Dynamics of silica and phytoplankton population under altered conditions of river flow in the Daugava River, Latvia

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Abstract. Three dams affect the flow of the lower Daugava River. The water reservoirs created by damming are relatively small with residence times from three to nine days. However, the water flow alteration is sufficient to cause a decrease in the phytoplankton biomass from an average of 246 to 96 mg m⁻³. The diatom community was dominated by single-cell and small ($d = 5-10 \mu m$) centric diatoms under the unaltered flow conditions. Under the altered flow conditions, chain-forming freshwater planktonic diatoms and singe-cell pennatae diatoms dominated the diatom community. The concentrations of dissolved silica varied between 51 and 121 µmol dm⁻³ and of biogenic silica from 1 to 12 µmol dm⁻³. In both cases the lowest values were observed during summer months. Furthermore, dissolved and biogenic silica concentrations were higher at stations representing unaltered flow conditions in comparison to those representing altered flow conditions during summer.

Key words: dissolved silica, biogenic silica, diatom community structure, rivers.

INTRODUCTION

Nitrogen and phosphorus are recognized as major nutrients because their availability governs overall algal growth (e.g. Schindler, 1977; Hecky and Kilham, 1988). At the same time, it has been discussed previously that a number of other elements might be limiting in certain ecosystems or for some organism groups. One of such elements is dissolved silica, whose availability can regulate phytoplankton species composition (Egge and Aksnes, 1992).

Dissolved silica in aquatic environments originates from the weathering and breakdown of silica-containing minerals and mostly is carried to marine environments by rivers (Tréguer et al., 1995). There are substantial variations in the delivery of dissolved silica from continents to the ocean due to different lithology of drainage areas, continental weathering intensity, climatic variations, and diatom production (Conley, 1997). In addition, it has been shown that anthropogenic factors, e.g. hydrological alteration of rivers as a result of construction of dams, can significantly reduce loads of dissolved silica to the sea (Garnier et al., 1999; Humborg et al., 2006), with adverse effects on the marine ecosystem (Conley et al.,

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1993; Humborg et al., 2000). The actual mechanism of a decrease of dissolved silica is still debated. For example, Humborg et al. (2000) argue that land-sea fluxes are smaller in the regulated than non-regulated boreal river systems as a result of the lower weathering flux of silica. It has been shown that major reservoirs built on boreal rivers can hold 30% to 70% of their annual water discharge (Dynesius and Nilsson, 1994), which can significantly decrease dissolved Si concentrations in rivers by providing preconditions for enhanced diatom growth and sedimentation of diatom frustules, and subsequent burial in sediments behind dams (Conley et al., 2000). Furthermore, the ability of small reservoirs with a short residence time of water to act as diatom traps and so affect silica landsea flux has been discussed. For example Friedl et al. (2004) argued that the residence time characteristic for small reservoirs of lowland rivers is not sufficient for the development of massive diatom blooms, so suggesting that some other explanation for the observed silica concentration decrease in lowland rivers is needed. At the same time it was argued that dams built on lowland rivers of the south-eastern Baltic with shorter residence times than those on boreal rivers can negatively affect silica land-sea fluxes (Humborg et al., 2006). Furthermore, it was demonstrated that even a relatively small reservoir with a short water residence time slows the river flow and that low flow conditions are essential for the formation of diatom blooms in rivers (e.g. Kiss and Genkal, 1993; Mitrovic et al., 2008).

Nevertheless, in our opinion there are too few direct studies on the impact of river flow alteration on land-sea silica fluxes due to alterations in diatom ecology. Therefore, we attempted to test the impact of an altered river flow on dissolved silica and the diatom population during the productive season along the heavily dammed Daugava River. We compared river areas unaffected and affected by damming. We also performed analysis of carbon, nitrogen, and silica in sediments of two reservoirs of different size to test the assumption of the dependence of the accumulation of silica of diatom origin on reservoir size.

MATERIALS AND METHODS

Study site

The Daugava River is 1005 km long with a catchment area covering 87 900 km². The catchment is composed of agricultural lands (50%), forest (40%), and lakes (2%) (Humborg et al., 2006). Consolidated sedimentary rocks dominate in the catchment, and the mean slope of the river is only 0.3%. The river flow velocity is highly variable: from 0.1 to more than 2 m s⁻¹ (Deksne et al., 2009). The long-term average runoff of the Daugava River is 21.1 km³ y⁻¹. The Daugava River is usually covered with ice in winter and experiences spring flood conditions.

