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EUROPEAN LARGE LAKES III

Strong dependence between phytoplankton and water chemistry in a large temperate lake: spatial and temporal perspective

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Abstract In lakes, spatial and temporal variability of water chemistry and phytoplankton are characteristic phenomena although often difficult to link together. This motivated us to study their interplay in Lake Vanajanselkä, a eutrophic lake in Finland. We hypothesized that in summer spatial and temporal differences in phytoplankton and water chemistry can be extended in comparison to spring and autumn. Therefore, chlorophyll *a* and water chemistry was examined by six sampling campaigns with 15 sampling sites over the lake in May–October 2009–2010. In summer, chlorophyll, pH, and oxygen were horizontally and vertically unevenly distributed in the lake, and in the epilimnion pH and oxygen showed a distinct diurnal variability suggesting high photosynthesis during the day. Daily >1 pH unit difference between the sites and 2.5 pH unit difference between the epi- and hypolimnion were found. In agreement with pH and oxygen, NO_3-N and NH_4-N could be unevenly distributed in the epilimnion. In autumn no spatial differences were found, however. The results emphasized that algae and cyanobacteria were responsible, at least partly, for the variability in water chemistry in the surface layer, and short- and long-term gradients in space and time need to be considered when productive lakes are studied.

Keywords Spatial variability · Temporal variability · Chemistry · Phytoplankton

Introduction

Spatial heterogeneity is a fundamental property of phytoplankton distribution (Cloern et al., 1992). It can result from various physical, chemical, and biological factors such as advective transport of cells (George & Edwards, 1973), horizontally and vertically unequally distributed physical and chemical resources (Salonen et al., 1984; Arvola et al., 1991; Anttila & Kairesalo, 2010), active migration (Arvola, 1984; Salonen & Rosenberg, 2001) and buoyancy of cells (e.g,. Reynolds, 2006). However, turbulence may easily smooth horizontal differences in the distribution of phytoplankton, and therefore vertical differences in phytoplankton can be pronounced, in particular, in small and sheltered lakes where mixing due to wind is less efficient than in larger lakes.

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The processes influencing phytoplankton distribution are dynamic and may have their own temporal fluctuations, such as the diurnal variability of photosynthetically active radiation (PAR) and convective mixing, but many of the factors are stochastic and difficult to analyse. According to Vilar et al. (2003), the factors that drive the spatial distribution of phytoplankton are still far from clear, and models proposed so far show only limited agreement with field observations. Recently, Della Rossa et al. (2013) have claimed that models, which contain phytoplankton, zooplankton and planktivorous fish, suggest zooplankton patchiness, while models not containing phytoplankton or fish do not. The interactions between phytoplankton and zooplankton, such as differences in grazing pressure caused by the unequal distribution of zooplankton, may produce patchiness in phytoplankton, which in turn may stimulate the patchiness of zooplankton (Riley, 1976). Spatial heterogeneity of the environment and organisms may also affect metabolism estimates of lake ecosystems (Van De Bogert et al., 2012), and, therefore, should be known.

It has been suggested that in eutrophic lakes, and especially in lakes with complex physical structures (e.g., a connected group of semi-isolated basins), spatial differences can be an important characteristic of plankton and water chemistry (see George & Heaney, 1978; Anttila & Kairesalo, 2010). Hutchinson (1967) proposed that factors such as vertical structure of light intensity or turbulence, which are continuously changing, are important in supporting a wide range of planktonic organisms.

In oligotrophic lakes the interplay between water chemistry and phytoplankton can be difficult to figure out because inorganic nutrient concentrations are often below the detection limit, and the metabolic activity of phytoplankton may be low as well (Wetzel, 2001). On the contrary, in eutrophic lakes the nutrient concentrations, including the inorganic fractions, can be higher and the same is true of the metabolic activity of phytoplankton. This motivated us to study the interplay between phytoplankton and water chemistry in Lake Vanajanselkä, a large and fairly open eutrophic temperate lake in southern Finland. Leppäranta et al. (2012) examined the ice season, while here we focused on the warm season for the spatial and temporal distribution of phytoplankton and water chemistry on a daily basis.

We first assumed that in summer phytoplankton may not be equally distributed over the lake area, and secondly that differences in all variables will be stronger in late than in early summer, and especially stronger when compared to autumn. The reason for these assumptions is that in late summer cyanobacteria usually dominate the phytoplankton community-forming surface scum. Also, thermal stratification is stronger in late summer than in the beginning of summer and, stratification is much stronger when compared to conditions in autumn. Thirdly, we expected that metabolic activity of plankton strengthens the variability in water chemistry in summer, but not in autumn. Because of this, we were interested in knowing whether the metabolic activity of plankton modifies the chemistry in the short-term, during a single day.

Materials and methods

Lake Vanajanselkä is the main basin of the Lake Vanajavesi water system, located in southern Finland (61°00′–61°20′N; 24°00′–24°30′E (Fig. 1), 120 km north of Helsinki. It is a large and shallow eutrophic lake with a median total phosphorus (TP) of 28 mg m^{-3} (whole year) and chlorophyll *a* of 19 mg m^{-3} (August) in the last 10 years (Hertta database, http://wwwp2.ymparisto.fi/scripts/hearts/welcome.asp, Finnish Environment Institute; see Table 1). The catchment area of Lake Vanajanselkä is 2,774 km^2, and the lake belongs to the drainage basin of River Kokemäenjoki, the fifth largest river basin in Finland. The lake has a long eutrophication history due to extensive human perturbations since the early 17th century. As a result, the lake had very poor water quality in the 1960s and 1970s (Kansanen, 1981), but since then the point loading has markedly decreased and the water quality of the lake has improved (Leppäranta et al., 2012). The lake is ice-covered on average for 5 months per year, from the beginning of December to the beginning of May.

