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Discussions

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Dynamics of auto- and heterotrophic picoplankton and associated viruses in Lake Geneva

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Abstract

Microbial dynamics has been rarely investigated in Lake Geneva, which is paradoxically the largest lake in Western Europe. From a 5 month survey, we report dynamic patterns of free living viruses, bacteria and small phytoplankton abundances in response to a variety of environmental parameters. For the first time, we fractionated the primary production to separate the contribution of different size-related biological compartments and measured both bacterial and viral production in addition to experiments conducted to appreciate virus-induced bacterial mortality. We observed marked seasonal and vertical variations in picocyanobacteria, bacteria and virus abundances and production. The contribution of picoplankton and nanoplankton production to the total primary production was high in November and spring-summer transition period respectively. The impact of viral lysis on both bacteria and picocyanobacteria was significantly higher than grazing activities. Virus-induced picocyanobacterial mortality reached up to 66 % compared to virus induced bacterial mortality that reached a maximum of 34 % in July. Statistical analyses revealed a complex interplay between biological abundances and/or activity with environmental factors in Lake Geneva. Our results provide new evidence on the critical role played by viruses in freshwater microbial dynamics and more globally on the functioning of the microbial food webs. This study highlights the importance of further considering this biological compartment for a better understanding of the plankton ecology of Lake Geneva, especially for modeling purposes and in a context of reoligotrophication and warming of this ecosystem.

1 Introduction

Picoplankton is an integral component of microbial community which seems to be ubiquitous in all seas and lakes (Azam et al., 1983; Callieri and Stockner, 2002). In aquatic microbial ecology, the term picoplankton traditionally refers to all cells which fall into the size class 0.2–3 μm that includes picocyanobacteria, heterotrophic bacteria, archaea

and small eukaryotic phototrophs referred to as picoeukaryotes (Li et al., 1983; Whitman et al., 1998; Worden and Not, 2008; Auguet et al., 2010). The ubiquitous distribution of picophytoplankton (cyanobacteria and picoeukaryotes) and their importance in terms of biomass and production make them a critical food web component and carbon cycling in a wide variety of aquatic environments (Worden et al., 2004). Compared to autotrophic picoplankton, heterotrophic bacteria contribute to a larger percentage to total plankton biomass and play a central role in the transformation and mineralization of organic matter in the biosphere, thereby contributing immensely to cycling of carbon and nutrients in aquatic systems (Sarmiento and Gruber, 2006).

The dynamics of picoplankton in aquatic ecosystems are not only controlled by various physico-chemical factors (temperature, light, and nutrients) but also by biotic interactions as well (viral lysis, predation and parasitism). In recent years, top-down control of picoplankton populations have evoked much interests among microbial ecologists with the finding of large numbers of viruses (10^8–10^{11} L^{-1}) in aquatic systems. Studies have now revealed that viral lysis can be a significant source of mortality which could be compared to bacterivory by protists (Pradeep Ram et al., 2005; Personnic et al., 2009a). Through their lysis activity, viruses also play an important role in regulating carbon and nutrient fluxes, food web dynamics and microbial diversity and diversifications in aquatic systems (Suttle, 2005; Jacquet et al., 2010; Brietbart, 2012).

The factors that influence viral abundance and dynamics in aquatic environments are complex and are found to vary with aquatic ecosystems (Clasen et al., 2008). Although a large majority of these studies have been focused on marine environments (Weinbauer and Suttle, 1997; Weinbauer, 2004), fewer investigations have been carried out in freshwater systems to study the influence of environmental factors on the dynamics of viral communities associated with autotrophic and heterotrophic picoplankton (Maranger and Bird, 1995; Clasen et al., 2008; Jacquet et al., 2010). Studies have shown that the viral abundance is influenced more by the bacterial abundance in marine environments and by chlorophyll *a* concentration in nutrient-rich lakes (Pradeep Ram et al., 2010). A few studies in the lacustrine environments have included the influ-

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ence of grazers in the picoplankton and bacterial abundances in studying viral dynamics (Personnic et al., 2009a,b; Berdjeb et al., 2011).

