Eesti Maaülikool
Estonian University of Life Sciences

PRODUCTIVITY AND NUTRIENT RETENTION OF LAKES ON SEASONAL, INTERANNUAL AND MORPHOMETRIC SCALES

JÄRVEDE PRODUKTIIVSUSE JA TOITEAINETE PEETUSE SESOONSUS, AASTATEVAHELISED ERINEVUSED NING SÕLTUVUS JÄRVEDE MORFOMEETRIAST

ALO LAAS

A Thesis
for applying for the degree of Doctor of Philosophy in Hydrobiology

Väitekiri
filosoofiadoktori kraadi taotlemiseks hüdrobioloogia erialal.

Tartu 2012

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Institute of Agricultural and Environmental Sciences,
Eesti Maaülikool, Estonian University of Life Sciences

According to verdict Nº 117 of September 3, 2012 Doctoral Committee for Agricultural and Environmental Sciences of the Estonian University of Life Sciences has accepted the thesis for the defence of the degree of Doctor of Philisophy in Hydrobiology.

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The English and Estonian language was edited by Tiina and Peeter Nõges.

The doctoral studies and the publication of the current thesis were supported by the Doctoral School of Ecology and Environmental Sciences created under the auspice of European Union Social Fund.

European Union
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ISBN 978-9949-484-46-1 (trükk)
978-9949-484-47-8 (pdf)

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which are referred to by their Roman number.

I **Laas, Alo**; Nõges, Peeter; Kõiv, Toomas; Nõges, Tiina (2012). High frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694(1), 57-74.

II Nõges, Tiina; Arst, Helgi; **Laas, Alo**; Kauer, Tuuli; Nõges, Peeter; Toming, Kaire (2011). Reconstructed long-term time series of phytoplankton primary production of a large shallow temperate lake: the basis to assess the carbon balance and its climate sensitivity. Hydrobiologia, 667(1), 205-222.

III Pall, Peeter; Vilbaste, Sirje; Kõiv, Toomas; Kõrs, Aive; Käiro, Kairi; **Laas, Alo**; Nõges, Peeter; Nõges, Tiina; Piirsoo, Kai; Toomsalu, Liina; Viik, Malle (2011). Fluxes of carbon and nutrients through the inflows and outflow of Lake Võrtsjärv, Estonia. Estonian Journal of Ecology, 60(1), 39-53.

IV Kõiv, Toomas; Nõges, Tiina; **Laas, Alo** (2011). Phosphorus retention as a function of external loading, hydraulic turnover time, area and relative depth in 54 lakes and reservoirs. Hydrobiologia, 660(1), 105-115.

CONTRIBUTIONS:

	I	II	III	IV
Concept	**AL**, TN, PN	TN, HA, +	PP, SV, +	TKõ, TN, **AL**
Design	PN, **AL**	TN, +	PP, +	TKõ
Data collection	**AL**	+, *	PP, TKõ, **AL,** +	TKõ, **AL**, TN
Data analyses	**AL**, PN	**AL**, TKa, +	PP, MV	TKõ
Manuscript preparation	**AL**, PN, +	TN, HA, **AL**, +	PP, SV, PN, +	TKõ, TN, **AL**

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ABBREVIATIONS

^{14}C	carbon 14
A/V ratio	lake area/volume ratio
BR	bacterial respiration
C	carbon
CCA analysis	canonical correspondence analysis
CDOM	coloured dissolved organic matter
Chl *a*	pigment chlorophyll *a*
Chl *B*	pigment chlorophyll *B*
CO_2	carbon dioxide
CODMn	chemical oxygen demand
DIC	dissolved inorganic carbon
DOC	dissolved organic carbon
DOM	dissolved organic matter
Fe	iron
GPP	gross primary production
I_{mix}	mean light intensity within the water column
Lat	latitude
N	nitrogen
NEP	net ecosystem production
O_2	oxygen
P	phosphorus
PAR	photosynthetically active radiation
PP	phytoplankton primary production
PP_{int}	integral primary production
Q	incident global radiation
R	community respiration
R_P	phosphorus retention of the lake
SD	standard deviation
Si	silicon
TIC	total inorganic carbon
TN	total nitrogen
TOC	total organic carbon
TP	total phosphorus
TranLat	transformation of the argument Lat
T_w	water temperature
U	wind speed
Z_{avg}	mean depth of the lake
Z_R	relative depth of the lake

1. INTRODUCTION

Despite the considerable percentage of inland waters in the temperate zone land cover, their role in the global carbon balance is not clear and the existing data suggest large type specific differences.

Respiratory CO_2 release from inland waters and the accumulation of carbon in lake sediments are major processes in the global carbon cycle, retaining more than half of the carbon flux from terrestrial sources that otherwise would reach the sea. The strongly lake-type-specific balance between primary production and respiration determines whether a lake acts regionally as a net sink or source of CO_2.

In the global change context even small changes in photosynthesis and respiration rates and/or in the loadings of organic matter or nutrients (e.g. phosphorus) may change the metabolic type of the lake and turn it from autotrophic to heterotrophic system or *vice versa*.

Todays *in situ* sondes fitted with sensitive and accurate optical oxygen probes have become a useful tool for estimating lake ecosystem metabolism through high frequency continuous measurements. The sonde method provides an alternative to more traditional methods of measuring metabolism that only use discrete samples. Continuous sampling by sondes overcomes many of the limitations of discrete samples and makes it possible to measure metabolism in a wide variety of systems.

Long-term observations across many years define the range of natural variability of ecological systems and provide a baseline from which to assess whether a system has changed significantly (Blenckner, 2005).

Regular hydrological data on large and shallow (area 270 km^2; mean depth 2.8 m) Lake Võrtsjärv have been collected for more than 80 years. Regular measurements of nutrients and ecosystem components started in 1960s. Lake Võrtsjärv was intensively studied for more than 50 years before the first monitoring buoy was deployed for high frequency measurements of physical and chemical parameters. Phytoplankton primary production *in situ* measurements with monthly frequency started in Võrtsjärv already in 1982 but the dataset has many gaps.

Present thesis summarizes for Lake Võrtsjärv: the first data on seasonal changes of the ecosystem metabolism based on high frequency measurements; the reconstruction of long term series of phytoplankton primary production by bio-optical modelling; the incoming and outgoing fluxes of carbon, nitrogen, phosphorus, and silicon; and gives an overview of phosphorus retention in Lake Võrtsjärv compared with 54 lakes and reservoirs in different climate regions around the world.

2. REVIEW OF THE LITERATURE

2.1. Lake monitoring – manual vs. high-frequency automatic

Lake monitoring has become an essential part of lake management as a tool to assess the health of the lake and to understand the impacts of human activities as well as natural processes. In addition, monitoring is a base for making good watershed management decisions and for evaluating the effects of these decisions. The monitoring techniques range from tests that can be performed occasionally by those with little training to full-scale, professional analyses of the physical, chemical, and biological aspects of a lake ecosystem.

Lake monitoring may provide early warning signs of ecosystem degradation resulting from contaminant inputs, nutrient addition, sediment runoff, and overuse of the resource. By monitoring the physical, chemical, and biological status of a lake as well as the changes of ecosystem structure and function can be detected quickly, and hopefully the harmful impacts could be eliminated before their consequences become unmanageable (Leiser *et al.*, 2005).

In order to perform efficient lake monitoring, at first the information has to be collected on the status of the lake for further understanding the changes. This, so called baseline inventory, should be done throughout one year at least.

Manual lake monitoring is a manpower- and time-consuming issue requesting specific conditions, e.g. good weather, as it is very complicated to perform field measurements at stormy or rainy weather. Therefore, hydrobiological monitoring typically has monthly, rarely weekly resolution of water chemical, physical and biological data series and only the linear changes between subsequent measurements could be assumed.

As the ecosystem processes and water quality changes are far quicker than could be reflected by monthly and even weekly monitoring, only high-frequency monitoring could provide a wealth of data on the natural dynamics of water systems that is impossible to obtain using manual monitoring (Fig. 2.1.1). It provides a much better picture of the true changes in water quality, whereas regular monitoring could provide only snapshots of a small number of moments in time (van den Broeke, 2007).

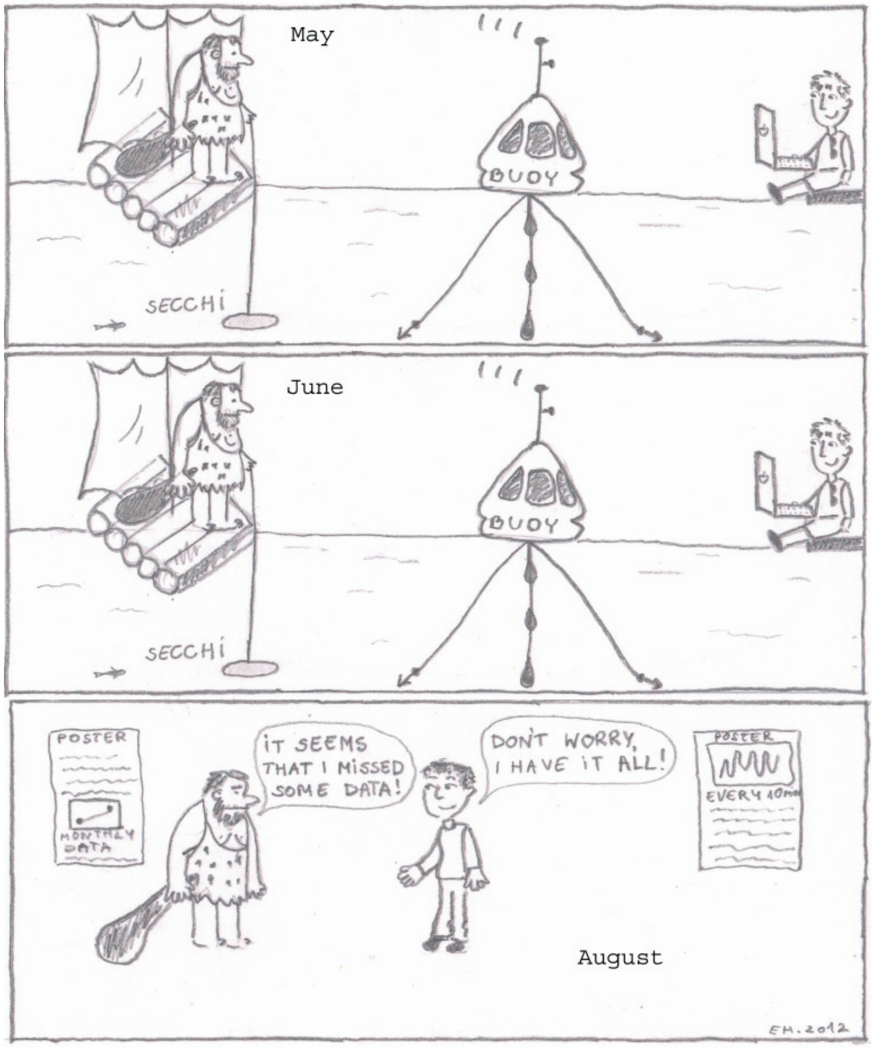

Figure 2.1.1. Manual lake monitoring vs. high-frequency automatic lake monitoring. Copyrights E. Heidok.

2.2. Organic matter production and decomposition in lakes

Primary production and respiration are the major metabolic pathways by which organic matter is produced and decomposed. Gross primary production (GPP) is the gross fixation of inorganic C by photosynthesis. Community respiration (R) is the remineralization of organic C to CO_2 by all organisms of the ecosystem. The net ecosystem production (NEP), i.e., the difference between gross primary production and community respiration, (NEP=GPP-R), can be used to define the metabolic type (net auto- or heterotrophic) of a lake. The potential of lakes to release CO_2 is huge - from the estimated 1.9 Pg of carbon that inland waters receive annually from the terrestrial landscape, less than half (0.9 Pg y^{-1}) is delivered to the oceans whereas respiratory CO_2 release constitutes the major part of this decrease (Cole *et al.*, 2007).

Recognising lakes as sites of intensive carbon processing, they are although often disregarded in models of the global carbon cycle due to their small percentage of the Earth's surface area (Sobek *et al.*, 2006). Several recent studies have demonstrated that lakes are significant sources of carbon dioxide and methane to the atmosphere (Huttunen *et al.*, 2003; Jonsson *et al.*, 2003; Cole *et al.*, 2007), and that they simultaneously bury more organic carbon in their sediments than the entire ocean (Downing *et al.*, 2008). Hence, lakes turn out to be disproportionately important sites of carbon cycling relative to their small areal extent. Lakes and reservoirs act as sentinels by providing signals that reflect the influence of climate change in their much broader catchments (Williamson *et al.*, 2008, 2009). In the context of global warming caused by the increase of greenhouse gases, it is important to know the role of each ecosystem type in the global carbon budget. It has been increasingly acknowledged that in many lakes, first of all in those located in cool-climate forested boreal regions, the heterotrophic processes are dominating over autotrophic ones turning the lakes into CO_2 sources (Algesten *et al.*, 2003; Sobek *et al.*, 2003).

2.2.1. Primary production

Phytoplankton primary production (PP) represents the major synthesis of organic matter in aquatic systems giving start to the food chains and forming the basis of the ecological pyramid. The amount of primarily synthesised organic matter indicates the trophic state of a waterbody, while the efficiency of its subsequent transformation in food chains results in a higher or lower fish production, and in a poorer or better water quality. To study the carbon metabolism of a lake, the first and the basic step would be the estimation of the amount of carbon fixed by the ecosystem. The importance of PP studies is impressively reflected in publication statistics of ISI Web of Science (ISI WoS), which showed that lake primary production has been analysed in ca. 1850 publications since 1990 with an increasing average yearly rate from ca. 60 until year

2000 to ca. 100 afterwards. The annual citation rate of these papers has exponentially increased from about 100 in 1992 to nearly 3300 in 2011. To understand climate sensitivity of the carbon metabolism, long-term changes of primary production need to be known. As stated already by Jassby *et al.* (1990), inter-annual changes of primary production remain one of the least investigated areas in limnology and this situation has not much improved during the last 20 years. The query on 'long term lake primary production' resulted in only in 180 publications in ISI WoS database since 1990. The average citation rate of one publication was more than 28 showing the high importance of the studies on this field.

2.2.2. Lake metabolism

There are several techniques for measuring the metabolic balance of natural waters. For lakes the most common method is based on measurements of the temporal and spatial variability of dissolved O_2 and/or CO_2 (Robertson *et al.*, 1993; Cole *et al.*, 2000; Hanson *et al.*, 2003; Lȯpez-Archilla *et al.*, 2004; Depew *et al.*, 2006; Staehr & Sand-Jensen, 2007; Coloso *et al.*, 2008; Effler *et al.*, 2008, Tsai *et al.*, 2008; Staehr *et al.*, 2010a,b). High frequency ($\geq 1h^{-1}$) O_2 measurements enable calculating the NEP (the difference between GPP and R) during the day and R during the night, thus yielding all three components necessary for the full budget. The probe method provides a useful alternative to more traditional methods of studying metabolism based on discrete samples. As shown by Staehr *et al.* (2012b), continuous measurements overcome many of the limitations of discrete samples and make it possible to measure metabolism in a wide variety of systems.

Lakes with high total phosphorus (TP) concentrations and low dissolved organic carbon (DOC) concentrations tend to be autotrophic (NEP>0), whereas lakes with low TP and high DOC tend to be heterotrophic (NEP<0) (Hanson *et al.*, 2003). Cole *et al.* (2000) showed that a lake has a net heterotrophic C balance at mean seasonal Chl *a* concentration below 20 mg m^{-2} and at GPP less than 1 g O_2 m^{-3} day^{-1} or 140 mmol C m^{-2} day^{-1} or, assuming a 200 day ice-free season, GPP below 330 g C m^{-2} $year^{-1}$. Brown-coloured lakes with increased humic matter or tannin content, often associated with forested or peaty catchments, should display stronger net heterotrophy than clear-water lakes (del Giorgio *et al.*, 1999; Sobek *et al.*, 2005).

Lakes become net heterotrophic only because they receive large allochthonous inputs of organic C which is respired in the lake. A review by Andersson & Sobek (2006) showed that switching from net autotrophy to net heterotrophy occurred at DOC concentrations higher than 4–6 mg l^{-1}, and del Giorgio *et al.* (1997) found that bacterial respiration (BR) tended to exceed NEP in aquatic systems with NEP below 100 mg C 1^{-1} day^{-1}. Net autotrophic systems produce significantly more organic material than they degrade. The excess organic material may either be exported to adjacent systems and/or accumulated within the system either in the sediment or as dissolved organic matter in the water (Staehr *et al.*, 2010b).

2.3. Nutrient and carbon fluxes through lakes

It has become increasingly important to quantify carbon and nutrient fluxes in the environment owing to their role in the processes of global warming, climate change, and eutrophication of water bodies. Generally, global warming intensifies the hydrological cycle and increases the magnitude and frequency of extreme climatic phenomena, including heavy rain falls in most parts of Europe (Christensen & Christensen, 2003), which cause abrupt fluctuations in the discharges of rivers (Graham *et al.*, 2006). Concentrations of different substances in river water are related to discharge but this relationship is commonly nonlinear (Volk *et al.*, 2002). High concentrations of dissolved organic matter may occur during floods as well as in low water periods. Although the content of dissolved organic matter is generally high in high water periods, the highest concentrations have been measured at relatively low water (Royer & David, 2005). The same phenomenon was also reported for mineral substances and nutrients (Järvet, 2003; Bärlund *et al.*, 2009).

2.4. Phosphorus retention in lakes

Human activities have markedly increased nutrient inputs from point and diffuse sources to watersheds. A portion of those nutrients enters to water bodies, degrading water quality and increasing nutrient input and subsequent eutrophication of lakes. Some part of those nutrients will flow out from lakes but a significant part of nutrients will stay.

Retention in lakes is of great importance when using a mass balance approach to assess nutrient sources and retention on regional level. Estimates of nutrient delivery from various sources will obviously be affected by permanent or temporary retention. Nitrogen and phosphorus in particular are usually subject to substantial retention. However, N and P retention is highly variable in time and space and could range between 0% and 100% depending on the flow paths and watercourse characteristics (e.g. presence of lakes in a drainage basin). Both the high nutrient load and long retention time will cause and affect the eutrophication of lakes.

As a major paradigm of limnology, phosphorus (P) availability is regarded as the most important determinant of productivity and water quality in lakes and reservoirs (Schindler, 1977; Vollenweider & Kerekes, 1980; Peters, 1986; Welch, 1992; Havens & Schelske, 2001). Phosphorus retention (R_P) is normally defined as the amount of externally loaded phosphorus that is biogeochemically transformed, retarded and retained (largely through sedimentation) within the water body (Dillon & Rigler, 1974; Søndergaard *et al.*, 2001). The rate of phosphorus loss within lakes is to a large extent related to the P loading rate and the depth of the lake (Brett & Benjamin, 2008). Thus, the physical 'structure' of a lake can also significantly influence its phosphorus concentration and retention (Håkanson, 2005). In this context, natural lakes and reservoirs could be considered similar, being driven in both cases by external factors such as morphology, hydrology and climate (Wetzel, 2001). Various formulations have been proposed for predicting P retention, mostly from areal phosphorus and hydraulic loading rate, settling velocity of phosphorus-containing particles, and mean depth (Brett & Benjamin, 2008). Predictive equations have been developed that link the phosphorus retention coefficient to the hydrological properties or mean depth of the water body (e.g. Kirchner & Dillon, 1975; Nürnberg, 1984; Hejzlar *et al.*, 2006). Nõges *et al.* (2007) showed an inverse relationship between the relative depth (Z_R) of the lake and the concentration of P in sediments, assuming that the potential for internal phosphorus loading and the resilience of ecosystem recovery after the removal of external phosphorus sources in large and shallow lakes with small Z_R should be less than in smaller and deeper lakes with greater relative depth. Accordingly, large and shallow lakes with small Z_R should have a lower phosphorus retention capacity than smaller and deeper lakes with bigger Z_R.

3. HYPOTHESIS AND AIMS OF THE STUDY

In the present thesis we have set the following aims:

1. Using the high frequency automatic monitoring data (**I**) to
    a. reveal the metabolic type of Lake Võrtsjärv as a representative of large, shallow, unstratified, eutrophic temperate lakes, and to determine its role in the regional and global carbon budgets,
    b. test the **hypothesis** of switching of the lake between net autotrophy and net heterotrophy,
    c. analyze the seasonal trends of gross primary production (GPP), community respiration (R) and net ecosystem production (NEP), and their environmental determinants that can improve our understanding of how future climatic conditions may impact the biological, chemical and physical stability of lake ecosystems.
2. To summarise the long-term primary production measurements in Võrtsjärv in order to receive reliable daily, monthly and annual PP estimates as the starting point in the lake's carbon balance calculations, and as the further basis for long-term studies of the ecosystem metabolism and its climate sensitivity (**II**).
3. To determine the incoming fluxes of dissolved inorganic (DIC), total (TOC) and dissolved organic carbon (DOC), nitrogen, phosphorus, and silicon into Lake Võrtsjärv via its four main inflows, posing the following questions (**III**):
    a. What is the magnitude of different fluxes?
    b. Which substances does the lake accumulate or release?
    c. Is there any seasonality in the fluxes of different substances?
4. To test the **hypothesis**, if large and shallow lakes with small relative depth (Z_R) have lower phosphorus retention capacity than smaller and deeper lakes with bigger Z_R (**IV**)

5. To examine differences of phosphorus retention among lakes and reservoirs with various morphometric parameters (**IV**)
6. To assess the impact of relative depth of the lake on the phosphorus retention capacities (**IV**).

4. MATERIAL AND METHODS

4.1. Study site

Lake Võrtsjärv (58°16' N 26°02' E) is located in Central Estonia (Fig. 1; **I**). Võrtsjärv is a large (270 km^2) shallow polymictic lake with a maximum depth of 6 m and a mean depth of 2.8 m, which, according to the classification by Lewis (1983) belongs to continuous rather than discontinuous cold polymictic lakes. Measurements of water currents carried out in 1995-1996 at 2 m depth at four stations in the lake (Kivimaa *et al.*, 1998) demonstrated that at moderate mean wind velocities (average 2.9 m s^{-1}, maximum 13.2 m s^{-1}), the average current velocities ranged from 2.7 to 8.6 cm s^{-1} at various stations with peak values exceeding 200 cm s^{-1}. Such strong wind induced currents mix the water horizontally resulting in a relatively homogenous water environment in the lake proper with an exception of the narrow, river-like southern end strongly affected by the main inflow. Võrtsjärv does not stratify: the mean difference between the surface (0.5 m) and bottom (2.5 m) temperatures over the ice-free period is approximately 0.1 °C with exceptional short term maxima reaching 4 °C on single calm days. We considered the effect of these single events negligible on average gas exchange rates at monthly time scales. The lake is eutrophic, characterised by the following mean concentrations: total phosphorus (TP) 54 µg l^{-1}, total nitrogen (TN) 1.6 mg l^{-1}, chlorophyll *a* (Chl *a*) 24 µg l^{-1} (Tuvikene *et al.*, 2004; Nõges *et al.*, 2007). Due to the influence of resuspended sediments, the Secchi depth is typically less than 1 m during the ice-free period. According to Reinart & Nõges (2004), the water colour has an average value of 60 mg Pt l^{-1}. Water colour has slight seasonal changes but there may be large differences between years. The lake is ice-covered for more than four months (average 135 days) of the year. The unregulated water level, which has annual mean amplitude of 1.4 m, the absolute range of 3.1 m, has proven by far the most influential factor in the lake. By altering the sediment resuspension rate, the variable water level affects the light climate (Nõges & Järvet, 1995), nutrient availability (Nõges & Nõges, 1999), and phytoplankton abundance and composition (Nõges *et al.*, 2003), both seasonally and in the long term. The water level reaches its seasonal maximum usually in April or May and declines steadily until the seasonal minimum, which is typically in September.

Within the 50 km^2 (19% of the lake area) covered by aquatic macrophytes, 35 km^2 is accounted for by submerged species, 12 km^2 by emergents and

3 km^2 by floating-leaved macrophytes (Feldmann & Mäemets, 2004). Due to high turbidity and strong wave induced turbulence, the submerged vegetation dominated by *Myriophyllum spicatum* L. is mostly sparse.

The 3100-km^2 catchment area of the large but very shallow Lake Võrtsjärv makes up about 7% of Estonian territory and, thus, may contribute significantly to the Estonian natural CO_2 budget. Võrtsjärv is strongly impacted by the inflow of DOM and nutrients due to its large catchment area (A) relative to lake volume (V) (Nõges & Järvet, 1998). The A/V ratio of Võrtsjärv (4.1 m^{-1} at mean water level) is larger than that of other well-studied large and shallow lakes such as Peipsi (1.9 m^{-1}) or Balaton (2.7 m^{-1}) and much larger than in the large and deep lakes such as Ontario (0.046 m^{-1}), Ladoga (0.08 m^{-1}), Onega (0.18 m^{-1}), and Vänern (0.27 m^{-1}) (ILEC World Lake Database). A specific feature of Võrtsjärv is the large natural climate-related variability of water level with a long-term absolute amplitude exceeding 3 m, which causes a more than 200% change in the water volume (Nõges *et al.*, 2003). Our earlier studies have shown that the fluctuating water level in Võrtsjärv resulting from meteorological forcing and major climate trends in the Northern Hemisphere, has a strong impact on the whole ecosystem (Nõges, 2004; Järvalt *et al.*, 2005; Feldmann & Nõges, 2007; Zingel *et al.*, 2007). According to Toming *et al.* (2009), climate-related hydrological changes cause large variation also in the absorption by coloured dissolved organic matter (CDOM) in Võrtsjärv (3.96 - 15.7 m^{-1}) that corresponds to DOC concentrations from 7 to 28 mg l^{-1}. Based on high DOC values, a net heterotrophic metabolism could be assumed while rather high average Chl *a* (24 mg m^{-3}) and TP (54 mg m^{-3}) might otherwise be expected to support net autotrophy.

4.2. Data collection

High frequency data for lake metabolism studies was collected from 30 April to 15 July in 2009 and from 20 April to 28 October in 2010 near the lake's deepest point. From 29 July to 11 August 2010, there are no data because of malfunctioning of the buoy. High frequency instrumentation and data collection are thoroughly described in paper **I**.

Phytoplankton primary production in Võrtsjärv has been measured *in situ* with ^{14}C-assimilation technique (Steeman-Nielsen, 1952) in 1982-1984, 1989, 1991, 1993-1998, 2000, 2003-2009. PP has been measured mainly during ice-free periods from April to October with weekly to monthly intervals. In 1983, 1984, 1991 and 1995, PP was measured also in winter under the ice. PP measurement techniques are thoroughly described in paper **II**.

Water samples for nutrient flux analyses were collected from the lower course of the inflows and from the outflow of Lake Võrtsjärv (Fig. 1, **III**) at weekly to monthly frequency in 2008 and 2009. Additionally, we used the data of nutrient concentrations drawn from the National Monitoring Programme. Details of sampling and analyses are thoroughly described in paper **III**.

Data on total phosphorus retention, internal/external loading, outflow losses and morphometry for 54 lakes and reservoirs in different climate regions around the world were compiled on the basis of published data sources (Table 1, Fig. 1; **IV**). Detailed methods are described in paper **IV**.

4.3. Lake metabolism and primary production modelling

Lake metabolism modelling was based on the algorithms published by Cole *et al* (2000), some minor changes were made to adjust the model to specific features of Lake Võrtsjärv dataset (see material and methods in paper **I**).

As the dynamics of lake metabolism indices (Fig. 2; **I**) followed shifted sinusoidal patterns, we fitted a sinusoidal curve to these data with the aim to quantify the phase shift between the series of GPP, R, and NEP and to compare it with the environmental sinusoidal variables – PAR and water temperature. Method is described in detail in paper **I**.

In parallel to *in situ* measurements (**II**), PP was estimated using a semi-empirical model elaborated by Arst *et al.* (2008). We developed two versions of the model: a spectral and an integral version. Detailed description of model is presented in paper **II**.

4.4. Statistical analyses

Relationships between metabolic rates, measured and modelled PP, physical, chemical and environmental factors (**I-IV**) were evaluated using the basic statistics and multiple regression modules of Statistica 8.0 (StatSoft, Inc. 1984-2007).

5. RESULTS AND DISCUSSION

5.1. Lake Võrtsjärv is seasonally switching between net autotrophy and net heterotrophy

5.1.1. Range, balance and sinusoidal seasonality of ecosystem metabolism in Võrtsjärv

In Lake Võrtsjärv GPP and R showed a large day-to-day variability with GPP mostly exceeding R in spring and early summer but remaining smaller than R in autumn (Table 1; **I**). The average of all GPP measurements exceeded slightly (but not significantly) that of R, but as the data was seasonally unbalanced (more measurements in spring), no conclusion on the metabolic type could be drawn on this basis. Due to the difference in the measurement periods in two years, the inter-annual differences cannot be assessed either and only the ranges of the values could be measured.

Days of net heterotrophy (NEP <0) occurred during all months, but were most frequent during late summer and autumn (Fig. 2; **I**).

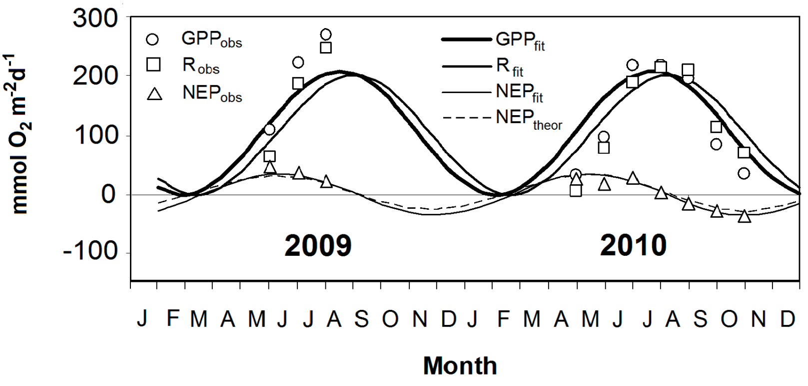

Figure 5.1.1.1. Observed ($_{obs}$) monthly mean values of respiration (R), gross primary production (GPP) and net ecosystem production (NEP) with fitted sine waves ($_{fit}$). The curve NEP$_{theor}$ shows the difference between GPP$_{fit}$ and R$_{fit}$. With modification from paper **I**.

The monthly averages of GPP, R, and NEP revealed a seasonal pattern well described by a sinusoidal fit (Fig. 5.1.1.1) (Fig. 2, Table 2; **I**). Given the good fit of the sine model to the metabolic variables (R^2 0.84 for GPP, 0.87 for R, and 0.93 for NEP), we analysed some of the model parameters to have an insight to the seasonality and to compare it with the sine wave fits of irradiance and water temperature. Among the simulated variables, NEP reached its seasonal peak in May, several weeks before the summer solstice (Fig. 5.1.1.2) (Fig. 4; **I**). GPP peaked in July or August, at approximately the same time with water temperature and 3-7 weeks after the peak of solar irradiance. The peak of community respiration was the last among the three and was reached in August, 1-4 weeks after the peak in water temperature. The fitting curve for solar irradiance (Q) peaked in both years on June 20, practically at the summer solstice. The curve fit for water temperature (T_w) peaked 31 or 32 days later. Despite markedly higher water temperatures in 2010 compared to 2009, (up to 8 °C in May and 4-6 °C in July – August, see Fig. 5; **I**), the timing of the peak according of the fitting curve showed little change. The timing of the simulated seasonal peaks of all three metabolic variables shifted about 25 days earlier in the warmer 2010 compared to 2009 and showed no obvious relationship to the timing of the Q and T_w peaks.

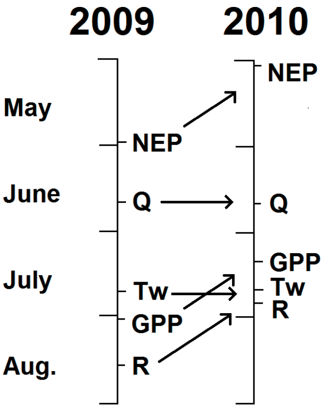

Figure 5.1.1.2. Timing if the seasonal peaks of solar irradiance (Q), water temperature (Tw), gross primary production (GPP), community respiration (R), net ecosystem production (NEP) in Võrtsjärv in 2009 and 2010 as derived from the fitting sine wave parameters. The arrows help to visualize the behaviour of the variables. From paper **I**.

The values of the constant *C* of the sinusoids characterising the mean levels of the metabolic parameters (in mmol O_2 m^{-2} d^{-1}) were 104 for GPP, 100 for R , and 0 for NEP, suggesting a balance (based on NEP) or a slight net autotrophy (based on GPP and R) of the lake on an annual scale. Converted to carbon units, the annual GPP estimate equalled 363 g C m^{-2} y^{1}. The dynamics of NEP was characterized by an autotrophic period lasting from early spring until August or September and a heterotrophic period for the rest of the year. The theoretical curve for

NEP (Fig. 5.1.1.1) (Fig. 2; **I**) calculated as the difference between the curves fits to GPP and R, matched well with the curve fitting the monthly NEP values. As the amplitudes of the GPP and R curves were almost equal, the sinusoidal behaviour of NEP was caused predominantly by the phase shift between GPP and R (without this phase shift the NEP curve would become flat).

