Proceedings of the Estonian Academy of Sciences,
2018, **67**, 1, 93–105
https://doi.org/10.3176/proc.2018.1.05
Available online at www.eap.ee/proceedings

ECOLOGY

# Changes in particulate organic matter passing through a large shallow lowland lake

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Received 30 June 2017, revised 5 January 2018, accepted 8 January 2018, available online 13 February 2018

**Abstract.** Different sources of particulate organic matter (POM) as well as its composition affect the biological food web and hence the self-purification potential and water quality of rivers. We studied the effect of a large shallow lake on the POM pool of the water passing through it. Over four years, we analysed monthly the amount and composition of POM and a set of environmental variables in the inflows and in the outflow of Lake Võrtsjärv (Estonia). In the inflows, the live pool of POM consisted of phytoplankton – small crypto-, dino-, and chlorophytes. The concentration of chlorophyll *a* (Chl *a*), as a proxy of phytoplankton biomass, was positively correlated with temperature and total phosphorus and negatively with dissolved silica, total nitrogen, and discharge. In the outflow, the share of the live component of POM was much larger than in the inflows but was also dominated by phytoplankton represented by grazing resistant filamentous cyanobacteria. Chl *a* was positively correlated with total phosphorus, temperature, pH, and precipitation, and negatively with dissolved silica, total nitrogen, and discharge in the outflow. The different amounts, composition, and seasonal dynamics of POM in the inflows and in the outflow have potentially substantial impacts on the food web with a predominating classical pathway in the inflows versus a detrital pathway in the outflow.

**Key words:** particulate organic matter, rivers, lakes, algal species, food web.

## INTRODUCTION

Particulate organic matter (POM) and dissolved organic matter (DOM) are the two fractions in which organic matter occurs in water bodies. Usually, these fractions have operative definitions: any organic material that does not pass through a particular filter is termed POM and the material that passes through a filter is termed DOM (Volkman and Tanoue, 2002). Commonly used filters for separating POM and DOM include glass fibre filters (GF/F), silver membrane fibres, or nitrocellulose filters.

In water bodies, POM consists of live planktonic, periphytic, and benthic microorganisms as well as dead organic matter that originates from the excrements and decay of various organisms. In streams and lakes of the temperate and boreal climate regions, the concentration of POM is usually lower than that of DOM (Niemirycz et al., 2006; Sobek et al., 2007; Tranvik et al., 2009). As it can be ingested by different metazoans POM enters the food web directly whereas DOM is utilized mainly via the microbial loop (Sobczak et al., 2002; Stutter et al., 2007; Drummond et al., 2014). In rivers, POM consists of autochthonous matter, originating in the stream biotic complex, and allochthonous matter, arriving from the catchment area, especially during snow melt or

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heavy rainfalls (Aufdenkampe et al., 2011). Transport of POM from the catchment is influenced by bedrock, soils (Chen and Jia, 2009), local climate conditions (Brooks et al., 2007), hydrology, and riverbank vegetation, but also by human activities (Rask et al., 1998; Ford and Fox, 2014). In many rivers, detrital matter constitutes the largest part of the POM (Vannote et al., 1980; Wallace et al., 1997; Drummond et al., 2014). Thorp and Delong (2002) suggested that algal derived carbon has more energy per unit mass compared with allochthonous carbon. Besides, algal cells contain labile forms of mineral and organic nutrients (Vieira and Myklestad, 1986; Malzahn et al., 2007). Riverine phytoplankton, consisting mostly of small-celled cryptophytes and diatoms (Sobczak et al., 2002; Piirsoo et al., 2007), the latter often originating in periphyton, are easily assimilated by aquatic invertebrates, especially collector-gatherers and filter feeders (Webster et al., 1999).

In lakes, POM is mainly derived from phytoplankton and the detritus originating from the decay of macrophytes (Boers and Boon, 1988). Cyanobacteria are increasingly becoming the dominating phytoplankton group in shallow lakes (Kosten et al., 2012; Nõges and Tuvikene, 2012); however, as they are not the preferred food for zooplankton, cyanobacteria fuel the microbial loop (Zingel et al., 2007) and the benthic food web (Cremona et al., 2014b). Therefore, differences in the composition and biomass of algal species between lakes and rivers may have a significant impact on the food webs in these systems.

Phytoplankton as a live component of POM has been distinguished from detrital matter by measuring a labile chemical marker such as chlorophyll *a* (Chl *a*) (Marker and Gunn, 1977; Savoye et al., 2012), adenosine triphosphate (ATP) (Nõges, 1989), and the C : N ratio (Taylor and Roff, 1984). However, also detailed information on phytoplankton composition has a great value for predicting the pathways of organic matter in food webs (Caroni et al., 2012), especially in the areas influenced by river inputs (Harmelin-Vivien et al., 2008). Streams and rivers are important interfaces between the mainland and lakes because they transport a wide range of organic carbon forms of different reactivity. In the present study, we used a combination of algal species composition, concentrations of Chl *a*, particulate organic carbon (POC, as a measure of POM), and seston (organisms and non-living matter) to assess the role of a shallow lowland lake in changing the proportions of classical and detrital food webs in connected streams.

The aims of this study were (i) to assess the main factors that control the concentrations and relative importance of phytoplanktonic versus detrital POM in rivers before and after passing a shallow eutrophic lake and (ii) to predict the potential impact of different species compositions of phytoplankton in the inflows and in the outflow on the food web structure in these systems. We set the following working hypothesis: considering that phytoplankton is assumingly more essential in lakes than in rivers, the relative importance of phytoplankton-based food chains versus detritus-based food chains is greater in the outflow compared with the inflows.

## STUDY AREA

The study was carried out in the five largest inflows and in the outflow of Lake Võrtsjärv in southern Estonia (north-eastern Europe), which belongs to the southern boreal forest zone (Fig. 1). The lake and its catchment (3104 km$^2$) are located in a flat lowland. Võrtsjärv is a large (270 km$^2$) eutrophic and very shallow (average depth 2.8 m) lake characterized by both seasonally and annually strongly fluctuating water level. Strong resuspension of bottom sediments due to shallowness and a large wind-exposed area cause high water turbidity (Secchi depth 0.5–1 m) (Kisand and Nõges, 2004). A detailed description of the lake is provided by Nõges and Nõges (2012).

