

Plankton metabolism and sedimentation in a small boreal lake — a long-term perspective

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We used weekly or biweekly data from the years 1990–2009 to analyse variation in primary production (PP), chlorophyll *a* (Chl) and respiration (*R*) of plankton, and organic matter sedimentation (*S*) in a small boreal lake with intense water colour. PP and *S* had a decreasing trend over the study period while no trend was found in Chl and *R*. PP and *R* were in balance except during the last five years when $R > PP$. The results indicated that light limited PP, while occasionally phosphorus, nitrogen and/or dissolved inorganic carbon could also act as limiting factors. The decrease in *S* coincided with that of PP although during the last five years allochthonous organic matter load seemed to compensate for the decrease in PP. Weather and hydrological conditions were the key drivers in modifying the properties of the lake while the metabolic processes were intercorrelated, and *R* correlated strongly with water temperature.

Introduction

In the last two decades many temperate lakes worldwide experienced an increase in dissolved organic carbon (DOC) concentration and water colour (e.g. Monteith *et al.* 2007). In boreal lakes, the brown colour of water is mostly due to humic substances of allochthonous origin (Hessen and Tranvik 1998, Peuravuori and Pihlaja 1999). Although humic substances are considered to be largely refractory against biological decomposition (Tulonen *et al.* 1992, Münster *et al.* 1999, Wetzel 2001), allochthonous organic matter (AOM) may contribute significantly to energy and carbon demand of food webs (Salonen *et al.* 1992a, 1992b, Kankaala *et al.* 2006a,

Jones *et al.* 2008). This is because of the overwhelmingly high contribution of allochthonous DOC to the total organic carbon (OC) pool in many humic lakes (Sarvala *et al.* 1981, Arvola *et al.* 1990, Einola *et al.* 2011).

As a consequence of high AOM load relative to the autochthonous production, plankton respiration may exceed primary production in humic lakes (Salonen *et al.* 1983, Cole *et al.* 2000) and lake ecosystems are usually supersaturated with CO₂ (Cole *et al.* 1994, Sobek *et al.* 2003, 2005). In addition, small boreal lakes may have elevated CH₄ concentrations which provide a link between AOM and food webs through consumption of methanotrophic bacteria (Kankaala *et al.* 2006a, 2006b).

In the northern hemisphere many catchments and lakes are recovering from acidification, which may be among the primary reasons for the increase in AOM load and brownification of the lakes (Monteith *et al.* 2007, Arvola *et al.* 2010) and rivers (Arvola *et al.* 2004, Erlandsson *et al.* 2008). Climate change is another complex driver including climate warming, changes in the frequency of episodic weather and consequently in the hydrological conditions (*see* Jylhä *et al.* 2010). They are factors which may influence the catchments and loading of nutrients and OM in boreal lakes (e.g. Schindler *et al.* 1996). The results of Sobek *et al.* (2007) suggest that climatic and topographic characteristics set the range of DOC concentrations of a certain region while catchment and lake properties regulate the DOC concentration in individual lakes as Arvola *et al.* (2010) showed for the study region.

Long-term data sets have proven useful to reveal causal relationships between physical, chemical and biological variables in lakes (Magnuson *et al.* 2004, 2006), and in particular when environmental conditions have changed, for instance, as a result of eutrophication or climate warming (Schindler 2009). Such data may be especially valuable if changes in lake ecosystems with irregular or cyclic fluctuations are interpreted (e.g. Talling and Heaney 1988, Gaedke and Schweizer 1993, Adrian *et al.* 1995). Intensive and extensive long-term studies on the metabolic processes are rare, and therefore many major conclusions regarding primary production and respiration of plankton are based on relatively short-term investigations and/or inter-lake comparisons. At the same time some results (e.g. Caffrey *et al.* 1998) suggest that the coupling between ecosystem primary production (~net ecosystem production) and respiration may vary between deep and shallow areas as well as between different seasons.

In this paper, we analyse the trends of primary production, respiration of plankton, chlorophyll *a* and sedimentation of OM in a 20-year long weekly data of a small pristine humic lake in southern Finland. The variables were analysed in relation to the fluctuations in nutrients, water colour and DOC. The lake and its catchment have been intensively studied since 1990 as a part of the "International Co-operative Pro-

gramme on Integrated Monitoring of Air Pollution Effects on Ecosystems" (Rask *et al.* 1998, Peltomaa and Ojala 2010, Huotari *et al.* 2011; *see* also other papers in this issue). Our primary aim was to study the variability and long-term trends of the metabolic processes of plankton, and the causal connections between these processes and abiotic factors. In the analysis, we focused on the uppermost, shallow water layer with most intense plankton biomass and metabolism (Keskitalo and Salonen 1998, Salonen *et al.* 1992a, 1992b, Peltomaa and Ojala 2010).

Material and methods

Study site

Lake Valkea-Kotinen is a small and shallow headwater lake (area 0.042 km², mean depth 2.5 m, max depth 6.5 m) with high water colour (> 100 mg Pt l⁻¹). The lake is located 130 km north of Helsinki in the Kotinen State Reserve in Hämeenlinna (Fig. 1). The catchment area around the lake (0.22 km²) has been intact for > 100 years and is covered by forest, of which 86% is growing on mineral soil and 14% on organic soil (peatlands). For details on the catchment and lake, *see* Vuorenmaa *et al.* (2014), and on the climatic conditions, *see* Jylhä *et al.* (2014). For changes in deposition, *see* Ruoho-Airola *et al.* (2014), and for details on the zooplankton, *see* Lehtovaara *et al.* (2014). One of the special features of the lake is its low pH which varied during the study period between ca. 5 and 5.5 (Vuorenmaa *et al.* 2014) while in the longer term (since the early 1900s to the 1970s) pH was mostly above 6 according to the diatom assemblages of the sediment (Liukkonen 1989).