5.1.2. Applicability of sinusoidal lake metabolism model in a stratified lake

A trial to apply our sinusoidal model to the monthly metabolic data of stratified Lake Frederiksborg Slotssø (Fig. 9; **I**), showed a 2-week lag between GPP and R in 2003 similar to that found in Võrtsjärv, that was not observed in 2004. This fits well with the higher GPP and smaller role of zooplankton grazing in 2003 described by Staehr & Sand-Jensen (2007). Our model explained 76% of GPP, 61% of R, and 52% of NEP monthly changes in this lake and suggested prevailing autotrophy from the end of March to mid-September in 2003 and from the end of April to the end of October in 2004 (mid-May to mid-September in the original work). The best fitting sinusoids, however, were unable to follow the high peaks of GPP and R in August or September, and the inter-annual differences. Thus, the model seems to be fit for describing the metabolism of turbid polymictic lakes like Võrtsjärv which have seasonally smooth changes in light and nutrient availability, and where strong light limitation forces the dynamics of GPP, R and NEP to follow better the sinusoidal changes of PAR and temperature. In stratified Frederiksborg Slotssø (Denmark) the metabolic variables were strongly controlled by changes in mixing depth, which determined nutrient availability by pulses and fluctuations in the mean available light levels in the mixed layer (Staehr & Sand-Jensen, 2007).

5.1.3. Regulation of ecosystem metabolism and impacts of climate change

In Võrtsjärv all metabolic variables showed positive relationships with solar irradiance and water temperature, and negative relationships with wind speed (U). GPP and NEP declined with seasonally declining water levels whereas R increased (Fig. 6; **I**).

Light limitation of phytoplankton growth is a common phenomenon in Võrtsjärv due to high plankton biomass, brownish water colour due to elevated humic matter content, and a continuously large impact of suspended sediments on light attenuation in the water during the ice-free period (Reinart & Nõges, 2004). As expected, GPP and NEP were stimulated by increasing irradiance whereas wind suppressed production processes likely by modifying the resuspension rate.

By autumn, a large amount of fresh sediment is produced. At the same time the lake reaches its lowest water levels. Both factors contribute to high rates of sediment resuspension, which increases linearly with decreasing mean depth of the lake (James *et al.*, 1997). The increased concentrations of particulate and dissolved matters raises the respiration rate causing a decline in NEP. As the fresh sediment in Võrtsjärv still contains intact algal cells and degradation products of algal pigments (Freiberg *et al.*, 2011), the observed increase of Chl *a* towards autumn is partially caused by resuspension and cannot be fully be attributed to algal growth and the reduction of zooplankton grazing pressure.

Increase in plankton respiration with increasing Chl *a*, TP, and DOC concentrations has been recurrently reported. Pace & Prairie (2005) analysed data from 70 different lakes, and found Chl *a* accounted for 71% and TP for 81% of the variance in community respiration, which they considered a typical pattern of lakes where primary production is strongly nutrient limited. In highly productive Frederiksborg Slotssø (Denmark) GPP and R increased with increasing Chla, TP and DOC (Staehr *et al.*, 2010b; 2012a). The rather low explanatory power of multiple regression models in Võrtsjärv (R^2 from 0.28 to 0.67) was most probably caused by the absence of high resolution data on Chl *a*, nutrients, and DOC, the influence of which will be the focus of our future studies on metabolic variables.

The best multiple regression models based on the frequently measured variables (PAR, T_w, U) and daily measured lake mean depth (Z_{avg}) explained 67% of the variability in log GPP, 36% in log R and 28% in NEP (Table 3: **II**). Increasing water temperature had a strong positive effects on GPP and R and a negative effect on NEP. GPP and NEP increased with increasing PAR, but the latter was not included in the best model describing respiration. Wind had negative effects on both GPP and NEP. Although having a negative correlation also with NEP, wind speed was not included in the best model for NEP. The decreasing average depth of the lake increased R and decreased NEP.

The factors governing GPP and R are partly overlapping. In our study, increasing water temperature had strong positive effects on GPP and R but a negative effect on NEP (Table 3, **I**). These results are fully in line with the findings by Staehr *et al.* (2010a) for Danish stratified lakes. Similar response of the metabolism of different types of lakes to temperature implies that climate warming is likely to support net heterotrophy of temperate lakes in general.

The intrinsic sensitivity of respiration to temperature was recently shown across aquatic ecosystems of contrasting thermal history (Perkins *et al.*, 2012). The positive relationship between T_w and GPP arises from the temperature dependence of R, which mathematically is one of the summands in GPP (Eq. 6; **I**). Temperature *per se* is not considered a growth limiting factor for phytoplankton, but may restrict or stimulate growth through various mechanisms such as shifted timing of the ice breakup (Adrian *et al.*, 1999; Weyhenmeyer *et al.*, 1999) or zooplankton grazing (Straile and Adrian, 2000), modified winter mixing in deep monomictic lakes and its consequences to nutrient availability (Salmaso, 2002, 2005; Straile *et al.*, 2003) or increased thermal stability of the water column crucial for development of cyanobacteria blooms (Paerl & Huisman, 2008). It is likely that the stimulating effect of T_w on lake heterotrophy can be attributed to the stronger temperature dependence of R rather than GPP.

5.1.4. Global and regional comparison of lake metabolism

The published mean daily GPP and R values for lakes range over more than five orders of magnitude (Fig, 5.1.4.1) (Table 4, Fig. 7; **I**) but are strongly correlated ($r=0.94$; $p<0.01$) and thus line up rather nicely along the 1:1 proportionality line. Among these 41 lakes located almost entirely within the temperate zone and characterized by a median GPP of 30 mmol O_2 m^{-3} d^{-1} and median R of 39 mmol O_2 m^{-3} d^{-1}, Lake Võrtsjärv occupies a mid position among the lakes staying very close to the proportionality line. Compared to the long-term primary productivity estimate of 208 g C m^{-2} y^{-1} in Võrtsjärv measured by the ^{14}C technique (**II**), the annual GPP estimate based on high frequency metabolism measurements (363 g C m^{-2} y^{-1}) was considerably higher. This difference can be explained by the fact that ^{14}C productivities lie between NEP and GPP values but are closer to NEP when long incubations are used and closer to GPP when short incubations are used and (Dring & Jewson, 1982; Bender *et al.*, 1999).

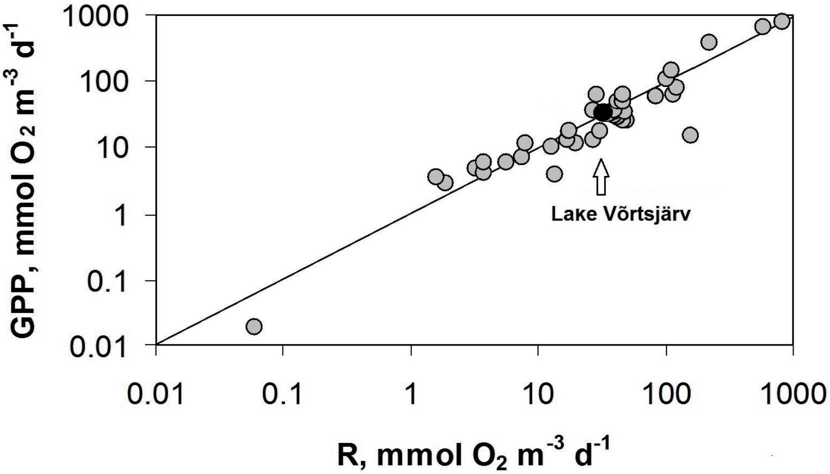

Figure 5.1.4.1. Scatterplot of published mean daily values of gross primary production (GPP) vs. community respiration (R) in lakes. From paper **I**.

The rather good proportionality of GPP and R shows that the main substrate for respiration in most lakes originates predominantly from primary production within the lake. Still there are deviations to both sides from the 1:1 line characterized by the GPP:R ratio ranging from 0.1 in Lake Hummingbird (MI, USA, Hanson *et al.*, 2003) to 2.5 in Lake Michigan (MI, USA, Ogdahl *et al.*, 2010). Although the GPP:R ratio is shown to be mostly a function of the lake trophic state (e.g. Cole *et al.*, 2000; Hanson *et al.*, 2003) and/or DOC loading (Andersson & Sobek, 2006), the analysis of published data show that also lake morphometry may play an important role in determining lake metabolism. Among the 41 lakes, volumetric GPP and R decreased highly significantly with the increasing mean depth of lakes (Fig. 8; **I**). A similar regularity was described by Staehr *et al.* (2012a) in 25 Danish lakes, which the authors explained by the generally lower trophic state of deeper lakes. In Võrtsjärv respiration increased with declining water levels also in the seasonal cycle but GPP did not show any dependence on water depth (Fig. 6; **I**). Among Danish lakes, GPP and R decreased also with increasing lake area but this result was not found in the set of lakes analysed by us. We found, however, highly significant positive relationships of GPP:R with lake area and volume (Fig. 8, **I**) showing that larger lakes tend to be more autotrophic. The mean depth of lakes *per se* had no significant effect on the auto-to-heterotrophy balance. The relative depth, which is the maximum depth of a lake as a percentage of mean diameter (Wetzel, 2001) and characterises the potential of thermal stratification (Escobar *et al.*, 2009; Tiberti *et al.*, 2010) and phosphorus retention (**IV**), had a significant impact towards heterotrophic conditions (decrease of GPP:R ratio) and a tendency towards lower NEP. Obviously the trend of relatively deeper lakes being more heterotrophic can be attributed to stronger thermal stratification in these lakes that leads to phosphorus depletion in the epilimnion during the growing season. In all relationships found between lake morphometric and metabolic variables, Võrtsjärv followed the general patterns and was never among outliers. The balance between annual GPP and R resulting in NEP=0, as found in Võrtsjärv, is not very common, as in 57% of the lakes included in Table 4 (**I**), annual NEP was negative, and a similar proportion (58%) was found among Danish lakes (Staehr *et al.*, 2012a).

During winter, the rate of photosynthesis in temperate lakes declines and remains negligible in lakes that freeze over (Salonen *et al.*, 2009). Decomposition of the organic matter continues, however, and the dissolved oxygen budget becomes negative in most lakes. Benthic oxygen demand of about 10 mmol O_2 m^{-2} d^{-1}, typical for highly eutrophic boreal lakes (Malve *et al.*, 2005), would deplete dissolved oxygen from a 1 m deep oxygen-saturated lake within 49 days. Anoxia formation and winter fish kills in boreal shallow lakes including Lake Võrtsjärv (Tuvikene *et al.*, 2002, Järvalt *et al.*, 2005) are common and give clear evidence of negative dissolved oxygen budgets. The ice breakup in spring brings about a tremendous change in light conditions while the commonly high transparency of water and the pool of re-mineralized nutrients enable the formation of a virtually unlimited pulse of algal growth. The timing of the vernal peak of phytoplankton is closely related to air temperature in spring, which mostly determines the timing of the ice breakup (Nõges *et al.*, 2010c). It can be assumed that during the vernal phytoplankton peak, most lakes become net autotrophic. Hence we can conclude that most lakes, at least in the boreal zone, switch in early spring from net heterotrophy to net autotrophy while the duration of the latter determines whether the lake becomes auto- or heterotrophic on an annual scale.

The fact that most of the substrate for respiration (plant, animal, and bacterial biomass, DOC) is produced within the lake during the annual cycle and exists in the organic form for a certain time before being re-mineralized, implies that seasonally the community respiration lags behind the GPP cycle whereas the phase shift is equal to the dominant mode of the organic matter turnover time in the food web. In Lake Võrtsjärv where the bulk of the plankton biomass is accounted for by slowly growing 'inedible' filamentous cyanobacteria, R lags behind GPP by two weeks, on average. For comparison, in the stratified Danish lakes GPP and R followed each other more strictly over time as reflected by NEP values near zero, GPP:R ratios near 1.0, and close positive correlations of daily GPP and R (r >0.9, Staehr *et al.*, 2010b, *cf.* 0.80 in Võrtsjärv), which the authors explained by relatively rapid respiration by bacteria and zooplankton of the newly produced organic matter. Only during development of algal blooms and their following collapse and degradation, was the synchrony between GPP and R lost.

5.2. Primary production of Lake Võrtsjärv and its long-term changes

5.2.1. *In situ* measured primary production

According to the 18-year measurements, the mean daily integrated PP was 558 mg C m^{-2} day^{-1} with monthly means changing from about 25 mg C m^{-2} day^{-1} in December and January to nearly 1300 mg C m^{-2} day^{-1} in June (Table 1; **II**). The scatter of single daily measurements in each month was rather large characterised by standard deviations (SD) making up from 49 to 184% of the monthly mean values. The daily PP was relatively most variable in November and March due to the onset and ending of the ice season. The maximum chlorophyll specific production rate at light saturation varied from 0.1 to 14.7 mg C mg Chl a^{-1} h^{-1} being on average 2.06 ± 1.72 mg C mg Chl a^{-1} h-^{1}. PP had a pronounced seasonality in Võrtsjärv, with two-third of the annual PP produced during one-third of the year from May to August. The mean daily PP from May to August formed on average 0.55% of the annual PP. We used this ratio to calculate the annual PP for years with incomplete data coverage. For the years to which both methods were applied, the integrated values corresponded well to the calculated values (Fig. 1; **II**). The measured annual average pelagic PP in Võrtsjärv was 205 g C m^{-2}. In the long-term, the measured PP had no significant trend either over single months or in the annually integrated values.

5.2.2. Modelled primary production and its comparison with *in situ* values

The vertical profiles of measured and modelled PP corresponded generally well with each other (Fig. 2, **II**). Also the modelled integral PP (PP_{int}, mg C m^{-2} h^{-1}) values that were computed by integrating vertical PP profiles over depth, were in good concordance with the measured PP_{int} values. For example, the profiles represented in Fig. 2 of paper **II**, gave measured PP_{int} values of 102 and 211 mg C m^{-2} h^{-1}, and modelled PP_{int} values of 113 and 223 mg C m^{-2} h^{-1}, respectively.

By the model we calculated PP_{int} in total for 6011 ice-free days in the 28-year period from 1982 to 2009. The median values of modelled and measured daily PP_{int} values were quite close in different months but the variation of the modelled values was smaller than that of the measured values (Fig. 4; Table 1; **II**). The average annual modelled pelagic PP_{int} in 1982–2009 was 200 g C m^{-2} $year^{-1}$ (Table 1; **II**). Considering approximately 4% underestimation of annual PP_{int} due to ignoring the under-ice production, the modelled average annual PP_{int} in Võrtsjärv would be 208 (min. 144, max. 306) g C m^{-2} $year^{-1}$, which is very close to the average of the measured values (205 g C m^{-2} $year^{-1}$). The yearly average modelled volumetric PP (PP_{int} divided by the mean depth of the lake) was 80 (min. 48, max. 148) g C m^{-3} $year^{-1}$ (Table 2; **II**).

For the 18 years when PP_{int} was both measured and modelled, the results were significantly correlated (R^2 = 0.32, P = 0.015) (Fig. 5; **II**), the modelled daily PP_{int}, however, exhibited significant linear increasing trends in all ice-free months over the whole study period (Fig. 6; **II**) while no trend was detected in the measured PP values. The increase in modelled PP_{int} was caused by the strong significant trends in Chl *a* one of the important input parameters, occurring from May to December over the whole study period (Fig. 7; **II**). The mean light intensity within the water column (I_{mix}) calculated from Secchi depth and water level, showed a bell-shape change over the years (Fig. 8A, **II**) with average light conditions for phytoplankton improving over 1980s and deteriorating again since the first half of 1990s. The percentage of Chl *a* in the total phytoplankton biomass (Chl% *B*) had opposite dynamics with an increasing trend since the beginning of 1990s (Fig. 8B; **II**).

The relationship between the annual PP_{int} values, based on measurements and modelling (R^2 = 0.32) was much weaker compared with the R^2 = 0.9

reported in Arst *et al.* (2008). However, in Arst *et al.* (2008) the results were obtained from 2-h measurement series of PP with full (without breaks) complex of initial data for model calculations, that is not so for long-term estimations. In general, there can be a number of errors included both in the modelling and the measured data. Excluding other methodological errors potentially included in the ^{14}C technique for measuring PP (see overview by Marra, 2002), the sources of error in summarising the measured data are included in the depth integration of the discrete vertical measurements, the extrapolation of the PP values around noon to the whole day (Richardson, 1991), but the major source of errors is included in the interpolation of the highly variable but infrequently measured daily PP values. The latter is largely avoided by modelling in which we used the true monthly mean values of daily irradiances and only the values of Chl *a*, a less variable parameter compared to PP, were interpolated between discrete measurements.

For the assessment of total PP of the lake and its long-term changes, we further used the modelled PP values. Multiplying the annual areal phytoplankton PP by the average lake area in each year, we got an estimate of 56 559 (min. 41 013, max. 77 064) tonnes of carbon fixed annually by phytoplankton primary production in Võrtsjärv. Considering the estimations that phytoplankton contributes 79% and macrophytes with their epiphyton 21% to the total PP in Võrtsjärv (Nõges *et al.*, 2010b), the total annual whole-lake carbon fixation of Võrtsjärv resulted in 71 268 (min. 51 679, max. 97 107) tonnes (Table 2; **II**).

5.2.3. Long-term trend of primary production

There are two interrelated possible explanations for the long-term stability of the measured PP on the background of increasing Chl *a*: (1) that the increase in Chl *a* was an adaptive response of phytoplankton to a deterioration of light conditions and (2) that some other factor caused the succession of dominating species having different rates of chlorophyll specific photosynthesis. Adaptation of phytoplankton to deteriorating light levels may include photoacclimation of existing species or, if exposure to dim light is prolonged, also succession of species in the favour of more shade tolerant ones. A simple strategy to survive sub-optimal light conditions is to increase the cellular content of light-harvesting pigments in order to maintain productivity (Falkowski & Owens, 1980; Dubinsky

& Stambler, 2009; Yacobi & Zohary, 2010). Phytoplankton species differ largely by their ability to increase cellular chlorophyll content (Johnsen & Sakshaug 2007). Experiments with *Limnothrix redekei* (Foy & Gibson, 1982), the species that dominated in Võrtsjärv in the beginning of our study period, showed the species ability to more than triple its cellular chlorophyll content under low light doses. In Võrtsjärv the long-term increase in cellular chlorophyll content observed in autumn was much smaller but still significant and covered the period from 1988 onward during which the proportion of *L. planctonica* among dominants was continuously increasing. In order to explain the increase of Chl *a* by a deterioration of light conditions, the latter has to be shown. Besides the underwater light climate calculations based on Secchi depth (Fig. 8A; **II**), also some other arguments suggest that light conditions have changed over the years: (1) although it seems a circular argument, the significant increase in Chl *a* itself (Fig. 7; **II**) must have had an effect on light conditions and, hence, the increase in Chl *a* could be caused by self-shading of phytoplankton; (2) a comparison of historical beam attenuation measurements from 1913 (Mühlen, 1918) with those from 2000 to 2001, Reinart & Nõges (2004) found that the absorption at 453 nm has significantly increased and therefore amount of dissolved organic matter in water may be higher nowadays than it was in the beginning of century. Given the general "browning" trends in many lakes over the northern hemisphere (Jennings *et al.*, 2010), an increase of humic matter content in Võrtsjärv over a longer period cannot be excluded. An increase in water colour coinciding with high water levels in 1978–1979 has been suggested as the main cause for the earlier switching of phytoplankton dominants from *Planktolyngbya limnetica* (Lemm.) J. Komarkova-Legnerova to *Limnothrix redekei* (Nõges *et al.*, 2010a; Tuvikene *et al.*, 2010); (3) chemical oxygen demand (CODMn), a common proxy for dissolved organic matter (DOM), was significantly lower in the period 1968–1977 compared with that in 1998–2008 and had a highly significant increasing trend within both periods (Tuvikene *et al.*, 2010). Potassium permanganate, a much milder oxidizer compared to the more often used potassium dichromate, is highly sensitive to variations in dissolved organic matter, including humic substances (Xia *et al.*, 2005). A correlations analysis between limnological variables in 102 Estonian lakes (Milius & Starast, 1999) found the strongest correlation among all analysed 14 variables between CODMn and water colour (r = 0.97) that allows using CODMn as a proxy for water colour. As a conclusion, an increase in Chl *a* and a decrease in chlorophyll specific production rate in response to deteriorated light conditions is the most likely explanation to the different long-term trends in modelled and measured PP. Figure 7 (**II**) shows that in the long-term, there was a breaking point in the trend of the Chl *a* series in the beginning of 1990s and that the biggest increase in Chl *a* has taken place in autumn. A comparison of these changes with the biomass dynamics of *Limnothrix planctonica* in Fig. 10 in paper **II** (Nõges *et al.*, 2004, updated) show a striking correspondence suggesting strongly that the Chl *a* change was caused by the emerging new dominant. Both *Limnothrix* species are considered true shade tolerants (Chomerat *et al.*, 2007; Padisa´k *et al.*, 2009) and occupy generally a similar niche in turbid polymictic lakes. Both species contain besides chlorophylls also phycocyanin, an additional photosynthetic pigment that has been shown as one of the main advantages in cyanobacteria in competition for light in turbid environments (Tilzer, 1987). The only major autecological difference between the two species in Võrtsjärv was expressed in their different seasonality and this may be the key to the observed inconsistency between Chl *a* and PP changes. The biomass of *L. planctonica* increases steadily during the vegetation period and, in the absence of major loss mechanisms, builds up a considerable standing stock by autumn. This standing stock is characterised by high Chl *a* which simulates a higher modelled PP for this period as seasonal or species specific differences in chlorophyll specific productivity are not included in PP model. It leads to some change of the specific absorption coefficients of the phytoplankton that was not taken into account in the model, which used the algorithm by Bricaud *et al.* (1995). The late autumn biomass was characterised also by higher cellular chlorophyll content that explains the positive trend in Chl *a*/B ratio over the period when the proportion of *L. lanktonica* increased in the phytoplankton community, i.e. since the early 1990s. This smooth succession of dominants could explain the absence of any significant trend in annual PP values. Still the question remains, what caused the succession between the two *Limnothrix* species. Resource limited conditions favour the species which has even a small advantage in exploiting the limiting resource. Building up a higher biomass by extending the growth period towards autumn may be a clear advantage in light-limited conditions. The earlier dominant and present subdominant *L. redekei* reaches its biomass peak in June but in summer its gas vacuoles collapse and the cells autolyse. The regular collapse of gas vacuoles in *L. redekei* in summer is a very common phenomenon not only in Võrtsjärv but has been mentioned also for Edebergsee, where trichomes with no or only small gas vacuoles dominated at high light intensities (Meffert &

Krambeck, 1977). Such collapse has not been described in *L. planctonica*, which has much smaller gas vacuoles per se. A study of the filament length structure in the two *Limnothrix* species (Nõges, 1999) suggested the selective sedimentation of longer filaments of *L. redekei* with collapsed gas vacuoles as the main loss factor of this species in summer. A CCA analysis for 44-year data on species composition and environmental variables (Nõges *et al.*, 2010a) showed that in Võrtsjärv *L. redekei* was favoured by increasing water level and *L. planktonica* by increasing temperatures in summer and autumn. Trend analysis for the period 1961–2004 (Nõges, 2009) revealed a highly significant ($P > 0.01$) upward trend for water temperature in August with a significant ($P > 0.05$) stepwise increase in 1989. Hence, we suppose that the initial breakthrough of *Limnothrix* species in early 1980s was caused by the sudden deterioration of light conditions following a water level increase in 1978/1979 (Nõges & Järvet, 1995; Nõges *et al.*, 2010a; Tuvikene *et al.*, 2010) while the consequent gradual increase of the proportion of *L. planktonica* could be more related to the late summer warming trend.

5.2.4. Primary productivity of Lake Võrtsjärv in the global scale

In the global context, Võrtsjärv occupies by its annual primary production a medium position among the World lakes for which data on PP were available for us (Table 3; Fig. 9; **II**). Annual areal PP of Võrtsjärv is very close to that of the other large and shallow lake close by, Lake Peipsi, but is also similar to the PP of much deeper large temperate lakes, such as Erie and Ontario. According to the data presented in Table 3 (**II**), the annual PP of 63 World's lakes was significantly negatively correlated with latitude ($R^2 = 0.23$, $n = 63$, $P > 0.001$). The strong effect of latitude (Lat) on lake productivity was stressed also by Håkanson & Boulion (2002) and Boulion (2003). These researchers showed a strong and significant decrease in phytoplankton primary production with increasing Lat, a relationship that could be successfully used to predict PP of inland waters. They found that 60% of the variation of annual PP could be explained by Lat according to linear equation: $PP = -130 * Lat + 8453$ and even 74% using the exponential equation: $PP = 647461 * \exp(-4.29 * TranLat)$ where $TranLat = (90/(90 - Lat))^{0.5}$. Data presented in Table 3 (**II**) showed somewhat weaker relationship also with the transformed values ($R^2 = 0.36$, $n = 63$, $P > 0.001$). Annual PP of Lake Võrtsjärv calculated according to the above described formulae of Håkanson & Boulion (2002) and

Boulion (2003) on the basis of Lat and TranLat gave the corresponding values of 880 and 480, which overestimate the real PP in the lake fourfold and twice, accordingly. Basing on this simple comparison, it is evident that besides global large-scale estimations, the direct measurements and local modelling are indispensable to calculate the carbon budget and to understand lake metabolism. Figure 9 in paper **II** shows, however, that Võrtsjärv is located rather close to the nutrient-saturated production boundary determined by Lat, where light limitation has the leading role. Theoretically, its productivity could increase if the relative proportion of chlorophyll among optically active substances (Chl *a*, yellow substance and suspended solids) would increase. On average, these three components account almost equally for light attenuation in Võrtsjärv (Nõges, 2000).

5.3. Fluxes of carbon and nutrients in the catchment-lake system of Võrtsjärv

Already in the first hydrochemical comprehensive study of Estonian water bodies by Simm (1975) it was shown that in our streams the content of inorganic substances is relatively high and the amount of dissolved organic matter never exceeds it. Because of the calcareous bedrock, the continuously high dissolved inorganic carbon (DIC) concentration is a characteristic feature of Estonian river waters. In the outflow of Lake Võrtsjärv, the mean concentration of inorganic carbon was twice as high and in the inflows even 2.5 to 3.5 times higher as that of organic carbon (Table 2; **III**). In the outflow of Võrtsjärv, the Emajõgi River, nutrient and DIC concentrations were generally lower than in the inflows. Among the inflows of Võrtsjärv the lowest dissolved (DOC) and total organic carbon (TOC) concentrations were found in the Tarvastu River and the highest values occurred mostly in the Tänassilma River. The Tänassilma River was the richest in phosphorus and the Tarvastu River, in nitrogen (Table 2; **III**). In the rivers the concentrations of TN and Si were higher in winter and lower in summer. The concentrations of TOC and DOC were higher from June to January and lower from February to June. The seasonal dynamics of DIC was quite indistinct except for a sharp decrease after ice breaks – a phenomenon characteristic of all rivers (Fig. 3; **III**). In 2008 the annual water discharge of the four inflows exceeded the outflow while in 2009 the outflow was higher than the inflows. A similar situation was observed for all studied substances (Table 3; **III**). In 2008, 21 400 t of TOC, 40 360 t of DIC, and 19 900 t of

DOC entered the lake via the four studied rivers. In 2009 the respective amounts were much lower, 18 300 t, 35 300 t, and 15 200 t. Similarly, in 2008 the incoming amounts of nutrients were higher, 2270 t of TN, 49 t of TP, and 2500 t of Si, while in 2009 the respective amounts were 1500 t, 44 t, and 2400 t. Data from 2008 showed that the inflow of water and the studied substances from the four main rivers alone were higher than the respective amounts carried out of the lake. In 2009 the outflow of water exceeded the inflow and this was also the case with TOC, DIC, and DOC. However, the incoming load of nutrients was continuously higher than the load of outgoing nutrients (Fig. 5; **III**).

The correlations between water discharge and loadings of substances were stronger than between concentrations and loadings (Table 4; **III**). In some cases, correlations between loadings and concentrations were nonsignificant or even negative as in the case of DIC in the inflows. There were significant negative correlations (from – 0.6 to – 0.84) also between DIC concentrations and water discharges in the inflows. We found strong positive correlations (>0.66) between water discharge and nitrogen concentration. Correlations between water discharge and phosphorus concentration were positive for some inflows, negative for some, and non-significant for some.

The concentrations of TOC and DOC in the river system studied by us were higher than those reported from a lotic system in Canada (Finlay *et al.*, 2010), from some streams in Germany (Sachse *et al*, 2005), and from lakes and rivers of Finland (Rantakari *et al.*, 2004; Mattsson *et al.*, 2007) and Poland (Siepak, 1999). Higher DOC concentrations were reported in the streams from draining peatland systems in Scotland (Dawson *et al*, 2004); however, a different determination method was used. The concentration of DIC varied more in our study compared with the study by Finlay *et al.* (2010). The loads of DOC into Lake Võrtsjärv via the four main inflows estimated for the period 1990 – 2002 were 1320 – 4934 t y^{-1} (Tamm *et al.*, 2008). Differences between our results and those reported by Tamm *et al.* (2008) are due to different estimation methods used. We calculated the carbon load directly from carbon content, which is a far more exact method than deriving it from the chemical oxygen demand. According to our calculations, DOC loading was more than four times higher than reported previously. However, the concentrations of TOC and DOC in our study may be overestimated. In the analysis we used the difference method of Dr. Lange TOC cuvette test and not the purging method (Kraatz & Wochnik, 1998). The used method presumes that TIC concentration is smaller than TOC concentration while in our samples TIC concentrations were higher than the respective TOC concentrations. There is an assumption that total carbon analysis may overestimate the organic carbon content in fresh waters in the presence of high DIC (Findlay *et al.*, 2010). In 1995 the estimated annual loadings of Võrtsjärv were 1930 t of N and 57 t of P (Nõges *et al.*, 1998) and the annual mean values for 23 years (1980–2002) were 2752 t and 78 t, respectively (Järvet, 2004a). In 1995, 986 t of N and 44 t of P were discharged from Lake Võrtsjärv via the outflow (Nõges *et al.*, 1998) and the respective values for the 23-year period were 1729 t and 39 t (Järvet, 2004a). Our results are in good accordance with the findings by Nõges *et al.* (1998) but show somewhat lower figures than those reported by Järvet (2004a). Here we have to consider the fact that there was a downward trend in the nutrient loadings and concentrations during two last decades (Järvet, 2004a; Iital *et al.*, 2010). In line with earlier findings (Nõges *et al.*, 1998; Järvet, 2004a), Võrtsjärv accumulated nutrients. We found that also Si has been retained in the lake as in both years the inflow of all N, P, and Si from the four tributaries exceeded their outflow.

Several studies have estimated only the concentrations of nutrients and DOC in stream water, without taking intro account the hydrology (Bernot *et al.*, 2006; Eimers *et al.*, 2008; Goodale *et al.*, 2009; Iital *et al.*, 2010). Discharge, however, is the primary factor determining the fluxes of nutrients and different carbon fractions into lakes. In 2008, when the discharge was 12.5% higher compared to 2009, all studied fluxes were also higher: TOC, 15%; DIC, 13%; DOC, 26%; TN, 34%; TP, 8%, and Si, 5%. Our findings are consistent with those of Pastor *et al.* (2003) and Eimers *et al.* (2008), who showed that changes in stream flow have an essential impact on concentrations of chemical substances such as DOC. Like in hard-water lakes in Canada (Finlay *et al.*, 2010), hydrologic inputs seem to play a more important part in carbon fluxes than lake metabolism. It was shown that in Finland weather-driven fluctuation in discharge is the main reason for changes in nitrogen and phosphorus fluxes (Vuorenmaa *et al.*, 2002; Bärlund *et al.*, 2009). Nõges *et al.* (1998) pointed out that the seasonal dynamics of the load of nutrients (N and P) from the catchment of Võrtsjärv depends on the hydrological load rather than on changes in nutrient concentrations. Also the load of Si is strongly linked to water discharge in the catchment of Võrtsjärv (Nõges *et al.*, 2008). The years 2008 and 2009 were different in respect of the hydrological regime of Lake Võrtsjärv (Figs 2 and 4; **III**). In 2008, the outflow accounted for only 91% of the four main inflows and water accumulated in the lake. In

2009, the respective figure was 130%, indicating that more water flowed out of the lake than entered it. The length of the ice-free period in the two years was also different. In 2008, Võrtsjärv froze only for a short period in January, while in 2009 the permanent ice cover lasted until late March. The difference between the inflow and outflow in late winter and early spring was positive in 2008 but negative in 2009 (Fig. 4; **III**). In the warm season differences in the discharges between the study years were not so distinct. The difference was negative from May to August in 2008 and from May to September in 2009. This is in good concordance with the annual mean water balance for Lake Võrtsjärv, which is negative for February, May, June, July, August, and September and positive for the remaining six months (Järvet, 2004b). As the discharge was the more important component of the loading, it is clear why the fluxes of substances differed between the study years.

5.4. Global analysis of the regulation of phosphorus retention in lakes

Lake Võrtsjärv is a highly eutrophic lake that receives nutrients from the catchment area mainly via four main rivers. The nutrient transport of each river reflects specific land use activities within the catchment; meteorological and hydrological conditions, and biogeochemical processes occurring in the soil, sediment and surface water. The results our ealrier unpublished study showed that the annual P runoff into Võrtsjärv decreased significantly from 1990s.

Our analysis (**IV**) based on the data from 54 lakes and reservoirs in different climate regions around the world revealed that on average the natural lakes retained 47 ± 28 (SD) % and the reservoirs 42 ± 22 (SD) % of external phosphorus loading. There was no statistically significant difference between these mean R_p values, so we treated lakes and reservoirs together in our analysis. Phosphorus retention ca 28% in large and shallow Võrtsjärv that has very small relative depth remains far below of the average level of this dataset (**IV**).

We also partially confirmed our hypothesis that waterbodies with greater relative depth retain more external phosphorus than waterbodies with lower relative depth, though this was corroborated only in waterbodies that had either quite large surface areas (> 25 km2, Fig. 5B; **IV**) or short hydraulic turnover times (<0.3 year, Fig. 6A; **IV**).