The largest inflow to Võrtsjärv, the Väike Emajõgi, contributes 41% of the total riverine water discharge to the lake (Nõges et al., 2008a). The other inflows are the Õhne, Tänassilma, Tarvastu, and Konguta (Fig. 1). The lengths of the inflows vary from 17 to 104 km and the catchment areas from 100 to 1291 km$^2$. The Väike Emajõgi and the Õhne originate in lakes, and the Tarvastu, Tänassilma, and Konguta streams rise from wetland or boggy areas. The average flow velocity in the lower course of the Väike Emajõgi is $<0.1$ m s$^{-1}$ with an average retention time of more than two weeks. The flow velocity of the other inflows is 0.1–0.3 m s$^{-1}$ (Järvekülg, 2001).

Luvisols are the dominant catchment soil type of the streams falling into Võrtsjärv from the north, north-east, and west; podzols prevail in the southern and south-western catchment parts while regosols are represented with an appreciable proportion only in the Väike Emajõgi catchment (Fig. 1). Fine sediments with prevailing silt and sand dominate in the lower course of the stream bottom, which is overlaid by mud or organic-rich silt in places (Miidel, 2004; Miidel et al., 2004).

Among macrophytes, the emergent *Phragmites australis* (Cav.) Trin. ex Steud., the floating-leaved *Nuphar lutea* (L.), and the helophyte *Sparganium emersum* Rehm. dominate. Besides these, green filamentous macroalgae from the genus *Cladophora* are abundant in the Väike Emajõgi and Tarvastu, while the water moss *Fontinalis antipyretica* Hedw. spreads on the bottom stones of the Õhne and Tarvastu.

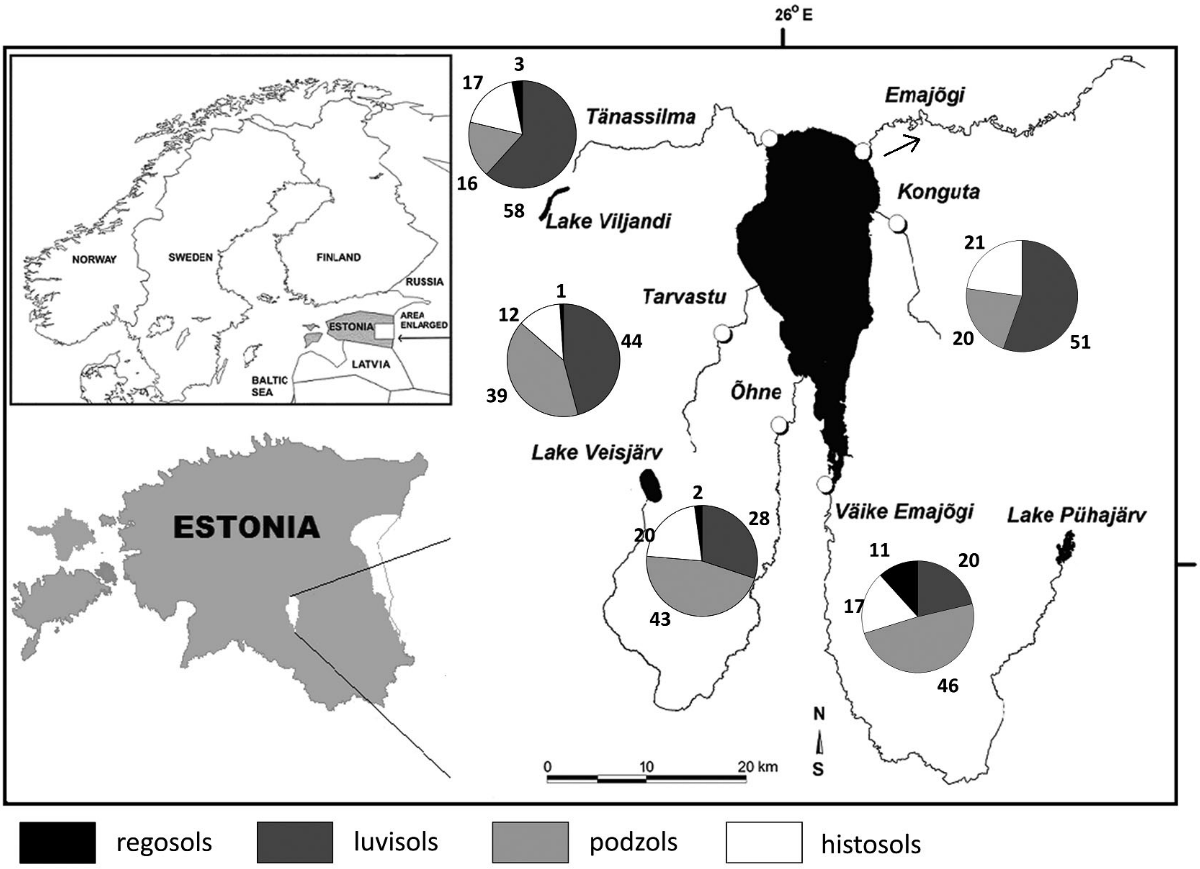

**Fig. 1.** Lake Võrtsjärv and the location of the sampling sites of the inflows: Tänassilma 58º23′55.3″N, 26º58′28.7″E; Tarvastu 58º13′43.5″N, 25º53′03.2″E; Õhne 58º08′47.6″N, 25º58′39.0″E; Väike Emajõgi 58º05′34.5″N, 26º03′10.4″E; Konguta 58º19′13.1″N, 26º11′20.9″E; and the outflow Emajõgi 58º23′6.33″N, 26º08′00.8″E. Circle sectors and numbers indicate the percentages of different soil types in the catchments of the inflows.

The outflowing Emajõgi is characterized by a very small mean stream gradient of 0.04 m km$^{-1}$ (Loopmann, 1979). Its water exhibits the integrated characteristics of Võrtsjärv.

