined by dividing the nitrate loss within the study reach by the river bottom area. River bottom area was calculated from water area estimated from Sentinel-2 bands using the Normalized Difference Water Index (sensing data from 09 September 2016 with discharge of 197 m$^3$ s$^{-1}$ at discharge gauging station Magdeburg).

We calculated gross primary production (GPP, g O$_2$ m$^{-2}$ d$^{-1}$) and ecosystem respiration (ER, g O$_2$ m$^{-2}$ d$^{-1}$) for each day using the one station method (Roberts and Mulholland 2007) at stations Westerhüsen and Werben. To estimate GPP and ER, the re-aeration of oxygen (gas exchange rate coefficient, $K_{600}$) throughout the river reach must be accurately determined (Raymond et al. 2012). Daily volumetric rates of GPP, ER, and $K_{600}$ were estimated from continuous dissolved oxygen, temperature, light, and discharge records with the stream Metabolizer package (Appling et al. 2018a). The streamMetabolizer is a new three parameter (GPP, ER, and $K_{600}$), multitad model which optimizes the calculation of the three variables simultaneously using a Bayesian hierarchical model. The streamMetabolizer program is using a Monte Carlo Markov Chain approach with a trapezoidal ordinary differential equation method to calculate the stream metabolism parameters. The model ensures similar $K_{600}$ values among days with similar physical conditions (e.g., discharge). For whole summer calculations, re-aeration was pooled in up to seven bins corresponding to discharge to achieve consistent estimates of $K_{600}$ (Appling et al. 2018b). Daily estimates of stream metabolism and $K_{600}$ were considered reliable by inspecting the model output for adequate convergence, fit of predicted dissolved oxygen measurements, model errors, and variability in the daily estimations of $K_{600}$, GPP, and ER. Rates of GPP and ER (g O$_2$ m$^{-3}$ d$^{-1}$) were standardized to river size by multiplying volumetric rates by daily estimates of depth. For Westerhüsen, we considered the mean water temperature differences between the Elbe dominated right site and the Saale dominated left site of the river (mean difference 0.5 °C). We calculated daily mean GPP for the Elbe study reach between Westerhüsen and Werben using the daily mean at both stations.

Assimilatory nitrate uptake was determined using net autotrophic production and the measured C/N stoichiometry of the algae biomass (see also Heffernan and Cohen 2010, Rode et al. 2016). Net primary production is GPP minus autotrophic respiration (Webster and Meyer 1997). Mean values of GPP for the Elbe river reach were calculated chlorophyll $a$-weighted.
roughly following an exponential increase from Westerhüsen downstream to Werben. Autotrophic respiration (AR), i.e., the difference between GPP and autotrophic net production, was estimated using the approach of Hall and Beaulieu (2013), where AR is calculated from daily metabolism data using quantile regression between GPP and 90% quantile of ER. For the summer period 2018, we determined AR values of 0.45 for station Westerhüsen and 0.50 for station Werben. These values are very close to mean values given streams by Hall and Beaulieu (2013) and Demar et al. (2015). Furthermore, we assumed that the net photosynthetic quotient is 1 (i.e., 1 mol O₂ produced corresponds to 1 mol C converted from CO₂ to organic biomass). The assimilatory N demand ($D_A$) was then calculated on a mass basis (with molar weights of 32 g mol⁻¹ for O₂ and 14 g mol⁻¹ for N):

$$\frac{O_2(g)}{N(g)} = 5.08 \times \frac{C}{N}$$

$$\frac{O_2(g)}{N(g)} = 4.57 \times \frac{C}{N}$$

for the upper and lower stations Westerhüsen and Werben, respectively (for details see Rode et al. 2016). Molar C/N ratios of the algae biomass were determined as 7.39 at Westerhüsen and as 7.27 at Werben. We calculated daily dissimilatory N demand by subtracting the areal assimilatory nitrate uptake from the total areal N uptake based on the N mass balance measured in the study reach.

Fig 2. Lateral averages of (a) chlorophyll a (Chl a), (b) nitrate-N, (c) dissolved silicon (Si₅₀), and (d) soluble reactive phosphorus (SRP) concentrations, and of molar (e) C:N and (f) C:P of seston along the River Elbe between river kilometers 318–585 at six samplings in the period 2007–2018. Error bars: Range of two samplings (2007, 2008, 2009, and 2013) or SD of three to five samplings 2017, 2018) (sometimes smaller than symbols). Arrows indicate simultaneous SRP decrease to detection limit and C:P increase of seston above around 130.
Fig 3. Relationships between the maximum chlorophyll \(\alpha\) concentrations (Chl \(\alpha\)) of longitudinal samplings and (a) mixing depth \((z_{\text{mix}})\), (b) average daily global radiation \((I_{\text{glob}})\), (c) the ratio of global radiation to mixing depth, and (d) between minimum soluble reactive phosphorus (SRP) concentration and maximum chlorophyll \(\alpha\) concentration. Regression lines were fitted by exponential functions.