The water balance of the lake is dominated by the inflow of River Lepaanvirta in the south, which brings about 90% of the total inflow (Jokiniemi, 2013). The outflow strait is situated almost opposite to the inflow, in the northwest, and discharges to Lake Rauttunselkä, another basin of the Lake Vanajavesi water system. The theoretical residence time of Lake Vanajanselkä is 450 days. Crossing Lake Vanajanselkä in a southeast–northwest alignment, is an underwater esker, which separates the lake into western and eastern sub-basins with almost identical surface areas (see Fig. 1).

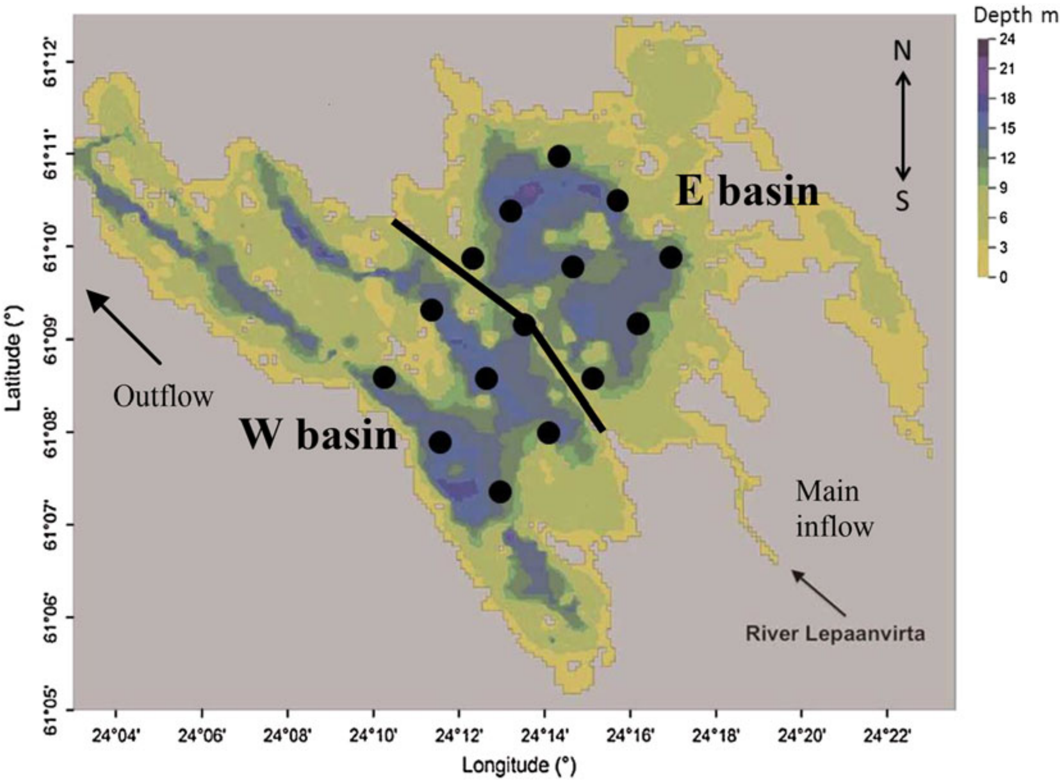


Fig. 1 Bathymetric map of Lake Vanajanselkä. The main inflow (R. Lepaanvirta) and outflow are indicated by *arrows*, locations of the sampling sites by *circles* (1–15). *Two black lines* in the middle of the lake indicate the ridge which goes through the lake from southeast to northwest. The two sub-basins are indicated as *W* and *E*

Table 1 Basic morphometric and hydrologic information on Lake Vanajanselkä

Variable	
Surface area (km^2)	103
Mean depth (m)	7.7
Max depth (m)	23.9
Volume, 10^3 (m^3)	793,100
Precipitation (mm a^{-1})	600
Discharge (m^3 s^{-1})	20
Residence time (d)	450
Above sea level (m)	79.4

Discharge represents River Lepaa, which contributes 90% of the total annual water inflow to the lake

Table 2 Discharge of River Lepaa at the times of the samplings, and the contribution of the inflowing water relative to the total lake volume and to the uppermost 5 m layer of the lake

Time	Discharge	% of volume d^{-1}	
Year/day	m^3 s^{-1}	Whole lake	Uppermost 5 m
2009			
9 Jun	13	0.14	0.34
5 Aug	7	0.08	0.18
28 Oct	10	0.11	0.26
2010			
31 May	36	0.39	0.94
3 Aug	3	0.03	0.08
23 Oct	8	0.09	0.21

During field campaigns in 2009 and 2010 the water discharge was low in comparison to the average annual discharge except in May 2010 (see Table 2). the daily inflow comprises <1% of the volume of the uppermost 5-m water layer, which is the thickness of the photic zone (Leppäranta et al., 2012). At 5-m depth the surface area of the lake contributes 61% of the total lake area and, respectively, the uppermost 5-m water layer makes 49% of the total volume of the lake.

During the period of open water data gathering was done three times per year on approximately the same dates: in May–June, early August and October. For more details of the study lake and the results from winter investigations, see Yang et al. (2012) and Leppäranta et al. (2012).