## MATERIAL AND METHODS

### Sampling

Water samples were collected monthly from February 2008 to December 2011 from the lower course of the inflows and from the upper course of the outflow of Võrtsjärv (Fig. 1). We took one-litre samples from a depth of 0.1 m from the thalweg, stored them in polyethylene bottles in the dark at 4 °C, and made chemical analyses within 24 h. Water temperature, pH, and electrical conductivity were measured in situ with a multisensor F/SET WTW (Wissenschaftlich-Technische Werkstätten GmbH, Germany). In 2008–2009 phytoplankton was sampled into one-litre bottles and was preserved with the acid Lugol solution.

### Laboratory work

We analysed phytoplankton samples according to the European standard EN 15204 (2006) using an inverted differential interference contrast microscope Nikon Eclipse T$_i$. The samples were left to settle in 2.5–10 mL Utermöhl (1958) chambers for 24 h. To obtain reliable estimates of the number of organisms, approximately 100 individuals from each most abundant species or at least 500 individuals in total were counted per sample, yielding a standard error of less than ±10% for the total count (Laslett et al., 1997). A detailed description of phytoplankton counting and biomass calculation is given in (Piirsoo et al., 2008). The wet weight biomass of phytoplankton (PB) was expressed in units of mg L$^{-1}$. The species richness of phytoplankton was expressed by the number of taxa (PT).

For Chl *a* (μg $L^{-1}$), 0.1–0.3 L of water was passed through a Whatman GF/F glass microfibre filter, and the concentrations were measured spectrophotometrically (Edler, 1979) at wavelengths of 665, 647, and 630 nm from 96% ethanol extracts of the filters according to the international standard ISO 10260 (1992).

For total suspended matter (TSM, mg $L^{-1}$), as a measure of seston, 0.2–0.6 L of water was passed through a pre-weighed Whatman GF/F filter. The concentration of the TSM was calculated from the difference in dried filter weight before and after the filtration procedure according to APHA (1989).

Determination of carbon compounds in water samples was based on the oxidation of organic compounds into carbon dioxide ($CO_2$), which was then detected quantitatively. The amount of POC was used as the carbon equivalent of POM and was calculated as the difference in the measured total organic carbon (TOC) and dissolved organic carbon (DOC) concentrations. A thorough description of the method can be found in (Piirsoo et al., 2012).

The concentrations of nitrogen, phosphorus, and silicon compounds were analysed from unfiltered water samples using standard methods (Grasshoff et al., 1999). The samples were digested with persulphate to determine total nitrogen (Tot-N, mg $L^{-1}$) as well as total phosphorus (Tot-P, mg $L^{-1}$). The concentration of Tot-N was determined by the cadmium reduction method. The formed highly coloured azo dye was measured by a spectrophotometer at 545 nm. The Tot-P concentration was determined by the ascorbic acid method, and the absorbance of the solution was measured at 880 nm. The concentration of dissolved silica compounds (DSi, mg $L^{-1}$) was determined by treating an acidified water sample with a molybdate reagent. The absorbance of the formed solution of the blue silicomolybdic complex was measured at 810 nm (Grasshoff et al., 1999). The data were added to the hydrochemical database of the inflows and the outflow of Lake Võrtsjärv (Vilbaste et al., 2015).

### Data collection

River discharges ($m^3$ $s^{-1}$) were calculated by multiplying the daily flows measured at the gauging stations by the coefficients that consider the gauged proportions of the river basins (Järvet, 2005). The water discharge data at the gauging stations and the monthly precipitation data at the Tartu–Tõravere weather station were provided by the Estonian Environment Agency.

The proportions of the different soil types within the river basins were calculated using a 1 : 10 000 scale digital soil map of Estonia (Maa-amet, 2001). The data on aquatic macrophytes for the summer period and the invertebrate data for the spring period in the inflows were obtained from the reports of the Estonian national monitoring programme (http://seire.keskkonnainfo.ee/).

### Statistical methods

We used STATISTICA 12 for Windows (Dell Inc., 2015) to analyse the data. The nonparametric Mann–Whitney U test was used to assess differences in the phytoplankton, POC, and hydrochemical characteristics between the inflows and the outflow. The Kruskal–Wallis ANOVA and median test were used to assess differences between the five inflows. The Spearman's Rank Order correlation was used to find relationships between the studied variables. The Kendall Seasonal Trend (K–S) test (Kendall, 1975; Hirsch et al., 1982; Hirsch and Slack, 1984) was used to characterize inter-annual changes in the phytoplankton and POC parameters; $p < 0.05$ was accepted as significant for all tests.

## RESULTS

The Kruskal–Wallis ANOVA and median test showed that the five inflows of Võrtsjärv did not differ statistically with respect to phytoplankton biomass, Chl *a*, or POC concentration and, hence, the data for the inflows were pooled. However, significant differences ($p < 0.5$) were noted between the inflows and the outflow. In the inflows, conductivity and nutrient concentrations (Tot-N, Tot-P, and DSi) were higher and the phytoplankton and chemical parameters exhibited broader ranges compared with the corresponding parameters for the outflow (Table 1). Phytoplankton biomass, POC, TSM, and pH were higher in the outflow ($p < 0.5$). The TOC concentrations did not differ significantly between the inflows and the outflow; however, the variation in TOC was five times lower in the outflow.

The seasonal dynamics of phytoplankton and POC were similar for the inflows with the highest values of phytoplankton biomass and the Chl *a* : POC ratio for summer (June–August) (Table 2, Fig. 2). However, significant differences ($p < 0.5$) were noted between the inflows and the outflow. The highest percentage of POC in TOC occurred in the inflows in winter (December–February). In the outflow, the richest phytoplankton, the highest Chl *a* and POC concentrations, and the highest percentage of POC in TOC occurred in late summer or autumn (Table 2, Fig. 2).