Fig 4. (a) N fractions nitrate-N, particulate nitrogen (PN) and total nitrogen (TN), (b) P fractions soluble reactive phosphorus (SRP), particulate phosphorus (PP) and total phosphorus (TP), and (c) particulate organic carbon (POC) along the River Elbe in 2018. Arrows indicate the mass of nitrate decrease and of POC increase between the continuous measurements of oxygen and nitrate at the ferries. (d) Correlation between POC and chlorophyll \(\alpha\) (Chl \(\alpha\)).
Results

Discharge did generally not increase within the first section of the river stretch (Fig. 1b). This was confirmed by almost identical discharge in Westerhüsen and Werben in 2018 (Fig. 1c, d). The only noteworthy tributary, the River Havel (mean low discharge 18.2 m$^3$/s$^1$), entered at km 438 and increased the discharge of the Elbe river only slightly (8%). Overall, dilution was not very high along the regarded river stretch.

The concentration of chlorophyll $a$ was low at moderate discharge in summer (2009) and autumn (2013) and at low discharge in autumn (2017; Fig. 2). It showed an increase along the investigated river stretch from 12 to 30 $\mu$g L$^{-1}$ (2009) and from 3 to 21 $\mu$g L$^{-1}$ (2017), or it remained constant between 10 and 13 $\mu$g L$^{-1}$ (2013). Regarding dissolved nutrients, inorganic nitrogen was dominated by nitrate whereas concentrations of ammonium and nitrite were two orders of magnitude lower (Fig. S3). Concentrations of nitrate nitrogen declined slightly, concentration of silica remained constant, and that of SRP decreased slightly (2009 and 2017) or did not change (2013) in these 3 years. In contrast, chlorophyll $a$ concentration either remained at high (60–90 $\mu$g L$^{-1}$; 2008) or very high level (150–180 $\mu$g L$^{-1}$; 2007), or it increased from 10 to > 100 $\mu$g L$^{-1}$ (2018) at low discharge in summer. The increase in 2018 was realized in a temperature range of 17.4–18.4°C (Fig. S4). During the 3 years with high chlorophyll values, concentrations of nitrate decreased more steeply and partly reached low values (2018). Concentrations of silicon declined linearly too and reached depletion in 2008. SRP concentration was depleted at km 388 (2007 and 2008) or it decreased linearly to depletion at km 470 (2018). Nevertheless, phytoplankton growth and decrease of silica and nitrate continued from there.

Molar C:N ratios of seston did not change along the river stretch and were below the Redfield ratio of 6.7 in autumns of 2013 and 2017 (Fig. 2e). The values were slightly higher than that ratio in summers of 2007 and 2009, and they showed an increase towards the downstream part in summers of 2008 and 2018. Molar C:P ratios did not vary and were below the Redfield ratio of 106 in summer of 2009 and autumn of 2017. It showed constantly values above that threshold at moderate discharge in autumn of 2013. In contrast, C:P ratios increased along the river stretch in the three summers with low discharge. The regression lines exceeded a C:P ratio of 130 at km 388 in summers of 2007 and 2008 when SRP was depleted, and later at km 470 in summer of 2018 corresponding to the later SRP depletion.

Maximum chlorophyll $a$ concentrations of longitudinal transects were only weakly correlated to the mixing depth due to the low chlorophyll maximum at low mixing depth in
September 2017 (Fig. 3a). The relationship was much stronger between chlorophyll and the average daily global radiation as a measure of overall light availability (Fig. 3b). The combination of global radiation and mixing depth explained 99% of chlorophyll variance (Fig. 3c). High chlorophyll concentration decreased the nutrient concentrations leading to low minimum SRP concentrations (Fig. 3d).

For the sampling with the most pronounced changes of chlorophyll and nutrients along the river stretch (summer of 2018), the dissolved, particulate and total fractions of N and P are shown (Fig. 4; for the other 5 years see Fig. S5). The linear decrease of nitrate was accompanied with an increase in particulate N until km 536. Total nitrogen was constant in the upstream reach, and decreased downstream. The decrease of nitrate between the continuous probe measurements (km 318–422) was 0.55 mg N L\(^{-1}\) which amounted to a mass of 20.4 t N during 52 h of travel time. The decrease in SRP was mirrored by an equivalent increase in particulate P. Total P was nearly constant except the last two sampling sites. Particulate organic carbon (POC) increased by 3.06 mg C L\(^{-1}\) between km 318 and 422 corresponding to a mass increase of 113 t C during 52 h. Concentration of POC was positively related to chlorophyll a concentration showing an intercept of 1.4 mg L\(^{-1}\) (Fig. 4d). The strong regression indicates that POC was dominated by phytoplankton.