Lake Geneva is a mesotrophic peri-alpine lake where past studies have suggested that *Synechococcus* is the most predominant species in the autotrophic picoplankton (APP) (Duhamel et al., 2006; Personnic et al., 2009b). Lake Geneva has been poorly investigated in terms of microbial dynamics and diversity, and information on virus-bacteria, flagellates-bacteria and picocyanobacteria-ciliates interactions is sparse (Duhamel et al., 2005; Tadonléké, 2005; Personnic et al., 2009a,b). Recently by using a PCR-based molecular approach, we showed that Lake Geneva displays clear seasonal variations in the diversity of viruses (Parvathi et al., 2012). However, information regarding the phytoplankton structure, production, ecology and dynamics of viruses are still lacking from this lake. Further, the influence of various chemical and physical parameters on viruses and different groups of plankton has not yet been well documented. Therefore, in the present study we proposed to highlight the seasonal and vertical variations in picoplankton abundance, production and different viral parameters in relation to both biotic and abiotic factors in Lake Geneva over a 5 month period including summer and fall.

Our aim was to bring out an understanding about the abundance of autotrophic and heterotrophic plankton and associated viruses and to elucidate the type and extent of relationship of various physical, chemical and biological factors in determining the abundance of various autotrophic and heterotrophic planktonic groups in Lake Geneva.

2 Materials and methods

2.1 Study site and sampling strategy

Lake Geneva which lies at an altitude of 372 m is the largest lake in Western Europe and forms the border between France and Switzerland at the north of the French Alps. The lake is 72 km long and 13 km wide with an area of 582 km^2. It is a meromictic

lake, never covered by ice, with temperature ranging between 4 and 22 °C. It holds an approximate volume of 89×10^9 m^3 and this lake was reported as eutrophic during the seventies. Later during the nineties, following restoration programs including measures to reduce phosphorus inputs, the lake changed to a mesotrophic state. In 2011, the lake had a total phosphorus content of 27 µg P L^{-1} (CIPEL report, 2012). In our study, samples were collected at the reference station (46°27′ lat. N 6°32′ long.), corresponding to the deepest part of the lake at monthly or bimonthly intervals from July to November 2011. The summer period extended from the end of July to September and autumn from October to November. The samples were collected at different depths (2, 7.5, 10, 15, 20, 25, and 30 m) using a niskin water sampler in two 20 L polycarbonate container and stored at ambient temperature, protected from light and heat, and brought to the laboratory within 3 h of collection.

2.2 Environmental parameters and plankton analysis

A multiparameter probe (CTD 90M, Sea and Sun Technology) was used to collect different parameters such as temperature, light, conductivity, chlorophyll *a* and oxygen profiles. Samples were analysed for nutrients namely nitrate (N-NO_3), nitrite (N-NO_2), total nitrogen (N_{tot}), phosphate (PO_4), total phosphorous (P_{tot}) and silicate (SiO_2) were analysed using standardised methods (Anneville et al., 2005). Raw water samples for the phytoplankton analysis were taken with a patented integrating instrument developed by Pelletier and Orand (1978) integrating the 0–20 m upper lit layer and fixed with a few drops of Lugol's solution. For each sample, 25 mL were poured into an Utermöhl room (cylinder surmounting a blade with sediment chamber; Utermöhl, 1931) and left to form a deposit during at least 12 h safe from light and heat. The qualitative and quantitative examination of the phytoplankton was carried out using inverted microscopy (Zeiss). For the zooplankton, vertical sampling from a depth of 50 m to the surface was carried out using a net of 212 µm mesh size. The samples were fixed with formol (5 % v/v). The enumeration of microcrustaceae presented here was achieved by means of a standard microscope (Olympus BX40) following Anneville et al. (2007).

HESSD
10, 1–32, 2013

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2.3 Flow cytometry analysis

Virus like particles (VLPs) were counted using a FACSCalibur flow cytometer (FCM) (Becton Dickinson) equipped with an air cooled laser providing 15 mW at 488 nm. Samples were fixed with glutaraldehyde (0.5 % final concentration, grade I, Merck) for 30 min, then diluted in 0.02 µm filtered Tris-EDTA buffer (referred to as TE, 0.1 mM Tris-HCL and 1 mM EDTA, pH 8), and incubated with SYBR Green I (at a final 10^{-4} dilution of the commercial stock solution; Molecular Probes), for 5 min at ambient temperature in the dark, followed by an incubation for 10 min at 75 °C, and then for another 5 min at room temperature prior to FCM analysis (Personnic et al., 2009a). FCM discriminated at least 3 sub groups of viruses, designated as VLP1, VLP2 and VLP 3 (virus like particles, group 1, 2 and 3). The analysis for determining heterotrophic bacterial abundance was performed as for the viruses but without heating at 75 °C and by using < 0.02 µm filter lake instead of TE. The picocyanobacteria and other smaller phytoplankters were analysed without fixing or staining but by using their natural autofluorescence. Analysis was made on samples to which a suspension of 1 µm beads had been added (Molecular Probes).