The composition of the phytoplankton community in the inflows and in the outflow had hardly any overlap. In the inflows, planktonic cryptophytes from the genera *Cryptomonas* and *Rhodomonas* dominated in the biomass for most of the year. Additionally, in spring (March–May) or autumn (September–November), the diatom *Nitzschia*

**Table 1.** Minimum, maximum, and median values of the phytoplankton and environmental parameters of the inflows and the outflow of Lake Võrtsjärv for 2008–2011. Abbreviations: *n* – number of samples; TSM – total suspended matter; POC – particulate organic carbon; TOC – total organic carbon; PB – phytoplankton biomass; PT – number of taxa; Tot-N – total nitrogen; Tot-P – total phosphorus; DSi – dissolved silica; Cond – electric conductivity; Disch – discharge; Precip – precipitation

| Parameter | Unit | Inflows | | | Outflow | | |
|---|---|---|---|---|---|---|---|
| | | *n* | Min–Max | Median | *n* | Min–Max | Median |
| TSM | mg L$^{-1}$ | 197 | 0.4–32.2 | 4.4 | 41 | 1.5–44.5 | 12.8 |
| POC | mg L$^{-1}$ | 247 | 0.1–26.2 | 1.8 | 51 | 0.2–17.5 | 3.5 |
| TOC | mg L$^{-1}$ | 247 | 3.5–56.0 | 18.6 | 51 | 12.9–36.2 | 20.0 |
| POC : TOC | % | 247 | <1–80 | 10 | 51 | 1–48 | 17 |
| Chl *a* | µg L$^{-1}$ | 224 | 0.04–49.3 | 2.2 | 51 | 1.6–60.0 | 25.3 |
| Chl *a* : POC × 1000 | | 247 | <0.1–132 | 1 | 51 | 0.2–138 | 7 |
| PB | mg L$^{-1}$ | 127 | <0.1–8.9 | 0.4 | 27 | 2.5–66.0 | 20.0 |
| PT | | 127 | 2–40 | 16 | 27 | 10–60 | 28 |
| Tot-N | mg L$^{-1}$ | 248 | 0.5–11.0 | 2.1 | 51 | 0.9–2.3 | 1.5 |
| Tot-P | mg L$^{-1}$ | 248 | 0.03–0.23 | 0.06 | 51 | 0.02–0.09 | 0.04 |
| DSi | mg L$^{-1}$ | 149 | 0.9–5.5 | 2.9 | 51 | 0.2–7.3 | 2.2 |
| pH | | 244 | 7.1–8.4 | 7.9 | 51 | 7.7–9.9 | 8.4 |
| Cond | µS cm$^{-1}$ | 248 | 210–748 | 464 | 51 | 288–428 | 360 |
| Disch | m$^3$ s$^{-1}$ | 200 | 0.1–56.6 | 3.2 | 51 | 5.5–57.0 | 35.0 |
| Precip | mm | 48 | 10.5–165 | 52.9 | | | |

**Table 2.** Seasonal median values of the phytoplankton and nutrient parameters in the inflows and the outflow of Lake Võrtsjärv for 2008–2011. For abbreviations and units, see Table 1

| Parameter | Median values for inflows | | | | Median values for outflow | | | |
|---|---|---|---|---|---|---|---|---|
| | Spring | Summer | Autumn | Winter | Spring | Summer | Autumn | Winter |
| TSM | 4.9 | 5.4 | 4.0 | 3.6 | 7.3 | 30.1 | 18.2 | 4.0 |
| POC | 1.2 | 1.9 | 2.0 | 2.0 | 2.5 | 5.5 | 5.0 | 2.7 |
| POC : TOC | 8 | 10 | 10 | 12 | 13 | 25 | 21 | 15 |
| Chl *a* | 2.0 | 4.6 | 2.4 | 0.4 | 8.7 | 30.7 | 34.4 | 11.6 |
| Chl *a* : POC × 1000 | 2 | 3 | 1 | 0.2 | 7 | 6 | 9 | 6 |
| PB | 0.5 | 0.7 | 0.3 | 0.1 | 14.7 | 38.6 | 36.8 | 10.0 |
| PT | 16 | 22 | 17 | 10 | 31 | 32 | 27 | 18 |
| Tot-N | 2.3 | 1.5 | 1.9 | 2.9 | 1.7 | 1.1 | 1.3 | 1.5 |
| Tot-P | 0.06 | 0.08 | 0.06 | 0.06 | 0.04 | 0.06 | 0.05 | 0.04 |
| DSi | 2.5 | 2.5 | 3.0 | 3.6 | 2.6 | 0.9 | 1.8 | 2.5 |

*acicularis* (Kützing) W. Smith and the chrysophytes *Synura* cf. *uvella* Stein em. Korschikov and *Dinobryon sertularia* Ehrenberg appeared in the water column. In summer, planktonic chlorophytes from the genera *Monoraphidium* and *Scenedesmus* and dinoflagellates from the genus *Peridinium* were present. Occasionally, the pseudoplanktonic diatom *Melosira varians* C.A. Agardh and the epiphytic/epilithic diatoms *Cocconeis placentula* Ehrenberg and *Gomponema parvulum* (Kützing) Kützing were washed into the water column.

In the outflow, the species composition of phytoplankton was quite homogeneous with filamentous cyanobacteria *Limnothix redekei* (van Goor) Meffert, *L. planktonica* (Wołoszynska) Meffert, and *Planktolyngbya limnetica* (Lemmermann) Komarkova-Legnerova *et* Cronberg dominating throughout the year. The cyanobacteria were accompanied by centric diatoms from the genus *Aulacoseira* in spring. Over the four-year period, inter-annual differences in POC and phytoplankton parameters were not significant.