CONCLUSIONS

1. A sinusoidal model fitted to primary production and respiration (R) seasonality of Lake Võrtsjärv showed that the metabolism of this lake switches between autotrophic and heterotrophic types. The autotrophic period starting from early spring lasts until August or September whereas during the rest of the year heterotrophy prevails. On an annual basis, gross primary production (GPP) of the pelagic part of Võrtsjärv is balanced or slightly exceeds R showing that from the CO_2 emission point of view, the lake can be considered carbon neutral (**I**).

2. In Võrtsjärv community respiration lagged behind GPP by about two weeks which could be explained by the bulk of the phytoplankton biomass accounted for by filamentous cyanobacteria that were inedible for zooplankton, which resulted in increased cyanobacteria biomass over the season, and also by increasing sediment resuspension with decreasing water levels towards autumn (**I**).

3. Stronger stimulating effect of temperature on R compared to GPP suggests that climate warming is likely to support heterotrophy in Võrtsjärv (**I**).

4. In a set of 41 lakes, Võrtsjärv followed the general relationships between morphometric and metabolic variables and was never among the outliers. The analysis supported earlier findings about declining GPP and R with increasing lake depth but also revealed a highly significant trend of larger lakes being more autotrophic (**I**).

5. According to the long-term mean annual primary production (PP) of 208 g C m^{-2} Võrtsjärv is located rather close to the nutrient-saturated production boundary determined by latitude where light limitation has the leading role. This assignment is supported by the phytoplankton composition dominated by eutrophic highly shade tolerant cyanobacteria species from the genus Limnothrix (**II**).

6. The semi-empirical primary production model based on continuous irradiance (PAR) measurements and

interpolated values for chlorophyll a (Chl *a*) concentration and light attenuation coefficient simulated sufficiently well the interannual changes in PP (**II**).

7. Increasing trend in the long-term modelled PP (induced by increasing Chl *a*) was not supported by measured PP. This controversy can be explained by an adaptive increase in the cellular Chl *a* content in phytoplankton in response to deteriorated light conditions, and the change of dominating species from *Limnothrix redekei* to *L. planctonica*, the lower chlorophyll specific productivity of which is not taken into account in the model (**II**).

8. Lake Võrtsjärv accumulated nutrients (nitrogen, phosphorus, and silicon) irrespective of the positive or negative water budget. When lake is gathering water, it also accumulates carbon, while in years of negative water budget Võrtsjärv also leaks carbon through its outflow (**III**).

9. The smallest differences between the incoming and outgoing nutrient and carbon fluxes occurred in the low water periods in summer and winter (**III**).

10. Our analysis based on the data from 54 lakes and reservoirs in different climate regions around the world revealed that phosphorus retention (R_p) in large and shallow Võrtsjärv (ca 28%) was below the average R_p in this set of the lakes (46%) (**IV**).

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SUMMARY IN ESTONIAN

Järvede produktiivsuse ja toiteainete peetuse sesoonsus, aastatevahelised erinevused ning sõltuvus järvede morfomeetriast

Hoolimata parasvöötme siseveekogude rohkusest ja heast uuritusest, ei ole meil senini selget ülevaadet nende veekogude rollist globaalses süsinikubilansis ja kirjandusest nähtuvad suured järvede tüübispetsiifilised erinevused.

Respiratoorne CO_2 vabanemine siseveekogudest ja süsiniku akumulatsioon järvesetetes on globaalse tähtsusega protsessid, mille käigus peetub enam kui pool maismaalt pärinevast süsinikuvoost, mis muidu jõuaksid maailmamerre. Oluline osa sellest vabanenud süsihappegaasist seotakse roheliste taimede ja veekogudes elutseva fütoplanktoni fotosünteesil taas orgaaniliseks aineks. Veekogudes toimuva primaarproduktsiooni ja hingamise vahekorra alusel saab järved jagada kahte ainevahetuse tüüpi: valdavalt CO_2 tootvateks (heterotroofseteks) ja valdavalt CO_2 talletavateks (autotroofseteks). Ka väike nihe primaarproduktsiooni ja hingamise tasakaalus, põhjustatuna näiteks orgaanilise aine või toiteainete (näiteks fosforiühendite) sissevoolu muutustest, võib muuta järve kui terviku ainevahetuse tüüpi.

Üldiste teadmiste ja oma varasemate Võrtsjärve uurimiste alusel oletasime, et järve ainevahetuse tüüp võib nii ööpäevaselt kui sesoonselt vahelduda. Jää- ja lumikatte all, aga samuti öötundidel, väheneb oluliselt vette jõudev valguse hulk, mis on vajalik fotosünteesi toimumiseks. Valguse ööpäevane ja aastaajaline muutlikkus ongi üheks peamiseks teguriks veekogude metabolismitüübi kujunemisel. Fotosünteesi ja hingamist mõjutavate tegurite muutused võivad toimuda üsna kiiresti (tundide ja päevade jooksul), mistõttu oli neist seni kord kuus toimunud vaatluste abil väga raske ülevaadet saada.

Mullu täitus sada aastat esimese Võrtsjärvele korraldatud kompleks-ekspeditsiooni algusest. Korrapärased toiteainete ja teiste vee keemiliste ning füüsikaliste näitajate mõõtmised algasid poole sajandi eest 1960. aastatel. Primaarproduktsiooni mõõtmistega tehti algust 1982. aastal, kuid kogutud andmeridades esineb kahjuks mitmeid “auke”. Võrtsjärve süsinikubilansi koostamiseks alustati 2008. aastal süsinikuühendite mõõtmisi järve suuremates sissevooludes ning väljavoolus. Tänu Euroopa Liidu toetusfondidele ja riiklikult sihtfinantseeritavale teadusteemale soetati 2009. ja 2010. aastal mitmeid uurimisseadmeid ning ka järvepoi, millede abil said Võrtsjärvel alguse pidevmõõtmised.

Töö eesmärgid:

Töö peamised eesmärgid võib koondada järgneva kuue põhipunkti alla:

1. Kasutades automaatseid tiheda sagedusega mõõtmisi seati eesmärgiks
    a. määratleda Võrtsjärve kui suure ja madala eutroofse parasvöötme järve metabolismitüüp ja roll regionaalses ja globaalses süsinikuringes (**I**);

    b. testida hüpoteesi, kas Võrtsjärve ainevahetuse tüüp muutub sesoonselt (**I**);

    c. analüüsida ökosüsteemi metabolismitüüpi määravate protsesside - koguproduktsiooni (GPP), hingamise (R) ja puhasproduktsiooni (NEP) hooajalisi trende ja neid mõjutavaid keskkonnategureid (**I**).

2. Anda ülevaade Võrtsjärve primaarproduktsiooni pikaajalistest muutustest ning täita modelleerimise abil lüngad andmestikus (nii puuduolevate kuude kui aastate osas). Saadud tulemused on oluliseks aluseks Võrtsjärve süsinikubilansi hindamisel ja edaspidistes metabolismiuuringutes (**II**).
3. Võrtsjärve sisse- ja väljavooludest mõõdetud lahustunud anorgaanilise süsiniku (DIC), kogu- (TOC) ja lahustunud orgaanilise süsiniku (DOC) ning lämmastiku, fosfori ja räni voogude alusel vastata küsimustele (**III**):
    a. Millised on järve sisenevad ainete koormused?

    b. Milliseid ühendeid järv akumuleerib ja milliseid vabastab?

    c. Kas erinevate ainete voogudes esineb sesoonseid erinevusi?

4. Testida hüpoteesi, kas suured ja madalad järved suudavad vähem toiteaineid kinni pidada kui väikesed ja sügavad järved, mille suhteline sügavus on suurem (**IV**).
5. Hinnata fosfori kinnipidamise erinevusi morfomeetriliselt erinevates järvedes (**IV**).
6. Selgitada järve suhtelise sügavuse mõju fosfori kinnipidamise võimele (**IV**).

Peamised tulemused:

1. Võrtsjärve metabolismitüüp muutub kaks korda aastas. Autotroofne periood algab varakevadel kohe peale jääminekut ning kestab kuni augusti keskpaiga või septembrini, seejärel muutub järv kuni varakevadeni heterotroofseks. Võrtsjärve koguproduktsioon on hingamisega ligikaudu võrdne või ületab seda vaid veidi, mistõttu järv ei toimi olulise CO_2 emiteerijana. (**I**).

2. Võrtsjärve ökosüsteemi hingamise tipp kujuneb välja umbes kaks nädalat peale suurima primaarproduktsiooni perioodi. Hingamiskiiruse tõusu põhjustavad suurte niitjate, zooplanktoni toiduks kõlbmatute sinivetikate domineerimine biomassis ning veetaseme alaneminsega kaasnev setete resuspensioon, mis suurendab aeroobsete bakterite aktiivsust (**I**).

3. Temperatuuri tõus intensiivistab hingamist rohkem kui fotosünteesi, mistõttu võib oletada, et kliima soojenemisel võib Võrtsjärve metabolismitüüp nihkuda heterotroofsuse suunas (**I**).

4. 41 järve võrdluses ei olnud Võrtsjärve metabolismināitajad erandlikud. Tehtud võrdlusanalüüs kinnitas eelnevate uuringute tulemusi selles osas, et nii primaarproduktsioon kui ka hingamine vähenevad järve sügavuse tõustes. Lisaks näitas meie analüüs, et suurematel järvedel on kalduvus olla autotroofsema metabolismiga (**I**).

5. Pikaajaliste primaarproduktsiooni (PP) mõõtmise tulemuste alusel seob Võrtsjärv keskmiselt 208 g C m^{-2} aastas. Võrtsjärv paikneb laiuskraadidel, kus valguse jõudmine vette limiteerib primaarproduktsiooni rohkem kui toiteainete kättesaadavus. See selgitab ka varjulembeste sinivetikaliikide (*Limnothrix*) esinemist Võrtsjärves (**II**).

6. Võrtsjärve jaoks kohaldatud poolempiiriline primaar-produktsiooni mudel, mis põhineb pealelangeva kiirguse, klorofüll a (Chl *a*) kontsentratsiooni ja valguse nõrgenemise koefitsiendil, võimaldab usaldusväärselt jäljendada muutuseid PP andmeridades (**II**).

7. Modelleeritud PP väärtustel ilmnes pikaajaline kasvutrend (mis tulenes Chl *a* kontsentratsiooni kasvust järves), mida ei toetanud järves mõõdetud PP väärtused. Vastuolu on ilmselt tingitud valgustingimuste pikaajalisest halvenemisest huumusainete hulga suurenemise tõttu, mida mudel ei suuda arvestada. Chl *a* kontsentratsiooni tõus on fütoplanktoni kohastumuslik reaktsioon, et halvenenud valgustingimustes säilitada fotosünteesi taset (**II**).

8. Võrtsjärv akumuleerib toiteaineid (lämmastik, fosfor, räni) hoolimata sellest, kas tema veebilanss on negatiivne või positiivne. Kui järv "kogub" vett, akumuleeritakse ka süsinikuühendeid, kuid negatiivse veebilansiga aastatel järv lekitab süsinikku (**III**).

9. Madalaveelistel suve- ja talveperioodidel on järve sisse ja sealt välja voolavate toiteainete ja süsinikuühendite koguste erinevused väiksemad kui veerohketel kevad- ja sügisperioodidel (**III**).

10. 54 maailma erineva kliimapiirkonna järve ja veehoidla analüüs näitas, et fosforipeetus suures ja madalas Võrtsjärves (28%) on tunduvalt väiksem, kui ülejäänud analüüsitud veekogudes keskmiselt (46%) (**IV**).

ACKNOWLEDGEMENTS

I am very grateful to my excellent supervisor Tiina Nõges, whose competence, expertise and ideas have inspired and guided me through the years of study. Dear Tiina, without your support, help and belief in me would not exists this work, those articles, projects and much much more what we have today. Tiina and Peeter you have been much more than just supervisors and co-workers to me – you are my best friends!

I want to give my warmest thanks to all my children (Johannes-Osvald, Eleonor and Birgit) who were very patient when I locked myself into my office and wasn't able to play with them. Special thanks to my wife Elen for her patience and support which helped me to work at home and gave me lots of motivation for writing this thesis.

My sincerest thanks will go to Helen Tammert, who encouraged me to start with my doctoral studies and have always offered constant support, even when she hadn't free time for herself.

I wish to express my sincere thanks to my co-authors of all papers. My special thanks will go to Peeter Nõges, who spent a lot of his valuable time with one of my paper and studied with me at the same time.

I want to thank my first two supervisors Arvo Tuvikene and Ain Järvalt who leaded me into the world of science.

I wish to acknowledge the Centre for Limnology for providing space and equipment when it was needed. I am grateful to the people in our Institute, in Centre for Limnology and other co-workers (Kaire Toming, Helen Tammert, Lea Tuvikene, Kersti Kangro, Helen Agasild, Anu Kisand, Alvi Rõigas, Helgi Arst, Sirje Vilbaste, Kai Piirsoo, Jüri Zirk, Ilmar Tõnno, Arvo Tuvikene, Ain Järvalt, Toomas Kõiv, Tõnu Feldmann, Priit Zingel, Rene Freiberg and many many others) who have never refused to help me with a good advice and who found free time and opportunity to spent the pleasant time together.

I am deeply grateful to my mother, my sisters and brothers – thank you for your support and love.

I would like to express my gratitude to the people who have or will participate in the projects of GLEON, NETLAKE and VeeOBS – you have given me the inspiration and knowledge to continue in the field of science.

This study was financed by Estonian target funding project SF0170011s08 of the Estonian Ministry of Education and Research, by grants 5594, 7156, 7600, 8729 and 9142 from Estonian Science Foundation, by 7th EU Framework Programme, Theme 6 (Environment including Climate Change) project REFRESH (Adaptive strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems, Contract No.: 244121), and by the Doctoral School of Earth Sciences and Ecology created under the auspice of European Social Fund.

I

ORIGINAL PUBLICATIONS

Laas, A; Nõges, P.; Kõiv, T. and T. Nõges, 2012.
HIGH FREQUENCY METABOLISM STUDY IN A LARGE
AND SHALLOW TEMPERATE LAKE REVEALS
SEASONAL SWITCHING BETWEEN NET
AUTOTROPHY AND NET HETEROTROPHY.
Hydrobiologia 694(1), 57-74.

Hydrobiologia (2012) 694:57–74
DOI 10.1007/s10750-012-1131-z

PRIMARY RESEARCH PAPER

High-frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy

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Received: 1 December 2011 / Revised: 11 April 2012 / Accepted: 24 April 2012 / Published online: 17 May 2012

Abstract Respiratory CO_2 release from inland waters is a major process in the global carbon cycle, retaining more than half of the carbon flux from terrestrial sources that otherwise would reach the sea. The strongly lake type-specific balance between primary production and respiration determines whether a lake acts regionally as a net sink or source of CO_2. This study presents two-year (2009, 2010) results of high-frequency metabolism measurements in the large and shallow polymictic eutrophic Lake Võrtsjärv (area 270 km^2; mean depth 2.8 m). We estimated the net ecosystem production (NEP), community respiration (R) and gross primary production (GPP) from continuous measurements of oxygen, irradiance, wind and water temperature. A sinusoidal model fitted to the calculated metabolic rates showed the prevalence of net autotrophy (mean GPP:$R > 1$) from early spring until August/September, whereas during the rest of the year heterotrophy (mean GPP:$R < 1$) prevailed, characterizing the lake as CO_2 neutral on an annual basis. Community respiration lagged behind GPP by approximately 2 weeks, which could be explained by the bulk of the phytoplankton biomass accounted for by filamentous cyanobacteria that are considered mostly inedible to zooplankton, and the seasonally increasing role of sediment resuspension. In the warmer year 2010, the seasonal peaks of GPP, R and NEP were synchronously shifted nearly 1 month earlier compared with 2009. The strong stimulating effect of temperature on both GPP and R and its negative effect on NEP revealed by the multiple regression analysis suggests increasing metabolic rates and increasing heterotrophy in this lake type in a warmer climate.

Keywords Lake metabolism · Sinusoid fitting · Seasonal shift · Temperature effect · Timing of peaks

Introduction

From the estimated 1.9 Pg of carbon that inland waters receive annually from the terrestrial landscape, less than half (0.9 Pg year^{-1}) is delivered to the oceans, whereas respiratory CO_2 release constitutes the major part of this decrease (Cole et al., 2007). Primary production and respiration are the major metabolic pathways by which organic matter is produced and decomposed. Gross primary production (GPP) is the gross fixation of inorganic C by photosynthesis. Community respiration (R) is the remineralization of organic C to CO_2 by all organisms of the ecosystem. The net ecosystem production (NEP), i.e. the

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Handling editor: David Philip Hamilton

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difference between GPP and community respiration, (NEP = GPP − R), can be used to define the metabolic type (net auto- or heterotrophic) of a lake.

There are several techniques for measuring the metabolic balance of natural waters. For lakes, the most common method is based on the measurements of the temporal and spatial variability of dissolved O_2 and/or CO_2 (Robertson et al., 1993; Cole et al., 2000; Hanson et al., 2003; López-Archilla et al., 2004; Depew et al., 2006; Staehr & Sand-Jensen, 2007; Coloso et al., 2008; Effler et al., 2008, Tsai et al., 2008; Staehr et al., 2010a, b). High-frequency (≥ 1 h^{-1}) O_2 measurements enable calculating the NEP (the difference between GPP and R) during the day and R during the night, thus yielding all the three components necessary for the full budget. The probe method provides a useful alternative to more traditional methods of studying metabolism based on discrete samples. As shown by Staehr et al. (2012b), continuous measurements overcome many of the limitations of discrete samples and make it possible to measure metabolism in a wide variety of systems.

Lakes with high total phosphorus (TP) concentrations and low dissolved organic carbon (DOC) concentrations tend to be autotrophic (NEP > 0), whereas lakes with low TP and high DOC tend to be heterotrophic (NEP < 0) (Hanson et al., 2003). Cole et al. (2000) showed that a lake has a net heterotrophic C balance at mean seasonal Chl a concentration below 20 mg m^{-2} and at GPP less than 1 g O_2 m^{-3} day^{-1} or 140 mmol C m^{-2} day^{-1} or, assuming a 200-day ice-free season, GPP below 330 g C m^{-2} year^{-1}. Brown-coloured lakes with increased humic matter or tannin content, often associated with forested or peaty catchments, should display stronger net heterotrophy than clear-water lakes (del Giorgio et al., 1999; Sobek et al., 2005).

Lakes become net heterotrophic only because they receive large allochthonous inputs of organic C which is respired in the lake. A review by Andersson & Sobek (2006) showed that switching from net autotrophy to net heterotrophy occurred at DOC concentrations higher than 4–6 mg l^{-1}, and del Giorgio et al. (1997) found that bacterial respiration (BR) tended to exceed NEP in aquatic systems with NEP below 100 mg C l^{-1} day^{-1}. Net autotrophic systems produce significantly more organic material than they degrade. The excess organic material may either be exported to adjacent systems and/or accumulated within the system either in the sediment or as dissolved organic matter in the water (Staehr et al., 2010b).

The 3,100-km^2 catchment area of the large but very shallow Lake Võrtsjärv makes up about 7% of Estonian territory and, thus, may contribute significantly to the Estonian natural CO_2 budget. Võrtsjärv is strongly impacted by the inflow of DOM and nutrients because of its large catchment area (A) relative to lake volume (V) (Nõges & Järvet, 1998). The A/V ratio of Võrtsjärv (4.1 m^{-1} at mean water level) is larger than that of the other well-studied large and shallow lakes, such as Peipsi (1.9 m^{-1}) or Balaton (2.7 m^{-1}), and much larger than in the large and deep lakes such as Ontario (0.046 m^{-1}), Ladoga (0.08 m^{-1}), Onega (0.18 m^{-1}) and Vänern (0.27 m^{-1}) (ILEC World Lake Database). A specific feature of Võrtsjärv is the large natural climate-related variability of water level with a long-term absolute amplitude exceeding 3 m, which causes a more than 200% change in the water volume (Nõges et al., 2003). Our earlier studies have shown that the fluctuating water level in Võrtsjärv resulting from meteorological forcing and major climate trends in the Northern Hemisphere, has a strong impact on the whole ecosystem (Nõges, 2004; Järvalt et al., 2005; Feldmann & Nõges, 2007; Zingel et al., 2007). According to Toming et al. (2009), climate-related hydrological changes cause large variation also in the absorption by coloured dissolved organic matter (CDOM) in Võrtsjärv (3.96–15.7 m^{-1}) that corresponds to DOC concentrations from 7 to 28 mg l^{-1}. Based on high DOC values, a net heterotrophic metabolism could be assumed, while rather high chlorophyll a (average 24 mg m^{-3}) and TP (average 54 mg m^{-3}) concentrations (Nõges et al., 2007) might otherwise be expected to support net autotrophy. Hence, Võrtsjärv, like many other northern temperate lakes with mid-range TP and DOC concentrations (Hanson et al., 2003), cannot be clearly classified into one of the two metabolic lake types. Because of the inconsistency between indicators of net heterotrophy and net autotrophy in the lake and its large climate-related hydrological and thermal variabilities caused by pronounced seasonality of the region, we hypothesized that the metabolic type of Lake Võrtsjärv might flip between net auto- and heterotrophy for shorter or longer periods. Earlier studies of carbon metabolism in lakes (e.g. Maier & Swain, 1978; Oxburgh et al., 1991; Sobek et al., 2006) have mostly been based on annual flux estimates, whereas seasonal studies (e.g. Staehr & Sand-Jensen, 2007; Staehr et al., 2010b) have been performed in stratified lakes.

Using the data of high-frequency automatic monitoring, this article aims to (i) reveal the metabolic type of Lake Võrtsjärv as a representative of large, shallow, unstratified, eutrophic temperate lakes, and to determine its role in the regional and global carbon budgets; (ii) test the hypothesis of switching of the lake between net autotrophy and net heterotrophy; and (iii) analyse the seasonal trends of GPP, *R* and NEP and their environmental determinants that can improve our understanding of how future climatic conditions may impact the biological, chemical and physical stabilities of lake ecosystems.

Materials and methods

Study site

Lake Võrtsjärv (58°16′N, 26°02′E) is located in Central Estonia (Fig. 1). Võrtsjärv is a large (270 km^2) shallow polymictic lake with a maximum depth of 6 m and a mean depth of 2.8 m, which, according to the classification by Lewis (1983) belongs to continuous rather than discontinuous cold polymictic lakes. Measurements of water currents carried out in 1995–1996 at 2-m depth at four stations in the lake (Kivimaa et al., 1998) demonstrated that at moderate mean wind velocities (average 2.9 m s^{-1}, maximum 13.2 m s^{-1}), the average current velocities ranged from 2.7 to 8.6 cm s^{-1} at various stations with peak values exceeding 200 cm s^{-1}. Such strong wind induced currents mix the water horizontally resulting in a relatively homogenous water environment in the lake proper with an exception of the narrow, river-like southern end strongly affected by the main inflow. Võrtsjärv does not stratify—the mean difference between the surface (0.5 m) and bottom (2.5 m) temperatures over the ice-free period is approximately 0.1°C with exceptional short-term maxima reaching 4°C on single calm days. We considered the effect of these single events negligible on average gas exchange rates at monthly time scales. The lake is eutrophic, characterized by the following mean concentrations: TP 54 µg l^{-1}, total nitrogen (TN) 1.6 mg l^{-1} and Chl *a* 24 µg l^{-1} (Tuvikene et al., 2004; Nõges et al., 2007). Owing to the influence of resuspended sediments, the Secchi depth is typically less than 1 m during the ice-free period. According to Reinart & Nõges (2004), the water colour has an average value of 60 mg Pt l^{-1}. Water colour has slight seasonal changes but there may be large differences between years. The lake is ice-covered for more than 4 months (average 135 days) of the year. The unregulated water level, which has an annual mean amplitude of 1.4 m, the absolute range of 3.1 m, has proven by far the most influential factor in the lake. By altering the sediment resuspension rate, the variable water level affects the light climate (Nõges & Järvet, 1995), nutrient availability (Nõges & Nõges, 1999) and phytoplankton abundance and composition (Nõges et al., 2003) both seasonally and in the long term. The water level reaches its seasonal maximum usually in April or May and declines steadily until the seasonal minimum, which is typically in September.

Within the 50 km^2 area (19% of the lake area) covered by aquatic macrophytes, 35 km^2 is accounted for by submerged species, 12 km^2 by emergents and 3 km^2 by floating-leaved macrophytes (Feldmann & Mäemets, 2004). Owing to high turbidity and strong wave-induced turbulence, the submerged vegetation dominated by *Myriophyllum spicatum* L. is mostly sparse.

According to Nõges et al. (2011), the mean daily integrated primary production (PP) of phytoplankton measured by the ^{14}C method is 558 mg C m^{-2} day^{-1} with monthly means ranging from about 25 mg C m^{-2} day^{-1} in December and January to nearly 1,300 mg C m^{-2} day^{-1} in June. By the mean annual PP (208 ± 27 g C m^{-2} year^{-1} in 1982–2009), Võrtsjärv is located rather close to the nutrient-saturated production boundary determined by latitude where light limitation has the leading role. The phytoplankton of the lake is dominated by two species of slowly growing highly shade tolerant cyanobacteria from the genus *Limnothrix* (Nõges et al., 2011). Being virtually inedible for the small-sized grazers community (Agasild et al., 2007), these species steadily increase their biomass over the annual cycle and reach the maximum shortly before ice formation.

High-frequency data

Data were collected from 30 April to 15 July in 2009 and from 20 April to 28 October in 2010 near the lake's deepest point. From 29 July to 11 August 2010, there are no data because of malfunctioning of the buoy.

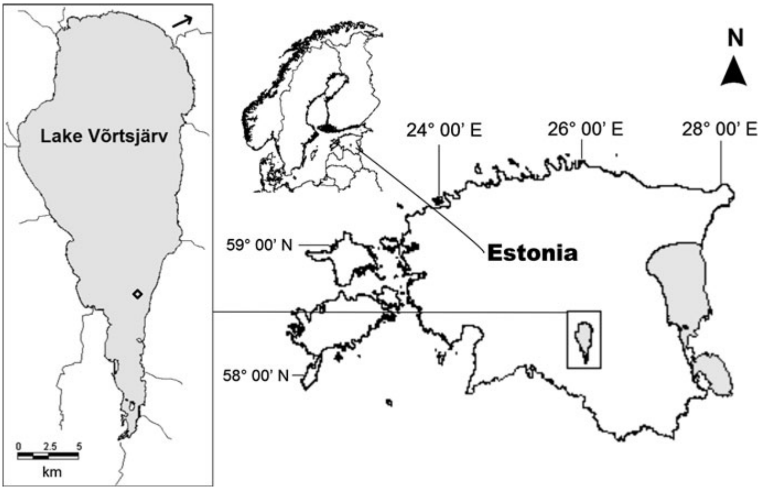


Fig. 1 Location map of Lake Võrtsjärv and the sampling station

The 3.1-m-deep measurement station was located at the long-term monitoring site of the lake, which has been considered generally representative of lake-wide conditions for a number of variables, such as phytoplankton abundance and composition (Nõges et al., 2004), bacterioplankton numbers (Tammert & Kisand, 2004), and DOC concentrations (Toming et al., 2009). In 2009, dissolved oxygen (DO) concentration, oxygen saturation and water temperature were measured using YSI model 6600 V2-4 multiparameter sonde fitted with a ROX optical oxygen sensor (model 6150) and temperature-conductivity sensor. The oxygen sensor was calibrated in air, with a correction for barometric pressure. Deployments lasted from 12 to 21 days, after which the probe was brought back to the lab for cleaning and prepared for the next deployment. All measurements were done at 1-m depth with 15 min intervals. For metabolism calculations, all data were hourly averaged.

In 2009, photosynthetically active radiation (PAR), wind speed and air temperature were measured by Estonian Meteorological and Hydrological Institute (EMHI) at Tõravere weather station located at a distance of 20 km from the lake. PAR was measured at 1-min intervals using a Li-Cor 190SA quantum sensor and converted to hourly sums. Wind speed was also measured every minute, and the hourly averages were used for calculations.

In 2010, a buoy was deployed in April at the measurement site, which recorded DO, water temperature and conductivity at 1-m depth. PAR, air temperature and wind speed were measured at 2 m above the lake, using a Vaisala Weather Transmitter WXT520 and a Li-Cor model 190SA quantum sensor for PAR. Electronic control and data collection were managed by a Campbell Scientific CR1000 data logger. DO and water temperature were measured in the same way as in 2009. To examine possible temperature stratification, two HOBO UA-001-08 Pendant water temperature loggers at 1.5- and 2.5-m depths were used in addition to YSI multisondes in both years.

We used regular monthly monitoring data of TP (standard ISO 15681-2), TN (standard EVS-EN ISO 11905-1) and chlorophyll *a* (Chl *a*) concentrations (96% ethanol extract analysed spectrophotometrically and calculated according to Lorenzen, 1967) to assess their effect on lake metabolism.

The water level was measured daily at the outlet of the lake by EMHI and the absolute values ($\mathrm{WL_{abs}}$) were converted into the mean depth of the lake (Z_{avg}, m) using the lake-specific bathymetric relationship (Nõges & Järvet, 1995):

$$Z_{\mathrm{avg}} = 0.71\ \mathrm{WL_{abs}} - 22.29 \quad \left(R^2 = 0.98\right) \tag{1}$$

The metabolism model

The model described by Cole et al. (2000) was used for calculating NEP, *R* and GPP from diel DO curves. NEP was calculated as

$$\mathrm{NEP_{hr}} = \Delta\mathrm{DO} - D/Z_{\mathrm{mix}}, \tag{2}$$

where ΔDO is the change in DO concentration over a 1-h interval, D is the diffusive exchange with the atmosphere in this period, and Z_{mix} is the mixing depth.

Diffusion was calculated as

$$D = k(\mathrm{DO} - \mathrm{DO_{sat}}), \tag{3}$$

where $\mathrm{DO_{sat}}$ is the concentration of oxygen in equilibrium with the atmosphere, and k is the coefficient of gas exchange of oxygen at a given temperature. The coefficient k was computed from the Schmidt number (Sc) and the gas piston velocity corresponding to a Schmidt number of 600 (k600). The Schmidt number is dependent on water temperature and was calculated at each time step using the DO-specific equation of Wanninkhof (1992). The k600 was estimated according to Cole & Caraco (1998) as a function of wind speed at 10 m above the lake surface (U):

$$\mathrm{k600}\ \left(\mathrm{cm\ h^{-1}}\right) = 2.07 + 0.215\ U^{1.7} \tag{4}$$

Assuming a neutrally stable boundary layer, wind speed at 10 m above the lake surface was calculated from our measurements at 2-m height using the relationship given by Smith (1985). During darkness, the change in gas concentration is assumed to be due to R and exchange with the atmosphere (D). During daylight hours, changes in gas concentrations are assumed to be due to R, D and GPP.

Our methods differed from those used by Cole et al. (2000) by lower sampling frequencies and by replacing the mixing depth by the daily mean depth in the nonstratified Lake Võrtsjärv. We calculated R for each 60-min interval from dusk to dawn. R_{night} was calculated as

$$R_{\mathrm{night}} = \Delta\mathrm{DO} - D \tag{5}$$

In line with the literature, we assumed that hourly daytime R equalled to hourly nighttime R (Carignan et al., 2000; Cole et al., 2000; Uehlinger, 2000; Hanson et al., 2003; Staehr & Sand-Jensen, 2007; Staehr et al., 2010a, b) and calculated R_{daylight} by multiplying hourly R by the number of hours during which PAR was >10 μmol $\mathrm{m^{-2}\ s^{-1}}$. Daytime NEP ($\mathrm{NEP_{daylight}}$) was calculated as mean hourly NEP during daylight multiplied by the number of hours during which PAR was >10 μmol $\mathrm{m^{-2}\ s^{-1}}$. GPP was calculated as

$$\mathrm{GPP} = \mathrm{NEP_{daylight}} + R_{\mathrm{daylight}} \tag{6}$$

Daily NEP was calculated as the averaged hourly NEP rate over the day multiplied by 24 h.

$$\mathrm{NEP} = \mathrm{mean\ NEP_{hr}} * 24 \tag{7}$$

This provides an estimate of daily NEP which is independent of errors in daily GPP and R, and which is calculated directly from changes in measured DO.

Volumetric values of GPP, R and NEP were multiplied by the daily Z_{avg} of the lake to get the areal estimates.

In order to compare the oxygen-based estimates of GPP with the ^{14}C primary production results, the former were converted to carbon units assuming that 1 mol of carbon dioxide is assimilated for every 1.25 mol of oxygen liberated (Ryther, 1956).

Statistical analysis

Relationships between metabolic rates and physical and environmental factors were evaluated using the basic statistics and multiple regression modules of Statistica 8.0 (StatSoft, Inc., 1984–2007). Frequency histograms of the variables showed that the GPP, R and the wind speed (U) were positively skewed, and so, before to statistical modelling, we $\log_{10}$ transformed these variables to reduce the potential influence of the minority of relatively high values in the dataset.