2.4 Fractionated primary production

Water samples (< 200 µm) collected from different depths (2.5, 7.5, 10, 15 and 20 m) were filled into two separate sets of three 250 mL glass bottles, with one of the three bottles being incubated at dark. Each flask was inoculated with 1 mL of labeled $NaH^{14}CO3$ (5 µ $CimL^{-1}$) and suspended at respective depths for a minimum of 5 h during the day. This fraction was treated for microphytoplankton (20–200 µm) production. After incubation, the samples were filtered through 20 µm filter and the contents were over washed with < 0.2 µm filtered water from the same depth. The filtrate (< 20 µm) was collected for filtration through 3 µm filter. The filter was over washed with < 0.2 µm water from the same area which was used for the nanophytoplankton production (3–20 µm). Similarly the 0.2–3 micron fraction was also obtained through filtration as the

HESSD
10, 1–32, 2013

picophytoplanktonic fraction. The water samples were immediately passed through a GF/F filter (0.7 µm) under gentle pressure (< 50 mm Hg) under diffused light conditions. The excess dissolved inorganic carbon ($DI^{14}C$) was removed by exposing the filters to fumes of concentrated hydrochloric acid for one minute. The filters were then placed in scintillation vials and a 5 mL scintillation cocktail was added. Radioactivity was measured using a liquid scintillation counter (Beckman coulter, USA). Production rate was calculated based on the photo-period of each day and expressed as $\mu g\,C\,L^{-1}\,d^{-1}$. Other details can be found elsewhere (Anneville et al., 2002; Tadonléké, 2010).

2.5 Bacterial and viral production

Water samples collected in polycarbonate bottles (in triplicates) were stored in ice and transported to the laboratory. Bacterial production was determined by incorporation of the nucleoside ^{3}H-Thymidine into bacterial DNA (Tadonléké, 2005). Briefly, a thirty milliliter water samples (in triplicates) along with trichloroacetic acid (TCA) killed control (1 % final concentration) was incubated with ^{3}H Thymidine (^{3}H-TdR) at a final concentration of 10 nM under in situ conditions in the dark for 1 h at ambient temperature. TdR incorporation was stopped by adding 1 % TCA. The samples were filtered through 0.22 µm (Millipore, USA) membrane filter, extracted in cold 5 % TCA and rinsed with 80 % ethanol. The dried filters were placed in scintillation vials and 0.5 mL of ethyl acetate was added to dissolve the filter. A 5 mL of scintillation cocktail was added and the radioactivity was measured using liquid scintillation counter (LS 6500 Scintillation counter, Beckman coulter, USA). The disintegration values per minute (dpm) after correcting for blank was converted to moles TdR incorporated as per Bell (1993) and converted to moles TdR of bacterial cells (2×10^{18} cells mol^{-1}) and bacterial carbon (20 fg C $cell^{-1}$).

Viral production was estimated by the virus reduction method (Wilhelm et al., 2002), similar to a previous study conducted at peri-alpine lake by Thomas et al. (2011). Briefly, 100 mL water sample was diluted with 3 volumes of ultra filtered sample

(< 0.02 µm, free of viruses) to reduce the number of free viruses in the sample significantly. This was divided into three replicates and samples were incubated in the dark for 24 h. Subsamples were drawn at every 2 hourly intervals to monitor the abundance of bacteria and viruses. The bacterial and viral abundances were determined using flow cytometry as described above.