In both summers the fieldwork, including in situ measurements and sampling, was started daily at 10:30 a.m. and finished at 4:00 p.m. (local summer time = GMT + 3 h, with solar noon at about 1:20 p.m. in summer). During fieldwork we had three boats with two people in each which made it possible to study a large number of sampling sites within a relatively short time. The samples were collected from 15 different sites, which made up a grid with rather evenly distributed points throughout the main part of the lake basin (Fig. 1). The samples were taken from the uppermost 1 m layer (in 2009) or at 1 m below the surface (in 2010) and at 1 m level above the bottom sediment. In 2009, the samples were taken with three lifts by a Limnos tube sampler (height 40 cm, volume 2.8 l) and in 2010 by a 100-cm long Limnos tube sampler (volume 7.0 l). The depths at the sampling sites varied from 10 to 21 m.

The data collected from the sampling sites included temperature and oxygen sounding profiles with a YSI instrument (0545, 556 MPS and Pro DO, Yellow Spring Instruments) and water samples for the water chemistry, and phytoplankton and zooplankton species composition as well as densities (phytoplankton and zooplankton data not shown here). From the chemistry samples, only inorganic nitrogen (nitrate + ammonium), phosphate phosphorus and water pH are analysed here, while the rest (total nitrogen and total phosphorus, alkalinity, electrical conductivity, colour, and dissolved organic carbon) are not shown. The determinations were carried out according to standard methods (see Keskitalo & Salonen, 1994; Arvola et al., 1996). Inorganic nitrogen ($NO_2 + NO_3$-N and NH_4-N), phosphate phosphorus (PO_4-P), and total nitrogen and total phosphorus concentrations were determined with a flow injection analyser (QuikChem®8000, Zellweger Analytics Inc., Lachat Instruments Division, Milwaukee, Wisconsin, USA) from the water samples, which had been filtered through Whatman GF/C filters (inorganic nutrients), or from non-filtered samples (total nutrients). Water pH was measured during the sampling day in the laboratory using an Orion pH meter. In addition, chlorophyll *a* was determined after hot ethanol extraction using a Shimadzu UV–Visible recording spectrophotometer UV-2100 at the wavelengths of 665 and 750 nm. The samples for inorganic nutrient and chlorophyll *a* determinations were filtered during the sampling day and analyzed in the following day or later; if later, the samples were kept in a refrigerator or in a deep-freezer (chlorophyll *a*).

Schmidt stability (*S*) and the heat content of the water column were calculated for each sampling day and site in 2009 and 2010. Schmidt stability gives the work needed for full mixing of the water body (Schmidt, 1928), and the zero reference of the heat content is the liquid state of water at 0°C.

At the time of the field campaigns the phytoplankton community was composed predominantly of cyanobacteria, primarily of *Microcystis* species, and a variety of diatom species accompanied by cryptophytes and chlorophytes. In 2009 cyanobacteria dominated especially in August and diatoms in spring and autumn, and the total biomass of phytoplankton varied between 0.5 and 4 g m^{-3} (wet weight; see Leppäranta et al., 2012) with lowest values in October. In 2010, diatoms (*Asterionella* and *Aulacoseira*) dominanted in spring and in August (*Fragilaria*) together with cyanobacteria. The zooplankton community consisted of small cladocerans (species belonging to the genus of *Bosmina* and *Eubosmina*), a few copepoda species (the most abundant were *Mesocyclops leuckarti* and *Eudiaptomus gracilis*), and a few more rotifers (the most abundant were a couple of *Keratella* species, *Kellicottia longispina*, *Polyarthra vulgaris*, and *Conochilus unicornis*). Cladocerans and copepods had their highest density in August and lowest in October while rotifers were most numerous in May/June. The phytoplankton and zooplankton data sets are not reported in detail in this paper.

The parametric *t* test was used for the comparisons of the water quality results from the eastern and western lake basins, and when this test could not be applied the nonparametric Mann–Whitney test was used. Pearson product-moment correlation analysis was used for the bivariate relationships of the different water quality parameters, and the Kolmogorov–Smirnov test was used for the validity of the normal distribution of the data sets. The statistical package used was SigmaStat3.0. The contour (isopleth) maps were produced by Sigma-Plot9.0. Non-transformed data sets were used for the statistical analyses.

Table 3 The means and the coefficients of variation (CV) at the 15 sampling sites of the chemistry variables and chlorophyll *a* during the sampling campaigns

	O_2 sat.		pH		NH_4-N		NO_3-N		PO_4-P		Chl α		Cond.	
	Mean	CV%	Mean	CV%	Mean	CV%	Mean	CV%	Mean	CV%	Mean	CV%	Mean	CV%
2009														
June														
Epi	106.7	5.6	7.69	59.8	18	40.0	672	6.6	2	34.4	14.2	23.9	119.0	1.5
Hypo	90.0	12.0	7.27	39.7	50	24.7	740	4.1	4	47.7	6.1	32.1	121.0	1.6
August														
Epi	113.9	7.2	8.64	68.1	9	24.5	354	7.0	1	29.6	15.4	6.0	117.0	1.7
Hypo	2.8	62.8	6.94	19.8	30	107.7	633	7.0	21	32.2	8.9	25.9	123.3	2.0
October														
Epi	120.9	0.7	7.63	15.2	9	24.5	233	7.0	9	29.6	7.0	6.0	120.9	0.7
Hypo	121.1	0.5	7.63	14.3	11	55.5	233	5.2	9	18.6	7.1	7.1	121.1	0.5
2010														
May														
Epi	114.2	4.9	7.81	32.0	12	46.5	716	7.5	2	66.5	14.9	24.3	108.6	5.4
Hypo	85.6	8.7	7.22	22.7	47	22.2	753	5.7	2	39.2	9.6	21.7	119.0	0.8
August														
Epi	115.4	5.7	8.52	56.6	8	55.7	297	13.3	2	31.1	30.8	20.3	113.8	0.5
Hypo	17.2	156.9	6.85	33.7	37	108.9	607	21.6	19	39.1	5.6	159.6	120.2	3.1
October														
Epi	94.5	2.8	7.58	26.0	11	14.7	157	3.5	8	13.0	5.0	10.4	114.4	0.4
Hypo	93.0	3.8	7.60	13.4	11	28.5	158	5.5	8	17.7	4.8	17.3	114.4	1.0