As the plot of the monthly average results (Fig. 2) suggested that the metabolic variables follow temporally shifted sinusoidal patterns, we fitted a sinusoidal curve to these data with the aim at quantifying the phase shift between the series of GPP, R and NEP, and to compare it with the environmental sinusoidal variables—PAR and water temperature. The best fit was found by the total least squares method modifying iteratively the sinusoidal equation parameters using the Solver tool of Microsoft Excel. The latter uses the Generalized Reduced Gradient nonlinear optimization code developed by Lasdon et al. (1978). In time series analysis, a sinusoidal model to approximate a sequence y_i can be written as

$$y_i = A\sin(\omega x_i - \varphi) + C + E_i \tag{8}$$

where A is the amplitude for the sinusoid, C is constant defining the mean level, ω is the angular frequency in radians per unit of time, x_i is the time

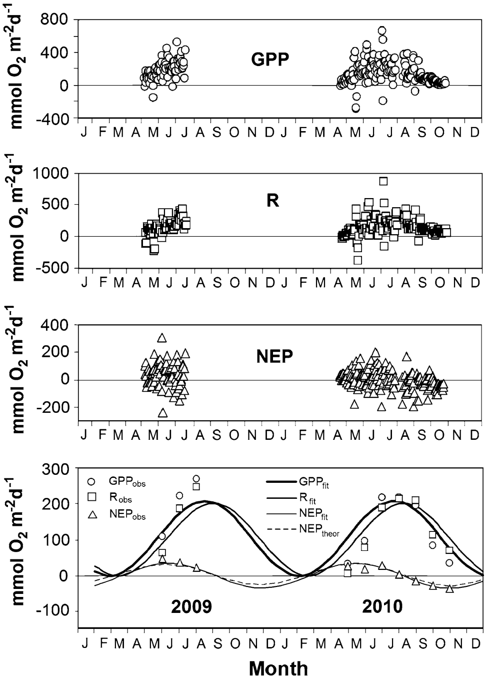


Fig. 2 Calculated daily values of GPP, community respiration (*R*), NEP in Võrtsjärv (*three upper panels*) and their monthly mean values with fitted sinusoids indicated with a subscript 'fit' (*lower panel*). The curve $\mathrm{NEP}_{\mathrm{theor}}$ shows the difference between $\mathrm{GPP}_{\mathrm{fit}}$ and R_{fit}

step, φ is the phase shift in radians and E_i is the error sequence in approximating the sequence y_i by the model. For each series, we took the half range between maximum and minimum values as the starting value for the amplitude, the mean value for the constant and $2\pi/365$ for the frequency. For both years, we calculated the phase shifts of the variables φ, and the dates of the model peak values (located at $\varphi + \pi/2$ rad). The fit was validated by the strength and significance of the correlation between observed and modelled series.

Results

The hydrological background

The water level followed a typical pattern in both years changing considerably the mean depth of the lake (Fig. 3a). During the study period in 2009, the water level dropped by 57 cm, corresponding to 42 cm or 15% decrease in the average depth of the lake. In 2010, the 1.15-m decline in the water level corresponded to 85 cm or 30% of the average depth.

Lake metabolism

GPP and *R* showed a large day-to-day variability with GPP mostly exceeding *R* in spring and early summer, but remaining smaller than *R* in autumn (Table 1). The average of all GPP measurements exceeded slightly (but not significantly) that of *R*, but as the data were seasonally unbalanced (more measurements in spring), no conclusion on the metabolic type could be drawn on this basis. Owing to the difference in the measurement periods in 2 years, the inter-annual differences cannot be assessed either, and Table 1 illustrates only the ranges of the values measured. Days of net heterotrophy (NEP < 0) occurred during all months, but were most frequent during late summer and autumn (Table 1; Fig. 2).

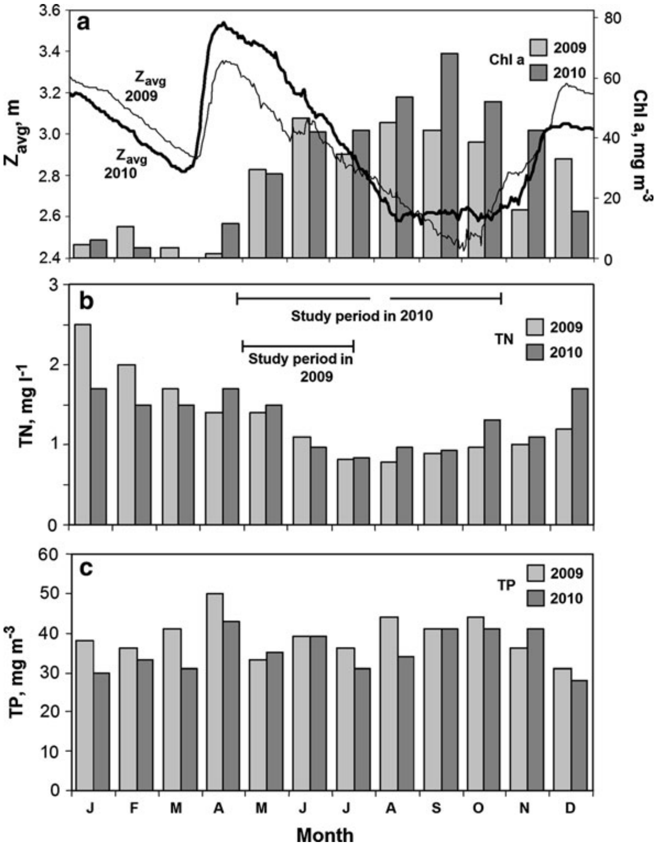
The log-normalized values of daily GPP and *R* were positively correlated ($r = 0.61$, $P < 0.0001$). The coefficient of correlation between untransformed GPP and *R* was 0.80. NEP was weakly positively correlated with log GPP ($r = 0.44$, $P < 0.0001$) and negatively with log *R* ($r = -0.24$, $P < 0.0001$).

The monthly averages of GPP, *R* and NEP revealed a seasonal pattern well described by a sinusoidal fit (Fig. 2; Table 2). Given the good fit of the sinusoidal model to the metabolic variables (R^2 0.84 for GPP, 0.87 for *R* and 0.93 for NEP), we analysed some of the model parameters to have an insight to the seasonality and to compare it with the sinusoidal fits of irradiance and water temperature.

Among the simulated variables, NEP reached its seasonal peak in May, several weeks before the summer solstice (Fig. 4). GPP peaked in July or August, at approximately the same time with water temperature and 3–7 weeks after the peak of solar irradiance. The peak of community respiration was the last among the three and was reached in August, 1–4 weeks after the peak in water temperature.

The fitting curve for solar irradiance peaked in both years on June 20, practically at the summer solstice. The curve fit for water temperature peaked 31 or 32 days later. Despite the markedly higher water

Fig. 3 Changes in the average depth of Võrtsjärv and chlorophyll *a* concentration (**a**), TN (**b**) and TP concentrations (**c**) over 2 years, 2009 and 2010, partly covered by high-frequency measurements of lake metabolism



temperatures in 2010 compared with 2009 (up to 8°C in May and 4–6°C in July–August, see Fig. 5), the timing of the peak according of the fitting curve showed little change. Temperature differences between surface (0.5–1 m) and bottom layers (2.5 m) showed little evidence of stratification. During the ice-free period in 2009, the mean daily temperature difference exceeded 1°C on 6 days and 2°C on two non-consecutive days. In the warmer year of 2010, there were 10 days in which the daily mean vertical temperature difference exceeded 1°C, but only 1 day with a more than 2°C difference.

The timing of the simulated seasonal peaks of all the three metabolic variables shifted about 25 days earlier in the warmer 2010 compared with 2009 and showed no obvious relationship to the timing of the Q and T peaks.

The values of the constant *C* of the sinusoids characterising the mean levels of the metabolic parameters (in mmol O_2 m^{-2} day^{-1}) were 104 for GPP, 100 for *R* and 0 for NEP, suggesting a balance (based on NEP) or a slight net autotrophy (based on GPP and *R*) of the lake on an annual scale. Converted to carbon units, the annual GPP estimate equalled 363 g C m^{-2} $year^{-1}$. The dynamics of NEP was characterized by an autotrophic period lasting from early spring until August or September and a heterotrophic period for the rest of the year. The theoretical curve for NEP (Fig. 2) calculated as the difference between the curves fits to GPP and *R*, matched well with the curve fitting the monthly NEP values. As the amplitudes of the GPP and *R* curves were almost equal, the sinusoidal behaviour of NEP was caused predominantly by the phase shift between GPP and

R (without this phase shift the NEP curve would become flat).

Regulation of ecosystem metabolism

All metabolic variables showed positive relationships with solar irradiance and water temperature, and negative relationships with wind speed (Fig. 6). GPP and NEP declined with seasonally declining water levels whereas R increased.

The monthly measured concentrations of TN and TP changed within a rather small range but that of Chl *a* almost tripled over the study period in 2010 (Fig. 3). Owing to the small number of measurements, these variables were not included in the statistical analysis.

The best multiple regression models based on the frequently measured variables (PAR, T_w and U) and daily measured Z_{avg} explained 67% of the variability in log GPP, 36% in log R and 28% in NEP (Table 3). Increasing water temperature had a strong positive effects on GPP and R and a negative effect on NEP. GPP and NEP increased with increasing PAR, but the latter was not included in the best model describing respiration. Wind had negative effects on both GPP and NEP. Although having a negative correlation also with NEP, wind speed was not included in the best model for NEP. The decreasing average depth of the lake increased R and decreased NEP.

Discussion

The published mean daily GPP and R values for lakes range over more than five orders of magnitude (Table 4; Fig. 7), but are strongly correlated ($r = 0.94$; $P < 0.01$) and thus line up rather nicely along the 1:1 proportionality line. Among these 41 lakes located almost entirely within the temperate zone and characterized by a median GPP of 30 mmol O_2 m^{-3} day^{-1} and median R of 39 mmol O_2 m^{-3} day^{-1}, Lake Võrtsjärv occupies a mid position among the lakes staying very close to the proportionality line. Compared to the long-term primary productivity estimate of 208 g C m^{-2} $year^{-1}$ in Võrtsjärv measured by the ^{14}C technique (Nõges et al., 2011), the annual GPP estimate based on high-frequency metabolism measurements (363 g C m^{-2} $year^{-1}$) was considerably higher. This difference can be explained by the fact that ^{14}C productivities lie

Table 1 Seasonal means (standard deviation) of meteorological, limnological and metabolic features of Lake Võrtsjärv

Parameters	Spring		Summer		Autumn	Entire study period
	01.05.2009–30.05.2009	20.04.2010–30.05.2010	01.06.2009–15.07.2009	01.06.2010–31.08.2010	01.09.2010–28.10.2010	
Wind speed (m s^{-1})	2.44 (0.84)	3.58 (1.83)	2.22 (0.98)	3.25 (1.9)	4.85 (2.63)	3.38 (2.07)
Air temperature (°C)	11.8 (3.0)	11.5 (5.23)	14.9 (3.65)	18.7 (4.43)	8.92 (3.71)	13.8 (5.6)
Water temperature (°C)	13.2 (1.65)	12.1 (4.61)	17.6 (2.74)	20.7 (3.83)	9.74 (4.27)	15.3 (5.73)
PAR (μmol m^{-2} s^{-1})	433 (155)	375 (152)	415 (150)	415 (168)	169 (87.4)	356 (177)
GPP (mmol O_2 m^{-3} day^{-1})	34.70 (26.86)	23.78 (37.67)	77.50 (38.03)	71.85 (44.06)	22.65 (21.44)	49.84 (43.26)
R (mmol O_2 m^{-3} day^{-1})	19.94 (32.46)	17.73 (36.87)	69.01 (30.47)	69.23 (47.12)	35.96 (20.0)	47.53 (42.39)
NEP (mmol O_2 m^{-3} day^{-1})	14.76 (21.10)	6.05 (17.22)	9.86 (33.85)	2.62 (24.56)	−13.31 (19.79)	2.55 (25.70)
TP (μg l^{-1})	36.0 (4.24)	39.0 (5.66)	40.0 (5.66)	48.7 (18.9)	40.7 (0.58)	41.6 (10.1)
TN (mg l^{-1})	1.25 (0.21)	1.6 (0.14)	0.80 (0.08)	0.93 (0.08)	1.12 (0.25)	1.12 (0.31)
Chlorophyll *a* (mg m^{-3})	45.4 (17.0)	21.8 (12.7)	47.8 (7.91)	44.2 (6.90)	63.6 (8.43)	44.4 (13.1)

PAR photosynthetically active radiation; *GPP* gross primary production; *R* community respiration; *NEP* net ecosystem production

Table 2 Parameters of the sinusoids fitted to the monthly mean values of gross primary production (GPP_{fit}), community respiration (R_{fit}), net ecosystem production (NEP_{fit}), daily solar irradiance (Q_{fit}) and daily surface water temperature (T_{fit}) in Lake Võrtsjärv

Parameter	GPP_{fit}	R_{fit}	NEP_{fit}	Q_{fit}[a]	T_{fit}[b]
Constant, mean level *C*	104	100	0	16	7
Amplitude *A*	104	100	35	15	15
Angular velocity (ω, rad day^{-1})	0.0184	0.0183	0.0186	0.0172	0.0172
Phase (φ, rad)	−2.798	−3.520	−1.557	−1.365	−1.902
Date of modelled peak in 2009	02/08/09	17/08/09	29/05/09	20/06/09	22/07/09
Date of modelled peak in 2010	10/07/10	26/07/10	02/05/10	20/06/10	21/07/10
R^2 modelled-observed	0.843	0.865	0.934	0.696	0.878
Significance *P*	0.0002	0.0001	0.0000	0.0000	0.0000

R^2 and *P* characterize the goodness of fit to the observed values. Units for the constant and amplitude are mmol O_2 m^{-2} day^{-1} for the metabolic variables: MJ m^{-2} day^{-1} for Q_{fit}, and °C for T_{fit}

[a] Fit for maximum values, i.e. for full sunshine

[b] Only the positive part of the fit is meaningful

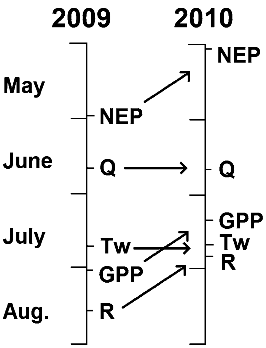


Fig. 4 Timing if the seasonal peaks of solar irradiance (*Q*), water temperature (T_w), GPP, community respiration (*R*), NEP in Võrtsjärv in 2009 and 2010 as derived from the fitting sinusoids parameters. The *arrows* help us to visualize the behaviour of the variables

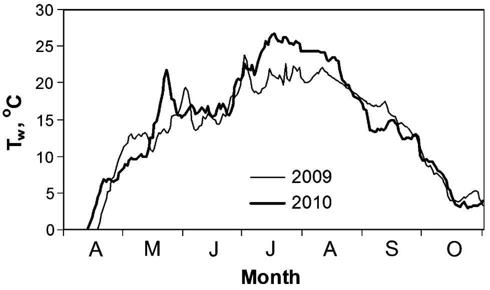


Fig. 5 Water temperature in Lake Võrtsjärv at 0.5–1-m depth during the ice-free periods of the study years

between NEP and GPP values, but are closer to NEP when long incubations are used and closer to GPP when short incubations are used and (Dring & Jewson, 1982; Bender et al., 1999).

The rather good proportionality of GPP and *R* shows that the main substrate for respiration in most lakes originates predominantly from primary production within the lake. Still there are deviations to both sides from the 1:1 line characterized by the GPP:*R* ratio ranging from 0.1 in Lake Hummingbird (MI, USA, Hanson et al., 2003) to 2.5 in Lake Michigan (MI, USA, Ogdahl et al., 2010). Although the GPP:*R* ratio is shown to be mostly a function of the lake trophic state (e.g. Cole et al., 2000; Hanson et al., 2003) and/or DOC loading (Andersson & Sobek, 2006), the analysis of published data shows that lake morphometry may also play an important role in determining lake metabolism. Among the 41 lakes, volumetric GPP and *R* decreased highly significantly with the increasing mean depth of lakes (Fig. 8). A similar regularity was described by Staehr et al. (2012a) in 25 Danish lakes, which the authors explained by the generally lower trophic state of deeper lakes. In Võrtsjärv, respiration increased with declining water levels also in the seasonal cycle, but GPP did not show any dependence on water depth (Fig. 6). Among Danish lakes, GPP and *R* decreased also with increasing lake area, but this result was not found in the set of lakes analysed by us. We found, however, highly significant positive relationships of GPP/*R* with lake area and volume (Fig. 8) showing that larger lakes tend to be more autotrophic. The

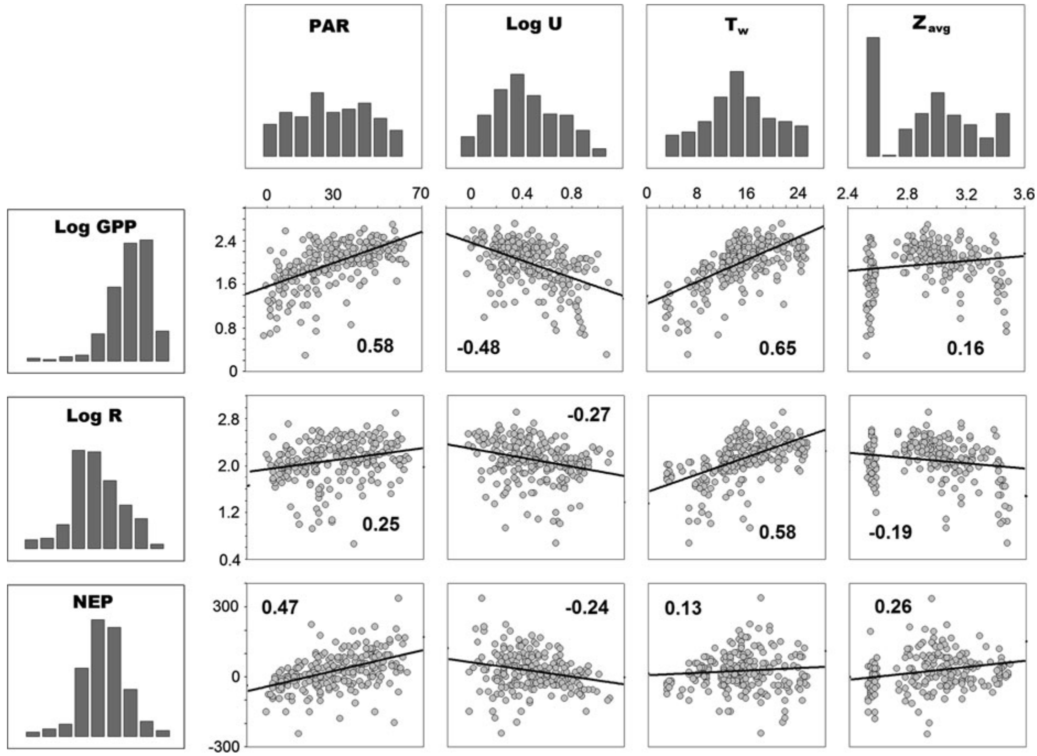


Fig. 6 Frequency distribution of variables and the correlation matrix relating metabolic variables GPP, R and NEP (all measured in mmol O_2 m^{-2} day^{-1}) with the environmental variables PAR (mol photon m^{-2} day^{-1}), U (m s^{-1}), T_w (°C) and Z_{avg} (m). *Straight lines* show linear fits and the numbers—Pearson correlation coefficients (r) of the relationships. All relationships are significant at $P < 0.01$

Table 3 Multiple regression of log GPP, log R and NEP as a function of water temperature (T_w), daily sum of PAR irradiance, logarithm of daily mean wind speed (log U), and mean lake depth (Z_{avg}) in Lake Võrtsjärv during the study periods in 2009 and 2010

Dependent variable	Parameter	R^2	Standardized regression coefficient	t	P
Log GPP	T_w	0.67	0.40	7.0	<0.0001
	PAR		0.24	4.1	<0.0001
	Log U		−0.21	−4.0	0.0001
Log R	T_w	0.36	0.57	10.8	<0.0001
	Z_{avg}		−0.15	−2.9	0.0044
NEP	PAR	0.28	0.53	8.4	<0.0001
	T_w		−0.24	−3.8	0.0002
	Log U		−0.17	−2.9	0.0036

The best model was selected with the stepwise procedure in Statistica 8.0 (StatSoft Inc., 1984–2007). Parameters are listed in order of decreasing importance, according to their t value

Table 4 Respiration (R) and GPP of some individual lakes in mmol O_2 m^{-3} day^{-1}

Lake name	State	Coordinate	Year of study	Area (ha)	Mean depth (m)	GPP	R	Authors
Yuan-Yang	Taiwan	24°35′N, 121°24′E	2004, 2005	3.6	1.5	0.02	0.06	Tsai et al. (2008)
Erie	USA	42°12′N, 81°12′W	2002	2,574,400	19	2.9	1.9	Depew et al. (2006)
Crampton	WI, USA	46°12′N, 89°28′W	2000	25.8	4.9	3.8	13.8	Hanson et al. (2003)
Michigan (near the Muskegon River inflow)	MI, USA	44°0′N, 87°0′W	2004, 2005	5,800,000	85	3.9	1.6	Ogdahl et al. (2010)
Müggelsee	Germany	52°26′N, 13°39′E	1994–1998	730	4.8	4.2	3.8	Gervais & Behrendt (2003)
Muskegon	MI, USA	43°13′N, 86°17′W	2004, 2005	1,700	7	4.6	3.1	Ogdahl et al. (2010)
Croche	QC, Canada	45°58′N, 74°01′W	2002–2003	19	5.1	5.9	3.8	Dubois et al. (2009)
Crystal	WI, USA	45°43′N, 89°25′W	2000	36.7	6.1	6.1	5.6	Hanson et al. (2003)
Trout	WI,USA	46°02′N, 89°40′W	2000	1090.9	14.9	7.3	7.4	Hanson et al. (2003)
Diamond	WI, USA	46°02′N, 89°42′W	2000	49.4	10.1	10.0	12.9	Hanson et al. (2003)
Ours	QC, Canada	45°58′N, 74°01′W	2002–2003	15	6.7	11.7	7.9	Dubois et al. (2009)
Big Muskellunge	WI, USA	46°01′N, 89°36′W	2000	396.3	7.92	11.8	20.0	Hanson et al. (2003)
Crampton	WI, USA	46°12′N, 89°28′W	2005	25.7	4.9	12.9	16.7	Coloso et al. (2008)
Hiawatha	WI, USA	45°54′N, 89°27′W	2000	14.6	~3.5	13.3	27.5	Hanson et al. (2003)
Hummingbird	MI, USA	46°14′N, 89°30′W	2000	0.8	~1.5	15.0	145.8	Hanson et al. (2003)
Paul	MI, USA	46°15′N, 89°30′W	1995–1998	1.2	5	17.6	31.1	Cole et al. (2000)
Peter	MI, USA	46°15′N, 89°30′W	2002, 2003	2.7	8.3	18.0	17.5	Van de Bogert et al. (2007)
East Long	MI, USA	46°14′N, 89°29′W	1995–1998	2.3	4.9	25.4	49.4	Cole et al. (2000)
East Long	MI, USA	46°14′N, 89°29′W	2000	2.3	4.9	25.5	45.9	Hanson et al. (2003)
Plum	WI; MI, USA	46°00′N, 89°30′W	2000	91	6.1	28.3	41.8	Hanson et al. (2003)
West Long	MI, USA	46°14′N, 89°29′W	2000	5.5	4.4	29.7	39.3	Hanson et al. (2003)
West Long	MI, USA	46°14′N, 89°29′W	1995–1998	5.5	4.4	30.4	41.8	Cole et al. (2000)
Tenderfoot	WI, USA	46°13′N, 89°31′W	2000	165.2	~ 4.8	30.5	39.4	Hanson et al. (2003)
Ward	WI, USA	45°60′N, 92°32′W	2000	2.7	4.87	32.1	35.4	Hanson et al. (2003)
Allequash	WI, USA	46°02′N, 89°37′W	2000	168.4	3.05	34.2	39.6	Hanson et al. (2003)
Võrtsjärv	Estonia	58°17′N, 26°02′E	2009, 2010	27,000	2.8	34.7	33.3	Model fit of the current study
Mary	WI, USA	45°54′N, 89°20′W	2000	1.2	2.7	35.0	47.3	Hanson et al. (2003)
Mar Chiquita	Argentina	30°54′S, 62°51′W	1992	57,700	3	36.7	27.4	Reati et al. (1997)
Brown	WI, USA	45°46′N, 89°29′W	2000	32.9	2.4	36.9	39.0	Hanson et al. (2003)
Muskellunge	WI, USA	45°57′N, 89°22′W	2000	110	3.96	47.9	41.6	Hanson et al. (2003)
Onondaga	NY, USA	43°05′N, 76°12′W	2000, 2001	1,200	10.7	50.0	46.6	Gelda & Effler (2002)
de Alcahozo	Spain	39°24′N, 2° 52′W	1992–1993	72	0.1	59.4	84.4	Florín & Montes (1998)

Table 4 continued

Lake name	State	Coordinate	Year of study	Area (ha)	Mean depth (m)	GPP	*R*	Authors
Peter	MI, USA	46°15′N, 89°30′W	2000	2.7	8.3	60.8	46.1	Hanson et al. (2003)
Ryans 1 Billabong	Australia	36°07′S, 146°58′E	1995	3.5	2.2	61.0	29.0	Ford et al. (2002)
Apopka	FL, USA	28°37′N, 81°37′W	1996–1997	12,400	1.7	61.2	116.5	Bachmann et al. (2000)
Kickapoo	MI, USA	46°13′N, 89°29′W	2000	7.9	~1	77.9	121.0	Hanson et al. (2003)
Frederiksborg Slotssø	Denmark	55°56′N, 12°17′W	2003, 2004	22	3.5	104.5	101.9	Staher & Sand-Jensen (2007)
Little Arbor Vitae	WI, USA	45°54′N, 89°37′W	2000	216.1	3.35	144.3	112.0	Hanson et al. (2003)
Salicor	Spain	39°28′N, 8°10′W	1992	52	0.09	378.5	222.2	Florín & Montes (1998)
Albardiosa	Spain	39°39′N, 8°18′W	1991	32	0.26	673.1	586.5	Florín & Montes (1998)
Santa Olalla	Spain	36°59′N, 6°28′W	1998–2000	35	0.37	769.5	832.0	López-Archilla et al. (2004)

All values are converted to volumetric rates by dividing the euphotic depth or epilimnion depth of the lake found from the literature. Lakes are sorted by the value of GPP. Most data refer to periods of only a few months, usually over the summer, when productivity is high, while in months with lower productivity, the status is supposedly different

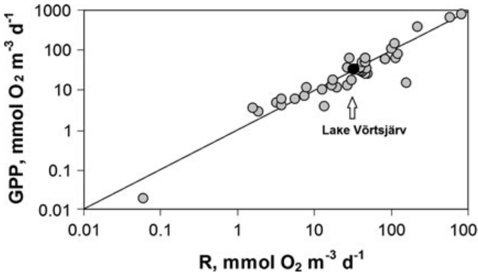


Fig. 7 Scatter plot of published mean daily values of GPP versus community respiration in lakes (see Table 4 for more details about the lakes)

mean depth of lakes per se had no significant effect on the auto-to-heterotrophy balance, whereas the relative depth, which is the maximum depth of a lake as a percentage of mean diameter (Wetzel, 2001) and characterises the potential of thermal stratification (Escobar et al., 2009; Tiberti et al., 2010) and phosphorus retention (Kõiv et al., 2011), had a significant impact towards heterotrophic conditions (decrease of GPP/*R* ratio) and a tendency towards lower NEP. Obviously, the trend of relatively deeper lakes being more heterotrophic can be attributed to stronger thermal stratification in these lakes, which leads to phosphorus depletion in the epilimnion during the growing season. In all relationships found between lake morphometric and metabolic variables, Võrtsjärv followed the general patterns and was never among outliers. The balance between annual GPP and *R* resulting in NEP = 0, as found in Võrtsjärv, is not very common, as in 57% of the lakes included in Table 4, annual NEP was negative, and a similar proportion (58%) was found among Danish lakes (Staehr et al., 2012a).

During winter, the rate of photosynthesis in temperate lakes declines and remains negligible in lakes that freeze over (Salonen et al., 2009). Decomposition of the organic matter continues, however, and the DO budget becomes negative in most lakes. Benthic oxygen demand of about 10 mmol O_2 m^{-2} day^{-1}, typical for highly eutrophic boreal lakes (Malve et al., 2005), would deplete DO from a 1-m-deep oxygen-saturated lake within 49 days. Anoxia formation and winter fish kills in boreal shallow lakes including Lake Võrtsjärv (Tuvikene et al., 2002; Järvalt et al., 2005) are common and give clear evidence of negative DO budgets. The ice breakup in spring brings about a

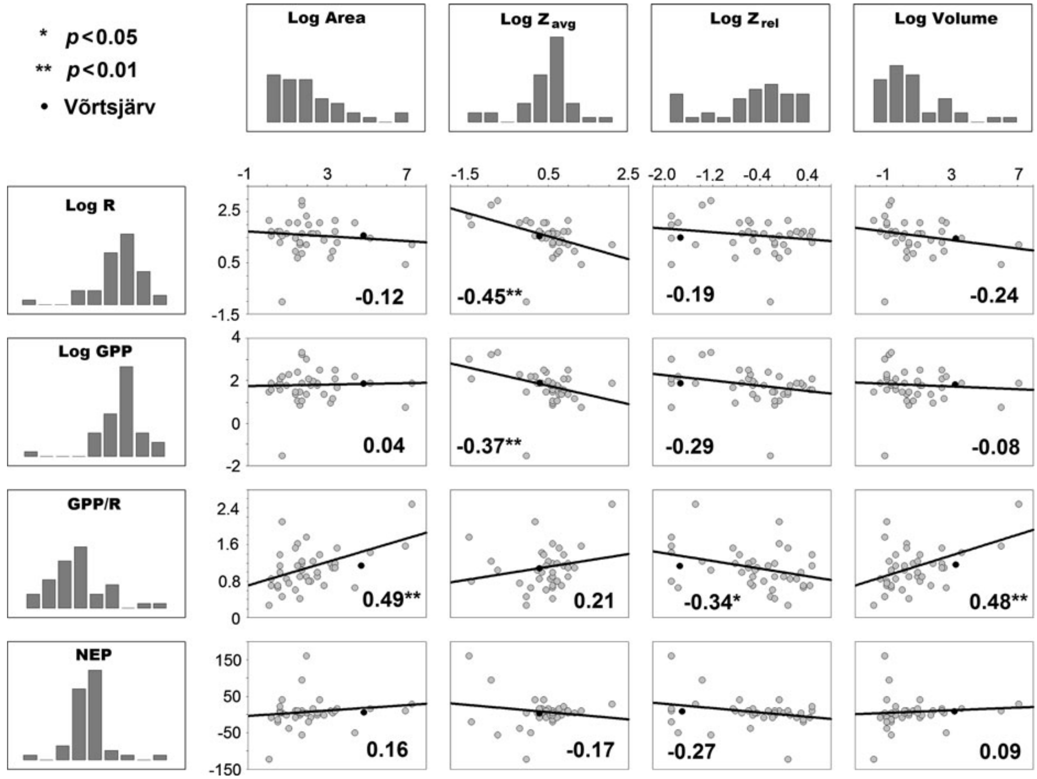


Fig. 8 Frequency distributions of variables and the correlation matrix relating lake metabolic characteristics GPP, *R*, NEP (mmol O_2 m^{-3} day^{-1}), and the GPP/*R* ratio with lake area (ha), mean depth (Z_{avg}, m), relative depth (Z_{rel}, %) and volume (10^6 m^3) for published data from 41 lakes. The position of Võrtsjärv is indicated with a *black dot*. *Straight lines* show linear fits and the numbers—Pearson correlation coefficients (*r*) of the relationships

tremendous change in light conditions, while the commonly high transparency of water and the pool of re-mineralized nutrients enable the formation of a virtually unlimited pulse of algal growth. The timing of the vernal peak of phytoplankton is closely related to air temperature in spring, which mostly determines the timing of the ice breakup (Nõges et al., 2010). It can be assumed that during the vernal phytoplankton peak, most lakes become net autotrophic. Hence, we can conclude that most lakes, at least in the boreal zone, switch in early spring from net heterotrophy to net autotrophy, while the duration of the latter determines whether the lake becomes auto- or heterotrophic on an annual scale.

The fact that the most of the substrates for respiration (plant, animal and bacterial biomasses and DOC) are produced within the lake during the annual cycle and exist in the organic form for a certain time before being re-mineralized implies that seasonally the community respiration lags behind the GPP cycle, whereas the phase shift is equal to the dominant mode of the organic matter turnover time in the food web. In Lake Võrtsjärv where the bulk of the plankton biomass is accounted for by slowly growing 'inedible' filamentous cyanobacteria, *R* lags behind GPP by 2 weeks, on average. For comparison, in the stratified Danish lakes GPP and *R* followed each other more strictly over time as reflected by NEP values near zero, GPP:*R* ratios near 1.0, and close positive correlations of daily GPP and *R* ($r > 0.9$, Staehr et al., 2010b, cf. 0.80 in Võrtsjärv), which the authors explained by relatively rapid respiration by bacteria and zooplankton of the newly

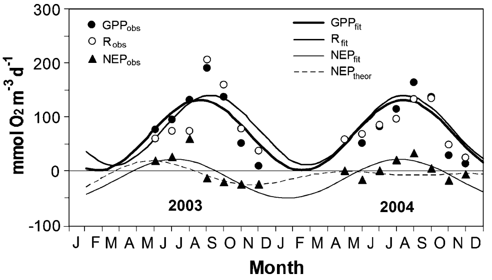


Fig. 9 Sinusoidal fitting applied to monthly mean values of GPP, *R* and NEP in Lake Frederiksborg Slotssø (data digitalized from Fig. 7 in Staehr & Sand-Jensen, 2007)

produced organic matter. Only during development of algal blooms and their following collapse and degradation was the synchrony between GPP and *R* lost.

A trial to apply our sinusoidal model to the monthly metabolic data of Lake Frederiksborg Slotssø (Fig. 9, data from Staehr & Sand-Jensen, 2007) showed a 2-week lag between GPP and *R* in 2003 similar to that found in Võrtsjärv, which was not observed in 2004. This fits well with the higher GPP and smaller role of zooplankton grazing in 2003 described by the authors. Our model explained 76% of GPP, 61% of *R* and 52% of NEP monthly changes in this lake and suggested prevailing autotrophy from the end of March to mid-September in 2003 and from the end of April to the end of October in 2004 (mid-May to mid-September in the original study). The best-fitting sinusoids, however, were unable to follow the high peaks of GPP and *R* in August or September and the inter-annual differences. Thus, the model seems to be more fit for describing the metabolism of turbid polymictic lakes like Võrtsjärv, which have seasonally smoother changes in light and nutrient availability, compared with stratified lakes, and strong light limitation forces the dynamics of GPP, *R* and NEP to follow better the sinusoidal changes of PAR and temperature. In Frederiksborg Slotssø (Denmark), the metabolic variables were strongly controlled by changes in mixing depth, which determined nutrient availability by pulses and fluctuations in the mean available light levels in the mixed layer (Staehr & Sand-Jensen, 2007).