2.6 Transmission electronic microscopy (TEM) analysis

Viral lytic infections were inferred from the percentage of visibly infected cells (FVIC) according to Sime-Ngando (1996). Bacterial cells contained in 8 mL of gluteraldehyde fixed samples (1 % final concentration) which were stored at 4 °C were harvested by ultracentrifugation onto 400 mesh NI electron microscope grids with carbon-coated Formvar film, by using a Beckman Coulter SW40 Ti Swing-Out-Rotor run at 70 000 × *g* for 20 min at 4 °C. Each grid was stained at room temperature (ca. 20 °C) for 30 s with uranyl acetate (2 % wt/wt), rinsed twice with 0.02 µm filtered distilled water and dried on a filter paper. Grids were then examined using a JEOL 1200E × TEM operated at 80 kV at a magnification of ×100 000. At least 600–800 prokaryotic cells per sample were examined to determine the frequency of visibly infected cells (FVIC). Cells were scored as infected if they contained five or more intracellular viruses. For each sample, the mean burst size (viruses bacteria^{-1}) was estimated from the number of viruses in visibly infected cells. Because mature phages are visible only late in the infection cycle, FVIC counts were converted to the frequency of infected cells (FIC) using the equation FIC = 9.524· FVIC-3.256 (Weinbauer et al., 2002). The FIC was then converted to viral-induced bacterial mortality (VIBM, as a percentage per generation) according to Binder (1999) using the equation VIBM = (FIC +0.6· FIC2)/(1 – 1.2· FIC).

2.7 Dilution experiments and viral parameters

The modified dilution approach was used to determine the grazing and viral-induced mortality on picoplankton and bacteria (Evans et al., 2003) as previously done by Per-

HESSD
10, 1–32, 2013

Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper |
Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

sonnic et al. (2009a) and Thomas et al. (2011). In this method, parallel dilution series (70, 40 and 20 %) of natural lake water was performed with 0.2 µm filtered sample to obtain the grazing rate and with 30kDa filtered sample to obtain grazing and viral lysis rates. Percentages of grazing and viral mortality were determined from the difference between the two dilution series keeping in mind that regression slopes have to be significant (Kimmance et al., 2007). Viral mortality rates (d^{-1}) were also calculated as the ratio of viral production and burst size. The lytic mortality rate was calculated from viral lysis rate and bacterial abundance.

2.8 Statistical analysis

Month wise statistical analysis to determine the variations of biological parameters with other environmental factors was performed using Spearman's correlation (with Excel-Stat). A two-way ANOVA analysis was performed to understand variations in biological and chemical parameters with depth and months. All the data were normalized using log transformation for factor analysis to reduce the multicolinearity of independent variables. The dependent variables in this study were the abundance values for bacteria, picocyanobacteria, other phytoplankton, VLP1, VLP2 and VLP. The variables that appeared influential in variations in dependent variables have been considered as explanatory variables (i.e. temperature, pH, turbidity, PO4, P tot, P part, Mg, COT, Na, Ca, NH_4, Cl, SO_4, Chl *a*, dissolved oxygen, N_{tot}, NO_3-N, NO_2-N, SiO_2-Si) but were found to be highly correlated indicating the presence of multicollinearity in the data. As such, the estimates of the model parameters obtained by the multiple linear regression method were unstable and unreliable. Hence, an alternative method of estimation, principal component regression (PCR) was used since multicollinearity was present in the data. The principle components were obtained by Eigen-value decomposition of the covariance or correlation matrix of the explanatory variables used for the analysis of one dependent variable. For PCR analysis of phytoplankton, picocyanobacteria and heterotrophic bacteria, only environmental factors which were dependent on each other were taken. For the analysis of variations in VLPs, biological factors such as the

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bacterial, picocyanobacterial and the other phytoplankton abundances were included as independent variables in factor analysis.

3 Results

3.1 Environmental factors

5 The mean along with standard deviation value of all the environmental parameters are provided in Table 1. Briefly, the average temperature during the study period was $14 \pm 5.2\,^{\circ}$C, with minimum and maximum value's of $6.2\,^{\circ}$C (November) and $21.5\,^{\circ}$C (August), respectively. Vertical profiles showed water temperature to decrease rapidly from surface ($19.6\,^{\circ}$C) to 30 m ($6.9\,^{\circ}$C). The water column was generally oxygenated with 10 dissolved oxygen content ranging from 5.2 to 10.9 mg L^{-1}. During the study period, the concentrations of TP and TN varied by 15 and 8 folds respectively. Both nitrogen and phosphorus values varied significantly ($p < 0.05$) with respect to months and depths. Chlorophyll *a* concentrations ranged from 0.8 to 6.8 µg L^{-1} with the highest and lowest values in July at 7.5 m and 30 m depths, respectively.