O_2%, oxygen saturation; pH, water pH; NH_4-N, ammonium nitrogen; NO_3-N, nitrate nitrogen; PO_4-P, phosphate phosphorus; Chl *a*, chlorophyll *a*; Cond., electrical conductivity (mS cm^{-1}, 25°C). The concentrations are given as mg m^{-3}

Results

Weather and water column stability

During the summer data gathering the weather was calm and sunny before mid-day and in the afternoon the conditions changed to slightly stronger wind and more clouds. In the autumn, the wind conditions were rather similar to those in the summer, although the days were not as sunny and warm. The maximum wind speed never exceeded 5 m s^{-1} on the sampling days. Due to daytime changes in cloudiness the solar radiation was variable but, in general, favourable for photosynthesis in the euphotic zone. The ice breakup day was April 27 in 2009 and April 21 in 2010.

In May/June the mean daily temperature varied between 13 and 16°C, and in August it was around 21°C. In both years the first days of fieldwork were performed soon after the spring overturn, and at that time the surface water temperature was still low (13°C). In spring 2009, the water temperature was clearly higher (11.2°C) in the hypolimnion than in spring 2010 (7.8°C). In August, the surface water temperature rose up to 23°C but the temperature was only 15°C in the hypolimnion. The Schmidt stability of the water column was clearly higher in August than in May/June (respectively, 30 and 52 J m^{-2} in spring 2009 and 2010, and 117 and 136 J m^{-2} in August) as well as the heat content (400 and 352 MJ m^{-2} in comparison to 605 and 630 MJ m^{-2}). In October, the water temperature was close to 6°C in both years and the water column was isothermal; consequently the stability was zero and the heat content about 200 MJ m^{-2}.

The horizontal variation of temperature was low in the epilimnion in both summer seasons. However, in August 2010 the water temperature increased during the course of the day and was on average 2°C higher during late afternoon than 4–5 h earlier when the sampling started. In autumn, the differences between the sampling sites were $\leq$0.4°C while in spring and summer the surface water temperature varied between 1.5 and 5.1°C, respectively.

Chlorophyll, pH, and oxygen

Chlorophyll *a* concentrations were on average higher in August than in May/June, distinctly higher in August 2010 (Tables 3, 4). In summer, the vertical stratification of chlorophyll was clear with substantially higher concentrations in the surface layer than in the hypolimnion. In October, the concentrations were lowest and at that time no difference between the water layers existed.

Similarly to chlorophyll *a*, water pH, and oxygen concentration were higher in the epilimnion than in the hypolimnion except in autumn (Table 3). For pH and oxygen the spatial variability was pronounced in summer, and the same was found to some extent in chlorophyll *a* as well (Table 3). The variability in pH between the sampling sites rose to 1 pH unit within one sampling day while between the surface and bottom layers the difference was as much as 2.5 pH units. However, in October no difference in the three constituents between the water layers was found.

The highest oxygen saturation (133%) was measured in August 2010 when the chlorophyll *a* concentration at the sampling site was above 30 mg m^{-3} and pH > 9.

Ammonium, nitrate, and phosphate

NH_4-N concentrations were lower in August and in October than in May/June in both years (Table 3). In August, the concentrations varied between 3 and 33 mg m^{-3}. For NO_3-N the lowest concentrations were recorded in October followed by August and May/June. However, in the bottom layers NH_4-N concentrations were clearly higher during the stratification period than in the surface layer while in October no vertical difference was found. In the case of NO_3-N, the bottom layer concentrations were distinctly higher only in August. In contrast, in summer PO_4-P concentrations were always below the detection limit (2 mg m^{-3}) in the

Table 4 The means and standard deviations (SD) of the chemistry variables and chlorophyll *a* from the sampling sites situated in the eastern ($n = 7$) and western ($n = 8$) part of the lake during the summer sampling campaigns

June, 2009							August, 2009						
	West		East					West		East			
	Mean	SD	Mean	SD	t	P		Mean	SD	Mean	SD	t	P
O2%	105.0	6.1	109.1	5.3	−1.420	NS	O2%	113.6	7.6	114.7	8.8	−1.113	NS
pH	7.7	0.2	7.8	0.2	−1.223	NS	pH	8.7	0.3	8.8	0.3	−0.185	NS
NH_4–N	20	7.9	16	6.8	1.089	NS	NH_4–N	10	3.7	7	2.4	1.999	0.065
NO_3–N	654	33.6	689	27.2	−2.291	0.038	NO_3–N	367	15.8	340	22.4	2.802	0.014
Chl *a*[a]	13.3		15.1		59.00	NS	Chl *a*	13.2	1.8	17.6	3.8	−2.976	0.010