Correlations between the studied variables were generally weaker for the inflows (Table 3) than for the outflow (Table 4). For the inflows, POC showed no significant relationships with any phytoplankton parameter and was positively correlated only with the amount of precipitation and negatively with Tot-N. The same two correlations were valid also for the outflow where, in addition, POC correlated positively with temperature, TSM, phytoplankton biomass, Chl *a*, and Tot-P, and negatively with DSi. Inflowing TSM was positively

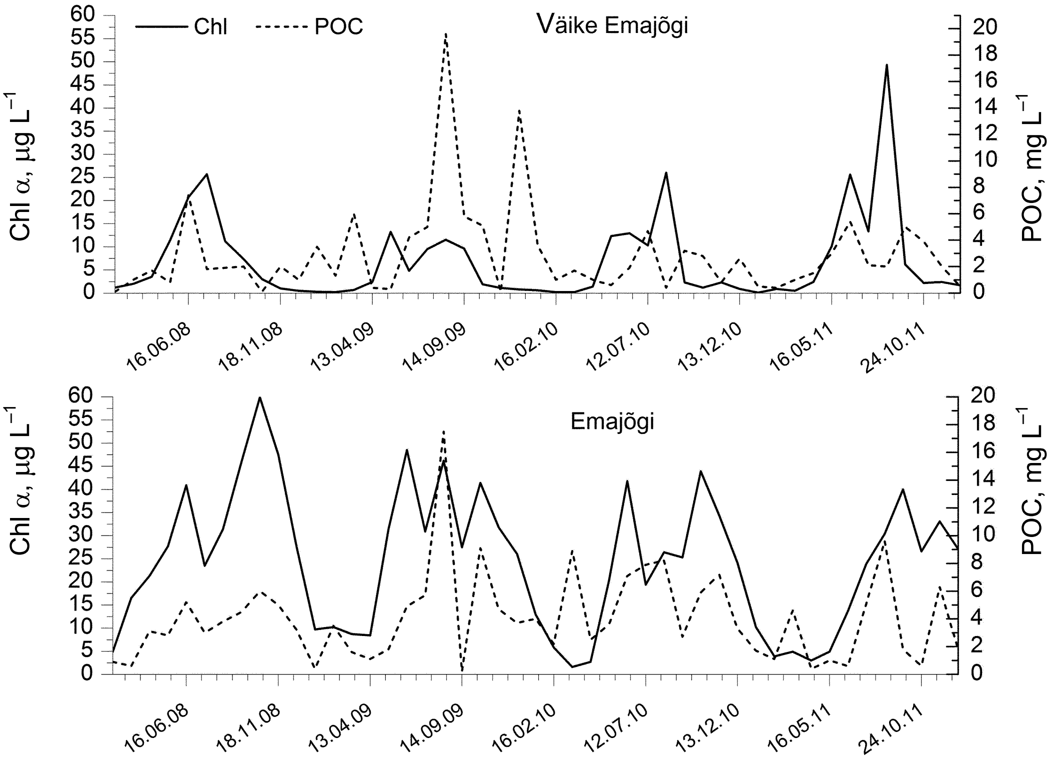

**Fig. 2.** Seasonal dynamics of Chl *a* and particulate organic carbon (POC) concentrations in the main inflow (Väike Emajõgi) and in the outflow (Emajõgi), 2008–2011.

**Table 3.** Spearman correlation coefficients of TSM, POC, and phytoplankton parameters with the environmental characteristics in the inflows of Lake Võrtsjärv for 2008–2011. For abbreviations, see Table 1; n.s. – not significant; absolute value of $R > 0.50$ is marked in bold

| | TSM | POC | Chl *a* | PB | PT |
|---|---|---|---|---|---|
| POC | n.s. | | | | |
| Chl *a* | 0.39 | n.s. | | | |
| PB | 0.34 | n.s. | **0.86** | | |
| PT | 0.44 | n.s. | **0.63** | **0.68** | |
| Tot-N | 0.17 | –0.13 | –0.32 | –0.29 | –0.19 |
| Tot-P | 0.42 | n.s. | 0.23 | n.s. | 0.19 |
| DSi | n.s. | n.s. | **–0.54** | **–0.70** | –0.43 |
| pH | n.s. | n.s. | 0.19 | n.s. | n.s. |
| Precip | n.s. | 0.20 | n.s. | n.s. | n.s. |
| Temp | n.s. | n.s. | **0.80** | **0.69** | **0.51** |
| Cond | 0.21 | n.s. | n.s. | n.s. | n.s. |
| Disch | –0.16 | n.s. | –0.22 | –0.21 | n.s. |
| TOC | 0.17 | 0.20 | n.s. | 0.18 | 0.27 |
| Luvisols | –0.17 | n.s. | n.s. | n.s. | –0.30 |
| Podzols | 0.17 | n.s. | n.s. | n.s. | 0.30 |
| Histosols | 0.32 | n.s. | n.s. | n.s. | n.s. |
| Regosols | –0.35 | n.s. | n.s. | n.s. | n.s. |

**Table 4.** Spearman correlation coefficients of TSM, POC, and phytoplankton parameters with the environmental characteristics in the outflow of Lake Võrtsjärv for 2008–2011. For abbreviations, see Table 1; n.s. – not significant; absolute value of $R > 0.50$ is marked in bold

| | TSM | POC | Chl *a* | PB | PT |
|---|---|---|---|---|---|
| POC | 0.50 | | | | |
| Chl *a* | **0.88** | **0.51** | | | |
| PB | **0.80** | **0.52** | **0.82** | | |
| PT | **0.57** | n.s. | n.s. | n.s. | |
| Tot-N | –0.42 | –0.28 | –0.44 | **–0.59** | n.s. |
| Tot-P | **0.80** | 0.34 | **0.74** | **0.72** | 0.46 |
| DSi | **–0.81** | –0.41 | –0.50 | **–0.71** | –0.44 |
| pH | **0.63** | n.s. | **0.58** | **0.64** | **0.52** |
| Precip | 0.48 | 0.39 | **0.51** | n.s. | n.s. |
| Temp | **0.65** | 0.34 | **0.64** | **0.66** | n.s. |
| Cond | –0.48 | n.s. | **–0.53** | n.s. | n.s. |
| Disch | n.s. | n.s. | –0.41 | n.s. | n.s. |
| TOC | **0.67** | **0.64** | **0.64** | **0.71** | n.s. |

correlated with conductivity, TOC, all phytoplankton parameters, and both main nutrients, and negatively with discharge. Inflowing TSM was also correlated with soil types: positively with the percentage of histosols and podzols, and negatively with the percentage of regosols and luvisols in the catchment area (Table 3). For the outflow, TSM was also correlated positively with the amount of precipitation, temperature, POC, Tot-P, and all phytoplankton parameters, and negatively with Tot-N, DSi, and conductivity. The Chl *a* concentration had positive correlations with temperature, pH, and Tot-P and negative correlations with Tot-N, DSi, and discharge, both for the inflows and for the outflow.