Sampling and determinations

Primary production (PP) and respiration (*R*) of plankton, and chlorophyll *a* concentration (Chl) were measured weekly, or every second week (since 2007), during the open-water period (from mid-May until the end of September). The sampling took place before noon at approx. 11:00 (local summer time = GMT + 3 hours, with solar

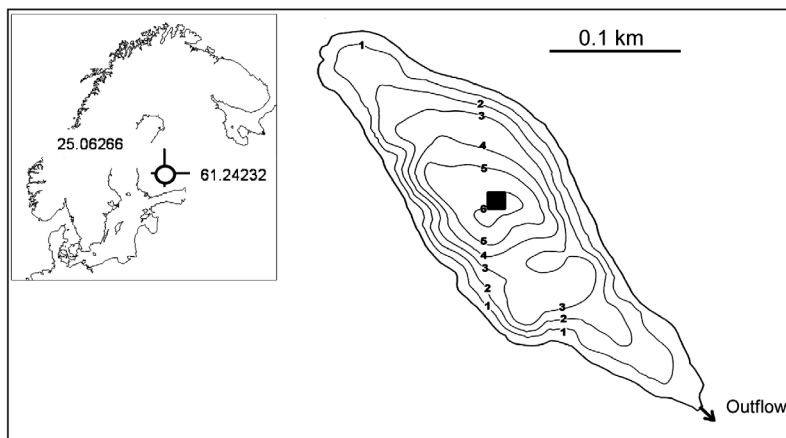


Fig. 1. Bathymetric map and location of Lake Valkea-Kotinen. Black square in the middle of the lake indicates the sampling and incubation point.

noon at about 13:20). Samples for Chl were taken successively down to 5 m depth with a 1-m-long tube sampler (6.7 l) from the deepest point of the lake. Samples for PP and *R* as well as for physical and chemical determinations were taken as composite water samples compiled from three lifts with a 0.3-m-long Limnos tube sampler (2.8 l) from around the boat. The sampling and incubation depths for PP and *R* were 0, 0.25, 0.5, and 1 m, and sampling depths for physical and chemical determinations 0, 1, 2, 3 and 5 m. Thermocline was defined as the depth where water temperature change was greatest.

Dissolved inorganic phosphate ($\text{PO}_4\text{-P}$), nitrate ($\text{NO}_3\text{-N}$) and ammonium ($\text{NH}_4\text{-N}$) concentrations were determined after the samples were filtered through $0.2 \mu\text{m}$ Millipore membrane filters. The detection limit for $\text{PO}_4\text{-P}$ was 2 mg m^{-3} and for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ it was 10 mg m^{-3} . Total phosphorus (P_{tot}) and total nitrogen (N_{tot}) concentrations were determined after wet oxidation with a Lachat FIA analyser (Koroleff 1983), equally with the inorganic nutrients. Water colour was determined with a spectrophotometer as absorption at 420 nm against Pt-Co standards (APHA 2000) after filtration through $0.2 \mu\text{m}$ membrane or GF/C glass fibre filters (no significant difference in the filtration efficiency between the filters was found). DOC was determined by combustion at 900–950 °C (Salonen 1979) or, since 2001, at 680 °C with a Shimadzu TOC 5000 analyzer. Methods for physical and chemical determinations are described in detail in Keskitalo and Salonen (1994).

PP was determined using acidification and bubbling modification of the ^{14}C -method (Schindler *et al.* 1972; see also Keskitalo and Salonen 1994) with a 24 h *in situ* incubation in light bottles. Dark fixation was determined correspondingly in bottles enclosed in closed aluminium tubes, and in calculations dark fixation was subtracted from the light fixation. *R* was determined as the increase in dissolved inorganic carbon (DIC) in dark bottles during 24 h *in situ* incubation. DIC was determined with the acidification and bubbling method of Salonen (1981). Water samples for Chl measurements were filtered through GF/C glass fibre filters. After 5 min extraction in hot (75 °C) ethanol, absorptions were measured at 665 and 750 nm wavelengths by a Shimadzu UV-2100 spectrophotometer. Chl concentration was calculated using an absorption coefficient of 83.4. Phytoplankton biomass was determined by using the Utermöhl (1958) technique and Lugol preserved samples. For details of sampling and biological determinations, see Keskitalo and Salonen (1994).

Sedimentation was measured using three 50 mm in diameter and 600 mm high cylinders suspended 2 m above the bottom in the deepest point of the lake. Sediment was removed from the traps every two-three weeks and no chemicals were used to preserve the samples either in the cylinder or after sampling. Portions of homogenized samples were filtered on ignited glass fibre filters and stored in a deep-freezer. After thawing, the sub-samples were dried for 24 h at 60 °C, weighed and round pieces from the filtering area were punctured for determina-

tions. Organic carbon was measured by combustion at 850 °C with an Uniquant TOC analyser (Salonen 1979). Parallel samples for the determination of organic matter (OM) were combusted in a muffle furnace at 500 °C for four hours. The amount of OM was calculated by subtracting the mass of the ignition residue from the dry mass of respective dried filters. N_{tot} was determined from the punctured samples after potassium persulphate digestion in an autoclave at 120 °C and dissolution in MQ water, and P_{tot} after ignition overnight at 450 °C and dissolution in 0.02 N H_2SO_4 . Both measurements were finally carried out with the Lachat FIA analyser.