May, 2010							August, 2010						
	West		East					West		East			
	Mean	SD	Mean	SD	t	P		Mean	SD	Mean	SD	t	P
O2%	115.6	7.5	112.8	2.7	2.825	NS	O2%	114.8	4.8	112.4	3.5	1.142	NS
pH	7.8	0.2	7.8	0.1	−0.009	NS	pH	8.5	0.2	8.7	0.3	−1.078	NS
NH_4–N	14	6.7	10	3.0	1.782	0.097	NH_4–N	10	6.0	8	4.5	0.612	NS
NO_3–N	673	30.2	759	31.7	−5.599	<0.001	NO_3–N	317	36.7	284	39.0	1.776	0.097
Chl *a*	12.2	2.0	17.6	2.7	−4.592	<0.001	Chl *a*	28.1	4.5	33.2	6.7	−1.798	0.094

The samples represent the uppermost 1 m water layer. The significance (P) values are given when $P < 0.1$. O_2%, oxygen saturation; pH, water pH; NH_4-N, ammonium nitrogen; NO_3-N, nitrate nitrogen; PO_4-P, phosphate phosphorus; and Chl *a*, chlorophyll *a*; NS, non-significant; *, instead of *t* test the Mann–Whitney rank Sum test was applied due to the non-equal variance. The concentrations are given as mg m^{-3}

[a] Median

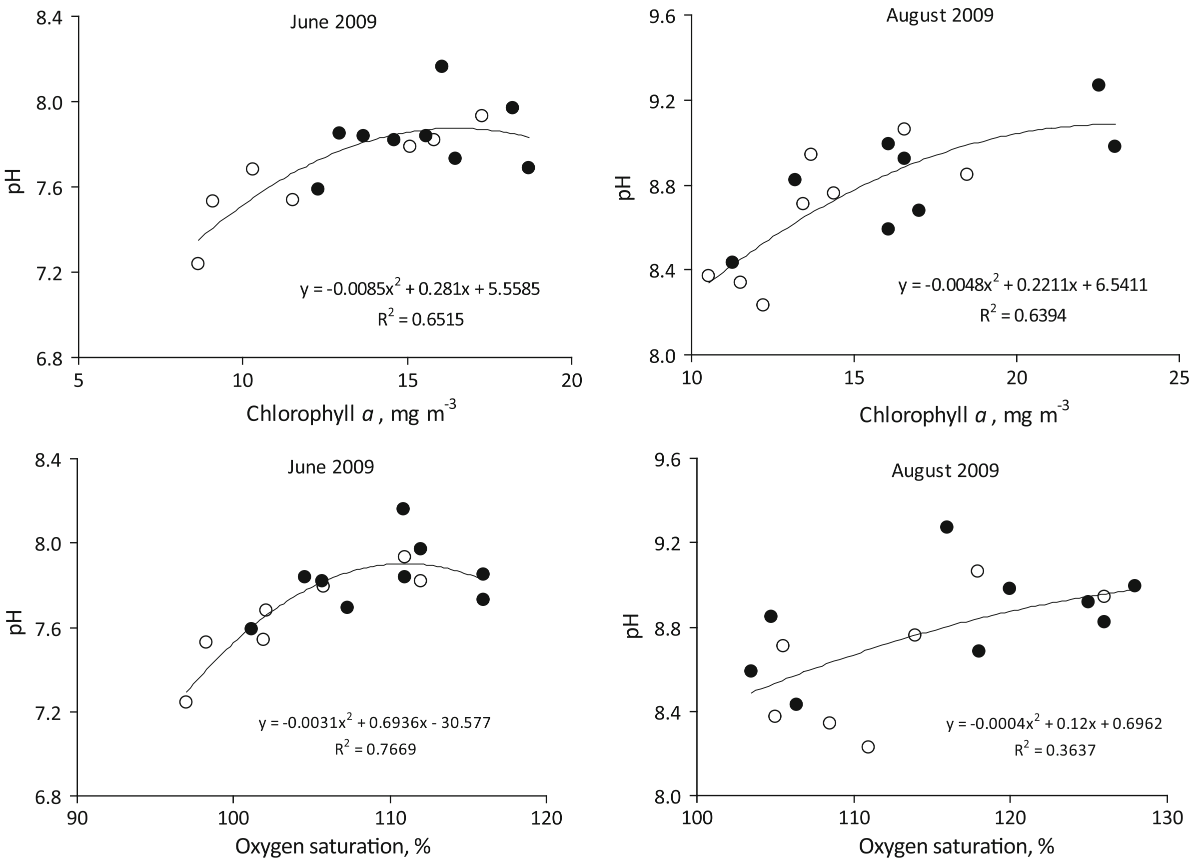


Fig. 2 The relationships between chlorophyll *a* and water pH, and oxygen saturation and pH in June and in August in 2009. The *points* represent different sampling sites over the lake's surface. *Open circles* indicate sampling sites in the W basin (see Fig. 1) and *black dots* in the E basin

surface layer while in the hypolimnion the concentrations were in August, on average, close to 20 mg m^{-3}.