Oxygen fluctuations were lower at the upstream site Westerhüsen (km 318) compared to the downstream site Werben (km 422; Fig. 5a). Consequently, gross primary production amounted to a daily mean of 6.45 g O\(_2\) m\(^{-2}\) d\(^{-1}\) (Westerhüsen station) and 20.5 g O\(_2\) m\(^{-2}\) d\(^{-1}\) (Werben station) or 2.44 and 7.69 g C m\(^{-2}\) d\(^{-1}\), respectively (period 26–29 June; Fig. 6; Table 2). The Elbe River was highly autotrophic with daily mean production: respiration ratios of 2.05 and 1.22 at stations Westerhüsen and Werben, respectively. Net primary production was 3.30 and 3.74 g O\(_2\) m\(^{-2}\) d\(^{-1}\) or 1.24 and 1.40 g C m\(^{-2}\) d\(^{-1}\) resulting in production: biomass ratios based on POC of 0.32 and 0.13 d\(^{-1}\). Given an average river width of 183 m and a stretch length of 104 km, these rates correspond to 51.1 t and 57.7 t C in 52 h (average 54.4 t C) which was lower than the POC increase obtained by point-measurements between Westerhüsen and Werben during the Lagrangian sampling in 2018 (113 t C). Nitrate concentration was higher in Westerhüsen (Fig. 5b). Calculated mean nitrate assimilatory demand by primary production was 464 mg N m\(^{-2}\) d\(^{-1}\). The total assimilatory N demand in the study reach amounted to 7.21 t N d\(^{-1}\) or 16.3 t N within 52 h. Denitrification was small and amounted to 28.3 mg N m\(^{-2}\) d\(^{-1}\) because calculated assimilatory N demand (395 mg N m\(^{-2}\) d\(^{-1}\)) was only slightly lower than net NO\(_3\) removal (423 mg N m\(^{-2}\) d\(^{-1}\)).

**Discussion**

In the present study, we detected high variations in phytoplankton development in the lower part of the Middle Elbe linked to different hydrological and seasonal settings. The phytoplankton densities in turn were linked to nutrient depletion in the Lagrangian sampling with strong nutrient depletion below the detection level for the limiting nutrient phosphorus at high phytoplankton development. This finding together with the estimates of N uptake suggests a predominant role of the phytoplankton in nutrient uptake. The strong link between nutrient uptake and phytoplankton dynamics makes this function highly variable but also predictable if phytoplankton control mechanisms are understood.

**Summer low water flow favors high phytoplankton density**

The concentrations of chlorophyll a were relatively low at low discharge in autumn and moderate discharge in summer and autumn (2009, 2013, and 2017). Only moderate growth of phytoplankton (chlorophyll increase from 12 to 30 μg L\(^{-1}\)) was observed at high discharge in summer 2009. Under such conditions, phytoplankton was probably light limited due to high mixing depth (Table 1). Phytoplankton did not grow at all along the stretch at high discharge in autumn 2013. Here, high water depth and only moderate sunlight in autumn coincided. Phytoplankton showed high growth rates (chlorophyll increase from 3 to 21 μg L\(^{-1}\) within 4 days) at low discharge in autumn 2017. However, it still remained at low biomass levels because the initial biomass in Magdeburg was very low. Reasons for this low biomass are unknown and might include low global radiation in autumn or top-down control by occasionally high abundances of planktonic grazers among metazoans and protozoans (Holst et al. 2002; Weitere et al. 2005). As a
consequence of low algal biomasses in 2009, 2013, and 2017. The C:P ratios of seston remained low in 2009 and 2017. They were higher in 2013 which was the only year with increasing discharge before sampling (Fig. S2) causing resuspension of phosphorus-leached particles which were characterized by the lowest concentrations of particulate phosphorus and the highest concentration of SRP of all years (Fig. S5).