15 3.2 Abundances of heterotrophic bacteria, picocyanobacteria and other phytoplankton

Heterotrophic bacterial population showed strong month-to-month and vertical variability with maximum abundance (5.76×10^6 cells mL^{-1}) observed in August at 10 m (Table 1). Bacterial abundance varied up to 5- and 11-folds with month and depth, re- 20 spectively. Similarly, the picocyanobacterial abundance was the highest at 10 m with an average of $1.1 \pm 0.7 \times 10^5$ cells mL^{-1} and the lowest at 30 m ($2.2 \pm 1.4 \times 10^3$ cells mL^{-1}). The picocyanobacterial abundance maximum was recorded in August (1.9×10^5 cells mL^{-1}) and minimum in November (2.1×10^2 cells mL^{-1}). Like bacterial and picocyanobactrial abundances, other FCM phytoplanktonic groups considered all together 25 also displayed vertical variations with the highest concentrations observed at 7.5 m

HESSD
10, 1–32, 2013

($8.0 \pm 1.45 \times 10^3$ cells mL^{-1}) in August and the lowest at 30 m ($3.6 \pm 2.1 \times 10^2$ cells mL^{-1}) in November (Fig. 1).

3.3 Virus-like particle abundances and lytic infection rates

Maximum abundances of the virus- like particles (VLPs) were observed at 2.5 m ($11.0 \pm 3.1 \times 10^7$ particles mL^{-1}) and the minimum at 30 m ($4.4 \pm 0.74 \times 10^7$ particles mL^{-1}). Highest and lowest VLP abundances were observed in September (1.3×10^8 particles mL^{-1}) and November (3.1×10^7 particles mL^{-1}), respectively. VLPs could be discriminated into two major groups, referred to as VLP1 and VLP2. Average VLP1 and VLP2 abundances were $7.2 \pm 2.9 \times 10^7$ particles mL^{-1} and $0.53 \pm 0.34 \times 10^7$ particles mL^{-1}, respectively. The highest and lowest VLP 1 and VLP 2 abundances were 1.2×10^8 and 2.9×10^7 particles mL^{-1} and 1.3×10^7 and 4.8×10^5 particles mL^{-1}, respectively and they were both measured at 2.5 and 30 m depth. The viral to bacterial ratio was highest at 20 m depth (56.6 ± 5.6) and lowest at 10 m (27.6 ± 12.2). The highest (170) and lowest (13.8) ratios were observed in July at different depths.

TEM analysis revealed that phages were mainly associated with oval and short rod morphotypes with an occurrence of 28 % followed by thin rods (25 %) and cocci (19 %). The burst size of these morphotypes was on average 46 for oval morphotypes and less than 15 for the short rods. The burst size ranged from 15 to 132 in July whereas the range was 21 to 35 in November. The average burst size ranged from 28 to 44 (mean = 32.6, Table 2). The frequency of virus infected cells ranged from 1.1 % in November to 2.7 % in July. Similarly the FIC was relatively low in November (7.2 %) and high in July (22.5 %). The viral induced bacterial mortality was calculated to vary between 8.2 % (November) and 34.9 % (July) (Fig. 6).

Virus-induced mortality on picocyanobacteria, assessed using the modified dilution method, was also found to be relatively high in July–August (reaching 66 %) while it could be insignificant at other periods, i.e. in November (Table 2). Comparatively,

the virus- mediated bacterial mortality ranged from 18.3 % (August) to 33.5 % (July) (Fig. 6).

3.4 Bacterial and viral production

Bacterial production (BP) ranged from 9.1 $\mu g C L^{-1} d^{-1}$ to 36.9 $\mu g C L^{-1} d^{-1}$. The lowest BP was measured in September and the highest in July. The BP values slowly recovered during October–November reaching a value of 15.5 $\mu g C L^{-1} d^{-1}$ (Fig. 2). The lowest viral production rate was found to be 1.24×10^7 particles $mL^{-1} d^{-1}$ in July. Thereafter it increased from August to October reaching up to 6.28×10^8 particles $mL^{-1} d^{-1}$ in October (Fig. 2).

3.5 Size fractionated primary production

Primary production measured at 5 depths between 2.5 and 20 m revealed marked seasonal and depth wise variations with various contributions of micro-, nano- and picoplankton to the total primary production. The total primary production maximum was estimated at 7.5 m depth in summer and at 2.5 m in fall. A maximum production rate of 18.5 $mg C m^{-3} h^{-1}$ was reported at 7.5 m in August. With 6.6 $mg C m^{-3} h^{-1}$ at 2.5 m, November was the least productive month. The production rates decreased rapidly below 10 m depth. The piocphytoplanktonic contribution was relatively high in October and November (Fig. 5), reaching up to 76 % while it was only 33 % in August. The depth at which the maximum picophytoplankton contribution was reported was at 15 m throughout the sampling period.