Because the ice-out day varied several weeks between the years, also sampling started at different times in different years, and that is why the data between the week-of-year 20 and 39 were chosen for the analyses, i.e. between the mid-May and the end of September.

Statistical analyses

Before further statistical analyses the normality of the data was verified using a Kolmogorov-Smirnov test. Student's *t*-test was used for the comparisons of the means and a Mann-Whitney rank sum test for the medians if the data was not normally distributed. A non-parametric Mann-Kendall test was used for long-term trend analyses, Pearson's product-moment correlation for correlation analyses, and a stepwise multiple regression analysis for the regression analyses. Multiple regressions with different factor combinations were used to explain weekly variation in PP and *R*, and annual variation in *S*. A principal component analysis was used to study multiple interrelationships among the data; the variables included were total and inorganic fractions of nutrients, water temperature, colour and DOC as well as primary production, respiration and chlorophyll *a*. The statistical packages used were Systat 9, SigmaStat 3.0 and SPSS 20. Because selection of the threshold *p* values indicating statistical significance of differences depends on both the magnitude of the effect and the sample size, *p* values between 0.1 and 0.05 should be seen only as tentative indications of possible statistical significance.

Results

Primary production, chlorophyll *a* and phytoplankton

The annual mean PP decreased significantly (Mann-Kendall test: $Z = -4.12$, $p < 0.01$, $n = 20$) during the study period (Fig. 2). The highest annual PP (158 mg C m⁻³ d⁻¹) in 1994 was three times higher than the lowest one in 2008 and almost two times higher than the 1990–2010 average (Table 1). Since the beginning of June (week 23) until the first week of September (week 36) PP was, on average, above 100 mg C m⁻² d⁻¹ but after that sharply declined and at the end of September it was < 40 mg C m⁻² d⁻¹ (Fig. 3). The long-term declining trend in weekly PP was strongest in August and September (Fig. 4, weeks 35–37). The annual average DIC concentration also increased during the study years ($Z = 1.849$, $0.05 < p < 0.1$, $n = 20$) with strongest increase in August (data not shown). DIC concentrations did not vary significantly within the uppermost 1-m water layer (Mann-Whitney rank sum test: $T = 44\ 674$, $p = 0.34$, $n = 214$) where PP and *R* measurements were done. The variability in PP was highest in 2001 (CV = 0.73) and lowest in 2008 (CV = 0.46). Seasonally, the variability was highest in late summer–early autumn when PP started to decline.

In Lake Valkea-Kotinen the attenuation of photosynthetically active radiation (PAR) along with depth was clearly stronger than the decrease in PP. The depth of the euphotic zone, estimated as 1% penetration of PAR, was 1.3–1.4 m, and the extinction coefficient for PAR was 3.6 m⁻¹ in 2009 (Turunen 2011). Seasonally, the ratio between PP at 0.1 m and 1 m depths decreased since the beginning of the measurements until mid-late June (minimum during week 26) after which it increased distinctly until the end of September. Considering the annual averages, the ratio increased in 2004 and during the following four years it remained at a significantly higher level than before (*t*-test: $t_{18} = -5.480$, $p < 0.001$; Fig. 5A).

For the study period 1990–2009, the mean chlorophyll (Chl) concentration in the uppermost 1-m water layer was 16.7 mg m⁻³ (Fig. 2), and its variability (CV = 0.48) was similar to that