## DISCUSSION

### Species composition and Chl *a*

Our results demonstrate significant differences in the phytoplankton composition between the inflows and the outflow of Lake Võrtsjärv. In the inflows, algae with a high surface-to-volume ratio and a rapid growth strategy were dominating. Domination of diatoms in spring and the increased proportion of small flagellates with a large variety of chlorophytes in summer are typical of streams and rivers of the temperate climate region (Reynolds et al., 1994; Tipping et al., 1997). These small crypto- and dinophytes, as well as spindle-shaped chlorophytes, being predominantly r-strategists according to Reynolds (1988), are able to sustain riverine conditions. The hydrological conditions of the major inflow of Võrtsjärv with an average retention time of more than two weeks are favourable for phytoplankton development as this period exceeds the maximum generation time of planktonic algae, i.e. two days (Reynolds, 2006). In addition, numerous tychoplanktonic algae in the inflows of Võrtsjärv may survive in the bottom sediments or maintain their growth in backwaters (Reynolds et al., 1994). The inflows of Võrtsjärv are also rich in the macrophytes *Phragmites australis* and *Nuphar lutea*, which suppress riverine turbulence and create an undisturbed habitat for invertebrates as well as provide a substrate for many epiphytic algae (Piirsoo et al., 2007; Vesterinen et al., 2016). However, both functional groups of algae are highly susceptible to grazing pressure by primary consumers, i.e. benthic invertebrates (Reynolds, 2006). According to monitoring reports, the filter-feeders *Unio pictorum* L., *U. crassus* Philipsson, and *Pisidium* sp., as well as the omnivorous larvae of *Chironomus* spp. are numerous in the inflows of Võrtsjärv. The small planktonic and attached microalgae in the inflows, the so-called live component of POM, serve as additional food for benthic invertebrates, especially in summer.

Low Chl *a* values (Koch et al., 2006; Stutter et al., 2007; Cai et al., 2008; Table 5) and a less than 10% phytoplankton contribution to POM (Lobbes et al., 2000; Wetzel, 2001) have been reported for many rivers of the arctic and temperate climate regions and are in line with our findings for the inflows of Võrtsjärv. In very large rivers, Chl *a* values can be much higher (Table 5) and the contribution of phytoplankton to POM is comparable to that of lakes, reaching 50% (Bianchi, 2007; Bukaveckas et al., 2011). In the inflows of Võrtsjärv, high summer and low winter values of Chl *a* (Table 2) indicate high photosynthetic activity during the warm season and the domination of the dead pool of POM during the cold season. The positive correlations of Chl *a* with temperature and Tot-P found in our study are consistent with some other studies (Basu and Pick, 1997; Yin et al., 2000; Bukaveckas et al., 2011). The negative correlation between Chl *a* and Tot-N (Table 3) is spurious and rather reflects a common dependence of these variables on discharge.

Phytoplankton biomass was negatively correlated with inflow discharge (Table 3); this result is consistent with the results of other studies (Reynolds, 1988; Everbecq et al., 2001; Putland et al., 2014). It can be explained by a reduction in the retention time as well as by a dilution effect due to increased discharge. The seasonal dynamics of DSi with a maximum concentration in winter accords with earlier results for the largest inflow of Võrtsjärv (Nõges et al., 2008a). The negative correlation between phytoplankton parameters and DSi concentration both for the inflows and for the outflow can probably be explained by the intensive development of diatoms in spring.

The relatively high electrical conductivity of the inflows of Võrtsjärv (Table 1) reflects the geochemistry of their catchments rich in Silurian carbonates, which is amplified by the relatively large proportion (24–40%) of highly mineralized groundwater in the average discharge of the inflows (Eipre, 1981). The lower conductivity in the outflow is attributable to calcite precipitation in the lake at increased pH resulting from photosynthesis.

Võrtsjärv represents the most common ‘shallow lake’ type in the world (Downing et al., 2006) with turbid water and a high phytoplankton biomass (Scheffer et al., 1993; Nõges and Tuvikene, 2012). The negative correlation between the outflow discharge and Chl *a* (Table 4) is caused by the large time lag between the spring flood peak, occurring around ice breakup, and the phytoplankton peak that forms during the summer low flow period. It has earlier been described as a negative relationship between water level and PB in this lake (Nõges and Tuvikene, 2012).

**Table 5.** Comparison of TSM, POC, and Chl *a* in small, large, and very large rivers; annual mean values are marked in bold; * summer data. For abbreviations and units, see Table 1