3.6 Statistical analysis

Monthly linear correlation analysis of various environmental factors showed seasonal variations. Summer months behaved differently with complex interactions between biological variables and physico-chemical parameters (turbidity, temperature, pH, O_2, $N\text{-}NO_3$, $N\text{-}NO_2$, SiO_2, total nitrogen etc). In July, bacterial abundance was significantly

correlated with picocyanobacteria, while picocyanobacteria were positively correlated with temperature, pH, O_2 and negatively with NO_3, SiO_2 and total phosphorus. VLP1 did not show any correlation with any of the biological factors including the bacterial abundance, but had significant correlation with physico-chemical factors like pH and total phosphorus and negative correlation with NO_3, SiO_2, total phosphorus and total nitrogen. VLP2 on the other hand had significant positive correlation with picocyanobacteria and other phytoplankton (Table 3). In our observation, temperature seemed to be the most determining factor for planktonic abundance when compared to Phosphorus (Figs. 3 and 4).

PCR analysis revealed temperature and pH as the most important significant factors likely to influence the abundance of bacteria and picocyanobacteria. For bacteria, factor 1, contributed to a eigen value of 4.34, with a factor pattern from 1 to 8. Factor 1 included temperature (0.87), pH (0.94), NO_3 (−0.87), SiO_2 (−0.93) and P_{tot} (0.70) (Fig. 7). For the picocyanobacteria, factors 1 and 2 also largely accounted for the variability in their abundance. Factor 2 had PO_4 (0.89) and P_{tot} (0.64) as the major components along with components listed under factor 1 as in the case of bacteria. For VLPs, biological factors such as bacteria, picocyanobacteria and other phytoplankton were included as independent variables for analysis. Factor 1 included bacteria (0.83), picocyanobacteria (0.94). phytoplankton (0.79), Temperature (0.84), pH (0.93), NO_3 (−0.87) and SiO_2 (−0.93). The eigen values obtained for analysis of VLPs had 6.41 for the factor 1.

4 Discussion

The main aim of the present study was to bring out the importance of physical, chemical and biological factors in influencing the abundance and activity of picocyanobacteria, bacteria and associated viruses. To reach this goal, not only abundances but also production measurements for phytoplankton, bacteria and viruses were performed. In

addition, we also estimated the mortality rates induced by viruses and small grazers on both picocyanobacteria and bacteria.

The abundances of viruses, bacteria and autotrophic picoplankton changed markedly with months and depths as revealed by two-way ANOVA (Table 4). Higher plankton abundance in August was likely attributed to higher temperatures and availability of light that favoured their growth. The significant difference in the planktonic dynamics could largely be contributed to temperature and the wind- induced waves as has previously been reported for perialpine lakes (Vinçon-Letie et al., 1989).

The planktonic community structure of an aquatic system largely depends on the lake's trophic state and contribution of picoplankton production to the total autotrophic production which could vary depending on the nutrient concentrations of the lakes (Stockner and Porter, 1988). The abundance of picocyanobacteria was high during the peak summer months (August–September) when the nutrient concentrations were higher (P_{tot} being $11.0 \pm 4.9\,\mu g\,P\,L^{-1}$ in summer) compared to autumn ($8.2 \pm 1.9\,\mu g\,P\,L^{-1}$). Even though the abundance was higher in summer, picoplankton production (constituted mainly by picocyanobacteria in Lake Geneva) contributed to a high percentage (76 %) of the total primary production during autumn (i.e. October and November) suggesting a significant functional role of the "smalls" in Lake Geneva. This could be explained by lower nutrient concentration of total nitrogen ($280\,\mu g\,L^{-1}$) and total phosphorus ($10\,\mu g\,L^{-1}$) during the fall period. It is reported that when nutrients become a limiting factor, autotrophic picoplankton cells strongly compete with the bigger phototrophic organisms (Raven, 1988; Callieri, 2007). Previous studies reported picocyanobacteria to be the major contributors to total primary production which tend to increase with depth (Platt et al., 1983) due to greater efficiency of their auxiliary pigments (typically phycoeyrhtrin) to utilize the blue-green light (Glover et al., 1985). The results obtained in the present investigation clearly suggest that picocyanobacteria play a crucial role in the trophic status of Lake Geneva as suggested in the past studies (Duhamel et al., 2006; Personnic et al., 2009b). Among the abiotic factors, temperature

HESSD
10, 1–32, 2013

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and pH were the most influential factors in determining the abundance of bacteria, picocyanobacterial and other phytoplankton which contributed to their monthly variability.