The factors governing GPP and *R* are partly overlapping. In our study, increasing water temperature had strong positive effects on GPP and *R* but a negative effect on NEP (Table 3). These results are fully in line with the findings by Staehr et al. (2010a) for Danish stratified lakes. Similar response of the metabolism of different types of lakes to temperature implies that climate warming is likely to support net heterotrophy of temperate lakes in general.

The intrinsic sensitivity of respiration to temperature was recently shown across aquatic ecosystems of contrasting thermal history (Perkins et al., 2012). The positive relationship between T_w and GPP arises from the temperature dependence of *R*, which mathematically is one of the summands in GPP (Eq. 6). Temperature per se is not considered a growth-limiting factor for phytoplankton, but may restrict or stimulate growth through various mechanisms such as shifted timing of the ice breakup (Adrian et al., 1999; Weyhenmeyer et al., 1999) or zooplankton grazing (Straile & Adrian, 2000), modified winter mixing in deep monomictic lakes and its consequences to nutrient availability (Salmaso, 2002, 2005; Straile et al., 2003) or increased thermal stability of the water column crucial for development of cyanobacteria blooms (Paerl & Huisman, 2008). It is likely that the stimulating effect of T_w on lake heterotrophy can be attributed to the stronger temperature dependence of *R* rather than GPP.

Light limitation of phytoplankton growth is a common phenomenon in Võrtsjärv due to high plankton biomass, brownish water colour due to elevated humic matter content, and a continuously large impact of suspended sediments on light attenuation in the water during the ice-free period (Reinart & Nõges, 2004). As expected, GPP and NEP were stimulated by increasing irradiance, whereas wind suppressed the production processes likely by modifying the resuspension rate.

By autumn, a large amount of fresh sediment is produced. At the same time, the lake reaches its lowest water levels. Both factors contribute to high rates of sediment resuspension, which increases linearly with decreasing mean depth of the lake (James et al., 1997). The increased concentrations of particulate and dissolved matters raises the respiration rate causing a decline in NEP. As the fresh sediment in Võrtsjärv still contains intact algal cells and degradation products of algal pigments (Freiberg et al., 2011), the observed increase of Chl *a* towards autumn is partially caused by resuspension and cannot be fully be attributed to algal growth and the reduction of zooplankton grazing pressure.

Increase in plankton respiration with increasing Chl *a*, TP and DOC concentrations has been recurrently reported. Pace & Prairie (2005) analysed data from 70 different lakes, and found that Chl *a* accounted for 71% and TP for 81% of the variance in community respiration, which they considered a typical pattern of lakes where primary production is strongly nutrient limited. In highly productive Frederiksborg Slotssø (Denmark), GPP and *R* increased with increasing Chl *a*, TP and DOC (Staehr et al., 2010b, 2012a). The rather low explanatory power of our multiple regression models (R^2 from 0.28 to 0.67) was most probably caused by the absence of high resolution data on Chl *a*, nutrients and DOC, the influences of which will be the focus of our future studies on metabolic variables.

Conclusions

A sinusoidal model fitted to monthly mean values of GPP, *R* and NEP from the large, shallow, polymictic Võrtsjärv showed that the metabolism of the lake switches between autotrophic and heterotrophic types. The autotrophic period starting from early spring lasts until August or September, whereas during the rest of the year heterotrophy prevails. On an annual basis, GPP of the pelagic part of Võrtsjärv is balanced or slightly exceeds *R* showing that, from the CO_2 emission point of view, the lake can be considered carbon neutral.

Community respiration lagged behind GPP by about 2 weeks which could be explained by the bulk of the phytoplankton biomass accounted for by filamentous cyanobacteria that were inedible for zooplankton, which resulted in increased cyanobacteria biomass over the season, and also by the increasing sediment resuspension with decreasing water levels towards autumn.

Stronger stimulating effect of temperature on *R* compared with GPP suggests that climate warming is likely to support heterotrophy in Võrtsjärv. As revealed from the sinusoid fitting to the seasonality of lake metabolic variables, the seasonal peaks of GPP, *R* and NEP were synchronously shifted about 1 month earlier in 2010 characterized by a warmer spring and summer compared to 2009.

Testing of the sinusoidal model on two lakes showed a good fit for describing the metabolism in the turbid polymictic Võrtsjärv where the dynamics of GPP, *R* and NEP followed better the sinusoidal changes of PAR and temperature, compared with the stratified Frederiksborg Slotssø, in which the metabolic variables were strongly controlled by changes in mixing depth, which determined nutrient availability by pulses and fluctuations in the mixed layer light levels.

Analysis of data from the literature supported the earlier findings on the important role of lake morphometry in determining lake metabolism. In a set of 41 lakes, Võrtsjärv followed the general relationships between morphometric and metabolic variables and was never among the outliers. The analysis supported earlier findings about declining GPP and *R* with increasing lake depth but also revealed a highly significant trend of larger lakes being more autotrophic.

Acknowledgments The study was supported by the Estonian target funding project SF 0170011508, by grants 7600, 8729 and 9102 from the Estonian Science Foundation and by 7th EU Framework Programme, Theme 6 (Environment including Climate Change) project REFRESH (Adaptive strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems, Contract No.: 244121).

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II

Nõges, T.; Arst, H.; **Laas, A.**; Kauer, T.;
Nõges, P. And K. Toming, 2011.
RECONSTRUCTED LONG-TERM TIME SERIES OF
PHYTOPLANKTON PRIMARY PRODUCTION OF A LARGE
SHALLOW TEMPERATE LAKE: THE BASIS TO ASSESS
THE CARBON BALANCE AND ITS CLIMATE SENSITIVITY.
Hydrobiologia, 667(1), 205 - 222.

Hydrobiologia (2011) 667:205–222
DOI 10.1007/s10750-011-0647-y

PRIMARY RESEARCH PAPER

Reconstructed long-term time series of phytoplankton primary production of a large shallow temperate lake: the basis to assess the carbon balance and its climate sensitivity

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Tuuli Kauer · Peeter Nõges · Kaire Toming**

Received: 4 November 2010 / Revised: 16 February 2011 / Accepted: 19 February 2011 / Published online: 4 March 2011

Abstract Aiming at building the carbon budget for further climate change impact research in the large and shallow northern temperate Lake Võrtsjärv, the present paper focuses on reconstructing the full phytoplankton primary production (PP) data series for the lake for the period of 1982–2009 covered by disconnected measurements, and testing the uncertainties involved both in the PP measurements and bio-optical modelling. During this 28-year period, in situ PP was measured in Võrtsjärv in 18 years with ^{14}C-assimilation technique. We reconstructed the full time series using a semi-empirical PP simulation model based on continuously measured PAR irradiance and interpolated values of monthly measured chlorophyll *a* (C_{chl}). The modelling results, which proved highly reliable during the calibration phase, correlated rather weakly with the annual PP estimates for the 18 years, which were based on 2-h incubations at midday, 1–2 times per month. Being based on continuous irradiance data, the modelled PP can be considered more reliable than the sparse measurements, especially for short to medium term studies. We demonstrate that in the long-term, the bio-optical method can be biased if changes in water colour or

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Handling editor: Luigi Naselli-Flores

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water level alter the light climate causing adaptive responses in the cellular chlorophyll content of light-limited phytoplankton.

Keywords Phytoplankton · Primary production · Võrtsjärv · Shallow eutrophic lake · Modelling · Light limitation

Introduction

Phytoplankton primary production (PP) represents the major synthesis of organic matter in aquatic systems giving start to the food chains and forming the basis of the ecological pyramid. The amount of primarily synthesised organic matter indicates the trophic state of a waterbody, while the efficiency of its subsequent transformation in food chains results in a higher or lower fish production, and in a poorer or better water quality. Lakes are sites of intensive carbon processing, although often disregarded in models of the global carbon cycle due to their small percentage of the Earth's surface area (Sobek et al., 2006). Several recent studies have demonstrated that lakes are significant sources of carbon dioxide and methane to the atmosphere (Huttunen et al., 2003; Jonsson et al., 2003; Cole et al., 2007), and that they simultaneously bury more organic carbon in their sediments than the entire ocean (Downing et al., 2008). Hence, lakes turn out to be disproportionately important sites of carbon cycling relative to their small areal extent. Lakes and reservoirs act as sentinels by providing signals that reflect the influence of climate change in their much broader catchments (Williamson et al., 2008, 2009). In the context of global warming caused by the increase of greenhouse gases, it is important to know the role of each ecosystem type in the global carbon budget. It has been increasingly acknowledged that in many lakes, first of all in those located in cool-climate forested boreal regions, the heterotrophic processes are dominating over autotrophic ones turning the lakes into CO_2 sources (Algesten et al., 2003; Sobek et al., 2003). To study the carbon metabolism of a lake, the first and the basic step would be the estimation of the amount of carbon fixed by the ecosystem. The importance of PP studies is impressively reflected in publication statistics of ISI Web of Science (ISI WoS), which showed that lake primary production has been analysed in ca. 1400 publications since 1990 with an increasing average yearly rate from ca. 60 until year 2000 to ca. 80 afterwards. The annual citation rate of these papers has exponentially increased from about 100 in 1992 to nearly 3000 in 2009, resulting on average 17 citations per item. However, to understand climate sensitivity of the carbon metabolism, long-term changes of primary production need to be known. As stated already by Jassby et al. (1990), interannual changes of primary production remain one of the least investigated areas in limnology and this situation has not much improved during the last 20 years. The query on 'long term lake primary production' resulted in only in 126 publications in ISI WoS database since 1990. The average citation rate of one publication was 26 showing the high importance of the studies on this field.

The present paper is the first step of the large-scale assessment of the carbon metabolism of Lake Võrtsjärv, a large and very shallow lake, the largest one remaining fully within the borders of Estonia. Its catchment area makes up 7% of Estonian territory and, thus, contributes significantly to Estonian natural CO_2 budget. Our aim was to summarise the long-term primary production measurements in Võrtsjärv in order to receive reliable daily, monthly and annual estimates of this parameter as the starting point in the lake's carbon balance calculations. The results will provide further basis for long-term studies of the ecosystem metabolism and its climate sensitivity.

Study site and dominant primary producers

Lake Võrtsjärv (58°16′N 26°02′E) is located in Central Estonia. With a surface area of 270 km^2 and a catchment area of 3374 km^2 (including the lake), it is the country's second largest lake. Võrtsjärv is shallow and polymictic with a maximum depth of 6 m and a mean depth of 2.8 m. The lake is eutrophic (OECD, 1982) characterised by the following annual mean concentrations: TP 54 $\mu g\ l^{-1}$, total nitrogen (TN) 1.6 $mg\ l^{-1}$, C_{chl} 24 $\mu g\ l^{-1}$ and has an average Secchi depth of 1.1 m (Tuvikene et al., 2004; Nõges et al., 2007). The water retention time is about 1 year and lake is ice-covered for more than 4 months (average 135 days) of the year. The unregulated water level has an annual mean amplitude of 1.4 m, the absolute range of 3.1 m, and exhibits a long-term periodicity with a period length of 20–30 years. The minimum and maximum water levels correspond to a 1.4-fold difference in the lake area, a 2.3-fold difference in the mean depth and a 3.2-fold difference in the water volume (Nõges et al., 2003).

Within the 50 km^2 (19% of the lake area at mean water level) covered by aquatic macrophytes 35 km^2 is accounted for by submerged, 12 km^2 by emergent and 3 km^2 by floating-leaved macrophytes (Feldmann & Mäemets, 2004). The earlier dominance of *Potamogeton perfoliatus* L. among submerged macrophyte is by now overtaken by *Myriophyllum spicatum* L.

Cyanobacteria compose the bulk (up to 95%) of the phytoplankton biomass during the ice-free period from May to October. The beginning of our study period coincided with a break through of two new dominants, *Limnothrix redekei* (van Goor) Meffert and *L. planktonica* (Wolosz.) Meffert. Both species are slow growing and highly shade tolerant that gives them an advantage in turbid waters. Seasonally *L. redekei* starts its growth earlier and reaches the biomass maximum in June while *L. planctonica* has its maximum usually in September–October. *L. redekei* reached its maximum in the years 1988–1990 forming on average more than 60% of filamentous cyanobacteria. By now, its share has decreased to an average of 20%. *L. planktonica*, which started to increase also in 1980s, became the main phytoplankton dominant since 1995 often building up more than 80% of the total biomass.

The lake underwent a rapid eutrophication during 1970s and 1980s. Since that, despite a considerable decrease in external nutrient loadings, the internal loading modulated by the long-term cyclic water levels has still prevented any significant decline in nutrient concentrations of the lake (Nõges & Kisand, 1999; Nõges et al., 2007, 2010c).

Materials and methods

PP measurements

Phytoplankton primary production (PP) in Võrtsjärv has been measured in situ with ^{14}C-assimilation technique (Steeman-Nielsen, 1952) in 1982–1984, 1989, 1991, 1993–1998, 2000, 2003–2009. PP has been measured mainly during ice-free periods from April to October with weekly to monthly intervals. In 1983, 1984, 1991 and 1995, PP was measured also in winter under the ice. The applied methodology and the detailed results have been published in a number of earlier papers (Nõges & Nõges, 1998; Nõges et al., 1998, 1999; Nõges, 1999b; Kisand et al., 2001; Kisand & Nõges, 2004; Agasild et al., 2007; Zingel et al., 2007). In situ PP (mg C m^{-3} h^{-1}) was measured at six different depths in the lake in two parallels. After incubation, the water was acidified to pH <2 with 0.5 N HCl to remove the remaining inorganic ^{14}C (Niemi et al., 1983; Hilmer & Bate, 1989; Lignell, 1992), after which the radioactivity of the sample was measured with a scintillation counter (LSC RackBeta 1211, Wallac, Finland) using external standardisation for decays per minute (DPM) calculations and Optiphase 'HiSafe 3' scintillation cocktail (Wallac, Finland). PP was calculated according to the standard formula (Nielsen & Bresta, 1984). Non-photosynthetic carbon fixation was measured in dark vials and subtracted from the light assimilation. Integral PP values (PPint) were calculated by integrating measured PP values over depth. We used 2-h incubations around midday, which measure rather the gross production (Vollenweider & Nauwerck, 1961). The daily gross PP (PP_{day}) was calculated using an equation relating day-long series of short incubations to hourly PP at midday (PP_{hour}), and the day length (DL) found for Lake Võrtsjärv (Nõges & Nõges, 1998):

$$PP_{day} = PP_{hour}/\left(0.230 - 890 \times 10^{-5} \times DL\right); \quad R^2 = 0.66,\ P < 0.01. \qquad (1)$$

We used two options to calculate annual PP values from the measurements. For years when PP was measured monthly or more frequently from April to October (1983, 1989, 1991, 1994, 1995–1997, 2000, 2004), we integrated the measured daily PP values over the time to achieve the yearly values. If not measured, the under-ice PP was assumed to be zero. For years when PP was measured only from May to August, we calculated yearly PP values from the average daily PP in May–August, which formed on average 0.55% of the yearly PP as calculated from the more complete data (Table 1).

Chlorophyll *a* and phytoplankton biomass

Phytoplankton abundance was measured as chlorophyll *a* concentration (C_{chl}, mg m^{-3}), and phytoplankton biomass on each occasion of PP

Table 1 Average daily, monthly and annual depth-integrated primary production of phytoplankton (PP_{int}) in Võrtsjärv measured and modelled in 1982–2009

Month	Daily PP_{int} (mg C m^{-2} day^{-1})						Monthly PP_{int} (g C m^{-2} $month^{-1}$)			
	Measured			Modelled			Measured		Modelled	
	AVG	*n*	SD	AVG	*n*	SD	AVG	% of annual	AVG	% of annual
January	24	9	16	3	28	14	0.7	0.4	0.1	0.0
February	40	8	35	0	28	0	1.1	0.5	0.0	0.0
March	183	12	169	14	28	52	5.7	2.8	0.4	0.2
April	516	28	395	352	28	276	15.5	7.6	10.6	5.3
May	1021	46	560	1077	28	250	31.7	15.5	33.4	16.6
June	1299	47	784	1299	28	378	39.0	19.1	39.0	19.4
July	1174	44	648	1235	28	274	36.4	17.8	38.3	19.1
August	1009	47	493	1088	28	173	31.3	15.3	33.7	16.8
September	557	40	316	852	28	267	16.7	8.2	25.6	12.7
October	359	35	247	492	28	115	11.1	5.4	15.2	7.6
November	482	20	889	130	28	90	14.4	7.1	3.9	1.9
December	28	10	21	13	28	25	0.9	0.4	0.4	0.2
Annual mean	558			546[a]			17		17	
Apr.–Nov. mean	848			816			25		25	
May–Aug. mean	1126			1175			35		36	
Annual PP_{int}, g C m^{-2} $year^{-1}$							205		200[a]	

In the modelling approach, the under-ice PP_{int} was assumed to be zero. The measured PP_{int} from December to March when the lake is generally frozen, constituted about 4% of the annual PP_{int}. As the mean values are based on different numbers of measurements (*n*) over the years, the table does not seek a strict comparison between the months, but is rather a condensed way of presenting the data

[a] Correction for under-ice production not applied

measurements. For C_{chl} analysis, plankton was collected on Whatman glass fibre filters (GF/F), pigments were extracted with 90% acetone (in 1982–2000) or 96% ethanol (since 2001), analysed spectrophotometrically, and calculated according to Lorenzen (1967). No statistically significant differences between the acetone and ethanol extractions were found for Võrtsjärv (Nõges & Solovjova, 2000).

Phytoplankton biomass (B, g m^{-3}) and the taxonomic composition were determined by microscopic counting and measuring the algae. Details of the methods are given in Nõges et al. (2010a).

PP modelling

In parallel with in situ measurements, long-term PP was estimated using an integral version of the semi-empirical model elaborated by Arst et al. (2008). The model used as input variables chlorophyll concentration, C_{chl}, the incoming irradiance, and the diffuse attenuation coefficient. We calculated C_{chl} values for each day by linearly interpolating the measured values. The irradiance and the diffuse attenuation coefficient were integrated over PAR region, correspondingly, q_{PAR}(inc), and $K_{d,PAR}$. As no spectral irradiance data was available for the whole period, we could not use the slightly better performing (Arst et al., 2008) spectral version of this model.

Incident global radiation, Q, was measured by the Estonian Institute of Hydrology and Meteorology (EMHI) at Tõravere (58°15′55N, 26°27′58″E), ca. 30 km from the eastern shore of Võrtsjärv. Before the year 2000, the values of Q were derived from direct and diffuse solar radiation, measured, correspondingly, with Janishevsky actionometer AT-50, and Janishevsky pyranometer model M-115M (Kondratyev, 1965). We calculated the incident photosynthetically active radiation, q_{PAR}(inc), as 0.436 * Q. Since the year 2000, q_{PAR}(inc) was measured directly with the irradiance quantum sensor Li-COR 190SA (Li-COR Biosciences).

Since, there were only few in situ measurements of $K_{\mathrm{d,PAR}}$ available for Võrtsjärv, we calculated its values from spectral beam attenuation coefficients, $K_{\mathrm{d}}(\lambda)$, measured from water samples using the model of Arst et al. (2002). Monthly depth-integrated samples were collected in 2002–2007 from one sampling point in Võrtsjärv, stored in plastic bottles in the dark at 4°C without any treatment until analyses (for maximum 12 h).

We extended $K_{\mathrm{d,PAR}}$ data series for the whole study period (1982–2009) using the regression with monitored chlorophyll *a* concentration (Eq. 2):

$$K_{\mathrm{d,PAR}} = 0.03C_{\mathrm{chl}} + 1.07 \quad \left(R^2 = 0.73,\ P<0.001\right) \tag{2}$$

The PP computing system based on the integral model (Arst et al., 2008) gives the values of $\mathrm{PP_{int}}$ in mg C $\mathrm{m^{-2}}$ $\mathrm{h^{-1}}$, and calculates the daily values by summing up the hourly values. However, our database contained mostly the daily sums of incident irradiance, which we could not use directly in our computing system. Dividing the daily sum of q_{PAR}(inc) by the day length (DL) we found the average hourly q_{PAR}(inc, av) for each day, which enabled us to calculate the corresponding average hourly $\mathrm{PP_{int}}$ for each day. Multiplying this by DL gave us the daily sum of $\mathrm{PP_{int}}$.

We compared the two calculation options for daily $\mathrm{PP_{int}}$ values during a special study in Võrtsjärv in 2009. From May to August, we recorded the incident global irradiance (Q) using Yanishevsky pyranometer (Kondratyev, 1965) placed on the roof of a building close to the coastal station in Võrtsjärv. We took q_{PAR}(inc) equal to 0.436 * Q(inc). The q_{PAR}(inc) readings taken each 2 min allowed to compute the hourly averages. There were 12 in situ measurements of C_{chl} and $K_{\mathrm{d,PAR}}$ within this period (more frequently than usually) that improved the reliability of the interpolated values. Using these data we calculated hourly PP profiles and $\mathrm{PP_{int}}$ values. By summing up these values we calculated the daily values referred further as $\mathrm{PP_{int}}$(model). For long-term PP modelling, we could use only the average daily q_{PAR}(inc) values from EMHI, and the corresponding $\mathrm{PP_{int}}$ values are referred further as $\mathrm{PP_{int}}$(appr). We used the regression formulae relating these two series during this 4-month study to make corrections in all $\mathrm{PP_{int}}$ values calculated on the basis of daily sums of incident irradiance.

Mean water column irradiance based on Secchi depth and water level

As we suspected that part of the C_{chl} changes in the long-term data might have occurred as an adaptive response of phytoplankton to a variable strength of light limitation due to changing water colour and/or depth (i.e. not directly related to PP dynamics as supposed by the model), we calculated another $K_{\mathrm{d,PAR}}$ value from its regression with the Secchi depth (S)

$$K_{\mathrm{d,PAR}} = 1.698\ \mathrm{S}^{-0.767} \quad \left(R^2 = 0.56,\ P < 0.001\right) \tag{3}$$

and applied that in the Lambert–Beer's law

$$I_z = I_0 \cdot \mathrm{e}^{(-K_{\mathrm{d,PAR}} \cdot Z)} \tag{4}$$

where I_z is the fraction of incident light at the surface (I_0) reaching the depth Z. Taking I_0 equal to 100% and the mean depth of the lake for Z (a variable depending on the largely fluctuating water level), we calculated the average irradiance in the mixed water column (I_{mix}; %) according to Riley (1957)

$$I_{\mathrm{mix}} = \frac{I_0 \cdot (1 - \mathrm{e}^{-K_{\mathrm{d,PAR}} \cdot Z})}{K_{\mathrm{d,PAR}} \cdot Z} \tag{5}$$

assuming that in Võrtsjärv the mixing depth increases simultaneously with the mean depth of the lake.

Results

Measured primary production

According to the 18-year measurements, the mean daily integrated PP was 558 mg C $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$ with monthly means changing from about 25 mg C $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$ in December and January to nearly 1300 mg C $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$ in June (Table 1). The scatter of single daily measurements in each month was rather large characterised by standard deviations (SD) making up from 49 to 184% of the monthly mean values. The daily PP was relatively most variable in November and March due to the onset and ending of the ice season. The maximum chlorophyll specific production rate at light saturation varied from 0.1 to 14.7 mg C mg C_{chl}^{-1} $\mathrm{h^{-1}}$ being on average 2.06 ± 1.72 mg C mg C_{chl}^{-1} $\mathrm{h^{-1}}$.

The mean daily PP from May to August formed on average 0.55% of the annual PP. We used this ratio to

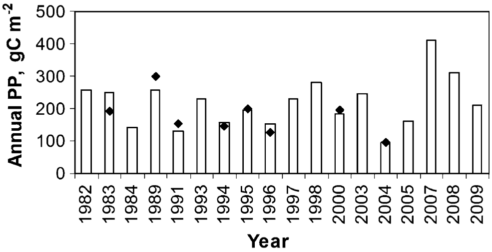

Fig. 1 Annual phytoplankton primary production estimates calculated as the integral over the ice-free period (*dots*), and from the average daily PP values in May–August assuming its correspondence to 0.551% of the yearly PP (*columns*)

calculate the annual PP for years with incomplete data coverage. For the years to which both methods were applied, the integrated values corresponded well to the calculated values (Fig. 1).

PP had a pronounced seasonality in Võrtsjärv, with two-third of the annual PP produced during one-third of the year from May to August. The monthly PP in June (39 g C m^{-2} $month^{-1}$) exceeded the average monthly PP (17 g C m^{-2} $month^{-1}$) by a factor more than two. The measured annual average pelagic PP in Võrtsjärv was 205 g C m^{-2}. In the long-term, the measured PP had no significant trend either over single months or in the annually integrated values.

Modelled primary production

Modelled versus measured primary production profiles

The vertical profiles of measured and modelled PP corresponded generally well with each other (Fig. 2). Also the modelled integral PP (PP_{int}, mg C m^{-2} h^{-1}) values that were computed by integrating vertical PP profiles over depth, were in good concordance with the measured PP_{int} values. For example, the profiles represented in Fig. 2, gave measured PP_{int} values of 102 and 211 mg C m^{-2} h^{-1}, and modelled PP_{int} values of 113 and 223 mg C m^{-2} h^{-1}, respectively.

Comparison of the two calculation options for daily PP_{int}

The relationship between the two integral primary production estimates computed from hourly irradiances over the day (PP_{int}(mod)) and the daily sums of irradiance (PP_{int}(appr)) was strong with a determination coefficient R^2 higher than 0.94 (Fig. 3). The regression formulae were slightly different for the two chlorophyll ranges, $C_{chl} < 35$ mg m^{-3} and $C_{chl} \geq 35$ mg m^{-3}, for which different algorithms were used in the model (Arst et al., 2008). We corrected all results of PP_{int} according to these formulae.

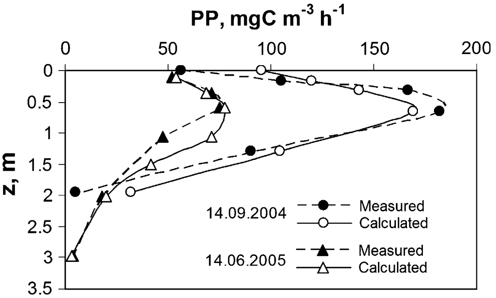

Fig. 2 Comparison of measured and modelled PP profiles in Võrtsjärv on 14.09.2004 and 14.06.2005 characterised by the respective C_{chl} values of 70 and 40 mg m^{-3}, q_{PAR}(inc) values of 1300 and 1003 µmol m^{-2} s^{-1}, and $K_{d,PAR}$ values of 2.5 and 2.2 m^{-1}

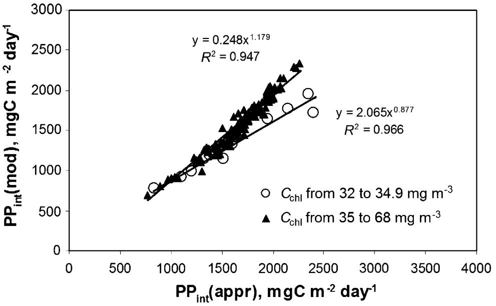

Fig. 3 Regression between the two integral primary production estimates for Võrtsjärv computed using hourly irradiances over the day (PP_{int}(mod)) and daily sums of irradiance (PP_{int}(appr)) for the days from May to August 2009 when C_{chl} was measured. Due to different algorithms in the model for $C_{chl} < 35$ mg m^{-3} and for $C_{chl} > 35$ mg m^{-3} (Arst et al., 2008), separate correction formulae were derived for these ranges

Modelled versus measured primary production time series

We calculated PP_{int}(mod) in total for 6011 ice-free days in the 28-year period from 1982 to 2009. The

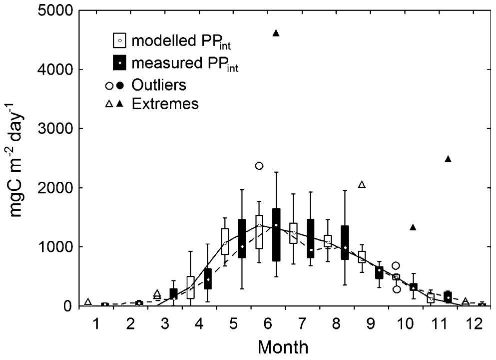

Fig. 4 Variation of measured (*black*) and modelled (*white*) daily primary production in Võrtsjärv in different months over the period 1982–2009. *Boxes* represent the median and quartiles, whiskers show the non-outlier range

median values of modelled and measured daily PP_{int} values were quite close in different months but the variation of the modelled values was smaller than that of the measured values (Fig. 4; Table 1).

The average annual pelagic PP_{int}(mod) in 1982–2009 was 200 g C m^{-2} $year^{-1}$ (Table 1). Considering approximately 4% underestimation of annual PP_{int} due to ignoring the under-ice production, the modelled average annual PP_{int} in Võrtsjärv would be 208 (min. 144, max. 306) g C m^{-2} $year^{-1}$, which is very close to the average of the measured values (205 g C m^{-2} $year^{-1}$). The yearly average volumetric PP (the ratio of the annual areal PP_{int}(mod) to the mean depth of the lake) was 80 (min. 48, max. 148) g C m^{-3} $year^{-1}$ (Table 2).

For the 18 years when PP_{int} was both measured and modelled, the results were significantly correlated ($R^2 = 0.32$, $P = 0.015$) (Fig. 5), the modelled daily PP_{int}, however, exhibited significant linear increasing trends in all ice-free months over the whole study period (Fig. 6) while no trend was detected in the measured PP values. A trial to detrend the modelled PP_{int} values did not improve the relationship with measured values and was given up.

The increase in modelled PP_{int} was caused by the strong significant trends in C_{chl}, one of the important input parameters, occurring from May to December over the whole study period (Fig. 7). The slope of the long-term chlorophyll trendline increased towards autumn and reached its maximum in September–October indicating the season in which the biggest changes in C_{chl} took place.

The mean light intensity within the water column (I_{mix}) calculated from Secchi depth and water level, showed a bell-shape change over the years (Fig. 8A) with average light conditions for phytoplankton improving over 1980s and deteriorating again since the first half of 1990s. The percentage of chlorophyll in the total phytoplankton biomass (Chl% *B*) had opposite dynamics with an increasing trend since the beginning of 1990s (Fig. 8B).

Total carbon fixation in the lake

For the assessment of total PP of the lake and its long-term changes, we further used the modelled PP values. Multiplying the annual areal phytoplankton PP by the average lake area in each year, we got an estimate of 56 559 (min. 41 013, max. 77 064) tonnes of carbon fixed annually by phytoplankton primary production in Võrtsjärv. Considering the estimations that phytoplankton contributes 79% and macrophytes with their epiphyton 21% to the total PP in Võrtsjärv (Nõges et al., 2010b), the total annual whole-lake carbon fixation of Võrtsjärv resulted in 71 268 (min. 51 679, max. 97 107) tonnes (Table 2).

Discussion

In the global context, Võrtsjärv occupies by its annual primary production a medium position among the World lakes for which data on PP are available (Table 3; Fig. 9).