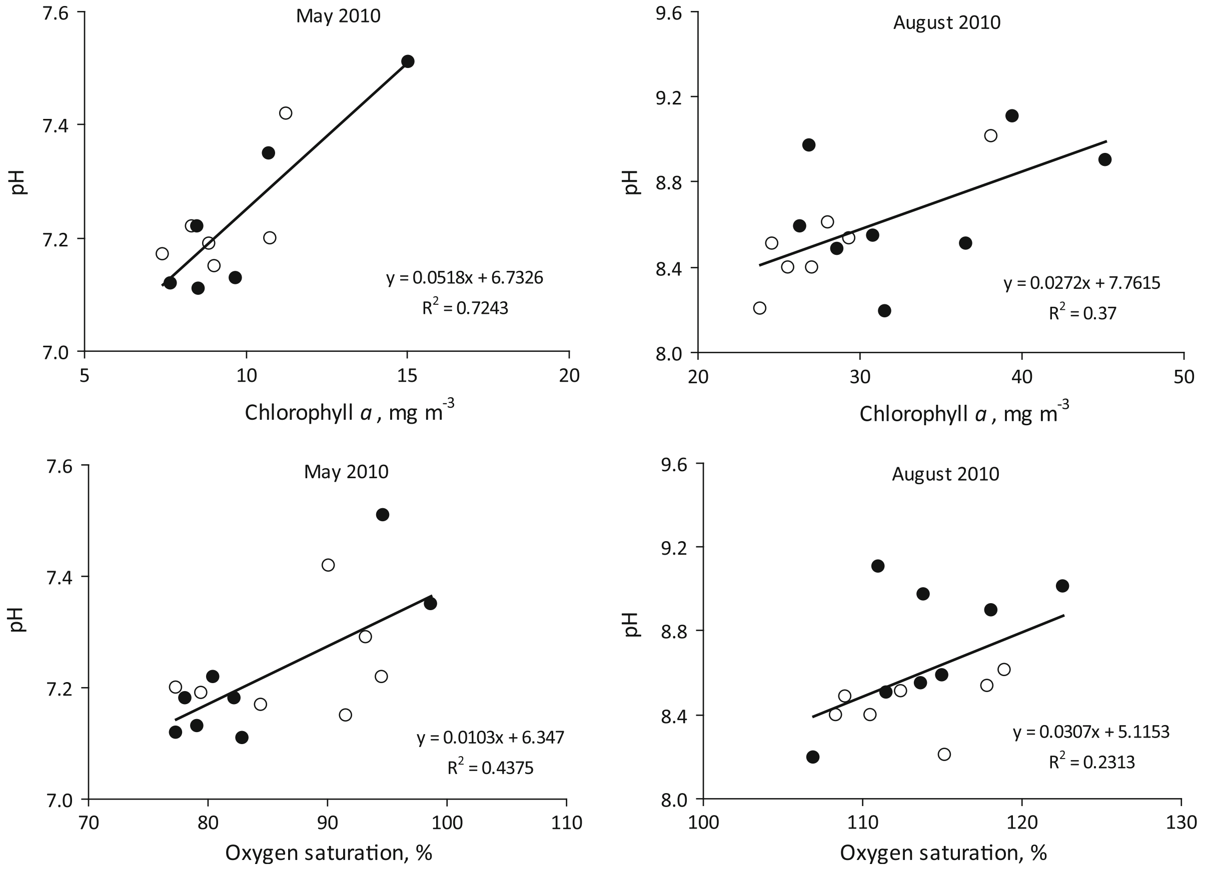
Besides random differences between the sampling sites, there was also systematic variability in summer between the eastern and western part of the lake (Table 4). For example, chlorophyll *a* concentration was higher and NH_4-N lower during all summer campaigns in the E basin (see Fig. 5).

Interactions between phytoplankton and water chemistry

In spring and summer, during both study years, the epilimnetic chlorophyll *a* concentrations were interrelated with pH (Figs. 2, 3). The relationship was stronger, however, in May and June than in August. A similar kind of relationship was also found between the oxygen saturation and pH, and again the connection between the variables was stronger in spring than in late summer (Figs. 2, 3).

Chlorophyll *a* was also correlated with NH_4-N and NO_3-N concentrations (Figs. 4, 5). Except in one case the relationship was reverse indicating that the concentrations of inorganic forms of nitrogen mostly declined when chlorophyll *a* concentrations increased. In June 2009, there was no correlation between chlorophyll *a* and NO_3-N while in May 2010 the relationship was strong and positive (Fig. 5). In October, chlorophyll *a* concentration did not vary between the sampling sites and the same was true with NH_4-N and NO_3-N concentrations. Thus, no correlations between chlorophyll *a* and NH_4-N or NO_3-N concentrations were found.

The above results clearly indicated that the spatial coherence between the chemistry variables and phytoplankton was strong in May/June and August during both years but not anymore in October (Figs. 2, 3, 4, 5). The spatial distributions of the different



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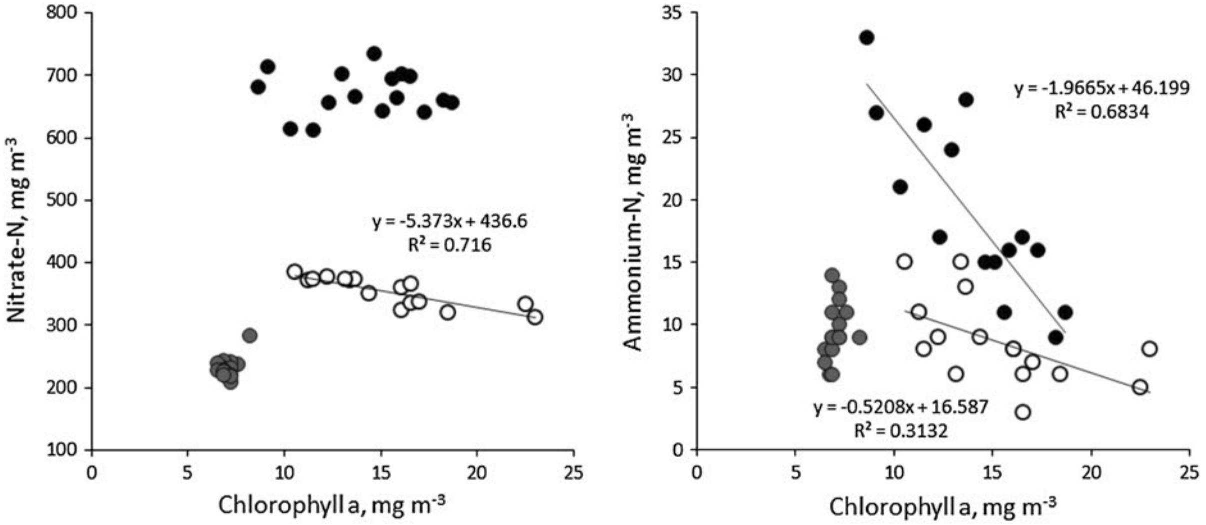