| River and study years | Climate region | TSM | POC | Chl *a* | References |
|---|---|---|---|---|---|
| **Brooks and small rivers** | | | | | |
| Inflows of Võrtsjärv, Estonia 2008–2011 | Temperate | **4.4** | **1.8** | **2.2** | This study, Table 1 |
| Outflow of Võrtsjärv, Estonia 2008–2011 | Temperate | **12.8** | **3.5** | **25.3** | This study, Table 1 |
| Chena river basin, USA 2005–2006 | Arctic | **10.5** | **1.0** | **4.1** | Cai et al., 2008 |
| Brooks, Finland 1997–1999 | Boreal | **0.7** | | | Mattsson et al., 2003 |
| Humber river basin, UK 1993–1995 | Temperate | | 0.2–67.0 | | Tipping et al., 1997 |
| Humber river basin, UK 1993–2005 | Temperate | *2.8–13.9 | *0.6–2.7 | *4.9–54.4 | Neal et al., 2006 |
| Thames river basin, UK 1993–2005 | Temperate | *2.8–11.1 | | *1.7–16.8 | Neal et al., 2006 |
| Dee river basin, UK 1992–1993 | Temperate | | **0.1–0.8** | | Hope et al., 1997 |
| Dee river basin, UK 2004–2005 | Temperate | | ***0.1–1.0** | ***0.6–5.1** | Stutter et al., 2007 |
| Dee river basin, UK 2008 | Temperate | ***0.2–1.2** | ***0.2–0.3** | ***0.2–1.8** | Dawson et al., 2012 |
| Don river basin, UK 1992–1993 | Temperate | | **0.5–0.8** | | Hope et al., 1997 |
| Glen Dye river basin, UK 1996–1998 | Temperate | | **0.4–0.9** | | Dawson et al., 2004 |
| Hudson river basin, USA 1998–2000 | Temperate | | 0.1–3.0 | | Raymond et al., 2004 |
| Hudson river basin, USA 2003 | Temperate | | **0.05** | | Longworth et al., 2007 |
| **Large and very large rivers** | | | | | |
| Russian rivers (*n* = 12) 1994–1995 | Arctic | | ***1.3** | | Lobbes et al., 2000 |
| Lena, Russia 2009–2011 | Arctic | ***19.9–494.0** | ***0.57–8.20** | | Winterfield et al., 2015a, b |
| Ob, Russia 2001 | Arctic-boreal | **5.6–18.0** | **0.4–0.9** | | Gebhardt et al., 2004 |
| Yenisei, Russia 2001 | Boreal | **3.2** | **0.4** | | Gebhardt et al., 2004 |
| Danube, Austria 1997–1998 | Temperate | | **1.6** | **21.0** | Hein et al., 2003 |
| Garonne, France 1976–1996 | Temperate | 5.0–835.0 | | | Veyssy et al., 1999 |
| Rhône, France 2007–2009 | Temperate | **141.0** | **3.1** | | Panagiotopoulos et al., 2012 |
| St. Lawrence, Canada 1994–1996 | Temperate | | 0.06–2.7 | 0.3–26.1 | Barth et al., 1998 |
| St. Lawrence, Canada 1998–2003 | Temperate | | **0.07–0.3** | | Hélie and Hillaire-Marcel, 2006 |
| Missouri, USA 2004–2006 | Temperate | ***125.0** | ***3.4** | ***19.7** | Bukaveckas et al., 2011 |
| Ohio, USA 1999 | Temperate | | | **4.0** | Koch et al., 2006 |
| Tennessee, USA 1999 | Temperate | | | **5.7** | Koch et al., 2006 |
| Cumberland, USA 1999 | Temperate | | | **14.8** | Koch et al., 2006 |
| Upper Mississippi, USA 2004–2006 | Temperate | ***38.0** | ***2.9** | ***32.3** | Bukaveckas et al., 2011 |
| Mississippi, Colorado, Rio Grande, 1996–1997 | Subtropical | **1.0–4185.0** | | | Kendall et al., 2001 |
| Lower Mississippi, USA 2003–2004 | Subtropical | **112.0** | **16.9** | | Bianchi et al., 2007 |
| San Pedro, USA 2001–2002 | Subtropical | | **0.6–320.0** | | Brooks et al., 2007 |

Algal growth in Võrtsjärv is largely dependent on nutrients via the resuspension processes (Nõges et al., 2004). Filamentous cyanobacteria, dominating in the outflow, are tolerant of light-limited conditions in turbid lakes. Besides, they are resistant to the grazing pressure of primary consumers (Reynolds, 2006). As a result, most of the primary production in Võrtsjärv provided by phytoplankton enters the decomposition pathway and, through the microbial loop, fuels the benthic consumers at low metazooplankton abundance (Zingel et al., 2007; Cremona et al., 2014b). The positive correlation between PB and POC concentration (Table 4) suggests that phytoplankton is an important component of POC in Võrtsjärv. The concentrations of Tot-P and Tot-N in the outflow coincide with average long-time values for Võrtsjärv (Nõges et al., 2008b). The positive correlations of phytoplankton with Tot-P and temperature and the negative correlation with Tot-N for the outflow (Table 4) are consistent with the results of earlier studies in Võrtsjärv (Nõges et al., 2008b).

## Concentrations of POC and TSM

In running waters, POC concentrations usually range from 1 to 30 mg $L^{-1}$, with a world average of 5 mg $L^{-1}$ but with considerable spatial and temporal variability (Tipping et al., 1997; Kendall et al., 2001). In small to large rivers, the major source of POM is detrital matter derived from the soil (Barth et al., 1998; Chen and Jia, 2009) while in very large rivers, plankton can be the major source of POM (Kendall et al., 2001; Bukaveckas et al., 2011).

The mean values of POC for the inflows of Võrtsjärv are comparable to those reported for some large rivers (Hein et al., 2003; Bukaveckas et al., 2011; Panagiotopoulos et al., 2012) but are considerably higher than those reported for several other European, North American, and Asian rivers in the temperate climate region (Table 5). The high POC concentration in the inflows of Võrtsjärv can be explained by the relatively large proportion of mud and organic-rich silt in the sediments (Miidel et al., 2004) as well as by the presence of detritus derived from the decay of abundant macrophytes, e.g. *Phragmites australis*, *Nuphar lutea*, and the green macroalga *Cladophora.* Extremely high POC concentrations are characteristic of large subtropical rivers in the semiarid region during the monsoon season (Brooks et al., 2007; Table 5). In the inflows of Võrtsjärv, POC made up about 10% of TOC (Table 1) and was positively correlated with the amount of precipitation (Table 3). The erosion flow caused by surface runoff is most likely the mechanism behind the positive relationship between POC and water discharge (Hein et al., 2003).

The about twice as high mean value of POC in the outflow compared with the inflows (Table 1) can be accounted for by the high phytoplankton biomass, turbidity, and resuspension in Võrtsjärv. The summer peaks of POC coincide with low-water periods (Cremona et al., 2014a).

The high Chl *a* : POC ratio for the outflow suggests a labile nature of POM in Võrtsjärv. The instability of the different types of POM ranks as follows: phytoplankton ≥ litter >> soil (Etcheber et al., 2007). Algal-derived labile POM containing e.g. fatty acids and proteins (Malzahn et al., 2007) can therefore be rapidly consumed by benthic communities (Drummond et al., 2014).