For the purposes of our experiment we chose a 240 km long section (Fig. 1) where three sequential dams for hydroelectric power plants erected create a chain of water reservoirs (Table 1). Altogether seven sampling stations for water analysis



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Fig. 1. Location of the sampling stations.

Table 1. Main characteristics of water reser	ervoirs of hydroelectric power plants
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Reservoir	Average depth, m	Maximum depth, m	Total volume, km ³	Water residence time, days	Dam construction year	Area, km ³
Plavinu	14.6	47.0	0.51	9	1966	35.0
Kegums	6.3	16.5	0.16	3	1939	24.9
Riga	7.1	17.4	0.34	6	1974	35.8

were chosen. Six stations (DG2–DG7) were placed above and below the respective dams to represent water conditions prior and after damming while one station (DG1) was chosen well above the area influenced by damming as a reference site. Station DG7 was located close to a long-term state monitoring site used in this study to calculate long-term average concentrations of dissolved silica and loads of dissolved silica to the Gulf of Riga. In addition, sediment samples were obtained from three stations in Keguma Reservoir (sampling depth 13 m) and from three stations in Plavinu Reservoir (sampling depth 45 m).

Sampling

Water samples, representing river surface water (0–1 m depth), were taken six times in 2009 from all seven stations using a Niskin-type sampler. The sampling of all seven stations was performed on the same day. The sampling mode, including sampling depth and sampling gear, as well as sampling occasions were chosen based on previous long-term (e.g. Andrushaitis et al., 1995 and state monitoring) and case (Humborg et al., 2006) studies to be compatible with previously obtained results. In order to cover the productive season when diatom forming and retaining by dams occur, the sampling started in April and ended in November. No samples were taken from December to March because during that period the Daugava was mostly covered by ice and so no significant diatom forming and subsequent loss could be expected. Immediately after sampling subsamples for physico-chemical and biological analyses were taken and transported to laboratory for further analysis.

Analytical methods

Temperature (T), turbidity (A750), conductivity (EC), and the concentrations of dissolved silica (DSi), biogenic silica (BSi), total suspended solids (TSS), and chlorophyll a (Chl a) were measured in all water samples. In addition, at stations DG1 (reference station) and DG7 the phytoplankton species composition and biomass were analysed. Water T and EC were measured according to standard procedures. Turbidity was measured with a spectrophotometer in a 100 mm cell under the wavelength of 750 nm. The concentration of DSi was determined colorimetrically according the method described by Koroleff (1983) and that of BSi was determined following the modified method of DeMaster (1979). The water, approximately 100–300 mL, was filtered through 0.6 µm polycarbonate filters. BSi was extracted with 1% sodium carbonate for a period of 3 h at 85°C. Then the subsamples were neutralized by 0.021 N HCl and analysed for DSi according the method described by Koroleff (1983). The content of TSS was measured gravimetrically after filtration of a known water volume through preweighed Millipore filters with 0.45 µm pore size. The Chl a samples (0.46-1.62 L) were filtered onto Whatman GF/C filters (d = 13 mm), and thereafter the filters were extracted with 96% ethanol for 24 h at room temperature before being measured with a spectrophotometer. Thereafter Chl a concentrations were calculated according to HELCOM guidelines (HELCOM, 2006a).

The phytoplankton samples (300 mL) were fixed with acid Lugol's solution. Subsamples of 10 and 25 mL of the fixed samples were settled in a sedimentation chamber for 24 h and counted according to the Utermöhl technique with an inverted microscope at 200× and 400× magnifications (Utermöhl, 1958; HELCOM, 2006b; Olenina et al., 2006). The total number of phytoplankton in all subsamples exceeded 500. The cell volume for phytoplankton biomass determination was calculated using geometrical formulas for various suitable geometrical shapes (Edler, 1979).

Data analyses

Data from the sampling stations were analysed for differences among stations using one-way ANOVA followed by Tukey's HSD post-hoc test to establish the impact of dams on concentrations of the measured parameters.

Daily water flow rates (Q) for 2009 were obtained from Plavinu hydroelectric power plant. These were subsequently used to calculate annual runoff.

The long-term average monthly concentrations of DSi were calculated from state monitoring programme data for the period 1991–2001. The corresponding monthly river flow values as well as annual runoff were calculated for the same period from daily flow measurements performed at Plavinu hydroelectric power plant.