In contrast, chlorophyll $a$ concentrations were much higher in summers at low discharge (2007, 2008, and 2018). Such concentrations were observed also in former years in the River Elbe (Guhr et al. 2003; Pusch and Fischer 2006; Hardenbicker et al. 2016) and are in the range of eutrophic rivers (Bowes et al. 2012). The strong positive relationship between the maximum chlorophyll $a$ concentration and global radiation (Fig. 3b) confirms the important role of light for phytoplankton growth in the River Elbe. To test the approach of an extended period of global radiation for phytoplankton growth (Várbiro et al. 2018), we included 5 days before the Lagrangian samplings which is the travel time needed in the free-flowing part of the Elbe between the dams close to the Czech-German border and the start of our investigation in Magdeburg. However, these data did not improve the relationship between maximum chlorophyll and global radiation ($R^2 = 0.77$ instead of $R^2 = 0.91$). Instead, the combination with internal light availability further improved that relationship (Fig. 3c): High light intensities due to low mixing depth enabled an increased time period for algal photosynthesis which was additionally supported by slightly higher residence time at low flow. Hosen et al. (2019) also reported recently that gross primary production was enhanced by higher temperature, lower turbidity and longer water residence times in the Connecticut River, i.e., under conditions of summer drought. Temperature seems to be less important than light in controlling growth of the autotrophic phytoplankton, at least within the main growing time from spring to autumn, and a study by Köhler et al. (2002) showed that net growth rate of river phytoplankton measured in dialyses chambers was not related to water temperature within a range of 4–23°C. The net-effect observed in our study (i.e., increased plankton growth with low discharge) is typical for rivers with low abundances of benthic filter feeders (Ruiz 2018), which is usually the case in the Elbe (Hardenbicker et al. 2016). Former studies showed on average a 4-fold increase of phytoplankton biomass along the 585 km of the German part of the Elbe (Guhr et al. 2003; Pusch and Fischer 2006). In this respect, the Elbe is different from e.g., the river Rhine where phytoplankton biomass is much lower due to occurrence of large benthic filter feeders which play a minor role in the Elbe (Weitere and Arndt 2002; Hardenbicker et al. 2016). Furthermore, the net growth rate of phytoplankton in the Elbe was found to increase with decreasing discharge (Guhr et al. 2003; Pusch and Fischer 2006). This is confirmed by our measurements of very high chlorophyll increase at the lowest discharge in 2018.

**Strong nutrient depletion only at high phytoplankton biomass**

Concentrations of dissolved nutrients showed a pronounced decrease in the 3 years with high summer phytoplankton biomass at low discharge. In 2007 and 2008, nutrient concentration decreased despite constant chlorophyll concentration indicating phytoplankton loss by sedimentation or grazing. In 2018, phytoplankton incorporated nitrate nitrogen so that particular N increased until km 536 parallel to significant decreases in nitrate. However, phytoplankton was probably not nitrogen limited as observed in other rivers (Kramer et al. 2018). Regarding phosphorus by contrast, SRP was nearly completely incorporated into particulate P by phytoplankton. Consequently, total P remained constant except the last two sampling sites where sedimentation occurred (see also chlorophyll data) due to backwater processes of the weir at Geesthacht. SRP depletion was measured in the River Elbe before (Rode et al. 2007; Hardenbicker et al. 2016; Ritz and Fischer 2019) and in the River Thames (Bowes et al. 2012) and Loire River (Minaudo et al. 2015). The increase of seston C:P ratios indicates that phytoplankton was P limited from km 388 in 2007 and 2008, and from km 470 in 2018 (compare C:P thresholds suggested for nutrient limitation by Hillebrand and Sommer 1999; Quigg et al. 2003). Nevertheless, nitrogen assimilation still continued after SRP depletion due to the variable nutrient stoichiometry of phytoplankton. Overall, however, phosphorus limitation of phytoplankton growth was restricted to downstream reaches of the River Elbe at low discharge conditions.