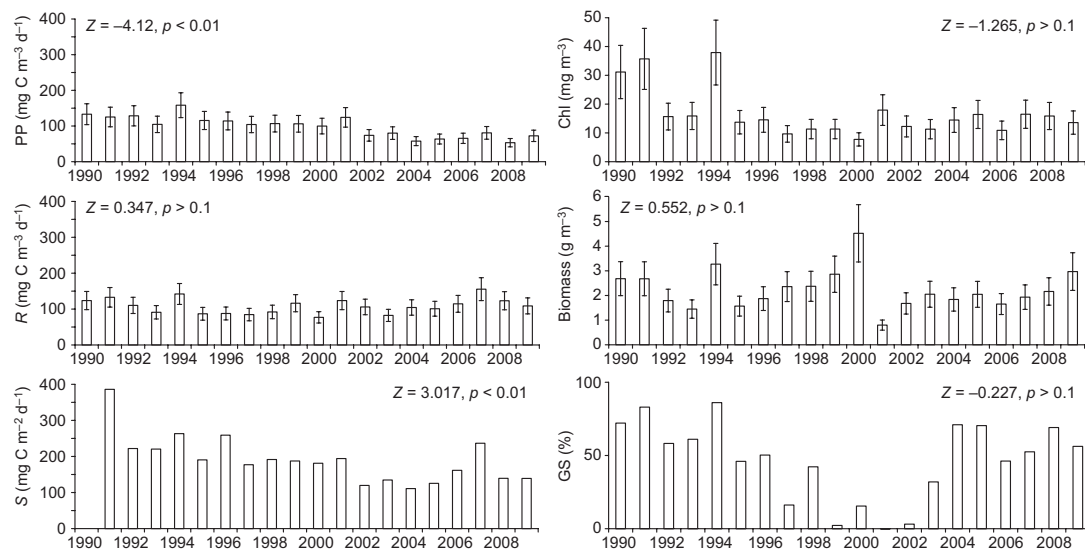


Fig. 2. Annual mean primary production (PP), chlorophyll *a* (Chl) and respiration (*R*) of plankton as well as phytoplankton biomass (Biomass), organic matter sedimentation (*S*) and share of *Gonyostomum semen* (GS; Raphidophyceae) of the phytoplankton biomass in the uppermost 1-m water layer in Lake Valkea-Kotinen. Mann-Kendall trend analysis results for annual (weeks 20–39) means are shown in the figure. The bars indicate standard deviations of the means.

of PP (CV = 0.47). The highest annual Chl concentration of 37.9 mg m⁻³ (1994) was 4.9 times higher than the lowest one (7.8 mg m⁻³ in 2000) and the three highest annual values were found during the first five years. Seasonally, the highest Chl concentrations (> 25 mg m⁻³) were usually recorded in early August (Fig. 3). No significant long-term trend ($Z = -1.265, p > 0.1, n = 20$) was

found in annual mean Chl concentrations. However, for individual weeks the Mann-Kendall test showed positive values from May to mid-July after which they turned negative until the middle of September (Fig. 4).

The highest annual phytoplankton biomass was found in 2000 and lowest in 2001 (Fig. 2), without any long-term trend during the study

Table 1. Characteristics of Lake Valkea-Kotinen: data (0–1 m) collected from week 29 to week 39 in 1990–2009 along with the results of the Kolmogorov-Smirnov test for normal distribution (K-S Dist., K-S Prob.). *n* = number of observations, PP = primary production (mg C m⁻³ d⁻¹), Chl = chlorophyll *a* concentration, *R* = respiration of plankton (mg C m⁻³ d⁻¹), N_{tot} = total nitrogen (mg m⁻³), NO₃-N = nitrate nitrogen (mg m⁻³), NH₄-N = ammonium nitrogen (mg m⁻³), P_{tot} = total phosphorus (mg m⁻³), PO₄-P = phosphate phosphorus (mg m⁻³), DOC = dissolved organic carbon (g m⁻³), Colour = water colour (g Pt m⁻³), and *T* = water temperature (°C).

Variable	<i>n</i>	Mean	Median	SD	Min	Max	K-S Dist.	K-S Prob.
PP	445	92	85	59	0	373	0.060	0.002
Chl	447	15.8	12.1	13.5	2.3	105.9	0.215	< 0.001
<i>R</i>	470	100	96	56	1	389	0.041	0.115
N _{tot}	470	465	458	58	314	765	0.070	< 0.001
NO ₃ -N	470	12	11	8	1	58	0.151	< 0.001
NH ₄ -N	470	14	11	14	2	139	0.226	< 0.001
P _{tot}	470	16	16	4	8	47	0.111	< 0.001
PO ₄ -P	470	1	1	1	0	7	0.394	< 0.001
DOC	447	12.2	12.2	1.5	7.8	17.6	0.051	0.008
Colour	401	148	145	27	78	250	0.065	0.002
<i>T</i>	445	16.4	16.6	3.7	5.1	24.1	0.052	0.014

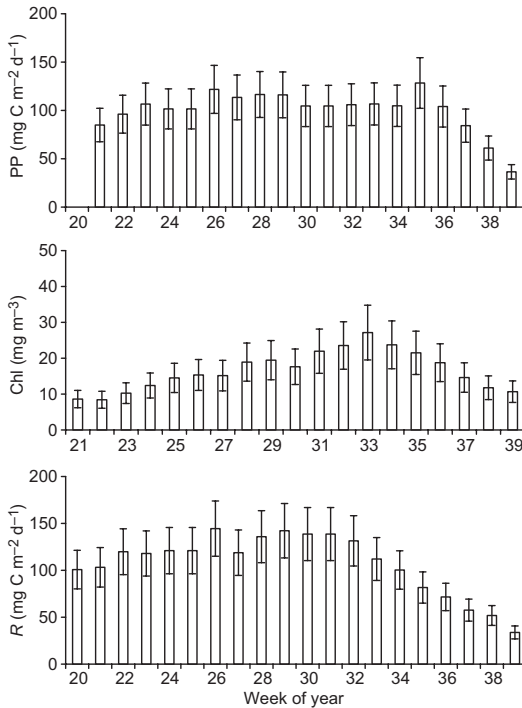


Fig. 3. Mean weekly development of primary production (PP), chlorophyll *a* (Chl) and respiration (*R*) of plankton in Lake Valkea-Kotinen. The bars indicate standard deviations of the means.

period ($Z = 0.552$, $p > 0.1$, $n = 20$). The most abundant phytoplankton taxonomical groups regarding average biomass over the whole study period were raphidophytes (43% of total phytoplankton biomass), dinophytes (15%), chrysophytes (12%), chlorophytes (10%), euglenophytes (9%), cryptophytes (4%), and diatoms (3%). During the first five years, *Gonyostomum semen* — a large raphidophyte — contributed