Fig. 4 The relationships between chlorophyll *a* and inorganic-nitrogen concentrations in 2009. *Black dots* indicate June, *open circles* August, and *grey dots* October

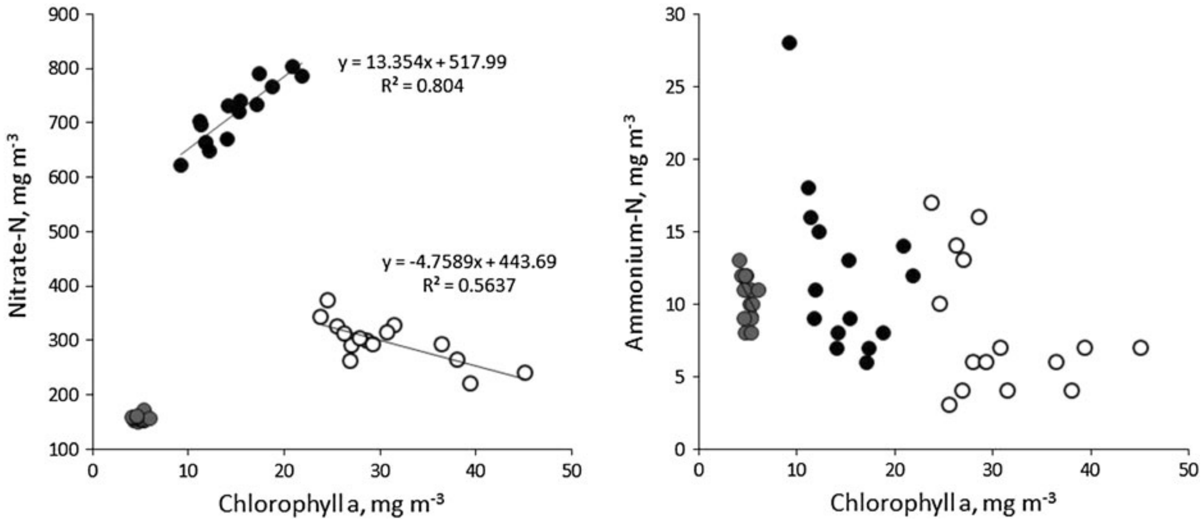

Fig. 5 The relationships between chlorophyll *a* and inorganic-nitrogen concentrations in 2010. *Black dots* indicate June, *open circles* August, and *grey dots* October

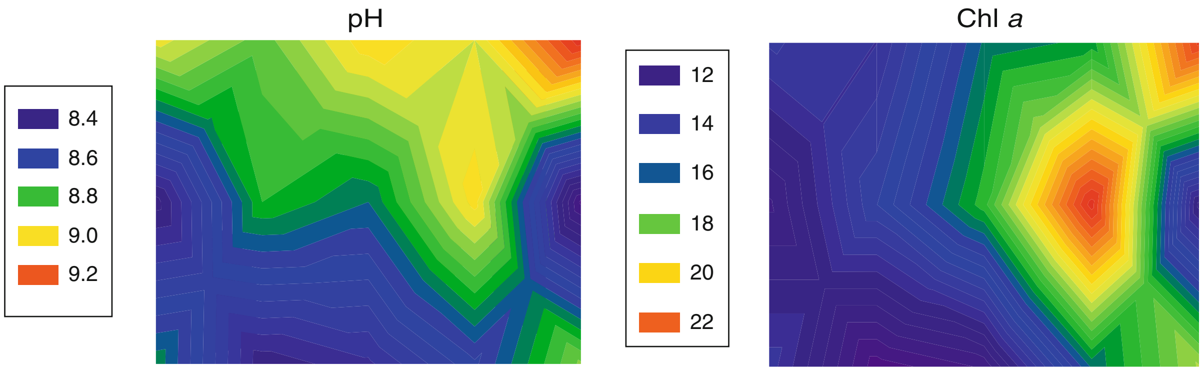

Fig. 6 Spatial distribution of chlorophyll *a* and water pH in the surface of L. Vanajanselkä in August 2010. *Plots* present interpolated distributions of quantities in the sampling grid

constituents were rather similar in both summer seasons with the highest chlorophyll *a* concentrations in the E part of the lake and highest pH and oxygen saturation values in the northern and eastern areas (Fig. 6). However, besides the spatial variability of chlorophyll *a* and the chemical properties, pH and oxygen saturation, in particular, had a strong daily temporal variation in August when their highest values were measured in the afternoon (Fig. 7).