**Dominant role of phytoplankton in riverine nutrient uptake**

The coupled nutrient—phytoplankton dynamics during the Langrangian sampling campaigns already suggested a predominant role of phytoplankton in nutrient dynamics. This is supported by the estimates of nutrient consumption and metabolism. The metabolism measurements showed a 3.4-fold increase in GPP between Westerhüsen and Werben, which is directly linked to a 7.4-fold increase in phytoplankton densities. Gross primary production was very high ranging between 6.45 g O m$^{-2}$d$^{-1}$ (Westerhüsen) and 20.5 g O m$^{-2}$d$^{-1}$ (Werben) leading to oxygen supersaturation and production: respiration ratios of 2.05 (Westerhüsen) and 1.22 (Werben; Table 2). High oxygen oversaturation in combination with high Chl $a$ concentrations (> 140 μg L$^{-1}$) was also observed in the upper Mississippi River during low flow summer conditions (Houser et al. 2015). The decrease in SRP and the equivalent increase of particulate P indicate a dominance of P uptake by phytoplankton and confirm the minor importance of macrophytes and periphyton in the Elbe River (Deutsch et al. 2009). Nitrogen biogeochemistry was dominated by assimilatory nitrate uptake whereas other processes were less important: Ammonium concentration was two orders lower than that of nitrate, and the nitrate input by the one main tributary, the River Havel (concentration 0.08 mg N L$^{-1}$; <1% of N load), was negligible. The
measured mean total NO$_3$ removal of 423 mg N m$^{-2}$ d$^{-1}$ for pronounced low flow conditions was similar to the total NO$_3$ removal reported by Ritz and Fischer (2019) who calculated 355 and 506 mg N m$^{-2}$ d$^{-1}$ (in summers 2011 and 2012, respectively) for the whole German Elbe River (length 585 km). Calculated assimilatory N demand of 395 mg N m$^{-2}$ d$^{-1}$ was in the range of fully light exposed river ecosystems during summer (Kunz et al. 2017). Only a small amount of denitrification could be detected because calculated assimilatory NO$_3$ uptake was only slightly lower than determined nitrate removal with a mean deviation of only 6.7% during the whole campaign. Our findings of assimilatory and dissimilatory NO$_3$ removal are in line with findings from a natural abundance $\delta^{18}$O and $\delta^{15}$N isotope study by Deutsch et al. (2009) who also found dominating assimilatory uptake due to a close to 1:1 ratio of the increase in $\delta^{18}$O and $\delta^{15}$N in NO$_3$. They showed that the share of denitrification of total NO$_3$ removal was limited and that the maximum loss of nitrate which could be attributed to denitrification was 25%. During their study campaign, discharge (309 m$^3$ s$^{-1}$) and water depth were higher than in our study and, therefore, the condition for primary production and assimilatory uptake were less favorable than in our study. Our low denitrification rates were considerably lower than those calculated by Ritz et al. (2018) using Membrane Inlet Mass Spectrometry which amounted to 432 mg N m$^{-2}$ d$^{-1}$ for the same reach in summer 2011. The dominant role of assimilatory nitrate uptake detected in the present study corresponds to findings for stream ecosystems from Mulholland et al. (2008) who quantified the share of denitrification on total NO$_3$ removal in a wide range of biomes to 16%. In large rivers total nitrate removal, and hence removal by denitrification, can be very limited as was found in impounded sections of the Upper Mississippi River (Loken et al. 2018). In our short-term measurement campaign, we used a rough estimate of the fraction of assimilatory respiration of GPP and hence of assimilatory N demand, because data for phytoplankton dominated systems and especially large rivers are extremely rare. Therefore, it has to be kept in mind that these assumptions are associated with considerable uncertainties because the mechanisms controlling variation in autotrophic respiration among large lotic systems remain unclear (Hall and Beaulieu 2013). However, long term GPP and ecosystem respiration estimates would allow better calculation of assimilatory N demand (Hall and Beaulieu 2013) and combined with long term mass balances improve also dissimilatory N removal estimates. The comparison of Lagrangian sampling and continuous probe measurement agreed well: The measured nitrate decrease between Westerhüsen and Werben in 2018 (20.4 t N) was in the range of probe estimates (16.3 t N).

**Conclusion**

The strong coupling of nutrient uptake to the development of the highly dynamic phytoplankton component makes nutrient uptake in large, plankton-rich rivers much more variable compared to streams, where benthic processes dominate. However, though variable, the dynamics are predictable when knowing the dominant control factors of phytoplankton. Here, summer low flow was an important condition for maximal algal development by cumulating ideal condition for phytoplankton growth with respect to water residence time and light availability. This finding is probably generalizable for rivers without significant loss processes of plankton, e.g., to benthic filter feeders, and drought conditions are expected to occur more frequently in many regions in the future (Humphrey et al. 2018). Another consequence of the dominant role of phytoplankton is that nutrients are hardly removed from the water column but rather converted into suspended biomass. This has probably significant consequences for the adjacent ecosystem, i.e., the estuary, in which high biomass and low suspended nutrients concentrations favor heterotrophic processes over autotrophic. Estuaries of eutrophic rivers, including the Elbe, often show high heterotrophic activity and corresponding oxygen depletion (Qian et al. 2018). Thus, riverine processes affect the predominant processes (i.e., autotrophic vs. heterotrophic) in the estuary.

**References**

Alexander, R. B., R. A. Smith, and G. E. Schwarz. 2000. Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. Nature **403**: 758–761. doi:10.1038/35015162

Appling, A. P., R. O. Hall, M. Arroita and C. B. Yackulic, 2018a. Streammetabolizer: models for estimating aquatic photosynthesis and respiration. R package version 0.10.9.