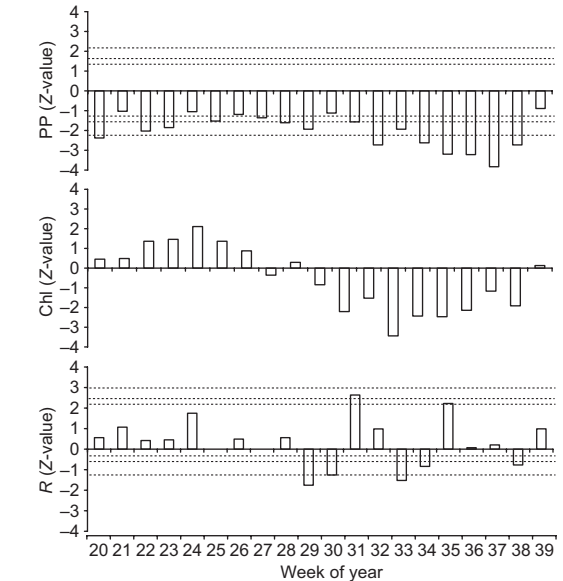
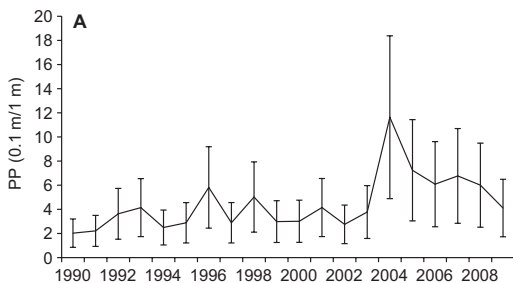


Fig. 4. Long-term weekly trends in primary production (PP), chlorophyll *a* (Chl) and community respiration (*R*). Dashed lines indicate the positive and negative Mann-Kendall test *Z*-values at $p < 0.01$, $p < 0.05$, and $0.05 < p < 0.1$.

occasionally > 95% to the phytoplankton biomass but since 1998 until 2004 its abundance was very low (Fig. 2).

Respiration

No long-term trend was found in annual mean respiration of plankton ($Z = 0.35$, $p > 0.1$, $n = 20$; Fig. 2). The mean daily *R* for the entire period was $106 \text{ mg C m}^{-3} \text{ d}^{-1}$ (CV = 0.47), and the highest annual value ($155 \text{ mg C m}^{-3} \text{ d}^{-1}$ in

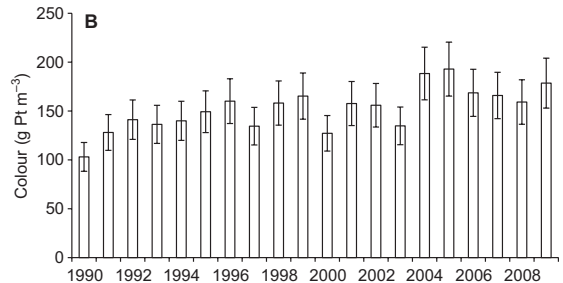


Fig. 5. (A) The ratio between weekly primary production (PP) at 0.1-m and 1-m depths from July until the end of September. The shift in the ratio in 2004 was nearly statistically significant (Cusum; maximum deviation = 6, $0.05 < p < 0.1$). (B) May–September mean colour values from the uppermost 1-m water layer. The bars indicate standard deviations of the means.

2007) was two times higher than the minimum ($77 \text{ mg C m}^{-3} \text{ d}^{-1}$ in 2000). Seasonally, there was a relatively strong positive correlation between R and water temperature (*see* below and Table 2).

The ratio between mean annual primary production and respiration of plankton decreased especially since 2003 (Fig. 6) which was largely due to the decrease in PP (Fig. 2).

Sedimentation

The annual mean sedimentation (S) rate of organic matter decreased significantly ($Z = 3.017$, $p < 0.01$, $n = 20$) from 1990 to 2009 (Fig. 2). Especially low sedimentation was recorded in 2002–2005, when it varied between 52 and $63 \text{ mg C m}^{-2} \text{ d}^{-1}$, but after that S increased and in 2006–2007 it was again at the 1990s level. The long-term average for the 20 year period was $89 \text{ mg C m}^{-2} \text{ d}^{-1}$ ($CV = 0.34$). The C/N mass ratio of the settled material was on average 14 with the maximum and minimum values of 19 and 10 in 1991 and in 1997, respectively. The respective mean C/P and N/P ratios were 159 and 11 with maximum and minimum values of 280/101 and 17/9.

Relationships between biotic and abiotic variables

The relationship between PP and Chl was weak, and the PP/Chl ratio varied between 1 and 61. The five highest annual PP/Chl ratios (8.4–12.9) were found for 1995–2000. On average, the

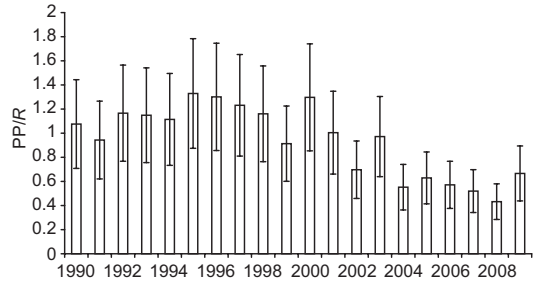


Fig. 6. The ratio between mean annual primary production and respiration (PP/R) of plankton in Lake Valkeakotinen. The bars indicate standard deviations of the means.

values decreased towards autumn and were lowest in August, at the time of highest Chl concentrations. In late summer (weeks 34–36), a negative relationship between PP at 1-m depth and water colour existed ($r^2 = 0.570$) suggesting decreasing availability of light for PP. In line with that the ratio between PP at the surface and 1-m depth increased relative to water colour ($r_p = 0.740$, $p = 0.0002$, $n = 20$), indicating a shallower productive layer.