RESULTS

The water flow rates (Table 2) observed during sampling events were mostly well in the range of long-term average values, exhibiting high values during spring floods in April and low values during summer. A deviation from the long-term average was observed in November when the registered flow rate substantially exceeded the value of the long-term average. At the same time, the calculated annual runoff for 2009 was $21.7 \text{ km}^3 \text{ y}^{-1}$, which is only slightly higher than the average annual runoff calculated from long-term data. The water temperature varied substantially over the period of experiment (Table 2) with the lowest values in April and the highest in July. The temperature variance among stations during a respective sampling event was mostly around 3%, reaching 9% only in June. The turbidity and conductivity values (Table 2) also varied seasonally over the observation period and similarly to temperature showed no significant difference between stations above and below dams.

Date	$\begin{array}{c} Q,\\ m^3 s^{-1} \end{array}$	T, ℃	$EC, \mu S cm^{-1}$	A750, absorption units
23.04.2009	1790	4.9	199	0.16
14.05.2009	502	13.3	234	0.06
11.06.2009	392	17.9	266	0.04
10.07.2009	359	21.0	302	0.04
13.08.2009	327	20.9	315	0.03
13.11.2009	1160	-	285	0.05

Table 2. Average water flow, temperature, conductivity, and turbidity of all stations during sampling events

- Not measured.



Fig. 2. Concentrations of dissolved silica (DSi) measured at the sites of the Daugava River (bars) and long-term (1991–2001) average (line) calculated from state monitoring data (Latvian Environment, Geology and Meteorology Center). Error bars represent standard error.

The concentrations of DSi varied seasonally between 51 and 121 μ mol dm⁻³ with significantly (ANOVA, p < 0.01) lower values in the period from May to August compared to those in April and November (Fig. 2) at stations DG3–DG7. Significantly (ANOVA, p < 0.01) higher concentrations of DSi than in other sites were registered at stations DG1 and DG2 in June and August (Fig. 2). Although no such significant difference between stations was registered in July, an apparent spatial concentration decrease pattern, the highest in DG1 and the lowest in DG7, could be observed. Generally seasonal concentration changes observed at station DG7 followed the long-term pattern. However, concentration levels registered during all sampling events exceeded long-term average values. The highest difference was registered in July and November.

The concentrations of BSi exhibited a general spatial decreasing tendency with higher concentrations at stations DG1 and DG2 and the lowest at stations DG6 and DG7 (Fig. 3a) in May–August, except for station DG4 in May and station DG3 in July. The observed overall decrease in the concentrations of BSi between stations DG1 and DG7 was 45% to 71% in May–July but only 8% in August. At the same time, a pattern of increasing concentration with the lowest values registered at station DG1 and the highest at station DG6 could be observed in April when on average concentration levels were higher than during the other months.

The concentrations of TSS (Fig. 3b) follow the same general spatial concentration decrease pattern as that of BSi in June–August and concentration increase pattern in April, but contrary to BSi exhibit no apparent concentration decrease



Fig. 3. Concentrations of biogenic silica (BSi) (a) and total suspended solids (TSS) (b) measured at the sites of the Daugava River.

pattern in May. Furthermore, the concentration of TSS registered at station DG1 in June was significantly higher than those registered at other stations during the same sampling occasion. Similarly to the concentrations of BSi, the TSS values were on average also the highest in April.

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The concentrations of Chl *a* demonstrated a clear spatial decrease pattern (Fig. 4) during all sampling occasions with the highest values at stations DG1 and DG2 and the lowest at station DG7, with the exception of station DG4 in May. However, contrary to BSi and TSS, the concentrations of Chl *a* measured in April did not exceed those measured during other sampling occasions.