Appling, A. P., R. O. Hall, C. B. Yackulic, and M. Arroita, 2018b. Overcoming equifinality: Leveraging long time series for stream metabolism estimation. J. Geophys. Res. Biogeosci. **123**: 624–645. doi:10.1002/2017JG004140

Aufdenkampe, A. K., E. Mayorga, P. A. Raymond, J. M. Melack, S. C. Doney, S. R. Alin, R. E. Aalto, and K. Yoo. 2011. Riverine coupling of biogeochemical cycles between land, oceans, and atmosphere. Front. Ecol. Environ. **9**: 53–60. doi:10.1890/100014

Baborowski, M., O. Büttner, and J. W. Einax. 2011. Assessment of water quality in the Elbe River at low water conditions based on factor analysis. Clean (Weinh) **39**: 437–443. doi:10.1002/clen.2010000373

Battin, T. J., L. A. Kaplan, S. Findlay, S. C. Hopkinson, E. Marti, A. I. Packman, J. D. Newbold, and F. Sabater. 2008. Biophysical controls on organic carbon fluxes in fluvial networks. Nat. Geosci. **1**: 95–100. doi:10.1038/ngeo101

Billen, G., and others. 2007. A long-term view of nutrient transfers through the Seine river continuum. Sci. Total Environ. **375**: 80–97. doi:10.1016/j.scitotenv.2006.12.005

Bouwman, A. F., G. Van Drecht, J. M. Knoop, A. H. W. Beusen, and C. R. Meinardi. 2005. Exploring changes in
river nitrogen export to the world’s oceans. Global Biogeochem. Cycles 19. doi:10.1029/2004GB002314

Bowes, M. J., E. Gozzard, A. C. Johnson, P. M. Scarlett, C. Roberts, D. S. Read, L. K. Armstrong, S. A. Harman, and H. D. Wickham. 2012. Spatial and temporal changes in chlorophyll-a concentration in the River Thames basin, UK: Are phosphorus concentrations beginning to limit phytoplankton biomass? Sci. Total Environ. 426: 45–55. doi:10.1016/j.scitotenv.2012.02.056

Caraco, N. F., J. J. Cole, and D. L. Strayer. 2006. Top down control from the bottom: Regulation of eutrophication in a large river by benthic grazing. Limnol. Oceanogr. 51: 664–670. doi:10.4319/lo.2006.51.1_part_2.0664

Deutsch, B., M. Voss, and H. Fischer. 2009. Nitrogen transformation processes in the Elbe River: Distinguishing between assimilation and denitrification by means of stable isotope ratios in nitrate. Aquat. Sci. 71: 228–237. doi:10.1007/s00027-009-9147-9

Friedrich, G., and M. Pohlmann. 2009. Long-term plankton studies at the lower Rhine/Germany. Limnologica 39: 14–39. doi:10.1016/j.limno.2008.03.006

Hall, R. O., M. A. Baker, E. J. Rosi-Marshall, J. L. Tank, and J. D. Newbold. 2013. Solute-specific scaling of inorganic nitrogen and phosphorus uptake in streams. Biogeosciences 10: 7323–7331. doi:10.5194/bg-10-7323-2013

Hall, R. O., and J. J. Beaulieu. 2013. Estimating autotrophic respiration in streams using daily metabolism data. Freshw. Sci. 32: 507–516. doi:10.1899/12-147.1

Hardenbicker, P., S. Rolinski, M. Weitere, and H. Fischer. 2014. Contrasting long-term trends and shifts in phytoplankton dynamics in two large rivers. Int. Rev. Hydrobiol. 99: 287–299. doi:10.1002/iroh.201301680

Hansen, J. B., and M. J. Cohen. 2010. Direct and indirect coupling of primary production and diel nitrate dynamics in a subtropical spring-fed river. Limnol. Oceanogr. 55: 677–688. doi:10.4319/lo.2010.55.2.0677

Hensley, R. T., M. J. Cohen, and L. V. Korhak. 2015. Hydraulic effects on nitrogen removal in a tidal spring-fed river. Water Resour. Res. 51: 1443–1456. doi:10.1002/2014WR016178

Hillebrand, H., and U. Sommer. 1999. The nutrient stoichiometry of benthic microalgal growth: Redfield proportions are optimal. Limnol. Oceanogr. 44: 440–446. doi:10.4319/lo.1999.44.2.0440

Hillebrand, H., G. Steinert, M. Boersma, A. Malzahn, C. L. Meunier, C. Plum, and R. Ptacnik. 2013. Goldman revisited: Faster growing phytoplankton has lower N:P and lower stoichiometric flexibility. Limnol. Oceanogr. 58: 2076–2088. doi:10.4319/lo.2013.58.6.2076

Holst, H., H. Zimmermann-Timm, and H. Kausch. 2002. Longitudinal and transverse distribution of plankton rotifers in the potamal of the river Elbe (Germany) during late summer. Int. Rev. Hydrobiol. 87: 267–280 10.1002/1522-2632 (200205)87:2<267::AID-IROH267>3.0.CO;2-F

Hosen, J. D., and others. 2019. Enhancement of primary production during drought in a temperate watershed is greater in larger rivers than headwater streams. Limnol. Oceanogr. 64: 1458–1472. doi:10.1002/lno.11127

Houser, J. N., A. Lynn, L. A. Bartsch, W. B. Richardson, J. T. Rogala, and J. F. Sullivan. 2015. Ecosystem metabolism and nutrient dynamics in the main channel and backwaters of the Upper Mississippi River. Freshw. Biol. 60: 1863–1879. doi:10.1111/fwb.12617