The total nitrogen (N_{tot}) concentration varied only little among years while the concentration of total phosphorus (P_{tot}) was lower between 1995 and 2006 after which it returned to the same level as at the beginning of the study period. The dissolved inorganic phosphorus ($\text{PO}_4\text{-P}$) concentration was mostly below the detection limit (2 mg m^{-3}); only at the beginning of the study it was more regularly detectable. The $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ concentrations were also below or close to the detection limit (10 mg m^{-3}) during the first

Table 2. Pearson product-moment correlation coefficients (r_p), statistical significance (p), and number of observations (n) between metabolic and abiotic variables. For the abbreviations, *see* Table 1.

		Temperature	Colour	DOC	$\text{NO}_3\text{-N}$	$\text{PO}_4\text{-P}$	$\text{NH}_4\text{-N}$	R	Chl
PP	r_p	0.194	-0.271	-0.242	-0.36	0.235	-0.365	0.451	0.401
	p	0.0003	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	n	343	313	383	382	287	389	357	386
Chl	r_p	0.129	-0.23	-0.0836	-0.0891	0.544	-0.17	0.394	
	p	0.0113	< 0.0001	0.0833	0.0653	< 0.0001	0.0004	< 0.0001	
	n	384	320	430	429	332	436	372	
R	r_p	0.569	-0.0636	-0.0268	-0.163	0.302	-0.233		
	p	< 0.0001	0.279	0.609	0.0015	< 0.0001	< 0.0001		
	n	333	292	368	380	307	386		

6–7 years, but after the summer of 1996 mostly above the detection limit.

In the uppermost 1 m, there was a weak correlation ($r_p = 0.451$, $p < 0.001$, $n = 357$) between PP and R , and between Chl and $PO_4\text{-P}$ ($r_p = 0.554$, $p < 0.001$, $n = 332$; Table 2). In late summer, P_{tot} (weeks 31–35) and dissolved inorganic nitrogen (weeks 34–36) had strong non-linear correlations with Chl (P_{tot} : $y = 0.074x^{2.042}$, $r = 0.786$, $n = 100$, $p < 0.001$; $NO_3\text{-N} + NH_4\text{-N}$: $y = 55.479x^{-0.822}$, $r = 0.697$, $n = 100$, $p < 0.001$). The ratio between Chl and P_{tot} varied from 0.1 to 4.5 with the lowest values (< 0.65) in early summer and the highest (> 1.06) in late summer. However, the inorganic fractions of N had clearly lower explanatory power (Table 2).

In multiple regressions, PP was best explained (28%) by $NO_3\text{-N}$, Chl and R (57%) by P_{tot} , temperature, PP and colour, and Chl (55%) by N_{tot} , PP and $PO_4\text{-P}$ (Table 3). Correspondingly, Chl and PP explained 77% of the annual variation in sedimentation. There was also a positive correlation between respiration and water

temperature at 1-m depth ($r_p = 0.569$, $p < 0.001$, $n = 333$; cf. Table 2).

Factor analysis based on the correlation matrix to extract the principal components confirmed that the three principal components (factors) explained 65.3% of the total variance of data. The first factor with highest loads consisted of phosphorus, respiration and chlorophyll, the second factor of nitrogen (nitrate and N_{tot}) and DOC (and colour), and the third one of water temperature. The first factor explained 31.7% of the variability, the second one 20.6% and third one 13.0%.

Discussion

The decrease in phytoplankton production was the most notable change in Lake Valkea-Kotinen during the 20-year study period. The most straightforward explanation would be that it was due to light limitation following increased water colour during the second half of the study period

Table 3. Results of the stepwise multiple regression analysis for PP, R and Chl as the dependent variables. For the abbreviations, see Table 1.

Dependent variable	Analysis of variance		Variables in model			
	F	p	Constant	Coef.	F	p
PP (df = 212) Adj $r^2 = 0.277$	28.498	< 0.001		96.16		
			$NO_2 + NO_3$	-2.79	32.81	< 0.001
			R	0.16	5.75	0.017
			Chl	1.27	27.19	< 0.001
R (df = 211) Adj $r^2 = 0.567$	71.437	< 0.001		-130.64		
			P_{tot}	5.95	135.85	< 0.001
			PP	0.11	4.67	0.032
			Col	0.17	4.10	0.044
			T	6.63	82.15	< 0.001
Chl (df = 208) Adj $r^2 = 0.552$	38.818	< 0.001		-34.12		
			PO_4	3.26	19.49	< 0.001
			NH_4	-0.65	10.52	0.001
			N_{tot}	0.09	24.23	< 0.001
			P_{tot}	0.50	5.08	0.025
			DIN	1.73	7.98	0.005
			PP	0.06	23.39	< 0.001
			Col	-0.07	5.00	0.026