Annual areal PP of Võrtsjärv is very close to that of the other large and shallow lake close by, Lake Peipsi, but is also similar to the PP of much deeper large temperate lakes, such as Erie and Ontario. According to the data presented in Table 3, the annual PP of 63 World's lakes was significantly negatively correlated with latitude ($R^2 = 0.23$, $n = 63$, $P < 0.001$). The strong effect of latitude (Lat) on lake productivity was stressed also by Håkanson & Boulion (2002) and Boulion (2003). They showed a strong and significant decrease in phytoplankton primary production with increasing Lat, a relationship that could be successfully used to predict PP of inland waters. They found that 60% of the variation of annual PP could be explained by Lat according to linear equation: $PP = -130 * Lat + 8453$ and even 74% using the exponential equation: $PP = 647461 * \exp(-4.29 * TranLat)$ where

Table 2 Modelled annual primary production of Võrtsjärv

Year	Areal pelagic PP, ice-free (g C m^{-2} y^{-1})	Areal pelagic PP, annual[a] (g C m^{-2} y^{-1})	Lake mean depth (m)	Volumetric pelagic PP, annual[a] (g C m^{-3} y^{-1})	Lake area (km^2)	Annual phytoplankton PP in the lake (Tonnes C y^{-1})	Annual total PP in the lake[b] (Tonnes C y^{-1})
1982	194	202	2.97	68	283	57062	71902
1983	182	190	2.66	71	273	51675	65115
1984	165	171	2.53	68	268	45931	57876
1985	216	225	2.75	82	275	61975	78094
1986	154	161	2.75	58	276	44273	55787
1987	138	144	3.00	48	284	41013	51679
1988	160	167	2.93	57	282	46978	59196
1989	234	244	2.81	87	278	67775	85402
1990	182	189	3.00	63	284	53796	67788
1991	166	173	2.98	58	283	48888	61602
1992	160	167	2.72	61	274	45843	57766
1993	186	194	2.38	81	263	50907	64147
1994	162	169	2.61	65	271	45760	57661
1995	185	193	2.71	71	274	52948	66719
1996	176	184	1.88	98	245	45100	56829
1997	199	207	2.38	87	263	54384	68529
1998	216	225	2.83	79	278	62682	78985
1999	188	196	2.80	70	277	54245	68353
2000	232	242	2.50	97	267	64635	81446
2001	202	211	2.55	82	269	56609	71332
2002	219	228	2.60	88	270	61575	77590
2003	211	220	2.17	101	255	56192	70806
2004	225	234	2.82	83	278	65053	81972
2005	219	229	2.84	80	279	63743	80321
2006	294	306	2.06	148	252	77064	97107
2007	251	262	2.36	111	262	68638	86489
2008	252	263	2.83	93	278	73149	92174
2009	223	232	2.98	78	283	65745	82844
Average	200	208	2.66	80	272	56559	71268
Min	138	144	1.88	48	245	41013	51679
Max	294	306	3.00	148	284	77064	97107
StDev	35	37	0.29	20	10	9504	11976

[a] Corrected for the 4% of under-ice production

[b] Corrected for the 21% of macrophyte and epiphyton production (Nõges et al., 2010b)

$\text{TranLat} = (90/(90 - \text{Lat}))^{0.5}$. Data presented in Table 3 showed somewhat weaker relationship also with the transformed values ($R^2 = 0.36$, $n = 63$, $P < 0.001$). Annual PP of Lake Võrtsjärv calculated according to the above described formulae of Håkanson & Boulion (2002) and Boulion (2003) on the basis of Lat and TranLat gave the corresponding values of 880 and 480, which overestimate the real PP in the lake fourfold and twice, accordingly. Basing on this simple comparison, it is evident that besides global large-scale estimations, the direct measurements and local modelling are indispensable to calculate the carbon budget and to understand lake metabolism. Figure 9 shows, however, that Võrtsjärv is located rather close to the

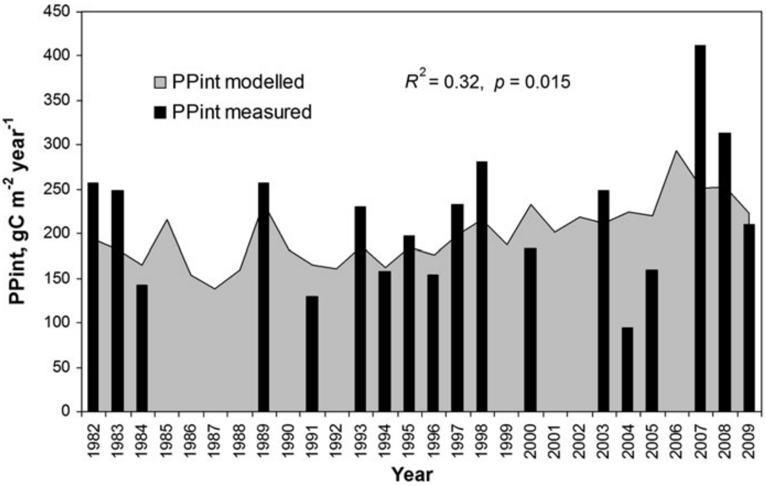

Fig. 5 Measured and modelled annual primary production in Võrtsjärv in years from 1982 to 2009

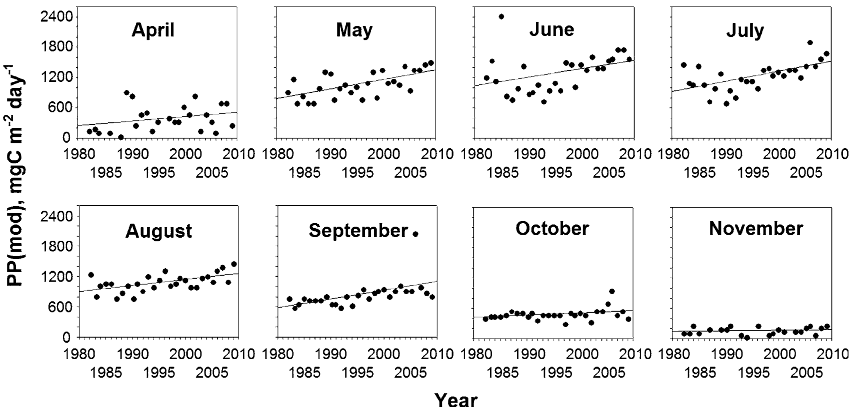

Fig. 6 Modelled daily primary production in Võrtsjärv during ice-free months over the study period of 1982–2009. *Straight lines* show linear trends (R^2 from 0.02 to 0.38, $P < 0.05$)

nutrient-saturated production boundary determined by Lat, where light limitation has the leading role. Theoretically, its productivity could increase if the relative proportion of chlorophyll among optically active substances (Chl, yellow substance and suspended solids) would increase. On average, these three components account almost equally for light attenuation in Võrtsjärv (Nõges, 2000).

Our measured PP database covers only 18 years while several other data series from Võrtsjärv started already in 1960s and by now cover a nearly 50-year time period. In order to fill the gaps in measurements and, potentially, to extend the PP data to the whole period of existing biological and chemical data, we selected the modelling approach. The bio-optical model developed for Võrtsjärv, which calculates primary production as a function of chlorophyll and light was a good descriptor for both volumetric and integral PP (Arst et al., 2008) giving strong and highly significant ($R^2 = 0.9$, $P < 0.0001$) correlations between synchronously measured and modelled PP. At daily and monthly scales, the modelled PP values, as based on real sums of irradiance, should be more accurate than the measured values which

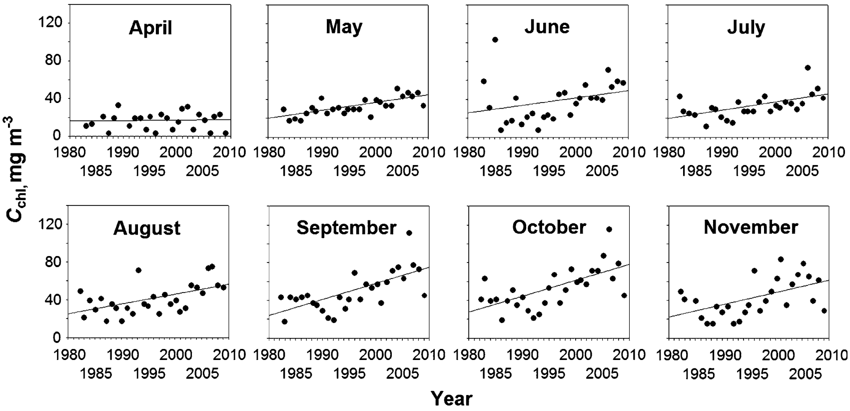

Fig. 7 Concentration of chlorophyll a (C_{chl}) in Võrtsjärv by months over the study period of 1982–2009. *Straight lines* show linear trends (since May, R^2 from 0.08 to 0.46, $P < 0.05$)

capture the light conditions of a couple of midday hours in single days only and introduce a large uncertainty to the daily estimates. The high daily and monthly variation of measured PP_{int} values (Fig. 4) show that the calculation of monthly average PP_{int} based on one or two measured daily values only, could give strongly erroneous estimates.

There are two interrelated possible explanations for the long-term stability of the measured PP on the background of increasing C_{chl}: (1) that the increase in C_{chl} was an adaptive response of phytoplankton to a deterioration of light conditions and (2) that some other factor caused the succession of dominating species having different rates of chlorophyll specific photosynthesis. Adaptation of phytoplankton to deteriorating light levels may include photoacclimation of existing species or, if exposure to dim light is prolonged, also succession of species in the favour of more shade tolerant ones. A simple strategy to survive sub-optimal light conditions is to increase the cellular content of light-harvesting pigments in order to maintain productivity (Falkowski & Owens, 1980; Dubinsky & Stambler, 2009; Yacobi & Zohary, 2010). Phytoplankton species differ largely by their ability to increase cellular chlorophyll content (Johnsen & Sakshaug 2007). Experiments with *Limnothrix redekei* (Foy & Gibson, 1982), the species that dominated in Võrtsjärv in the beginning of our study period, showed the species ability to more than triple its cellular chlorophyll content under low light doses. In Võrtsjärv the long-term increase in cellular chlorophyll content observed in autumn was much smaller but still significant and covered the period from 1988 onward during which the proportion of *L. planctonica* among dominants was continuously increasing.

In order to explain the increase of C_{chl} by a deterioration of light conditions, the latter has to be shown. Besides the underwater light climate calculations based on Secchi depth (Fig. 8A), also some other arguments suggest that light conditions have changed over the years: (1) although it seems a circular argument, the significant increase in C_{chl} itself (Fig. 7) must have had an effect on light conditions and, hence, the increase in C_{chl} could be caused by self-shading of phytoplankton; (2) a comparison of historical beam attenuation measurements from 1913 (Mühlen, 1918) with those from 2000 to 2001, Reinart & Nõges (2004) found that the absorption at 453 nm has significantly increased and therefore amount of dissolved organic matter in water may be higher nowadays than it was in the beginning of century. Given the general “browning” trends in many lakes over the northern hemisphere (Jennings et al., 2010), an increase of humic matter content in Võrtsjärv over a longer period cannot be excluded. An increase in water colour coinciding with high water levels in 1978–1979 has been suggested as the main cause for the earlier switching of phytoplankton dominants from *Planktolyngbya limnetica* (Lemm.) J. Komárková-Legnerová to *Limnothrix redekei* (Nõges et al., 2010a; Tuvikene et al., 2010); (3) chemical

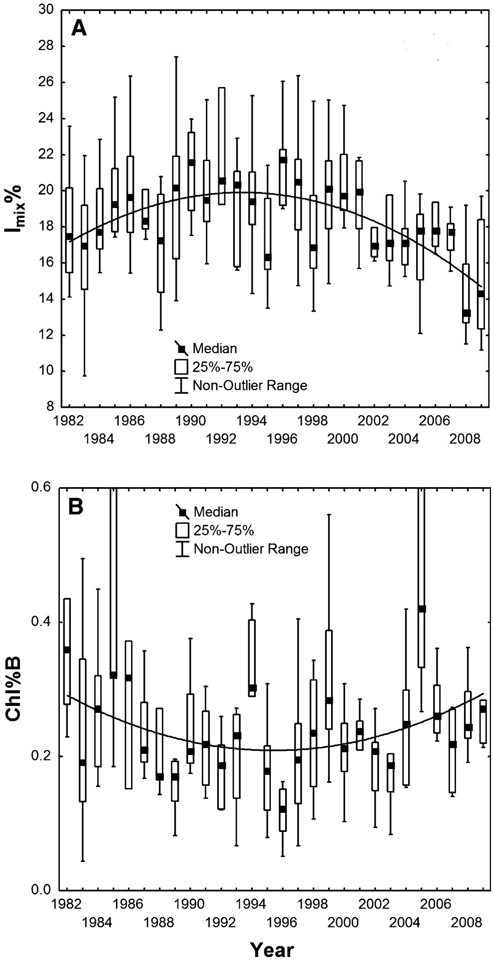

Fig. 8 Long-term adaptive response of phytoplankton to changing light conditions in Võrtsjärv. **A** Average solar irradiance in the mixed water column as the fraction of incident irradiance at the water surface during ice-free period; **B** percentage of chlorophyll *a* in total phytoplankton biomass during the ice-free period. *Curves* show the quadratic fitting line

oxygen demand COD_{Mn}, a common proxy for dissolved organic matter (DOM), was significantly lower in the period 1968–1977 compared with that in 1998–2008 and had a highly significant increasing trend within both periods (Tuvikene et al., 2010). Potassium permanganate, a much milder oxidizer compared to the more often used potassium dichromate, is highly sensitive to variations in dissolved organic matter, including humic substances (Xia et al., 2005). A correlations analysis between limnological variables in 102 Estonian lakes (Milius & Starast, 1999) found the strongest correlation among all analysed 14 variables between COD_{Mn} and water colour ($r = 0.97$) that allows using COD_{Mn} as a proxy for water colour.

As a conclusion, an increase in C_{chl} and a decrease in chlorophyll specific production rate in response to deteriorated light conditions is the most likely explanation to the different long-term trends in modelled and measured PP.

Figure 7 shows that in the long-term, there was a breaking point in the trend of the C_{chl} series in the beginning of 1990s and that the biggest increase in C_{chl} has taken place in autumn. A comparison of these changes with the biomass dynamics of *Limnothrix planctonica* in Fig. 10 (Nõges et al., 2004, updated) show a striking correspondence suggesting strongly that the C_{chl} change was caused by the emerging new dominant. Both *Limnothrix* species are considered true shade tolerants (Chomérat et al., 2007; Padisák et al., 2009) and occupy generally a similar niche in turbid polymictic lakes. Both species contain besides chlorophylls also phycocyanin, an additional photosynthetic pigment that has been shown as one of the main advantages in cyanobacteria in competition for light in turbid environments (Tilzer, 1987). The only major autecological difference between the two species in Võrtsjärv was expressed in their different seasonality and this may be the key to the observed inconsistency between C_{chl} and PP changes. The biomass of *L. planctonica* increases steadily during the vegetation period and, in the absence of major loss mechanisms, builds up a considerable standing stock by autumn. This standing stock is characterised by high C_{chl} which simulates a higher PP(mod) for this period as seasonal or species specific differences in chlorophyll specific productivity are not included in PP model. It leads to some change of the specific absorption coefficients of the phytoplankton that was not taken into account in the model, which used the algorithm by Bricaud et al. (1995). The late autumn biomass was characterised also by higher cellular chlorophyll content that explains the positive trend in C_{chl}/B ratio over the period when the proportion of *L. planktonica* increased in the phytoplankton community, i.e. since the early 1990s. This smooth succession of dominants

Table 3 Phytoplankton primary productivity (PP) of some individual lakes in g C m^{-2} y^{-1}

Lake name	Latitude	PP	Reference
Verkhneye, Schirmacher Oasis, Antarctica	68.6	0.6	Kaup (1994)
Mexcut L1, USA	39.0	1.3	Dodson et al. (2000)
Long, USA	40.1	1.5	Dodson et al. (2000)
Latnjajaure, Swedish Lappland	68.4	2.7	Dodson et al. (2000)
LaCaldera, Spain	37.1	3.4	Dodson et al. (2000)
Char, USA	74.7	4.1	Dodson et al. (2000)
Toolik, USA	68.6	5.5	Dodson et al. (2000)
Imikpuk, Alaska	71.3	8.4	Dodson et al. (2000)
Watts Lake, Vestfold Hills, Antarctica	68.6	10	Heath (1988)
Onega, Russia (May-Oct)	61.5	11	Syarki & Tekanova (2008)
Great Bear Lake, Canada	66.0	18	De Vooys (1979)
Lake 239 ELA, Canada	49.7	21	Dodson et al. (2000)
Eckarfjärden, Sweden	60.4	24	Andersson & Kumblad (2006)
Tahoe, Sierra Nevada, USA	39.1	36	De Vooys, 1979
Great Slave Lake, Canada	61.7	37	De Vooys (1979)
Lawrence, USA	42.4	41	Dodson et al. (2000)
Mirror, USA	43.9	47	Dodson et al. (2000)
Superior, USA	47.7	60	De Vooys, (1979)
Paul, USA	46.2	60	Dodson et al. (2000)
Huron, USA	44.8	85	De Vooys (1979)
Biwa, Japan	35.3	88	Dodson et al. (2000)
Little Rock, USA	46.0	91	Dodson et al. (2000)
Superior, USA	47.7	94	Sterner (2010)
Washington	47.6	96	Dodson et al. (2000)
Gull, USA	42.4	102	Dodson et al. (2000)
Trek, USA	43.1	110	Hoffmann & Dodson (2005)
Baikal, Russia	53.5	113	De Vooys (1979)
Sparkling, USA	46.0	134	Dodson et al. (2000)
Michigan, USA	44.0	145	De Vooys (1979)
Crystal, USA	46.0	149	Dodson et al. (2000)
Trout, USA	46.1	153	Dodson et al. (2000)
Constance, Lower Basin, Switzerland	47.7	164	De Vooys (1979)
Krankesjön, Sweden (May-Sept)	55.7	166	Blindow et al. (2006)
Thonotosassa, USA	28.0	166	Dodson et al. (2000)
Acton, USA	39.6	181	Dodson et al. (2000)
Ontario, USA	43.7	185	De Vooys (1979)
Plusssee, Germany	54.2	187	Dodson et al. (2000)
Memphremagog, Canada	45.1	197	Hoffmann & Dodson (2005)
Hall, USA	47.8	200	Hoffmann & Dodson (2005)
Peipsi, Estonia/Russia	58.7	200	Nõges et al. (2001)
Võrtsjärv, Estonia	58.3	208	Present study
Erie, USA	42.2	240	De Vooys (1979)
Fish, USA	43.2	292	Dodson et al. (2000)
Buckeye, USA	43.1	310	Hoffmann & Dodson (2005)

Table 3 continued

Lake name	Latitude	PP	Reference
Mendota, USA	43.1	342	Dodson et al. (2000)
Monona, USA	43.1	343	Dodson et al. (2000)
Wingra, USA	43.1	345	Dodson et al. (2000)
Wintergreen, USA	42.4	369	Dodson et al. (2000)
IJssel, The Netherlands	52.6	400	De Vooys (1979)
Börringesjön, Sweden (May-Sept)	55.5	413	Blindow et al. (2006)
Nakuru, Africa	0.4	467	De Vooys (1979)
St. George, USA	44.0	548	Dodson et al. (2000)
Suwa, Japan	36.0	557	Dodson et al. (2000)
Tjeukemeer, Netherlands	52.1	567	Hoffmann & Dodson (2005)
Highway, USA	43.1	572	Hoffmann & Dodson (2005)
Portage, USA	43.2	575	Hoffmann & Dodson (2005)
Ziegler, USA	43.2	605	Hoffmann & Dodson (2005)
Kasumigaura, Japan	36.2	608	Dodson et al. (2000)
Kinneret, Israel	32.8	619	Dodson et al. (2000)
Lanao, Philippines	8.8	621	Dodson et al. (2000)
Valencia, Venezuela	10.1	821	Dodson et al. (2000)
Clear, California, USA	39.1	913	De Vooys (1979)
MadMetro2B, USA	43.0	1300	Dodson et al. (2000)

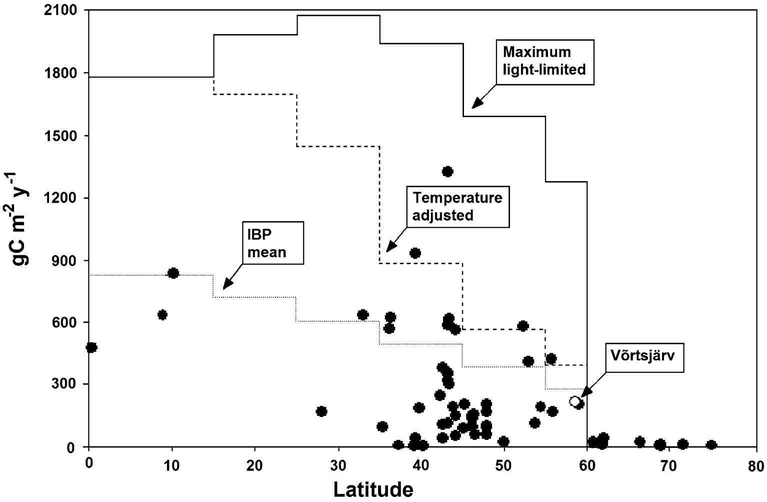

Fig. 9 Latitudinal trends in primary production (PP) redrawn from Lewis (1996) and combined with data on single lakes presented in Table 3. *Top line*: modelled maximum PP for nutrient-saturated conditions if there was no thermal gradient with latitude (the latitudinal trends can be traced mainly to latitudinal gradients in minimum monthly solar irradiance); *middle line*: the same adjusted for the temperature effect on optimum photosynthesis rate (Q_{10} about 2); *bottom line*: empirical mean of measurements within the International Biological Program. According to this scheme, Võrtsjärv is located very close to light limitation boundary

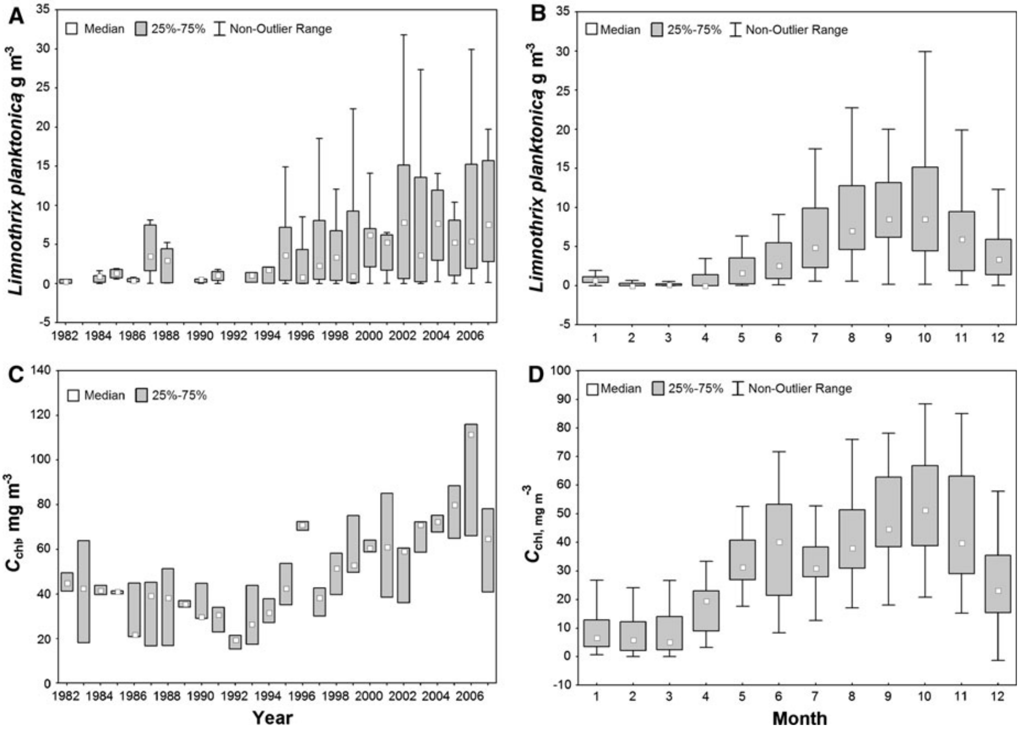

Fig. 10 Long-term (**A**) and average seasonal dynamics (**B**) of *L. planctonica* biomass in Võrtsjärv (modified from Nõges et al., 2004) compared to long-term autumn C_{chl} in September–December (**C**) and average seasonal changes of C_{chl} (**D**) over the study period 1982–2009

could explain the absence of any significant trend in annual PP values.

Still the question remains, what caused the succession between the two *Limnothrix* species. Resource limited conditions favour the species which has even a small advantage in exploiting the limiting resource. Building up a higher biomass by extending the growth period towards autumn may be a clear advantage in light-limited conditions. The earlier dominant and present subdominant *L. redekei* reaches its biomass peak in June but in summer its gas vacuoles collapse and the cells autolyse. The regular collapse of gas vacuoles in *L. redekei* in summer is a very common phenomenon not only in Võrtsjärv but has been mentioned also for Edebergsee, where trichomes with no or only small gas vacuoles dominated at high light intensities (Meffert & Krambeck, 1977). Such collapse has not been described in *L. planctonica*, which has much smaller gas vacuoles *per se*. A study of the filament length structure in the two *Limnothrix* species (Nõges, 1999) suggested the selective sedimentation of longer filaments of *L. redekei* with collapsed gas vacuoles as the main loss factor of this species in summer. A CCA analysis for 44-year data on species composition and environmental variables (Nõges et al., 2010a) showed that in Võrtsjärv *L. redekei* was favoured by increasing water level and *L. planktonica* by increasing temperatures in summer and autumn. Trend analysis for the period 1961–2004 (Nõges, 2009) revealed a highly significant ($P < 0.01$) upward trend for water temperature in August with a significant ($P < 0.05$) stepwise increase in 1989. Hence, we suppose that the initial breakthrough of *Limnothrix* species in early 1980s was caused by the sudden deterioration of light conditions following a water level increase in 1978/1979 (Nõges & Järvet, 1995; Nõges et al., 2010a; Tuvikene et al., 2010) while the consequent gradual increase of the proportion of

L. planktonica could be more related to the late summer warming trend.

The relationship between the annual PP_{int} values, based on measurements and modelling found in this paper ($R^2 = 0.32$) is much weaker compared with the $R^2 = 0.9$ reported in Arst et al. (2008). However, in Arst et al. (2008) the results were obtained from 2-h measurement series of PP with full (without breaks) complex of initial data for model calculations, that is not so for long-term estimations. In general, there can be a number of errors included both in the modelling and the measured data.

Excluding other methodological errors potentially included in the ^{14}C technique for measuring PP (see overview by Marra, 2002), the sources of error in summarising the measured data are included in the depth integration of the discrete vertical measurements, the extrapolation of the PP values around noon to the whole day (Richardson, 1991), but the major source of errors is included in the interpolation of the highly variable but infrequently measured daily PP values. The latter is largely avoided by modelling in which we used the true monthly mean values of daily irradiances and only the values of C_{chl}, a less variable parameter compared to PP, were interpolated between discrete measurements.

Conclusions

- Our aim was to summarise the long-term primary production measurements in Võrtsjärv in order to receive reliable daily, monthly and annual estimates of this parameter as the first step in the lake's carbon balance calculations. The results will provide further basis for long-term studies of the ecosystem metabolism and its climate sensitivity.
- According to the long-term annual PP (208 ± 27 g C m^{-2} y^{-1}) Võrtsjärv is located rather close to the nutrient-saturated production boundary determined by latitude where light limitation has the leading role. This assignment is supported by the phytoplankton composition dominated by eutrophic highly shade tolerant cyanobacteria species from the genus *Limnothrix.*
- The semi-empirical primary production model based on continuous irradiance (PAR) measurements and interpolated values for chlorophyll concentration and light attenuation coefficient simulated sufficiently well the interannual changes in PP.
- Increasing trend in the long-term PP(mod) series (induced by increasing C_{chl}) was not supported by measured PP. This controversy can be explained by an adaptive increase in the cellular C_{chl} content in phytoplankton in response to deteriorated light conditions, and the change of dominating species from *Limnothrix redekei* to *L. planctonica.* The latter is characterised by a seasonally later biomass peak in Võrtsjärv and lower chlorophyll specific productivity not taken into account in the model.
- We consider the developed PP model a useful tool for filling the gaps in the measured data and potentially extending the PP data series over periods for which other biological and chemical data are available. The model can be improved, however, by including seasonal and species specific correction factors to the chlorophyll specific productivity.

Acknowledgments The study was supported by Estonian target funding project SF 0170011508, by grants 5594, 7156 and 7600 from Estonian Science Foundation, by 7th EU Framework Programme, Theme 6 (Environment including Climate Change) project REFRESH (Adaptive strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems, Contract No.: 244121), and by the Doctoral School of Earth Sciences and Ecology created under the auspice of European Social Fund.

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Pall, P.; Vilbaste, S.; Kõiv, T.; Kõrs, A.; Käiro, K.; **Laas, A**.; Nõges, P.;
Nõges, T.; Piirsoo, K.; Toomsalu, L. And M. Viik, 2011.
FLUXES OF CARBON AND NUTRIENTS THROUGH THE
INFLOWS AND OUTFLOW OF LAKE VÕRTSJÄRV, ESTONIA.
Estonian Journal of Ecology, 60(1), 39 - 53.

Estonian Journal of Ecology, 2011, **60**, 1, 39–53 doi: 10.3176/eco.2011.1.04

Fluxes of carbon and nutrients through the inflows and outflow of Lake Võrtsjärv, Estonia

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Received 1 June 2010, revised 12 January 2011

Abstract. We determined the incoming fluxes of total organic carbon (TOC), dissolved inorganic (DIC) and organic carbon (DOC), nitrogen, phosphorus, and silicon via four main inflows into Lake Võrtsjärv and compared these with the outgoing fluxes from the lake during 2008–2009. The discharge and loads of the studied substances from the four main rivers alone were higher than the amounts carried out of the lake in 2008. In 2009, the outflow of water exceeded the inflows and this was the case with the amounts of TOC, DIC, and DOC as well. However, the incoming load of nutrients was continuously higher than the outgoing load. The lake accumulated nutrients (nitrogen, phosphorus, and silicon) irrespective of whether water retention was positive or negative, but the balance between carbon accumulation and carbon emission depended on the lake's water budget.

Key words: carbon, inflows, Lake Võrtsjärv, nutrients, outflow.

Abbreviations: TOC – total organic carbon, DIC – dissolved inorganic carbon, DOC – dissolved organic carbon, TC – total carbon, TIC – total inorganic carbon, DC – dissolved carbon, TN – total nitrogen, TP – total phosphorus.

INTRODUCTION

It has become increasingly important to quantify carbon and nutrient fluxes in the environment owing to their role in the processes of global warming, climate change, and eutrophication of water bodies. Generally, global warming intensifies the hydrological cycle and increases the magnitude and frequency of extreme climatic phenomena, including heavy rainfalls in most parts of Europe (Christensen & Christensen, 2003), which cause abrupt fluctuations in the discharges of rivers (Graham et al., 2006). Concentrations of different substances in river water are related to discharge but this relationship is commonly nonlinear (Volk et al., 2002). High concentrations of dissolved organic matter may occur during floods as well as in low water periods. Although the content of dissolved organic matter is generally high in high water periods, the highest concentrations have been measured at relatively low water (Royer & David, 2005). The same phenomenon was also reported for mineral substances and nutrients (Järvet, 2003; Bärlund et al., 2009).

Lake Võrtsjärv, the second largest lake in the Baltic countries, represents one of the most intensively investigated inland water bodies in Estonia (Haberman et al., 2004 and references therein). The catchment area of the lake is 3104 km^2 and it receives DOC and nutrients via four main inflows (Väike Emajõgi, Õhne, Tänassilma, and Tarvastu).

Earlier calculations of the nitrogen and phosphorus budgets of Lake Võrtsjärv were based on monthly data from 1988–1991 (Nõges & Järvet, 1998), on weekly measurements in 1995 (Nõges et al., 1998), as well as on the annual mean for 23 years (1980–2002) (Järvet, 2004a). A downward trend for the total loadings of nitrogen and phosphorus into Lake Võrtsjärv since the early 1990s was reported by Järvet (2004a), and a downward trend for nutrient concentrations for several inflows was reported by Iital et al. (2010). There are no calculations of silicon loadings into the lake. A single study exists of the temporal dynamics of silicon fluxes into the lake via one inflow (Väike Emajõgi) (Nõges et al., 2008). Tamm et al. (2008) studied the import of DOC into the lake; in their paper the loading of DOC was calculated indirectly from the chemical oxygen demand (COD_{Mn}). Until now there are no data about direct measurements of carbon fluxes into Lake Võrtsjärv.

This study is part of a larger project whose goal was to establish a budget of organic matter and nutrients of Lake Võrtsjärv in order to answer the question whether the lake is a carbon-emitting or a carbon-binding system. The aim of this study was to determine the incoming fluxes of carbon (TOC, DIC, DOC), nitrogen, phosphorus, and silicon into Lake Võrtsjärv via the four main inflows. The main objective was to compare these incoming fluxes with the outgoing fluxes from the lake. We posed the following questions: (i) What is the magnitude of different fluxes? (ii) Which substances does the lake accumulate or release? (iii) Is there any seasonal regularity in the course of fluxes of different substances?

MATERIAL AND METHODS

Lake Võrtsjärv is located in the southern part of Estonia (Fig. 1). Through the outflowing Emajõgi River its catchment area forms a sub-catchment of Lake Peipsi, the fourth largest lake in Europe. Forest and wetlands occupy more than 50% of the catchment area of Lake Võrtsjärv (Table 1). The lake is natural and unregulated. The main four inflows make up about 75% of total discharge from the catchment (Järvet et al., 2004).

Long-term fluctuations and changes of the water level of the lake during the study period are presented in Fig. 2. The years 2008 and 2009 were hydrologically different for Lake Võrtsjärv. From January to December 2008 the water level rose

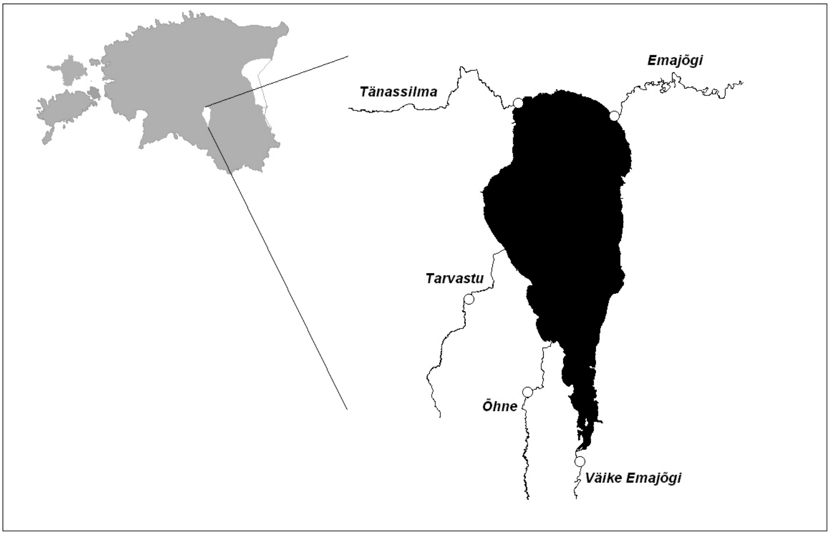

Fig. 1. Sampling stations of the four main inflows and the outflow of Lake Võrtsjärv.

Table 1. River characteristics and land types in the catchment areas according to Järvet (2003)

River	Length, km	Catchment area, km^2	Land type, %			
			Forest	Wetland	Agricultural	Other
Väike Emajõgi	83	1380	61	2	33	4
Õhne	94	573	61	6	32	1
Tänassilma	34	454	57	5	35	3
Tarvastu	22	108	51	0.5	48	0.5

significantly but in December 2009 it was only slightly lower than in December 2008. This means that in 2008 the lake collected water but lost only a small part of it in 2009. In 2008 the annual mean air temperature was 7.2 °C and total precipitation was 875 mm. In 2009 the respective figures were 6.0 °C and 806 mm.