Howarth, R. W., and others. 1996. Regional nitrogen budgets and riverine N&P fluxes for the drainages to the North Atlantic Ocean: Natural and human influences. Biogeochemistry 35: 75–139. doi:10.1007/BF02179825

Humphrey, V., J. Zscheischler, P. Ciais, L. Gudmundsson, S. Sitch, and S. I. Seneviratne. 2018. Sensitivity of atmospheric CO2 growth rate to observed changes in terrestrial water storage. Nature 560: 628–631. doi:10.1038/s41586-018-0424-4

Ibiñe, C., and J. Peñuelas. 2019. Changing nutrients, changing rivers. Science 365: 637–638. doi:10.1126/science.aay2723

Julian, J. P., M. W. Doyle, and E. H. Stanley. 2008. Empirical modeling of light availability in rivers. J. Geophys. Res. 113: G03022. doi:10.1029/2007JG006601

Kamjunke, N., and others. 2013. Biogeochemical patterns in a river network along a land use gradient. Environ. Monit. Assess. 185: 9221–9236. doi:10.1007/s10661-013-3247-7

Keck, F., and F. Lepori. 2012. Can we predict nutrient limitation in streams and rivers? Freshw. Biol. 57: 1410–1421. doi:10.1111/j.1365-2427.2012.02802.x

Klausmeier, C. A., E. Litchman, T. Daufresne, and S. A. Levin. 2008. Phytoplankton stoichiometry. Ecol. Res. 23: 479–485. doi:10.1111/j.1128-4008.0470-8

Köhler, J., M. Bahnwart, and K. Ockenfeld. 2002. Growth and loss processes of riverine phytoplankton in relation to
water depth. Int. Rev. Hydrobiol. 2-3: 241–254. doi:10.1002/1522-2632(200205)87:2<3241::AID-IRH241>3.0.CO;2-A
Kramer, B. J., T. W. Davis, K. A. Meyer, B. H. Rosen, J. A. Goleksi, G. J. Dick, G. Oh, and C. J. Gobler. 2018. Nitrogen limitation, toxin synthesis potential, and toxicity of cyanobacterial populations in Lake Okeechobee and the St. Lucie River Estuary, Florida, during the 2016 state of emergency event. PLoS One 13: e0196278. doi:https://doi.org/10.1371/journal.pone.0196278

Kunz, J. V., R. Hensley, L. Brase, D. Borchardt, and M. Rode. 2017. High frequency measurements of reach scale nitrogen uptake in a fourth order river with contrasting hydromorphology and variable water chemistry (Weisse Elster, Germany). Water Resour. Res. 53: 328–343. doi:10.1002/2016WR019355

Loken, L. C., and others. 2018. Limited nitrate retention capacity in the Upper Mississippi River. Environ. Res. Lett. 13. doi:10.1088/1748-9326/aacd51

Minaudo, C., M. Meybeck, F. Moatar, N. Gassama, and F. Curie. 2015. Eutrophication mitigation in rivers: 30 years of trends in spatial and seasonal patterns of biogeochemistry of the Loire River (1980–2012). Biogeosciences 12: 2549–2563. doi:10.5194/bg-12-2549-2015

Mulholland, P. J., and others. 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading. Nature 452: 202–246. doi:10.1038/nature06686

Ockenfeld, K., and H. Guhr. 2003. Groyne fields: Sink and source functions of “flow-reduced zones” for water content in the River Elbe (Germany). Water Sci. Technol. 48: 17–24. doi:10.2166/wst.2003.0420

Peterson, B. J., and others. 2001. Control of nitrogen export from watersheds by headwater streams. Science 292: 86–90. doi:10.1126/science.1056874

Pusch, M., and H. Fischer. 2006. Stoffdynamik und Habitatstruktur in der Elbe. In Konzepte für die nachhaltige Entwicklung einer Flusslandschaft, Band 5. Berlin: Weißensee Verlag.

Qian, W., and others. 2018. Current status of emerging hypoxia in a eutrophic estuary: The lower reach of the Pearl River Estuary, China. Estuar. Coast. Shelf Sci. 205: 58–67. doi:10.1016/j.ecss.2018.03.004

Quigg, A., and others. 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. Nature 425: 291–294. doi:10.1038/nature01953

Raymond, P. A., C. J. Zappa, D. Butman, T. L. Bott, J. Potter, P. J. Mulholland, A. E. Laursen, W. H. McDowell, and D. Newbold. 2012. Scaling the gas transfer velocity and hydraulic geometry in streams and small rivers. Limnol. Oceanogr. 2: 41–53. doi:10.1215/21573689-1597669