VLP abundances were significantly correlated with bacterial and picocyanobacterial abundances in general. High abundances of VLPs were observed in the top 20 m layer. Similar trend was noticed for VLP1, VLP2 groups and heterotrophic bacteria. Previous studies have shown a tight coupling of VLP1 and VLP2 with bacterial and picocyanobacterial abundance, respectively (Duhamel et al., 2006; Personnic et al., 2009b). In our study, the correlation of viruses with bacteria and picocyanobacteria varied with respect to sampled months suggesting that these shifts are probably due to succession of hosts and its viruses (Parvathi et al., 2012). Month wise variations in viral and bacterial abundance suggested environmental factors had strong influence on the standing stock, as reported in other freshwater systems (Pradeep Ram et al., 2005). In our study, phytoplankton viruses did not contribute significantly to the total virus pool, and that the positive effect of an increase in chlorophyll *a* with heterotrophic bacteria is not directly beneficial to virus production. However, we are aware that chl *a* represents only a crude approximation of the algal biomass and thus is probably not the best parameter to use while attempting to identify virus/parasite relationships (Gasol and Duarte, 2000). Moreover, the specificity of viruses to their hosts implies that phytoplanktonic groups must also be taken into consideration (Zhong et al., 2013). Therefore the relationships between viral parameters and other factors are not always predictable.

VLP abundance was high in the upper 20 m depth likely because bacterial growth was stimulated by both high temperatures, organic and inorganic nutrients as suggested by our results of production rates (Weinbauer, 2004). It is also possible that there were larger initial virioplankton and bacterioplankton populations in the summer months and in the beginning of autumn (Personnic et al., 2009b). A quite similar seasonal pattern was observed for the virioplankton in other temperate lakes, where highest viral abundance occurred in autumn (Bettarel al., 2005; Padeep-Ram et al., 2010). Significant seasonal co-variations were recorded for viruses and heterotrophic bacteria and between viruses and picocyanobacteria between July and October. High VBR

in autumn (October and November) and its increase with depth suggested important phage-host interactions and that the impact of viruses on bacteria is more significant in deeper waters than at the surface, as previously observed in this lake and others (Colombet et al., 2006; Personnic et al., 2009b). Such relationships between these groups were clearly confirmed with the measurements of high virus induced mortality on both bacteria and picocyanobacteria for which we also demonstrated seasonal variations. High viral production rates (up to 2.6×10^7 particles mL^{-1} h^{-1}) corroborated this strong viral impact and high viral production coincided indeed with high virus induced bacterial (23 %) and picocyanobacterial mortality (19 %). Thus, it was not really surprising that for both bacteria and picocyanobacteria, the percentage loss due to grazing was always lower than viral lysis (as estimated by the dilution method when applicable). These mortality rates were comparable with earlier reports of grazing mortality and viral lysis reported for Lake Geneva and other lakes (Weinbauer and Hofle, 1998; Bettarel, 2004; Duhamel et al., 2006; Personnic et al., 2009a). All in all, it was found that viral activity was particularly high in autumn, and co-varied with the picoplankton production during the same time period, a result already suggested by past for these peri-alpine lakes (Personnic et al., 2009a).

Principle component regression analysis was useful to assess factors that influence the abundance of autotrophic and heterotrophic plankton in Lake Geneva. Factors like temperature, pH, NO_3, P_{tot}, SiO_2 and Chl *a* explained 65 % variability in bacterial abundance. In the case of picocyanobacteria and other phytoplankton, the above mentioned factors accounted for a variability of 90 and 60 % respectively. In the case of VLPs host abundances (bacteria, picocyanobacteria and other phytoplankton) also played important role in determining their variations (Fig. 6). Principle component regression analysis revealed that temperature, pH, NO_3, P_{tot}, SiO_2, Chl *a* together with host abundances (bacteria, picocyanobacteria and other phytoplankton) attributed 77 % variability in VLP1, 72 % in VLP2 and 78 % in total VLP abundances. Clearly many factors are likely to play an important role and influence various autotrophic and heterotrophic planktonic components to various extents in Lake Geneva. It was shown that viruses

HESSD
10, 1–32, 2013

are potentially an important explanatory variable of picoplankton dynamics and diversity (Parvathi et al., 2012, this study) and this compartment should not be neglected anymore in attempts to explain plankton dynamics, distribution and succession in Lake Geneva.