The total phytoplankton biomass in the reference station DG1 was on average 246 mg m⁻³ and in station DG7, 96 mg m⁻³, varying seasonally from 128 to 326 mg m^{-3} with the highest values in July and August, respectively. On average diatoms formed from 40% (DG1) to 50% (DG7) of the total biomass. The rest was taken up by cryptophytes, mainly Cryptomonas spp. (27%), unidentified small $(d = 5-7 \mu m)$ flagellates (12%), chlorophytes (10% at DG1 and 6% at DG7), and cyanobacteria (8% at DG1 and 3% at DG7). The total diatom biomass was substantially (from 29% in April to 77% in June) higher in station DG1 than in station DG7 during all sampling occasions except for August when the diatom biomass observed in station DG7 exceeded that in station DG1 (Fig. 5). Furthermore, the diatom species composition between stations differed significantly (Fig. 5). Singlecell diatoms, mostly Synedra spp., and small ($d = 5-10 \,\mu\text{m}$) centric Cyclotella spp. and Stephanodiscus spp. were abundant in the upriver station DG1, forming from 77% to 91% of the diatom biomass during the whole study period (Fig. 5a). At the same time, the diatom composition at station DG7 was from 55% to 70% dominated by chain-forming freshwater planktonic diatoms (Aulacoseira islandica v. islandica, A. granulata v. granulata, and Melosira varians) during the summer period, while in spring and autumn singe-cell pennatae diatoms (Asterionella



Fig. 4. Concentrations of chlorophyll a measured at the sites of the Daugava River.





Fig. 5. Biomass of most abundant diatom species in stations DG1 (a) and DG7 (b).

formosa, *Diatoma vulgaris* v. *vulgaris*, *Navicula* spp., and *Synedra* spp.) dominated comprising 74% and 66%, respectively, of the total spring and autumn diatom biomass (Fig. 5).

DISCUSSION

The results of our study confirm the assumption that the alteration of river flow by building dams results in a decrease of the DSi concentration in the water column during the phytoplankton growth season and so reduces the silica land–

sea flux as suggested by Humborg et al. (2006). It has been argued that the observed decrease in the DSi concentration can be associated with increased concentrations of BSi (e.g. Humborg et al., 2006) where silica is transferred from the dissolved to the particulate silica pool due to the assimilation of silica by diatoms. However, the decrease in the DSi concentration from on average 92 μ mol dm⁻³ in April to 62 µmol dm⁻³ in May observed in our study was not reflected in an increased BSi concentration. Quite the opposite, BSi concentration values in May were lower than in April (Fig. 3a). Although no spring phytoplankton bloom was registered, the diatom community was already developed during April (Fig. 5). Therefore, we have to assume that the development of diatoms is not the main factor controlling the seasonally occurring decrease in the DSi concentration. At the same time high water flow rates (Table 2) indicate that spring flood conditions were still observable in April. As a result, a large amount of particles, both resuspended from the river bottom and freshly eroded from land, along with phytoplankton cells were in the water column, which was reflected in the measured TSS values. The TSS concentration exhibited a clear correlation ($R^2 = 0.74$) with BSi (Fig. 6) while there was no correlation between BSi and Chl a if April data were included. Therefore we can conclude that during April the enhanced BSi concentration was mostly sustained by particles resuspended from the river bottom or transported from land.

The correlation between BSi and Chl *a* was positive ($R^2 = 0.42$) if only May– August data were used (Fig. 7). This suggests that a significant proportion of BSi measured during these months originates from diatoms. In order to estimate the proportion of living diatoms in the measured BSi, we attempted to recalculate the particulate silica concentration from the diatom biovolume. For this we assumed



Fig. 6. Correlation between biogenic silica (BSi) and total suspended solids (TSS).



Fig. 7. Correlation between biogenic silica (BSi) and chlorophyll a.

that the dry biomass of algae was 20% of the biomass estimated from biovolume (Strickland, 1966) and silica constituted on average 60% by dry weight of diatoms (Sicko-Goad et al., 1984). The concentration of BSi calculated from diatom biomass constituted only 10–15% of the BSi concentrations at respective observation occasions, except for July when 21% of BSi at both stations and in April when 5% at station DG7 was bound in diatom cells. These estimated values could be underestimations of actual values. However, we have to assume that part of the material measured as BSi was actually phytoliths, which are considered to be an important source of BSi in soils (Conley, 2002) and can enter riverine ecosystems via soil surface erosion and constitute a major source of the suspended load (Cary et al., 2005). This pathway seems to be most plausible in April when spring flood conditions with a capacity to erode the soil surface, which according to Cary et al. (2005) is a precondition for phytolith transport from soil to river, can be observed. During the rest of the observation period, rivers received water mostly through groundwaters and so no major soil surface erosion was expected. As we counted only living cells, we can assume that a substantial part of the measured BSi, especially during May-August, originated from empty frustules of diatoms that were overlooked during the counting procedure and were kept in water by the turbulent flow.