Reynolds, C. S., J. P. Descy, and J. Padiak. 1994. Are phytoplankton dynamics in rivers so different from those in shallow lakes? Hydrobiologia 289: 1–7. doi:10.1007/BF00007404

Reynolds, C. S., and J.-P. Descy. 1996. The production, biomass and structure of phytoplankton in large rivers. Arch. Hydrobiol. 10: 161–187. doi:10.1127/lt/10/1996/161

Ritz, S., K. Dähneke, and H. Fischer. 2018. Open-channel measurement of denitrification in a large lowland river. Aquat. Sci. 80: 11. doi:10.1007/s00204-017-0560-1

Ritz, S., and H. Fischer. 2019. A mass balance of nitrogen in a large lowland river (Elbe, Germany). Water 11: 2383–2400. doi:10.3390/w11112383

Roberts, B. J., and P. J. Mulholland. 2007. In-stream biotic control on nutrient biogeochemistry in a forested stream, West Fork of Walker branch. J. Geophys. Res. Biogeoisci. 112. doi:10.1029/2007JG000422

Rode, M., U. Suhr, and G. Wriedt. 2007. Multi-objective calibration of a river water quality model: Information content of calibration data. Ecol. Model. 204: 129–142. doi:10.1016/j.ecolmodel.2006.12.037

Rode, M., S. Halbedel Angelstein, M. R. Anis, D. Borchardt, and M. Weitere. 2016. Continuous in-stream assimilatory nitrate uptake from high frequency sensor measurements. Environ. Sci. Technol. 50: 5685–5694, DOI: 10.1021/acs.est.6b00943

Rulz Albizuri, J. R. 2018. Effects of global warming on phytoplankton and its biocontrol in large rivers: Insights from a model analysis. PhD thesis, Univ. of Osnabrück, 153 pp.

Seitzinger, S. P., R. V. Styles, E. W. Boyer, R. B. Alexander, G. Billen, R. W. Howarth, B. Mayer, and N. Van Bremen. 2002. Nitrogen retention in rivers: Model development and application to watersheds in the northeastern U.S.A.Biogeochemistry 57: 199–237. doi:10.1023/A:1015745629794

Tank, J. L., E. J. Rosi-Marshall, M. A. Baker, and R. O. Hall. 2008. Are rivers just big streams? A pulse method to quantify nitrogen demand in a large river. Ecology 89: 2935–2945. doi:10.1890/07-1315.1

Tittel, J., O. Büttner, and N. Kamjunke. 2012. Non-cooperative behaviour of bacteria prevents efficient phosphorus utilisation of planktonic communities. J. Plankton Res. 34: 102–112. doi:10.1093/plankt/fbr094

Várbiró, G., J. Padišák, Z. Nagy-László, A. Abonyi, I. Stanković, M. G. Udović, V. B-Beres, and G. Borics. 2018. How length of light exposure shapes the development of riverine algal biomass in temperate rivers? Hydrobiologia 809: 53–63. doi:10.1007/s10750-017-3447-1

Webster, J. R., and J. L. Meyer [eds.]. 1997. Stream organic matter budgets. J. N. Am. Benthol. Soc. 16: 3–161. doi:10.2307/1468223

Weitere, M., and H. Arndt. 2002. Top-down effects on pelagic heterotrophic flagellates (HNF) in a large river (River Rhine): Do losses to the benthos play a role? Freshw. Biol. 47: 1437–1450. doi:10.1046/j.1365-2427.2002.00875.x

Weitere, M., A. Scherwass, K.-T. Sieben, and H. Arndt. 2005. Planktonic food web structure and potential carbon flow.
in the Lower River Rhine with a focus on the role of protozoans. River Res. Appl. 21: 535–549. doi:10.1002/rra.825
Welker, M., and N. Walz. 1998. Can mussels control the plankton in rivers? A planktological approach applying a Lagrangian sampling strategy. Limnol. Oceanogr. 43: 753–762. doi:10.4319/lo.1998.43.5.0753
Wollheim, W. M., C. J. Voosmarty, B. J. Peterson, S. P. Seitzinger, and C. S. Hopkinson. 2006. Relationship between river size and nutrient removal. Geophys. Res. Lett. 33. doi:10.1029/2006GL025845
Yang, S., O. Büttner, J. W. Jawitz, R. Kumar, P. S. C. Rao, and D. Borchardt. 2019b. Spatial organization of human population and wastewater treatment plants in urbanized river basins. Water Resour. Res. 55: 6138–6152. doi:https://doi.org/10.1029/2018WR024614
Yang, X. Q., S. Jomaa, O. Büttner, and M. Rode. 2019a. Autotrophic nitrate uptake in river networks: A modeling approach using continuous high-frequency data. Water Res. 157: 258–268. doi:10.1016/j.watres.2019.02.059

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