Water samples were collected from the lower course of the inflows and from the outflow of the lake (Fig. 1) at least monthly in 2008 and 2009. Additionally, we used the data of nutrient concentrations drawn from the National Monitoring Programme.

The content of TOC, DIC, and DOC was quantified at the Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, using the TOC analyser and standard methods (ISO 8245, 1987; EN 1484, 1992). All

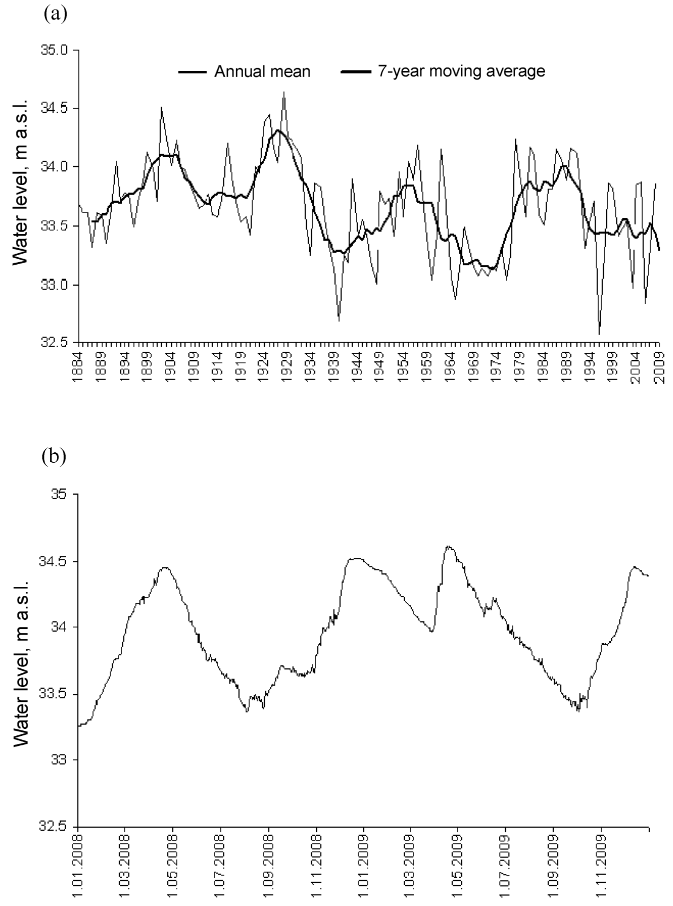

Fig. 2. Long-term fluctuations (1884–2009) (a) and changes during the study period (2008–2009) (b) of the water level of Lake Võrtsjärv (a.s.l. – above sea level).

methods for determining carbon compounds in the water samples were based on the oxidation of organic compounds into carbon dioxide (CO_2), which was then detected quantitatively. The Dr. Lange TOC cuvette tests LCK 380 involve wet chemical oxidative digestion followed by photometric determination of the CO_2. Oxidation of organic compounds took place at 100 °C in the thermostat Hach/Lange LT 200, with a reaction time of 2 h. The CO_2 from the digestion cuvette was passed through a gas-permeable membrane into an indicator cuvette. The resulting colour change in the indicator was evaluated with Dr. Lange photometer DR 2800. We used the difference method: TC – TIC = TOC. Dissolved organic carbon was measured from filtrated water in the same way: DOC = DC – DIC (Kraatz & Wochnik, 1998).

Analysis of the content of nutrients (TN, TP, Si) was carried out in the laboratory of Tartu Environmental Research Ltd. The obtained data are comparable and reliable owing to the implementation of a quality assurance programme and the annual international inter-laboratory testing of chemical laboratories according to the standard ISO/IEC 17025: 2005 for analysing monitoring samples.

Daily flow values and water level data were obtained from the National Monitoring Programme. To calculate the water discharge of the rivers, the daily flow measured in the gauging station of the river was multiplied by a coefficient that considers the distance of the gauging station from the river mouth and the peculiarities of the river basin (Järvet, 2005).

Water chemistry values were linearly interpolated between the sampling dates and the calculated values were multiplied by the values of the daily discharge to obtain daily loads. Further, monthly and annual loads were calculated.

We calculated Spearman's Rank Order Correlations to relate discharges, loadings, and concentrations. Differences at the $p < 0.05$ level were accepted as significant. The software STATISTICA for Windows 8.0 (StatSoft, Inc., 2007) was applied.

RESULTS

The lowest mean and median nutrient and DIC concentrations were recorded in the outflow of the lake (Table 2). The lowest DOC and TOC concentrations were found in the Tarvastu River. The highest DOC and TOC values occurred mostly in the Tänassilma River. The real maximum, however, was registered in the Väike Emajõgi River. The Tänassilma was the richest in phosphorus and the Tarvastu, in nitrogen (Table 2). The concentrations of TN and Si were higher in winter and lower in summer. The spring decrease appeared earlier in the concentration of Si than in TN. The concentration of TP rose from April to January and decreased thereafter. The concentrations of TOC and DOC were higher from June to January and lower from February to June. The seasonal dynamics of DIC was quite indistinct except for a sharp decrease after ice breaks – a phenomenon characteristic of all rivers (Fig. 3).

The daily hydrological load from the four main inflows varied from 0.4×10^6 m^3 (11.06.2008) to 14.7×10^6 m^3 (8.04.2009) and from the outflow, from 0 to 4.2×10^6 m^3 (1.05.2009). The lake had no outflow in the periods 22.01.–23.01.2008, 1.11.–8.11.2008, and 28.10.–29.10.2009 when a backflow (max 0.37×10^6 m^3 d^{-1}) occurred in the Emajõgi. The inflow of water from the four studied rivers predominated over the outflow in winter and spring 2008, in spring 2009, and in some periods in the autumn of both years (see Fig. 4).

In 2008 the annual discharge of the four inflows exceeded the outflow; in 2009, vice versa, the outflow was higher than the inflows. A similar situation was observed for all studied substances (Table 3). In 2008, 21 400 t of TOC, 40 360 t of DIC, and 19 900 t of DOC entered the lake via the four studied rivers. In 2009

Table 2. Ranges of the concentrations (mg L^{-1}) of total organic carbon (TOC), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), total nitrogen (TN), total phosphorus (TP), and silicon (Si) in the main inflows and in the outflow of Lake Võrtsjärv in 2008–2009

Substance	*n*	Mean	Median	Minimum	Maximum
Väike Emajõgi					
TOC	26	22.53	20.35	12.00	53.40
DIC	26	43.58	45.00	26.50	54.90
DOC	26	18.76	18.55	3.00	47.60
TN	45	1.54	1.50	0.52	3.10
TP	45	0.05	0.05	0.03	0.07
Si	27	2.90	3.00	1.50	4.30
Õhne					
TOC	26	21.88	21.10	11.70	32.30
DIC	26	41.15	44.05	22.00	52.60
DOC	26	19.43	19.55	10.00	30.10
TN	45	1.77	1.70	0.77	3.30
TP	43	0.05	0.05	0.03	0.09
Si	27	2.55	2.50	1.30	4.50
Tänassilma					
TOC	26	23.52	22.50	11.60	37.00
DIC	26	51.85	51.30	34.60	72.20
DOC	26	21.44	21.40	7.10	33.80
TN	45	2.21	2.20	0.57	4.60
TP	45	0.07	0.07	0.01	0.13
Si	27	2.30	2.10	0.30	4.60
Tarvastu					
TOC	26	20.22	16.85	9.40	48.40
DIC	26	51.35	54.00	32.70	64.00
DOC	26	16.95	15.80	2.90	33.40
TN	39	2.62	2.50	0.91	5.10
TP	39	0.05	0.05	0.03	0.08
Si	27	2.60	2.60	1.40	3.90
Emajõgi (outflow)					
TOC	26	21.58	21.95	12.90	36.20
DIC	26	35.72	35.15	28.00	46.70
DOC	26	17.72	18.20	12.00	21.60
TN	51	1.43	1.40	0.28	3.60
TP	50	0.04	0.04	0.02	0.08
Si	36	1.94	2.05	0.17	3.10

the respective amounts were much lower, 18 300 t, 35 300 t, and 15 200 t. Similarly, in 2008 the incoming amounts of nutrients were higher, 2270 t of TN, 49 t of TP, and 2500 t of Si, while in 2009 the respective amounts were 1500 t, 44 t, and 2400 t.

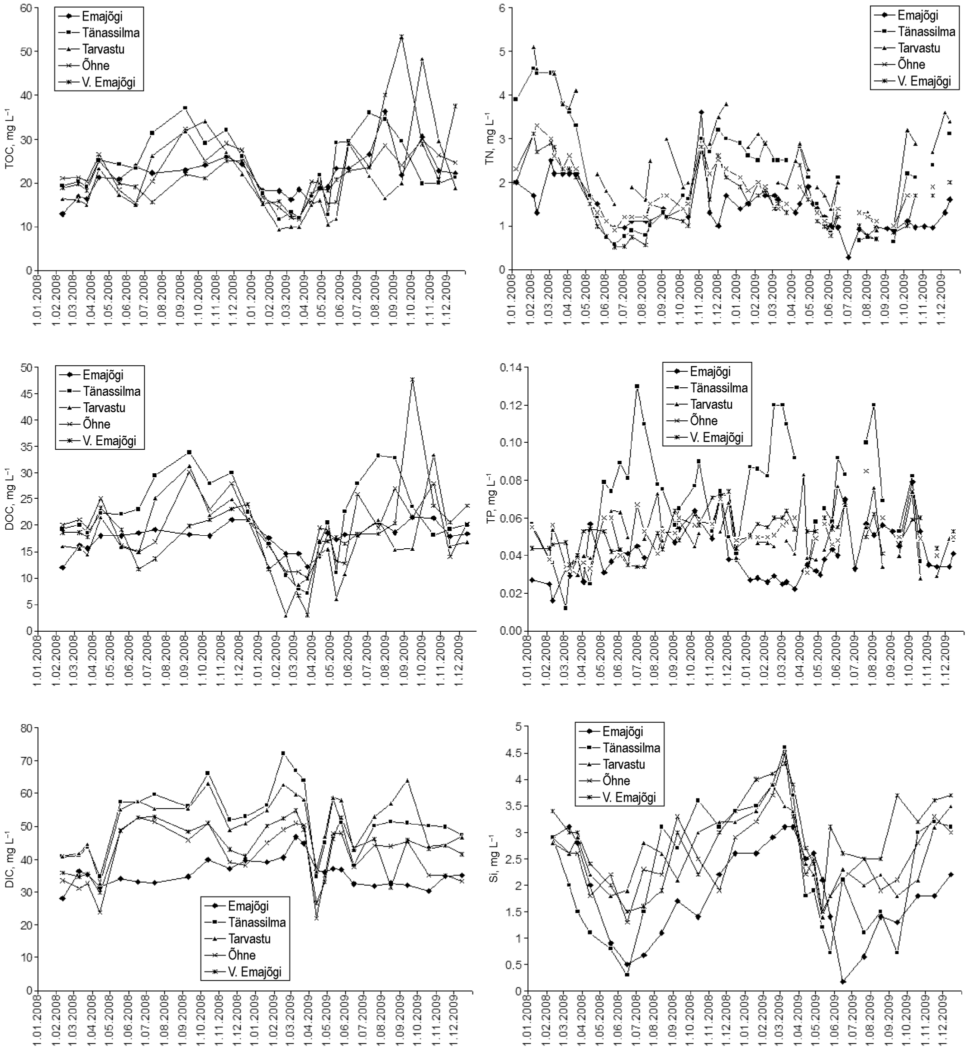

Fig. 3. Dynamics of the concentrations of total organic carbon (TOC), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total nitrogen (TN), total phosphorus (TP), and silicon (Si) in the outflow (Emajõgi) and in the main inflows (Väike Emajõgi, Õhne, Tänassilma, Tarvastu) of Lake Võrtsjärv in 2008 and 2009.

Data from 2008 showed that the inflow of water and the studied substances from the four main rivers alone were higher than the respective amounts carried out of the lake. In 2009 the outflow of water exceeded the inflow and this was also the case with TOC, DIC, and DOC. However, the incoming load of nutrients was continuously higher than the load of outgoing nutrients. More detailed data are presented in Fig. 5.

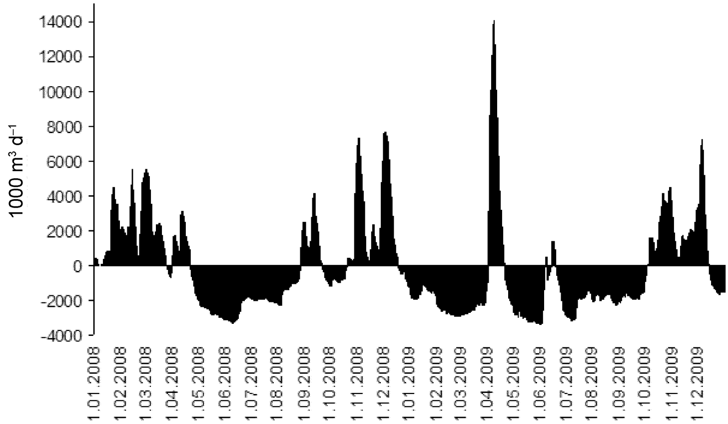

Fig. 4. Daily differences between the sum of discharge from the four main inflows (Väike Emajõgi, Õhne, Tänassilma, Tarvastu) and the outflow (Emajõgi) of Lake Võrtsjärv in 2008 and 2009.

Table 3. Discharge (Q, 10^6 m^3) and loadings (tonnes) of total organic carbon (TOC), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), total nitrogen (TN), total phosphorus (TP), and silicon (Si) into Lake Võrtsjärve via four main inflows and in the outflow in 2008 and 2009

River	Year	Q	TOC	DIC	DOC	TN	TP	Si
Väike Emajõgi	2008	445	9 490	18 722	8 859	944	24	1 301
	2009	401	9 329	17 378	7 432	668	22	1 302
Õhne	2008	231	5 591	9 139	5 153	534	12	574
	2009	206	4 651	7 836	3 937	343	10	562
Tänassilma	2008	207	5 348	10 369	4 996	632	11	536
	2009	166	3 430	8 119	3 195	383	10	432
Tarvastu	2008	44	981	2 131	896	156	2	122
	2009	39	865	1 924	658	100	2	106
Emajõgi (outflow)	2008	788	17 029	27 484	14 422	1 216	34	1 306
	2009	1 052	23 307	39 197	18 692	1 329	41	1 993

Spearman's nonparametric correlations were stronger between water discharge and loadings of substances than between concentrations and loadings (Table 4). In some cases, correlations between loadings and concentrations were non-significant or even negative as in the case of DIC in the inflows. There were significant negative correlations (from –0.6 to –0.84) also between DIC concentrations and water discharges in the inflows. We found strong positive correlations

(>0.66) between water discharge and nitrogen concentration. Correlations between water discharge and phosphorus concentration were positive for some inflows, negative for some, and non-significant for some. Correlations between water discharge and TOC and DOC concentrations for the Õhne River were weak but significant.

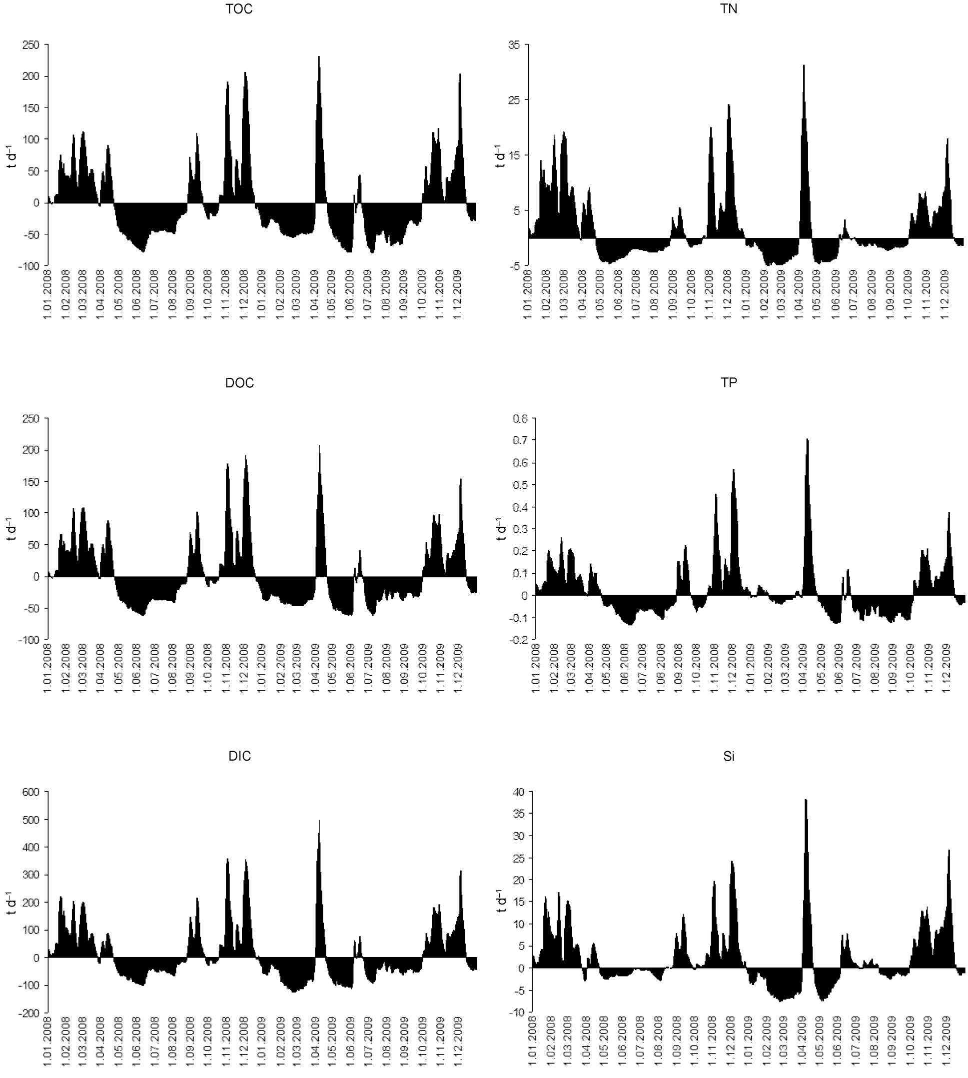

Fig. 5. Daily differences between the sum of loads of total organic carbon (TOC), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total nitrogen (TN), total phosphorus (TP), and silicon (Si) in the main inflows (Väike Emajõgi, Õhne, Tänassilma, Tarvastu) and the outflow (Emajõgi) of Lake Võrtsjärv in 2008 and 2009.

Table 4. Spearman's Rank Order Correlations between discharges (Q), loadings (L), and concentrations (C) of total organic carbon (TOC), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), total nitrogen (TN), total phosphorus (TP), and silicon (Si) in the main inflows and in the outflow of Lake Võrtsjärv; $p < 0.05$, n.s. – not significant

Variable	Correlations between		
	Q and L	Q and C	C and L
Väike Emajõgi			
TOC	0.87	n.s.	0.51
DIC	0.97	−0.72	−0.57
DOC	0.86	n.s.	0.69
TN	0.97	0.82	0.92
TP	0.98	0.34	0.45
Si	0.96	n.s.	0.47
Õhne			
TOC	0.94	0.48	0.70
DIC	0.96	−0.84	−0.69
DOC	0.95	0.47	0.71
TN	0.96	0.71	0.85
TP	0.95	n.s.	n.s.
Si	0.94	n.s.	0.39
Tänassilma			
TOC	0.90	n.s.	n.s.
DIC	0.98	−0.60	−0.49
DOC	0.89	n.s.	n.s
TN	0.93	0.66	0.87
TP	0.79	−0.70	n.s.
Si	0.80	n.s.	0.55
Tarvastu			
TOC	0.87	n.s.	0.66
DIC	0.98	−0.84	−0.74
DOC	0.88	0.27	0.64
TN	0.92	0.69	0.90
TP	0.92	−0.36	n.s.
Si	0.94	n.s.	0.44
Emajõgi (outflow)			
TOC	0.83	n.s.	n.s.
DIC	0.96	n.s.	0.46
DOC	0.91	n.s.	n.s.
TN	0.81	n.s.	0.48
TP	0.58	n.s.	0.56
Si	0.67	n.s.	0.74

DISCUSSION

Already in the first hydrochemical comprehensive study of Estonian water bodies by Simm (1975) it was shown that in our streams the content of inorganic substances is relatively high and the amount of dissolved organic matter never exceeds it. Because of the calcareous bedrock, the continuously higher amount of DIC, compared to DOC, is a characteristic feature of Estonian river waters. In the outflow of Lake Võrtsjärv, the mean concentration of inorganic carbon was twice as high and in the inflows even 2.5 to 3.5 times as high as that of organic carbon (Table 2).

The concentrations of TOC and DOC in the river system studied by us were higher than those reported from a lotic system in Canada (Finlay et al., 2010), from some streams in Germany (Sachse et al, 2005), and from lakes and rivers of Finland (Rantakari et al., 2004; Mattsson et al., 2007) and Poland (Siepak, 1999). Higher DOC concentrations were reported from streams draining peatland systems in Scotland (Dawson et al, 2004); however, a different method was used. The concentration of DIC varied more in our study compared with the study by Finlay et al. (2010).

The loads of DOC into Lake Võrtsjärv via the four main inflows estimated for the period 1990–2002 were 1320–4934 t y^{-1} (Tamm et al., 2008). Differences between our results and those reported by Tamm et al. (2008) are due to different methods used. We calculated the carbon load directly from carbon content, which is a far more exact method than deriving it from the chemical oxygen demand. According to our calculations, the amount of DOC was more than four times higher than reported previously. However, the concentrations of TOC and DOC in our study may be overestimated. In the analysis we used the difference method of Dr. Lange TOC cuvette test and not the purging method (Kraatz & Wochnik, 1998). The used method presumes that the TIC concentration is smaller than the TOC concentration in the water samples. In our samples the TIC concentrations were higher than the respective TOC concentrations. There is an assumption that total carbon analysis may overestimate the organic carbon content in fresh waters in the presence of high DIC (Findlay et al., 2010).

In 1995, 1930 t of N and 57 t of P were introduced into Lake Võrtsjärv (Nõges et al., 1998) and the annual mean values for 23 years (1980–2002) were 2752 t and 78 t, respectively (Järvet, 2004a). In 1995, 986 t of N and 44 t of P were discharged from Lake Võrtsjärv via the outflow (Nõges et al., 1998) and the respective values for the 23-year period were 1729 t and 39 t (Järvet, 2004a). Our results are in good accordance with the findings by Nõges et al. (1998) but show somewhat lower figures than those reported by Järvet (2004a). Here we have to consider the fact that there was a downward trend in the nutrient loadings and concentrations during more than the last 20 years (Järvet, 2004a; Iital et al., 2010). In line with earlier findings (Nõges et al., 1998; Järvet, 2004a), Lake Võrtsjärv accumulated nutrients. We found that also Si has been retained in the lake as in both years the inflow of all N, P, and Si from the four tributaries exceeded their outflow. There were, however, some differences between 2008 and 2009.

In 2008, all incoming fluxes were higher than the outgoing fluxes: only 80% of the introduced TOC was carried out of the lake. For DIC, DOC, TN, TP, and Si, the respective percentages were 68, 72, 54, 70, and 52. As we measured only the fluxes from the four main inflows but not the total flux, the percentages should even be lower. This means that Lake Võrtsjärv accumulated all the above substances in 2008.

In 2009, more carbon was carried out of the lake than was discharged via the four main inflows. Export was 127% for TOC, 111% for DIC, and 123% for DOC. Still, the percentage was lower than 100 for all nutrients: 89, 94, and 83 for TN, TP, and Si, respectively.

Several studies estimated only the concentrations of nutrients and DOC in stream water, without taking account of hydrology (Bernot et al., 2006; Eimers et al., 2008; Goodale et al., 2009; Iital et al., 2010). Discharge, however, is the primary factor determining the fluxes of nutrients and different carbon fractions into lakes. In 2008, when the discharge was 12.5% higher compared to 2009, all studied fluxes were also higher: TOC, 15%; DIC, 13%; DOC, 26%; TN, 34%; TP, 8%, and Si, 5%.

Daily differences between the values of the loads of the studied substances in the four main inflows and the outflow are presented in Fig. 5. In the case of positive values more substances entered than left the lake via the rivers. Negative values in the figure do not indicate that the lake necessarily emitted the substances as we only took into account four inflows. Daily differences in the loads of the substances (Fig. 5) and in the discharge (Fig. 4) vary only slightly and one may conclude that the lowest accumulation takes place in low water periods – in summer and under the ice cover in winter. Nevertheless, it is evident that nutrient uptake, which leads to the accumulation of N, P, and Si in the lake, is more intensive during the vegetation period, i.e. in summer. This was once again confirmed by our study (Fig. 3). As the retention period of water in Lake Võrtsjärv is about one year (Järvet et al., 2004) and the loading of substances is far more discharge-dependent than concentration-dependent (Table 4), comparison of daily differences may lead to confusing conclusions. Therefore, a longer period should be considered.

Our findings are consistent with those of Pastor et al. (2003) and Eimers et al. (2008), who showed that changes in stream flow have an essential impact on concentrations of chemical substances such as DOC. Like in hard-water lakes in Canada (Finlay et al., 2010), hydrologic inputs seem to play a more leading part in carbon fluxes than lake metabolism. It was shown that in Finland weather-driven fluctuation in discharge is the main reason for changes in nitrogen and phosphorus fluxes (Vuorenmaa et al., 2002; Bärlund et al., 2009). Nõges et al. (1998) pointed out that the seasonal dynamics of the load of nutrients (N and P) from the catchment of Lake Võrtsjärv depends on the hydrological load rather than on changes in nutrient concentrations. Also the load of Si is strongly linked to water discharge in the catchment of Lake Võrtjärv (Nõges et al., 2008).

The years 2008 and 2009 were different in respect of the hydrological regime of Lake Võrtsjärv (Figs 2 and 4). In 2008, the outflow accounted for only 91% of the four main inflows and water accumulated in the lake. In 2009, the respective figure was 130%, indicating that more water flowed out of the lake than entered it. The length of the ice-free period in the two years was also different. In 2008, Lake Võrtsjärv froze only for a short period in January, while in 2009 the permanent ice cover lasted until late March. As is evident from Fig. 4, the difference between the inflow and outflow in late winter and early spring was positive in 2008 but negative in 2009. In the warm season differences in the discharges between the study years were not so distinct. The difference was negative from May to August in 2008 and from May to September in 2009. This is in good concordance with the annual mean water balance for Lake Võrtsjärv, which is negative for February, May, June, July, August, and September and positive for the remaining six months (Järvet, 2004b). As the discharge was the more important component of the loading, it is clear why the fluxes of substances differed between the study years.

CONCLUSIONS

Tens of thousands of tonnes of TOC, DIC, and DOC, thousands of tonnes of TN and Si, and tens of tonnes of TP enter Lake Võrtsjärv annually. The lake accumulated nutrients (nitrogen, phosphorus, and silicon) irrespective of whether water retention was positive or negative. However, the balance between the amounts of incoming and outgoing carbon via the rivers was much more dependent on the water budget of the lake. The smallest differences between the incoming and outgoing fluxes occurred in the low water periods in summer and winter. Within the scope of this study we cannot yet answer the question whether the lake is a carbon-emitting or a carbon-binding system. For this purpose, a number of missing components of the carbon budget of Lake Võrtsjärv need to be studied.

ACKNOWLEDGEMENTS

Funding for this research was provided by target-financed project SF0170011s08 of the Estonian Ministry of Education and Research and grant No. ETF7600 of the Estonian Science Foundation. We thank two reviewers for helpful comments on the manuscript.

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Süsiniku ja toitesoolade koormus Võrtsjärve sissevooludes ning väljavoolus

Peeter Pall, Sirje Vilbaste, Toomas Kõiv, Aive Kõrs, Kairi Käiro, Alo Laas, Peeter Nõges, Tiina Nõges, Kai Piirsoo, Liina Toomsalu ja Malle Viik

On arvutatud nelja peamise sissevoolu (Tänassilma, Tarvastu, Õhne, Väike Emajõgi) kaudu Võrtsjärve tuleva ja sealt Emajõe kaudu väljuva üldise orgaanilise süsiniku (TOC), lahustunud orgaanilise süsiniku (DOC), lahustunud anorgaanilise süsiniku (DIC), lämmastiku, fosfori ning räni koormused kahe aasta jooksul (2008–2009). Aastas tuleb jõgede kaudu järve kümneid tuhandeid tonne TOC-i, DOC-i ja DIC-i; tuhandeid tonne lämmastikku ja räni ning kümneid tonne fosforit. Nii vooluhulk kui ka uuritud nelja jõe kaudu järve kantavate ainete koormused olid 2008. aastal, võrreldes järvest väljakantavate kogustega, suuremad. 2009. aastal aga ületas väljavool neli uuritud sissevoolu nii vooluhulga kui ka süsiniku koormuse poolest. Sissetulev toitesoolade hulk oli aga väljuvast endiselt suurem. Järv akumuleeris lämmastikku, fosforit ja räni, sõltumata järve veebilansist. Süsiniku puhul oli akumuleerumine või järvest väljakandumine rohkem veebilansiga seotud.

IV

Kõiv, T.; Nõges, T. and **A. Laas**, 2011.
PHOSPHORUS RETENTION AS A FUNCTION OF
EXTERNAL LOADING, HYDRAULIC TURNOVER TIME,
AREA AND RELATIVE DEPTH IN 54 LAKES AND
RESERVOIRS.
Hydrobiologia, 660(1), 105 - 115.

Hydrobiologia (2011) 660:105–115
DOI 10.1007/s10750-010-0411-8

EUROPEAN LARGE LAKES II

Phosphorus retention as a function of external loading, hydraulic turnover time, area and relative depth in 54 lakes and reservoirs

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Received: 5 November 2009 / Accepted: 10 August 2010 / Published online: 27 August 2010

Abstract We analysed phosphorus retention as a function of external loading, hydraulic turnover time, area and relative depth on the basis of published data from 54 lakes and reservoirs in different climate regions around the world. Our analysis demonstrated that reservoirs and lakes that received higher areal loading of phosphorus (TP_{in}) also retained more P per m^2 but the proportion of the external P loading retained in the waterbody (retention coefficient, R_P) remained generally independent of TP_{in}. The waterbodies with longer hydraulic residence times (T_R) retained larger proportions of external P and the correlation between R_P and T_R was much stronger in lakes with areas larger than 25 km^2 than in the whole data set. TP_{in} and T_R together determined 78% of the variation in R_P in large lakes. We also partially confirmed our hypothesis that waterbodies with bigger relative depths (Z_R) retain more of the external phosphorus than larger and shallower waterbodies with lower Z_R. The hypothesis was, however, validated only for lakes larger than 25 km^2 and for those with T_R <0.3 year, where R_P increased significantly with increasing Z_R. In stratified lakes, increasing relative depth correlated with reduced P retention capacity, demonstrating the complex nature of phosphorus biogeochemistry in lake ecosystems.

Keywords Phosphorus retention · Phosphorus mass balance · Lake morphometry · Relative depth

Introduction

As a major paradigm of limnology, phosphorus (P) availability is regarded as the most important determinant of productivity and water quality in lakes and reservoirs (Schindler, 1977; Vollenweider & Kerekes, 1980; Peters, 1986; Welch, 1992; Havens & Schelske, 2001). Excessive input of P is considered to be the main cause of eutrophication of inland surface waters, and there have been many attempts to assess and control the external loading and retention of P in order to restrain eutrophication (Sas, 1989; Anderson et al., 2005). Nutrient retention, a fundamental property of every aquatic ecosystem, is linked to its geomorphological, hydrological, edaphic and biotic characteristics (Vitousek & Reiners, 1975; Hansson et al., 2005).

Guest editors: T. Blenckner, T. Nõges, L. Tranvik, K. Pettersson, R. Naddafi / European Large Lakes II. Vulnerability of large lake ecosystems - Monitoring, management and measures

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Phosphorus retention is normally defined as the amount of externally loaded phosphorus that is biogeochemically transformed, retarded and retained (largely through sedimentation) within the water body (Dillon & Rigler, 1974; Søndergaard et al., 2001). Sediment P may also be released by various mechanisms and returned to the water column in dissolved form. It is generally accepted that oxic lake sediments retain P more efficiently than anoxic sediments (Søndergaard et al., 2001; Wetzel, 2001). Under oxic conditions and at about neutral pH, iron precipitates as a trivalent iron oxyhydroxide, which has a large capacity to co-precipitate and/or adsorb phosphate. Under anoxic conditions, reductive dissolution of the solid Fe(III) oxyhydroxide results in parallel dissolution of the previously bound phosphate. However, the ultimate release of P from sediments does not depend only on hypolimnetic oxygen conditions, but also on Fe availability and sulphide production rate, i.e. anoxia does not necessarily result in benthic P release in lakes with high iron but low sulphate concentration (Gächter & Müller, 2003). In addition to the biogeochemical transformations mentioned above, the rate of phosphorus loss within lakes is to a large extent related to the P loading rate and the depth of the lake (Brett & Benjamin, 2008). Thus, the physical ‘structure’ of a lake can also significantly influence its phosphorus concentration and retention (Håkanson, 2005). In this context, natural lakes and reservoirs could be considered similar, being driven in both cases by external factors such as morphology, hydrology and climate (Wetzel, 2001). Studies calculating P retention in lakes and reservoirs do not generally take macrophytes, periphyton and benthic algae into account as is done for wetlands, rivers and streams (Engelhardt & Ritchie, 2001; Dodds, 2003; Schulz & Köhler, 2006), although their contribution to phosphorus dynamics could be rather significant (Carpenter & Lodge, 1986; Rooney et al., 2003).