Earlier findings indicate that slow-flow conditions are essential preconditions for the formation of diatom blooms (e.g. Kiss and Genkal, 1993; Mitrovic et al., 2008), which in turn enable the transfer of silica from the DSi to the BSi pool. However, both pools demonstrated a simultaneous spatial decreasing tendency along the altered river section. Furthermore, the phytoplankton biomass was higher in the station representing unaltered conditions during all sampling events

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(Fig. 5). Therefore we considered other factors that can affect diatom community development. The most relevant physical–chemical factors, besides water turbulence and DSi concentration, affecting diatom growth, and so the uptake of DSi, are temperature (e.g. Vandonk and Kilham, 1990; Yang et al., 2012), deficiency of underwater light (e.g. Reynolds, 1995; Reynolds and Descy, 1996), and availability of reactive phosphorus (e.g. Urrea and Sabater, 2009; Chessman and Townsend, 2010; Yang et al., 2012).

The temperature regime in the Daugava River is similar to that of other rivers of eastern Baltic, e.g. the Oder and Vistula, while the concentration of TSS (on average 4 mg dm⁻³) in the Daugava is substantially lower than in the Oder (22 mg dm⁻³) and Vistula (17 mg dm⁻³) rivers (Humborg et al., 2006). At the same time, substantially higher concentrations of BSi were observed in both the Oder and the Vistula (Humborg et al., 2006). Therefore, it is not likely that the observed lower concentration of BSi in the Daugava could be due to differences of either temperature or turbidity. The mean concentrations of reactive phosphorus (DIP, 1.5 μ mol dm⁻³) and dissolved inorganic nitrogen (DIN, 41 μ mol dm⁻³) observed in the Daugava (Jurgensone and Aigars, 2012) also seem to be sufficiently high not to be limiting algal growth. Moreover, the observed concentrations are well in the range of values observed by Pastuszak et al. (2012) in the Oder (approximately 1.25 and 142 µmol dm⁻³ of DIP and DIN, respectively) and the Vistula (approximately 2.5 and 107 μ mol dm⁻³ of DIP and DIN, respectively). However, the presence of several phytoplankton species, e.g. Stephanodiscus hantzshii, Aulacoseira islandica v. islandica, and Aulacoseira granulata v. granulata that are characteristic in phosphorus-limited systems with a high Si:P ratio (Donk and Kilham, 1990; Ferris and Lehman, 2007) suggests that the growth of algae in the Daugava still might be limited by phosphorus availability. The assumption is indirectly supported by recent findings of Jurgensone and Aigars (2012) indicating that on average up to 56% of phosphorus measured in the Daugava as dissolved is actually associated with particles of different size and colloids. Therefore, it can be assumed that at least partly the development of the algal community might be inhibited by phosphorus availability. Still, further research is needed for a more definite conclusion.

Our results clearly show that an alteration of the river flow results in distinct changes of the diatom community. This is clearly demonstrated by the shift from species of the genera *Aulacoseira*, *Cyclotella*, *Melosira*, *Stephanodiscus*, and *Synedra*, observed in our study at the site unaffected by damming, to chainforming diatoms such as *Aulacoseira* and *Melosira*, observed at the sites affected by the river flow alteration. The species of the genera *Aulacoseira*, *Cyclotella*, *Melosira*, *Stephanodiscus*, and *Synedra* are usually associated with turbulent waters since their cells rely on water turbulence to keep them in the photic zone (e.g. Sherman and Webster, 1998; Clarson et al., 2009), while chain-forming diatoms are known to dominate under low-flow conditions. Plausibly species characteristic for turbulent waters were not observed in the river sections affected by dams because most likely the series of water reservoirs cumulatively can alter

the river flow to low-flow conditions although each reservoir individually has a very short residence time. Therefore, in those river sections where the water flow is altered the turbulence is not sufficient to prevent cell sinking as demonstrated elsewhere by Bormans and Webster (1999). At the same time, the chain-forming diatoms most likely were not abundant upstream of the series of water reservoirs as their chains tend to break in turbulent waters, which in turn negatively affects their growth.

CONCLUSIONS

The results of our study clearly demonstrated that the alteration of the river flow due to damming results in a shift of the phytoplankton species composition as well as a decrease in their biomass. The latter contradicts conclusions from studies conducted at other rivers according to which the construction of reservoirs results in phytoplankton blooms. Therefore we assume that the phytoplankton community is limited by the availability of phosphorus.

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