(Vuorenmaa *et al.* 2014). However, in contrast to PP, no consistent long-term trend was found for Chl. Although the photic zone became shallower especially since 2004, this does not necessarily mean that in the lake phytoplankton became more light limited. This is because flagellated algal species, which overwhelmingly dominated the phytoplankton community in Lake Valkea-Kotinen (Peltomaa *et al.* 2013), can optimize their vertical position in relation to light and other abiotic resources (e.g. Arvola *et al.* 1991). Therefore, phytoplankton might be able to compensate the darker water colour and consequent light limitation by moving closer to the surface (Smolander and Arvola 1988), and PP might not be affected. Neither the chlorophyll nor phytoplankton results allow for any final conclusion whether this really happened in the lake because we took composite samples from the uppermost 1-m water layer. Further, phytoplankton in Lake Valkea-Kotinen have been found to harvest hypolimnetic nutrients (Salonen and Rosenberg 2000), so that even reduced thickness of the epilimnion does not necessarily diminish nutrient availability. Consequently, the observed long-term decrease in PP may be biased, but on the other hand it is supported by the concurrent decrease in annual sedimentation rate. However, because the lowest sedimentation rate coincided with the drought in 2002–2003 and sedimentation again increased after the high precipitation in 2005, sedimentation is to a great extent controlled by the hydrological conditions. In this context, it is necessary to mention that no major changes in thermal stability and/or heat content could be found in Valkea-Kotinen between the two decades in spite of differences in annual and seasonal scale. Also no clear change in the depth of the epilimnion was found.

Besides PAR and UV radiation, that attenuates in the uppermost few ten millimetres in Lake Valkea-Kotinen (Vähätalo *et al.* 2000, Arst *et al.* 2008), other factors influencing PP in the lake include shortage of dissolved inorganic carbon (DIC) as well as nitrogen and phosphorus. Low DIC concentration evidently affected the PP results during the 24 h bottle incubations. It is likely that phytoplankton were not able to sustain their DIC requirements as the long incubation time prevented the exchange

of CO₂ between water and the atmosphere, and the retrieval of CO₂ from deeper DIC rich water layers. Schippers *et al.* (2004) concluded that fresh waters with low alkalinity are sensitive to atmospheric CO₂, and its elevation may thus enhance primary production of phytoplankton if CO₂ is a limiting resource (*see* Jansson *et al.* 2012). Due to low ambient CO₂ concentration of Valkea-Kotinen water, it is possible that proportion of ¹⁴C fixed in photosynthesis is increasingly recycled by bacteria during the 24 h PP incubations, another factor which may have decreased PP results. On the other hand, due to low pH of the water (pH varied mostly between 5.0 and 5.5), CO₂ contributed to > 90% of DIC, which did not change much during the 20 years (Vuorenmaa *et al.* 2014). However, the DIC concentrations increased during the latest years especially in August when the mean concentration was up to > 0.5 g C m⁻³ in comparison with 0.2 g C m⁻³ during the early 1990s. The increase in DIC was in line with the decrease in the PP/R ratio, and indicated better availability of CO₂ for photosynthesis during the study years (*see* also Huotari *et al.* 2009).

Limitation of PP by nutrients was highlighted during the two-year drought in 2002–2003 and the following exceptionally wet summer 2004 when nutrient and AOM loads were high (Arvola *et al.* 2010). The ratio between PP and R decreased in the dry summer of 2002 rather dramatically, after which it remained at a much lower level during the rest of the study period. We propose that there were two major consecutive factors influencing the decrease. The first one was the drought itself in the summers 2002 and 2003 which resulted in a downward shift in the level of groundwater and inflow to the lake and a substantial decrease in nutrient loading. The second one was the abnormally rainy summer in 2004 which resulted in an upward shift in hydrology and an increase in DOC loading and consequently higher colour in the lake. Then, elevated concentration of humic compounds may have decreased the availability of nutrients (Jones 1998).

In addition, since 2002 no clear change in R has been found, however, which contradicts some previous findings that R and/or bacterial activity may respond to changes in allochtho-

nous OC load (e.g. Tranvik 1988, Kankaala *et al.* 1996, Drakare *et al.* 2002). The increase in sedimentation after the summer of 2004 suggests that allochthonous OM compensated the decrease in PP in Lake Valkea-Kotinen (Vuorenmaa *et al.* 2014). The results demonstrated how a change in hydrology following the shift from drought to wet conditions can modify the chemical properties of a headwater lake, and cause an increase in water colour, and N and P concentrations as well.

Nutrient data (Vuorenmaa *et al.* 2014) together with previous nutrient-enrichment experiments (Järvinen 2002) suggested that in the 1990s phytoplankton was limited by both P and N but during the last ca. 10 years P limitation became more severe than N limitation. It is noteworthy that in the topmost 1-m water layer PO₄-P almost never exceeded the detection limit of the analytical method, i.e. ~2 mg m⁻³, and NO₃-N and NH₄-N concentrations, in turn, were always higher in May and September than during the rest of the summer. Evidently in mid-summer the biological uptake of both nutrients by plankton was most intense. Earlier Jansson *et al.* (2001) found that the overall mobilization of energy by bacterioplankton and phytoplankton in small humic lakes in northern Sweden was restricted by the lack of inorganic nitrogen rather than phosphorus. The results of Järvinen (2002) suggest nutrient competition between bacteria and phytoplankton in Lake Valkea-Kotinen, but the conditions in the lake differ from those in the incubation bottles of his experiments. In the lake, phytoplankton is able to migrate and retrieve nutrients from deeper water layers and/or from the sediment while in the bottles this is not possible. Bacteria, on the other hand, are not able to move as much as algae and thus have limited ability to exploit spatially unevenly distributed resources. This difference may reduce resource competition between bacteria and algae, and also explain why the migratory algal cells dominate the phytoplankton communities in many humic lakes (Arvola *et al.* 1999).