Various formulations have been proposed for predicting P retention, mostly from areal phosphorus and hydraulic loading rate, settling velocity of phosphorus-containing particles, and mean depth (Brett & Benjamin, 2008). Hydraulic residence time is an important determinant of the impact of nutrient input on lake ecosystems. In general, a longer residence time causes more extensive recycling and greater nutrient retention. Reservoirs with high hydraulic residence times and high inflowing P concentrations also tend to have high phosphorus retention (Straškraba et al., 1995). The Vollenweider models (1969, 1975) have demonstrated that natural lakes with higher flushing rates retain less P than lakes with longer hydraulic residence times (Søndergaard et al., 2001).

As the European Water Framework Directive (European Union, 2000) requires that all waterbodies should achieve Good Ecological Status by 2015, there is an urgent need to quantify R_P in order to establish a reliable phosphorus budget and identify the important phosphorus sources. The most accurate quantification of R_P is based on measured mass balances, which are time-consuming and expensive to establish. Therefore, predictions of R_P from the lakes’ morphometric and hydrological characteristics would be potentially valuable. Predictive equations have been devised that link the phosphorus retention coefficient to the hydrological properties or mean depth of the water body (e.g. Kirchner & Dillon, 1975; Nürnberg, 1984; Hejzlar et al., 2006). Nõges et al. (2007) showed an inverse relationship between the relative depth (Z_R) of the lake and the concentration of P in sediments, assuming that the potential for internal phosphorus loading and the resilience of ecosystem recovery after the removal of external phosphorus sources in large and shallow lakes with small Z_R should be less than in smaller and deeper lakes with greater relative depth. Accordingly, large and shallow lakes with small Z_R should have a lower phosphorus retention capacity than smaller and deeper lakes with bigger Z_R. The aim of the present article was to test this hypothesis. We examined differences of R_P among lakes and reservoirs with various morphometric parameters and assessed the impact of relative depth on their phosphorus retention capacities.

Materials and methods

Data on total phosphorus retention, internal/external loading, outflow losses and morphometry for 54 lakes and reservoirs in different climate regions around the world were compiled from published sources (Table 1, Fig. 1). The data set covered wide ranges of morphological, hydrological and phosphorus loading conditions (Table 2). Climate regions were distinguished according to Köppen–Geiger (Kottek et al., 2006).

Table 1 Sources of data analysed

	ID	Site	Locations	Climatic region	Number of cases	Source
Lakes	1	Verevi	Estonia	Dfb	1	Nõges (2005)
	2	Cameron	Canada	Dfb	2	Dillon (1975)
	3	Four Mile Lake	Canada	Dfb	2	Dillon (1975)
	4	Sempachersee	Switzerland	Dfb	2	Moosmann et al. (2006)
	5	Baldeggersee	Switzerland	Dfb	2	Moosmann et al. (2006)
	6	Hallwilersee	Switzerland	Dfb	2	Moosmann et al. (2006)
	7	Pfäffikersee	Switzerland	Dfb	2	Moosmann et al. (2006)
	8	Greifensee	Switzerland	Dfb	2	Moosmann et al. (2006)
	9	St. Clair	Canada/USA	Dfa	4	Lang et al. (1988)
	10	Apopka	USA	Cfa	2	Canfield et al. (2000), Coveney et al. (2005)
	11	Müggelsee	Germany	Cfb	1	Köhler et al. (2005)
	12	Frank Lake	Canada	Dfb	1	White & Bayley (2001)
	13	Võrtsjärv	Estonia	Dfb	1	Nõges et al. (1998)
	14	Chapala	Mexico	Aw	2	de Anda et al. (2001)
	15	Whitemere	England	Cfb	2	Kilinc & Moss (2002)
	16	Taihu	China	Cfa	3	Kelderman et al. (2005)
	17	Lough Neagh	Ireland	Cfb	1	Gibson et al. (2001)
	18	Karhijärvi	Finland	Dfb	1	Krogerus & Ekholm (2003)
	19	Malham Tarn	England	Cfb	1	Talling & Parker (2002)
	20	Little Mere	England	Cfb	2	Beklioglu et al. (1999)
	21	Brienz	Switzerland	Dfb	1	Müller et al. (2007)
	22	Belau	Germany	Dfb	1	Schernewski (2003)
	23	Pyhäjärvi	Finland	Dfb	1	Ekholm et al. (1997)
	24	Köyliönjärvi	Finland	Dfb	1	Wright et al. (1993)
	25	Villikkalanjärvi	Finland	Dfb	1	Knuuttila et al. (1994)
	26	Tuusulanjärvi	Finland	Dfb	1	Ojanen (1979)
	27	Kotojärvi	Finland	Dfb	1	Knuuttila et al. (1994)
	28	Rotorua	New Zealand	Af	1	Burger et al. (2007)
	29	Peipsi	Estonia	Dfb	1	Nõges et al. (2003)
	30	Baikal	Russia		2	Tarasova & Mescheryakova (1992), Callender & Granina (1997)
	31	Kortowskie	Poland	Dfb	6	Dunalska (2002)
	32	Dal	India	Dsb	1	Solim & Wanganeo (2008)
	33	Trichonis	Greece	Csa	2	Bertahasa et al. (2006)
	34	Blankensee	Germany	Dfb	1	Ramm & Scheps (1997)
	35	Tarawera	New Zealand	Af	1	Hamilton et al. (2006)
	36	Skipout	USA	Cfa	1	Wagner (1996)
	37	Kasumigaura	Japan	Cfa	1	Havens et al. (2001)
	38	Dong Hu	China	Cfa	1	Havens et al. (2001)
	39	Okeechobee	USA	Cfa	1	Havens et al. (2001)
	40	Mälaren	Sweden	Dfb	1	Kvarnäs (2001)

Table 1 continued

	ID	Site	Locations	Climatic region	Number of cases	Source
Reservoirs	41	Broa	Brazil	Cfa	1	Miranda & Matvienko (2003)
	42	Sahela	Morocco	Csa	1	Alaoui Mhamdi et al. (2007)
	43	Bort-Les-Orgues	France	Cfb	1	Brigault & Ruban. (1998)
	44	Ceské údolí	Czech Republic	Dfb	2	Duras & Hejzlar (2001)
	45	Marne	France	Cfb	3	Garnier et al. (1999)
	46	Aube	France	Cfb	2	Garnier et al. (1999)
	47	Seine	France	Cfb	2	Garnier et al. (1999)
	48	Eau Galle	USA	Dfa	3	James & Barko (1997)
	49	Kesikköprü	Turkey	Dsb	1	Pulatsü (2003)
	50	Lago de Cidra	Puerto Rico	Am	1	Ginés (1998)
	51	Eagle Creek	USA	Dfa	1	Raftis et al. (2005)
	52	Saguling	Indoneasia	Af	1	Hart et al. (2002)
	53	Williams Fork	USA	Dfb	2	LaBaugh & Winter (1984)
	54	Gross	USA	Dfb	2	LaBaugh & Winter (1984)

Fig. 1 Global map of the locations of lakes and reservoirs considered in this study. Lakes: *open circles*, reservoirs: *full circles*

The majority of the data originated from the temperate zone of Europe and North America. As the data for some lakes and reservoirs covered more than 1 year, there are 85 records in the data set. Wherever possible, data from the same lake under different trophic conditions were used. All but one (Broa, Brazil) of

Table 2 General statistics of the parameters analysed

	Abbreviation, unit	*n*	Mean	Median	Min	Max	SD
Area	A, km^2	85	1002.9	10.2	0.03	31,494	4,805
Mean depth	Z_M, m	82	30.31	5.9	0.5	758	117.7
Relative depth	Z_R	85	0.98	0.51	0.00	6.66	1.25
Hydraulic retention time	T_R, year	70	11.56	0.48	0.01	350	58.52
External loading	TP$_{in}$, g m^{-2} year^{-1}	80	3.14	0.83	0.00	44.90	6.96
Phosphorus retention	R_P, year^{-1}	85	0.46	0.5	0.00	0.93	0.26

the reservoirs included in this study were strictly stratified; in the natural lakes, stratification and/or circulation was mainly controlled by heat, although some lakes (Verevi and Baldeggersee) were partially or fully meromictic.

Data on total phosphorus external loading (TP$_{in}$) and outflow (TP$_{out}$), both in g m^{-2} year^{-1}, were taken mainly from mass balance studies. TP retention (R_P) was expressed as a proportion of external loading:

$$R_P = \frac{TP_{in} - TP_{out}}{TP_{in}}$$

Figure 2 shows that for nine lakes in the database, TP export was greater than TP input. Negative retention indicates some source of phosphorus that is not considered in the mass balance. Such data were therefore not considered in further analysis, where we included only the waterbodies with positive R_P.

The relative depth was calculated from the ratio between maximum depth and average depth, and the mean of the lake was determined using the lake area as shown by Håkanson (2004):

$$Z_R = \left(D_{\max} \cdot \sqrt{\pi}\right) / \left(20.0 \cdot \sqrt{A}\right),$$

where A is the lake water area and $D_{\max}$ is the maximum depth. The relative depth in stratified lakes and reservoirs ranged from 0.15 to 6.6 (mean 1.5) and in non-stratified water bodies from 0 to 1.6 (mean 0.23).

For statistical analysis, we used the program package Statistica for Windows 8.0 (StatSoft, Inc., 2007). The data set was screened for outliers and non-realistic values were excluded. R_P data appeared to follow a normal distribution (Kolmogorov–Smirnov test, $P > 0.2$ for non-normality). The other parameters (lake area, mean depth, relative depth, external loading and hydrological retention time) were not normally distributed but achieved normality after log transformation, and the transformed data of these characteristics were used for statistical analysis.

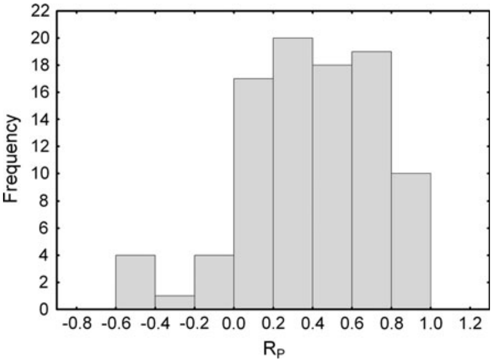


Fig. 2 A histogram of the values of total phosphorus retention coefficient (R_P) in the 85 lakes analysed in this study. A negative R_P could reflect the release of phosphorus from sediments and indicates that lakes are not in steady state. Lakes with negative R_P were excluded from further analysis

Results

On average the natural lakes retained 47 ± 28 (SD) % and the reservoirs 42 ± 22 (SD) % of external phosphorus loading. There was no statistically significant difference between these mean R_P values, so we treated lakes and reservoirs together in our analysis. However, natural lakes and reservoirs are marked differently in the figures. Our correlation analysis demonstrated that the reservoirs and lakes that received higher areal loading of P also retained more P per m^2 (Fig. 3), but the retention coefficient (R_P) remained generally independent of the amount of areal P input (TP$_{in}$) that the waterbody received ($r = -0.151$, $P = 0.186$). The waterbodies with longer hydraulic residence times (T_R) retained more

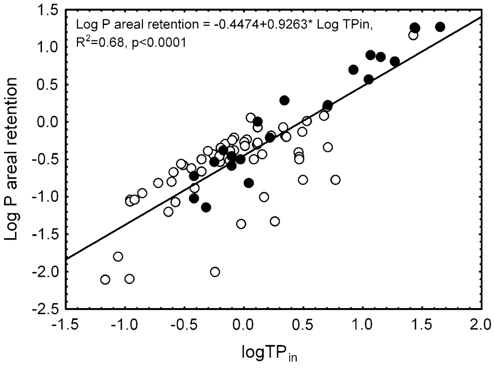


Fig. 3 The areal total phosphorus retention correlates strongly with areal total phosphorus loading. Lakes: *open circles*, reservoirs: *full circles*

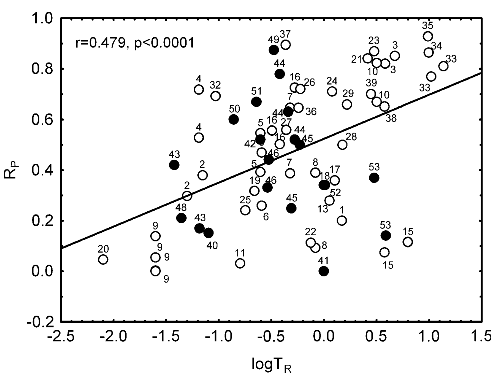


Fig. 4 Waterbodies with longer hydraulic residence times (T_R, years) retain significantly more external P—their phosphorus retention coefficient (R_P) is higher. Lakes: *open circles*, reservoirs: *full circles*. Numbers denote ID as in Table 1

of the external P (Fig. 4), and the correlation between R_P and T_R was much stronger in lakes larger than 25 km^2 ($r = 0.77$, $P < 0.0001$) than in the whole data set ($r = 0.48$, $P < 0.0001$). TP$_{in}$ and T_R together explained only 22% of the variation of R_P in the whole data set, but 78% of the variation of R_P in lakes larger than 25 km^2:

$$R_P = 0.656 \pm 0.046\ (\mathrm{SE}) + 0.495 \pm 0.078 * \log T_R + 0.442 \pm 0.148 * \log \mathrm{TP_{in}}$$
$$(R^2 = 0.777,\ n = 22,\ P < 0.0001)$$

In the whole data set we found no significant relationship between R_P and the relative depth Z_R of the waterbody ($r = -0.098$, $P = 0.393$), while in lakes larger than 25 km^2 and in lakes with T_R < 0.3 year, R_P increased significantly with increasing Z_R (Figs. 5 and 6, respectively). R_P decreased significantly with increasing Z_R in stratified lakes ($r = -0.366$, $P = 0.009$).

Discussion

The results of our work confirm previous reports suggesting that waterbodies receiving higher areal loading of P also retain more P per m^2 (Kirchner & Dillon, 1975; Nürnberg, 1984; Fig. 3) and that those with longer hydraulic residence times retain more of the external P (Søndergaard et al., 2001; Fig. 4). However, in some cases, the rate of TP loss might also increase when the hydraulic retention time decreases (Welch, 1992). Brett & Benjamin (2008) have discussed this curiosity, reasoning that lakes with short hydraulic retention times might receive relatively greater inputs of allochthonous, mineral-bound particulate phosphorus than do lakes with longer retention times. As this particulate P tends to be more susceptible to settling (House et al. 1986; Driscoll et al. 1993), lakes with shorter hydraulic retention times might have greater instantaneous TP loss rates than those with longer T_R.

A novel finding of our study was that the retention coefficient is much more strongly determined by external P loading and by hydrological residence time in large lakes than in smaller lakes. We developed a regression equation, which enables us to determine the proportion of the P retained in large lakes (area larger than 25 km^2) with 80% power, if their residence time and the external P loading are known. The sustainable and cost-effective management of large lakes requires a proper understanding of the relevant relationships. The relationship between the efficiency of management efforts and the morphological properties of lakes, and therefore the relationship developed in our study, could be used widely to estimate the effect of such management measures as the reduction of external P loading on the P retention capacity of the lake and to evaluate its effect on lakes with different hydraulic residence times.

We also partially confirmed our hypothesis that waterbodies with greater relative depth retain more external phosphorus than waterbodies with lower

Fig. 5 Relationship between total phosphorus retention coefficient (R_P) and relative depth (Z_R) in waterbodies larger (**A**) and smaller (**B**) than 25 km^2. Lakes: *open circles*, reservoirs: *full circles*. Numbers denote ID as in Table 1

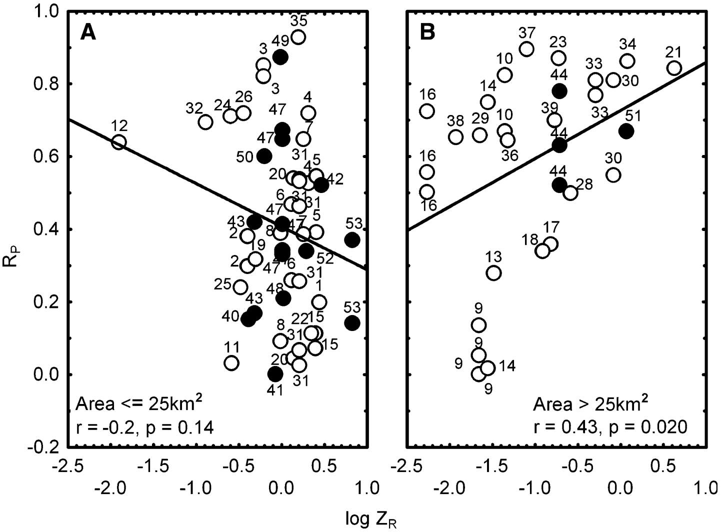
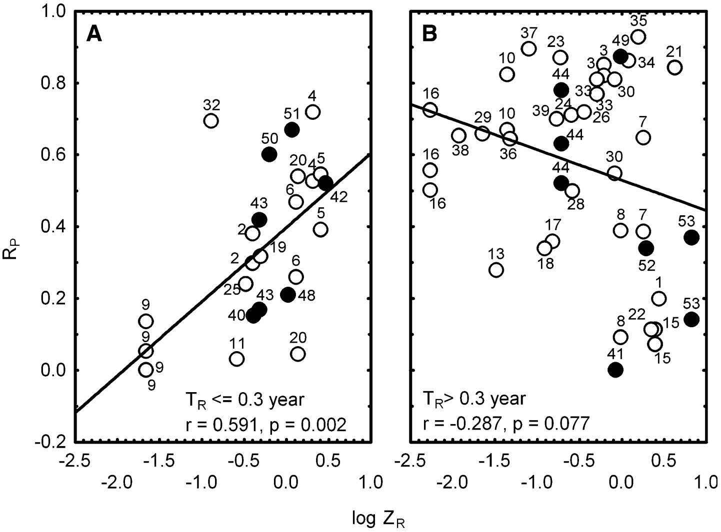


Fig. 6 Relationship between total phosphorus retention coefficient (R_P) and relative depth (Z_R) in waterbodies where the hydraulic residence time is shorter (**A**) or longer (**B**) than 0.3 year. Lakes: *open circles*, reservoirs: *full circles*. Numbers denote ID as in Table 1



relative depth, though this was corroborated only in waterbodies that had either quite large surface areas (>25 km^2, Fig. 5B) or short hydraulic turnover times (<0.3 year, Fig. 6A). On the basis of our earlier study of 15 lakes, which showed an inverse relationship between relative lake depth and the concentration of P in surface sediments (Nõges et al., 2007), we assumed that in large and shallow polymictic lakes (small Z_R) where bottom sediments are permanently stirred up and washed during the whole ice-free period so that labile P is not allowed to accumulate, the phosphorus retention capacity should be lower than in smaller and deeper lakes with bigger Z_R. Our results showed that the assumed positive relationship between R_P and Z_R appeared to be valid only for lakes with specific morphological and hydrological features such as quite large surface area and short hydraulic residence time. Large surface area is commonly linked with long wind fetch and more intensive wave action, which stimulate sediment resuspension and prevent sedimentation of particles; also, a high flushing rate interferes with sedimentation processes. Our study demonstrated that the relationship between R_P and Z_R was non-linear and could be positive only under conditions, in which sedimentation is assumed to be suppressed. Relative depth has frequently been used to compare the morphologies of lakes and to explain their limnological behaviour. Z_R is a good characteristic of the stability and thermal or chemical stratification of water masses, and could also be applied as a predictor of oxygen conditions and redox status in lakes (Håkanson, 2004). Mass balance calculations show that much of the phosphorus load to a lake is retained largely through sedimentation, and the role of sedimentation in phosphorus retention is usually greater than that of assimilation by biota (de Anda et al., 2001; Havens et al., 2001; Schernewski, 2003; Kelderman et al., 2005). Håkanson (2005) stressed that gross sedimentation is a function of relative depth as well as total lake phosphorus concentration, so lake morphometry is a very important factor in the gross sedimentation value.

Our study showed that the retention coefficient of P in stratified lakes might decrease when the relative depth of the waterbody increases. In stratified lakes, where sedimentation is much more distinct than in polymictic lakes, the correlation between R_P and Z_R was negative. The stronger and deeper stratification in lakes with higher Z_R presumably supports phosphorus release from sediments through different geochemical mechanisms. This reduces the overall P reduction capacity compared with R_P in stratified lakes with smaller Z_R and, thus, weaker stratification. Lakes with sharp physical and chemical stratification and high relative depth might have a special ecosystem structure (see Tyler & Vyverman, 1995; Wetzel, 2001; Ott et al., 2005), where phosphorus retention is determined by multiple heterogeneous factors. Sharp stratification could be accompanied by the depletion of hypolimnetic oxygen bringing about the release of large amounts of phosphorus from anaerobic sediments. During the mixing periods this released phosphorus is transported from the hypolimnion to the epilimnion in the form of phosphates (Nürnberg, 1994). Although the epilimnion of a stratified lake can lose up to half its total phosphorus through sinking loss during the stagnation period (Guy et al., 1994), sharp and stable stratification could also mean that a large part of the phosphorus is recycled in the epilimnion and metalimnion. The sharp decline of temperature in the metalimnion might decrease the rate of sinking of organic matter particles and therefore intensify phosphorus recycling in the epilimnion (Gliwicz, 1979). Phosphorus retention in stratified and oxygenated lakes is frequently higher than in lakes with anoxic hypolimnia (Nürnberg, 1984). On the other hand, the release of phosphorus from sediments depends not only on a hypolimnetic oxygen condition, but also on the balance between sedimentation and resuspension of organic matter, and the P, Fe and sulphide contents of the sediment (Gächter & Müller 2003; Hupfer & Lewandowski, 2008).

Considering the different structures of shallow and stratified systems it is not surprising that the calculated P retention values vary widely. In natural lakes the relative depth is usually <2%. However, Z_R might be more than 5% in permanently stratified or meromictic systems (Doyle & Runnels, 1997), while several lakes, also represented in our study, maintain stratified conditions despite rather low relative depths. Nixdorf & Deneke (1997) demonstrated how shallow lakes become structurally more diverse with increasing depth and thus more sensitive to the effect of wind on the mixing depth and type. Gradual increase or decrease of the depth might result in an intermediate situation, where the lakes are too shallow for stability and too deep for intense polymixis. Under such conditions, the role of relative depth in phosphorus retention is difficult to estimate.

Conclusions

Our study revealed that:

- Reservoirs and lakes that receive higher areal loading of phosphorus also retain more P per m^2.
- Waterbodies with longer hydraulic residence times retain more of the external P and this relationship is most obvious in lakes with areas larger than 25 km^2.
- Large lakes and reservoirs (>25 km^2) retain more of the external P if their relative depth is bigger.
- Lakes and reservoirs with high flushing rates (>3 $year^{-1}$) retain more of the external P if their relative depths are bigger.

- Stratified lakes and reservoirs retain less of the external P if their relative depths are bigger.

Acknowledgments The study was supported by SF 0170011508 and by grant 7600 from the Estonian Science Foundation.

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CURRICULUM VITAE

General information

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Education

Since 2006	PhD student at Estonian Univesity of Life Sciences
2002–2004	MSc in hydrobiology, Estonian Agricultural University
1998–2002	BSc in hydrobiology, University of Tartu
1995–1998	Lähte Ühisgümnaasium
1986–1995	Lähte Secondary School

Professional experience

Since 2010	Researcher at Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Centre for Limnology
2008–2009	Head of the Nurmiko Hulgi OÜ, Tartu department
2005–2008	Senior officer of water management at Ministry of the Environment, Tartu County Environmental Department
2005–2008	Laboratory assistant at Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Centre for Limnology
2002–2005	Laboratory assistant at Estonian Agricultural University, Institute of Zoology and Botany, Võrtsjärv Limnological station
2001–2005	Senior officer of fishery at Ministry of the Environment, Viljandi County Environmental Department.

Scientific and research activities

Main research interest:

High frequency changes of biological and physical parameters in aquatic ecosystems.

Publications

Laas, A., Nõges, P., Kõiv, T., Nõges, T., 2012. High frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694(1), 57-74.

Read, J.S., Hamilton, D. P., Desai, A. R., Rose, K. C., MacIntyre, S., Lenters, J. D., Smyth, R. L., Hanson, P.C., Cole, J. J., Staehr, P. A., Rusak, J. A., Pierson, D. C., Brookes, J. D., Laas, A., Wu, C. H., 2012. Lake-size dependency of wind shear and convection as controls on gas exchange. Geophysical Research Letters. doi 10.1029/2012GL051886

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Kõiv, T., Nõges, T., Laas, A., 2011. Phosphorus retention as a function of external loading, hydraulic turnover time, area and relative depth in 54 lakes and reservoirs. Hydrobiologia, 660(1): 105-115.

Pall, P., Vilbaste, S., Kõiv, T., Kõrs, A., Käiro, K., Laas, A., Nõges, P., Nõges, T., Piirsoo, K., Toomsalu, L., Viik, M., 2011. Fluxes of carbon and nutrients through the inflows and outflow of Lake Võrtsjärv, Estonia. Estonian Journal of Ecology, 60(1): 39-53.

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Ott, I., Timm, H., Rakko, A., Mäemets, H., Kübar, K., Tammert, H., Laas, A., Tambets, M., Järvet, A., Kübar, R., 2006. Viljandi järv - kas looduslik või oluliselt muudetud? Sammul, Marek (Toim.). Eesti Loodusuurijate Seltsi aastaraamat. Tartu: Eesti Looduseuurijate Selts: 76 – 93.

Järvalt, A., Laas, A., Nõges, P., Pihu, E., 2005. The influence of water level fluctuations and associated hypoxia on the fishery of Lake Võrtsjärv, Estonia. Ecohydrology & Hydrobiology, 4: 487 - 497.

Moss, B., Steohen, D., Alvarez, C., Becares, E., VandeBund, W., Collings, S. E., VanDonk, E., DeEyto, E., Feldmann, T., FernindezAliez, C., FernindezAliez, M., Frankeng, R. J. M., GarckaCriado, F., Gross, E., Gyllström, M., Hansson, L.–A., Irvine, K., Järvalt, A., Jenssen, J.–P., Jepesen, E., Kairesalo, T., Kornijow, R., Krause, T., Künnap, H., Laas, A., Lill, E., Lorents, B., Luup, H., Miracle, M. R., Nõges, P., Nõges, T., Nykänen, M., Ott, I., Peczula, W., Peeters, E. T. H. M., Phillips, G., Romo, S., Russell, V., Salujõe, J., Scheffer, M., Siewertsen, K., Smal, H., Tesch, C., Timm, H., Tuvikene, L., Tõnno, I., Virro, T., Wilson, D., 2003. The determination of ecological quality in shallow lakes – a tested system (ECOFRAME) for implementation of the European Water Framework Directive. Aquatic Conservation. Aquatic Conservation-Marine and Freshwater Ecosystems, 13: 507 - 549.

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International courses attended:

- Global lake ecological observatory network (GLEON) 8 meeting/workshop “Lake Modelling” Hamilton, University of Waikato, New Zealand, February 1-7, 2009
- GLEON 9 meeting/workshop “Physical Limnology” Camp Manito-wish, Boulder Junction, Wisconsin, USA, October 12-15, 2009
- Nordic Research Training Course in Joensuu “Advanced Technologies in Measurements of Physical and Biological Interactions in Pelagic Systems of Large Lakes”, University of Eastern Finland, Joensuu, 31 May-11 June, 2010.
- GLEON 12 meeting/workshop “Introduction to Lakebase: VADER, Lakebase and more” Ramot, Sea of Galilee, Israel, April 4-8, 2011.
- Nordforsk Research Training course “Automated Monitoring and High-Frequency Data Analysis”, Erken Laboratory, Uppsala University, Sweden, July 25-31, 2011.
- GLEON 13 meeting/workshop “Communicating Science” Lake Sunapee, New Hampshire, USA October 10-14, 2011

International conferences:

- International Symposium on Wetland Pollutant Dynamics and Control (WETPOL 2007), Tartu, Estonia, 16-20 September, 2007. Oral presentation: Laas, A., Järvet, A. & Nõges. T. “Long-term changes of N and P retention in Lake Võrtsjärv, the influence of catchment processes and climate”
- Global lake ecological observatory network (GLEON) 8, Hamilton, University of Waikato, New Zealand, February 1-7, 2009. Poster presentation: Laas, A. & Nõges, T. “Recording of water chemical and physical parameters with an automatic monitoring station in Lake Võrtsjärv, Estonia”
- GLEON 9, Camp Manito-wish, Boulder Junction, Wisconsin, USA, October 12-15, 2009. Poster presentation: Laas, A. & Nõges, T. “Assessing Lake Võrtsjärv (Estonia) metabolism using high frequency water measurements”
- GLEON 12 Ramot, Sea of Galilee, Israel, April 4-8, 2011. Poster presentation and oral presentation in COOL THINGS session: Laas, A., Nõges, T., Nõges, P. & Kõiv, T. “First high frequency metabolism studies in large shallow Lake Võrtsjärv, Estonia”.

- GLEON 13 Lake Sunapee, New Hampshire, USA October 10-14, 2011. Poster presentation: Laas, A., Vanni, M., Yacobi, Y. Y., Staehr, P. A. Rose, K. C., Arst, H. & Nõges, P. ”How comparable are the bioproduction estimates yielded by different methods?”.

Membership of societies:

Since 2012	Member of Association for the Sciences of Limnology and Oceanography (ASLO)
Since 2009	Member of Global Lake Ecological Observatory Network (GLEON)
2007–2009	Member of Improved regional development and CBC in the Estonian-Russian border region through partial implementation of Lake Peipsi Management Programme, project lead group
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Haridus

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Publikatsioonide loetelu

Laas, A., Nõges, P., Kõiv, T., Nõges, T., 2012. High frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia 694(1), 57-74.

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Moss, B., Steohen, D., Alvarez, C., Becares, E., VandeBund, W., Collings, S. E., VanDonk, E., DeEyto, E., Feldmann, T., FernindezAliez, C., FernindezAliez, M., Frankeng, R. J. M., GarckaCriado, F., Gross, E., Gyllström, M., Hansson, L.–A., Irvine, K., Järvalt, A., Jenssen, J.–P., Jepesen, E., Kairesalo, T., Kornijow, R., Krause, T., Künnap, H., Laas, A., Lill, E., Lorents, B., Luup, H., Miracle, M. R., Nõges, P., Nõges, T., Nykänen, M., Ott, I., Peczula, W., Peeters, E. T. H. M., Phillips, G., Romo, S., Russell, V., Salujõe, J., Scheffer, M., Siewertsen, K., Smal, H., Tesch, C., Timm, H., Tuvikene, L., Tõnno, I., Virro, T., Wilson, D., 2003. The determination of ecological quality in shallow lakes – a tested system (ECOFRAME) for implementation of the European Water Framework Directive. Aquatic Conservation. Aquatic Conservation-Marine and Freshwater Ecosystems, 13: 507-549.

Tuvikene, A., Melikidze, J., Laas, A., 2003. The fate of plycyclic aromatic hydrocarbons in Lake Võrtsjärv, Estonia. In: Lake ecosystems: biological processes, antropogenic transformation, water quality. Proceedings of the II International Scientific Conference: September 22-26, 2003, Minsk-Naroch. 2003: 98-101.

Erialane enesetäiendamine:

- Koolitus "Lake Modelling" Global lake ecological observatory network (GLEON) 8. koosolekul, Waikato ülikool, Hamilton, Uus-Meremaa, 1.-7. veebruar, 2009.

- Koolitus “Physical Limnology” GLEON 9. koosolekul, Camp Manitowish, Boulder Junction, Wisconsini osariik, USA, 12.-15. oktoober, 2009.
- Kursus “Advanced Technologies in Measurements of Physical and Biological Interactions in Pelagic Systems of Large Lakes” programmi Nordic Research Training raames, Ida-Soome Ülikool, Joensuu, Soome, 31. mai-11. juuni, 2010.
- Koolitus “Introduction to Lakebase: VADER, Lakebase and more” GLEON 12. koosolekul, Ramot, Iisrael, 4.-8. aprill, 2011.
- Kursus “Automated Monitoring and High-Frequency Data Analysis” programmi Nordforsk Research Training raames, Erkeni laboratoorium, Uppsala Ülikool, Rootsi, 25.-31. juuli, 2011.
- Koolitus “Communicating Science” GLEON 13. koosolekul. Sunapee, New Hampshire osariik, USA, 10.-14. oktoober, 2011

Osalemine rahvusvahelistel konverentsidel/kohtumistel:

- International Symposium on Wetland Pollutant Dynamics and Control (WETPOL 2007), Tartu, Eesti, 16.-20. september, 2007. Suuline ettekanne: Laas, A., Järvet, A. & Nõges. T. “Long-term changes of N and P retention in Lake Võrtsjärv, the influence of catchment processes and climate”.
- Global lake ecological observatory network (GLEON) 8, Waikato Ülikool, Hamilton, Uus-Meremaa, 1.-7. veebruar, 2009. Stendiettekanne: Laas, A. & Nõges, T. “ Recording of water chemical and physical parameters with an automatic monitoring station in Lake Võrtsjärv, Estonia”.
- GLEON 9, Camp Manito-wish, Boulder Junction, Wisconsini osariik, USA, 12.-15. oktoober, 2009. Stendiettekanne: Laas, A. & Nõges, T. “ Assessing Lake Võrtsjärv (Estonia) metabolism using high frequency water measurements”.
- GLEON 12, Ramot, Sea of Galilee, Iisrael, 4.-8. aprill, 2011. Poster ja suuline ettekanne COOL THINGS sessioonil: Laas, A., Nõges, T., Nõges, P. & Kõiv, T. “First high frequency metabolism studies in large shallow Lake Võrtsjärv, Estonia”.

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Teadusorganisatsiooniline tegevus:

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7. september 2012

ISBN 978-9949-484-46-1 (trükk)
ISBN 978-9949-484-47-8 (pdf)

roheline trükis

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