Discussion

The results showed convincingly that besides chlorophyll *a*, water pH, oxygen concentration, and inorganic N and P concentrations varied substantially in space and time in the study lake. The spatial variability was high especially in summer, soon after the spring mixing at the time of the biomass peak of diatoms, and later in summer at a time of the cyanobacteria bloom. Such a high variability was more than expected and clearly higher than that of the electrical conductivity. Because the main body of the lake is open and large with a maximum wind fetch of >10 km, a necessary prerequisite for the variability in plankton and water chemistry is calm weather; otherwise spatial gradients are disturbed as the autumn results showed. In addition, in August 2009 and 2010 there was a surface scum formed by *Microcystis*, which made the conditions favourable for the study.

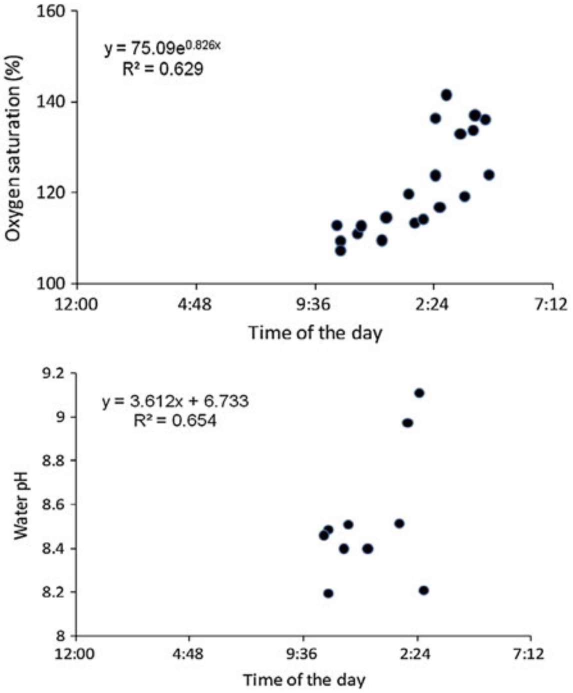

Fig. 7 Variability of oxygen and pH within a day, August 3, 2010. The *points* represent different sampling sites over the surface

If light and temperature are commodious (Reynolds, 2006; Verspagen et al., 2006), nutrients are known to be the primary factors controlling the growth of algae and cyanobacteria (Wetzel, 2001; Kalff, 2002). The observed spatial and temporal differences in water chemistry and chlorophyll *a* raised the question, however, of which was the cause and which was the effect? Intense carbon dioxide (and bicarbonate) and nutrient uptake for photosynthesis and growth may result in high pH and oxygen concentration, and simultaneous decrease of nutrients, including inorganic carbon (e.g., Kairesalo, 1980). Water pH, in particular, seemed to be sensitive to changes in metabolism, and therefore, together with oxygen (see, e.g., Staehr et al., 2012, and references therein), it has been used as a proxy for the metabolic processes in lakes (e.g., Verduin, 1957). This explains why pH, as well as oxygen saturation, was strongly correlated with chlorophyll *a*.

The results further showed that pH and oxygen were correlated with NH_4-N and NO_3-N concentrations, a phenomenon not commonly found in temperate lakes. The results suggest that differences in phytoplankton biomass and its metabolism between the sampling sites primarily produced the observed short-term differences in the chemical properties of the lake. At the same time it is obvious that the observed changes in nutrient concentrations also influenced phytoplankton and its metabolic activity, although at night chemistry gradients set up during daytime may easily flatten due to convective mixing (Boehrer & Schultze, 2008). At the time of the samplings the impact of inflowing water on the spatial differences in lake chemistry was negligible because of the very low discharge relative to the lake volume.

The results proved that in Lake Vanajanselkä the NO_3-N concentration decreased remarkably during the summer season, a result in agreement with the observations of Weyhenmeyer et al. (2007) who showed that in many European lakes NO_3-N concentrations may decrease in summer and may cause potential nitrogen limitation for phytoplankton. Whether nitrogen became a limiting nutrient in this lake cannot be confirmed, however, although the ammonium concentrations were very low and nitrate concentrations also decreased to almost zero in some sampling sites. The reason is that in summer, in the epilimnion, PO_4-P concentrations were always below the detection limit (ca. 2 mg m^{-3}), and because of that the role of PO_4-P cannot be analyzed. On the contrary, the high NH_4-N and PO_4-P concentrations in the hypolimnion indicated poor redox conditions and intense organic matter mineralization later in summer.

As a whole the results supported our first expectation that in summer-time phytoplankton may not be equally distributed over the whole lake area. The second assumption was also supported, although the horizontal differences were found to be distinct also during the early summer. The third expectation was likewise supported by the results, which clearly demonstrated the dynamic nature of the lake system and close linkage between the biotic and abiotic processes. We suggest that differences in phytoplankton and its metabolism strongly affect the observed short-term differences in the chemical properties. This was indirectly indicated by the results from autumn when the spatial variation of water chemistry was low in comparison to spring and summer. The low variability in autumn coincided with the low chlorophyll *a* concentration relative to the spring and summer, suggesting much weaker metabolic response to water chemistry in autumn. Besides, the isothermal conditions in autumn supported more efficient water mixing than in spring and summer.

In conclusion, in summer the variability of inorganic nutrients and chlorophyll *a* was shown to be significant in Lake Vanajanselkä in both space and time. In deeper water layers the chemical conditions were generally more stable than at the surface, however. The results suggest that sensors, which are capable of collecting data at short time-intervals may be useful in studying water chemistry and phytoplankton when spatial and temporal gradients exist (cf. Van De Bogert et al., 2012).

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