The decrease in OC sedimentation relative to N_{tot} and P_{tot} during the first 11 years suggested a rather dramatic change in the biogeochemistry of the major nutrients. Therefore, an intriguing question is whether there was a link between

the observed decrease in C/N and C/P of the settled material and the higher lake water NO₃-N and NH₄-N concentrations during late 1990s. Both results suggest that N limitation may have decreased since the middle of the 1990s, although in the Valkea-Kotinen catchment the atmospheric deposition of N has decreased since the end of the 1980s (Ruoho-Airola *et al.* 2014). This is interesting, because earlier findings of Bergström *et al.* (2005) and Bergström and Jansson (2006) indicated that in unproductive lakes in Europe and North America high atmospheric N deposition elevated inorganic nitrogen concentrations and caused a shift from N limitation to P limitation.

At the same time with a shift in limiting nutrient the abundance of *Gonyostomum semen*, a raphidophyte alga with high chlorophyll-*a* content, decreased to a very low level (Peltomaa *et al.* 2013). Its annual maximum abundance decreased in 1999 and remained during the subsequent four years at a significantly lower level than before (*t*-test: $t_{12} = 3.143$, $p < 0.001$; see also Peltomaa and Ojala 2010). The species recovered by 2004 and again reached high cell densities similar to those in the early 1990s. In Lake Valkea-Kotinen *Gonyostomum semen* is known to carry out extended diurnal vertical migrations (Salonen and Rosenberg 2000) which may allow the cells to retrieve nutrients from the hypolimnion and even from the bottom sediments (cf. Eloranta and Råike 1995). In addition, the species is capable of mixotrophic nutrition (Rengefors *et al.* 2008), which can be beneficial in steeply stratified humic lakes where different resources are spatially distinctly separated (Angeler *et al.* 2012). In our study lake, the highest Chl values were recorded usually in August and coincided with the maximum abundance of *Gonyostomum*. According to Peltomaa and Ojala (2010) it is a species with relatively high efficiency in C incorporation, and in Lake Valkea-Kotinen the highest PP values usually coincide with high abundance of *Gonyostomum*. Therefore, the disappearance of *Gonyostomum* in 1999–2003 may be difficult to explain as a consequence of changes in nutrient ratios or other abiotic factors especially when the species “re-appeared” to the lake. This is why we suggest that in Lake Valkea-Kotinen food web

interactions need to be taken into consideration when the inter-annual differences in *Gonyostomum* abundance and seasonal dynamics are evaluated, although previous studies have indicated that grazing may have a minor influence on the species (Lebret *et al.* 2012).

The “drought–flood” episode between 2002 and 2004 manifested how strongly the upstream lakes can be influenced by their catchment areas and by climate as was pointed out earlier by Magnuson *et al.* (2005, 2006) and Drakare *et al.* (2002; see also Einola *et al.* 2011 and Ojala *et al.* 2011). Valkea-Kotinen clearly had a long response time for this kind of environmental change, a very similar phenomenon as Jennings *et al.* (2012) showed in a larger nearby lake, Pääjärvi, after the flood in summer 2004. As discussed above, the complexity of the ecosystems complicates interpretation of many important relationships between the metabolic processes and the multiple environmental variables and stressors (see Palmer and Yan 2013), in spite of the available frequent and harmonized long-term data. Besides the physical and chemical drivers, phytoplankton may have also been influenced by higher trophic levels of the food web such as zooplankton (Lehtovaara *et al.* (2014) and fish (Rask *et al.* 2014).

According to Lehtovaara *et al.* (2014) in Lake Valkea-Kotinen crustacean zooplankton was affected by water colour, alkalinity and phosphorus while rotifers were also affected by competitive and/or predatory interactions with cladocerans and copepods. It seems that during the early years of the study period the zooplankton community was more associated with primary production and during the latest years with water colour (Lehtovaara *et al.* 2014). These results together with our results and results of Rask *et al.* (2014) and Vuorenmaa *et al.* (2014) suggest that OM and water colour were strongly shaping the ecological conditions, including plankton metabolism in Lake Valkea-Kotinen. However, the details on how zooplankton and the higher trophic levels of the food web influenced phytoplankton and the metabolic processes in the lake are not known.

In conclusion, the results suggested that the availability of light and nutrients and water temperature were among the key abiotic factors

regulating the changes in metabolic processes of Lake Valkea-Kotinen. The decline in PP was interpreted to be a result of climatic forcing and consequent hydrological conditions which determined the nutrient and DOC loading to the lake, and which finally affected the metabolic processes of plankton and sedimentation patterns. From a research perspective, a very useful period in the lake was the episodic drought–flood period of 2002–2004 which demonstrated the effect of high precipitation on the AOM load to the lake which, in turn, enhanced the sedimentation rate in the lake during the successive years. This verifies that the Valkea-Kotinen system has a long response time (memory) for such kind of environmental change stressors, and highlights the value of long-term intensive data when complex relationships and multiple stressors are studied.

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