The TSM as an indirect metric of water clarity is one of the most variable characteristics of water bodies with an annual variation from 1 to 10 000 mg $L^{-1}$ (Thomas and Meybeck, 1996). Soil leaching is the major source of TSM (Lobbes et al., 2000). Our TSM results (5.5–15.0 mg $L^{-1}$) are within the range of the values measured in other rivers of the boreal and temperate climate regions (Gebhardt et al., 2004; Neal et al., 2006; Dawson et al., 2012; Table 5). Extremely low TSM values are characteristic of lowland rivers of the arctic and boreal climate regions (Thomas and Meybeck, 1996), e.g. Finnish brooks with low erosion in the catchment (Mattsson et al., 2003; Table 5). High TSM values in rivers are first of all related with major flood events (Kendall et al., 2001; Bianchi et al., 2007; Panagiotopoulos et al., 2012; Table 5).

## CONCLUSIONS

- The concentration of Chl *a* and the Chl *a* : POC ratio, and hence the share of phytoplankton, peaked in the inflows in summer and in the outflow in autumn. Considerably higher Chl *a* as well as the higher Chl *a* : POC and POC : TOC ratios in the outflow compared with the inflows indicate the lake's substantial contribution to the live component of POM. The weaker correlations between phytoplankton and environmental variables for the inflows compared with the outflow indicate the higher spatial heterogeneity of riverine versus lacustrine ecosystems.
- Contrary to our working hypothesis, the observed change in the phytoplankton composition towards a higher share of cyanobacteria potentially increases the domination of the detritus-based food chain in the outflow compared to the inflows.

## ACKNOWLEDGEMENTS

This study was supported by the institutional research funding (IUT 21-2) of the Estonian Ministry of Education and Research and by the MARS project 'Managing Aquatic Ecosystems and Water Resources under Multiple Stress' funded under the 7th EU Framework Programme, Theme 6 'Environment including climate change' (Contract No. 603378). We are grateful to Dr. Jonne Kotta and to the two anonymous reviewers for valuable comments on the manuscript. Mrs Ester Jaigma kindly revised the English text of the manuscript. The publication costs of this article were covered by the Estonian Academy of Sciences.

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# Partikulaarse orgaanilise aine muutused läbiminekul suurest madalast järvest

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Töö eesmärk oli: 1) uurida peamisi keskkonnategureid, mis mõjutavad nii partikulaarse orgaanilise aine (POA) kontsentratsiooni kui ka POA koostisse kuuluva fütoplanktoni ja lagunenud orgaanilise aine (detriidi) omavahelist suhet madala eutroofse järve sissevooludes ning väljavoolus; 2) hinnata fütoplanktoni kui POA olulise komponendi mõju toiduahelale jõgedes ja järvedes.

Töö hüpotees oli, et kuna vooluvetega võrreldes on fütoplanktoni biomass madalates järvedes tunduvalt suurem, domineerib järvedes fütoplanktonil baseeruv toiduahel ja jõgedes detriidil baseeruv toiduahel.

Veeproovid ja fütoplanktoni materjal koguti igakuiselt Võrtsjärve viie suurema sissevoolu (Väike Emajõgi, Õhne, Tänassilma, Tarvastu, Konguta) alamjooksult ning väljavoolu (Emajõgi) ülemjooksult vastavalt aastail 2008–2011 ja 2008–2009 (joon 1).

Uuringu põhjal võib järeldada: 1) Võrtsjärve sissevoolude fütoplanktonis domineerisid krüpto-, dino- ja klorofüüdid ning epifüütsed ränivetikad, mis väikeste mõõtmete tõttu on potentsiaalseks lisatoiduallikaks madalaveeliste jõgede põhjaloomastikule eriti vetikate suvisel maksimumperioodil (biomass 0,7 mg $L^{-1}$, klorofüll *a* sisaldus 4,6 µg $L^{-1}$; tabel 2, joon 2); 2) POA keskmine kontsentratsioon Võrtsjärve väljavoolus (3,5 mg $L^{-1}$) oli ligikaudu kaks korda suurem kui sissevooludes (1,8 mg $L^{-1}$; tabel 1) ja selle peamiseks põhjuseks oli fütoplanktoni suur biomass järves (keskmine 20,0 mg $L^{-1}$, klorofüll *a* sisaldus 25,3 µg $L^{-1}$; tabel 1). Väljavoolus domineerisid eutroofsetele järvedele iseloomulikud tsüanobakterid perekonnast *Limnothix* ja *Planktolyngbya* ning nende biomassi maksimum (38,6 mg $L^{-1}$, klorofüll *a* sisaldus 34,4 µg $L^{-1}$; tabel 2, joon 2) langes kokku POA suure kontsentratsiooniga (5,5 mg $L^{-1}$) hilissuvel ja sügisel (tabel 2, joonis 2). Positiivne korrelatsioon fütoplanktoni biomassi ja POA vahel ($r = 0{,}52$, tabel 4) näitas fütoplanktoni olulisust POA koostises, kuid järves on niitjad tsüanobakterid tarbitavad mitte otseselt, vaid detriidil baseeruva toiduahela kaudu; 3) väikesed korrelatsiooninäitajad nii POA kui ka fütoplanktoni biomassi ja keskkonnatingimuste vahel sissevooludes annavad järvede ökosüsteemidega võrreldes (tabelid 3 ja 4) tunnistust vooluvete ökosüsteemide suuremast heterogeensusest.

Vastupidiselt töös püstitatud hüpoteesile domineerib madalates eutroofsetes järvedes niitjate tsüanobakterite rohkuse tõttu detriidil baseeruv toiduahel. Väikesemõõtmeliste vetikate rohkuse pärast on vooluvetes suhteliselt suurema tähtsusega vetikatel baseeruv toiduahel. Seega mõjutavad vetikate koosseis ja biomass seisu- ning vooluvete ökosüsteemide toiduahelaid erinevalt.