5 Conclusions

The present study highlighted complex relationships among the microbial components of Lake Geneva where physical, chemical and biotic interactions parameters intervene in the dynamics and activity of the picoplankton size community. The results clearly suggest that the picophytoplanktonic size fraction can be responsible for a significant part of the production of this lake and also show how viral lysis can be a driving force in the dynamics of these populations. The study clearly highlights the complex interplay of various biological variables and environmental parameters which are involved in determining the dynamics of autotrophic and heterotrophic (pico) plankton communities in aquatic ecosystems. Lake Geneva can be considered as a model ecosystem for large and deep temperate lakes and our analysis, even restricted to a few months, point thus the importance of considering now the viral compartment in freshwater plankton ecology. This could be particularly important for modelers.

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HESSD
10, 1–32, 2013

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Table 1. Minimum, maximum, mean and standard deviation values for all the variables measured in Lake Geneva in this study from July to November 2011. Abbreviations are mentioned in the text.

Variables	Min	Max	Mean	SD
Bacteria (cells mL^{-1})	5.27×10^5	5.76×10^6	2.15×10^6	1.33×10^6
Picocyanobacteria (cells mL^{-1})	2.11×10^2	1.94×10^5	5.72×10^4	5.82×10^4
Other phytoplankton (cells mL^{-1})	1.48×10^1	3.21×10^4	4.05×10^3	7.64×10^3
VLP1 mL^{-1}	2.92×10^7	1.21×10^8	7.16×10^7	2.92×10^7
VLP2 mL^{-1}	4.83×10^5	1.30×10^7	5.25×10^6	3.41×10^6
VLP mL^{-1}	3.06×10^7	1.29×10^8	7.69×10^7	3.23×10^7
VPR	13.18	170.35	36.5	25.4
Temperature (°C)	6.22	21.53	14.0	5.15
Turbidity (FTU)	0.71	2.01	1.16	0.30
PAH ($\mu g\,L^{-1}$)	23	35	28.5	3.84
PC ($\mu g\,L^{-1}$)	0.14	1.48	0.66	0.417
pH	7.71	8.73	8.14	0.34
Par_w (µE)	0.58	730.2	92.8	164
O_2 ($\mu g\,L^{-1}$)	5.19	10.92	8.69	1.43
NO_2 ($\mu g\,L^{-1}$)	0.0	11.0	3.0	2.0
PO_4 ($\mu g\,L^{-1}$)	2.0	14	4.0	1.9
Ppart ($\mu g\,L^{-1}$)	1.0	11.2	4.0	2.0
COT (mgC L^{-1})	0.23	1.61	1.05	0.23
NO_3 ($\mu g\,L^{-1}$)	80	610	340	187
SiO_2 ($\mu g\,L^{-1}$)	9.0	159	63.2	48.4
P_{tot} ($\mu g\,P\,L^{-1}$)	2.0	29.0	10	4.0
NH_4 ($\mu g\,L^{-1}$)	1.0	24.0	8.0	5.0
N_{tot} ($\mu g\,N\,L^{-1}$)	170	980	529	173
SO_4 ($mg\,L^{-1}$)	0.67	49.54	48.4	0.674
TAC (meg L^{-1})	0.13	1.79	1.61	0.135
CHLA	0.80	6.778	3.62	1.48
Microplankton production ($mg\,C\,m^{-3}\,h^{-1}$)	0.0025	5.30	1.41	1.62
Nanoplankton prod. ($mg\,C\,m^{-3}\,h^{-1}$)	0.0076	2.41	0.68	0.74
Picoplankton prod. ($mg\,C\,m^{-3}\,h^{-1}$)	0.05	4.40	1.55	1.38

HESSD
10, 1–32, 2013
Dynamics of auto- and heterotrophic picoplankton in Lake Geneva
A. Parvathi et al.

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Table 2. Mean values for the frequency of viral infected cells (FVIC), frequency of infected cells (FIC), viral induced bacterial mortality (VIBM) and average burst size (BS) as estimated using transmission electron microscopy. Grazing and viral induced mortality obtained from the dilution experiments are represented as PCGM and PCVM for the picocyanobacteria and grazing mortality), and BGM and BVM for the heterotrophic bacteria.

Sample	TEM ANALYSIS				DILUTION EXPERIMENTS			
	FVIC	FIC	VIBM	BS	PCGM (%)	PCVM (%)	BGM (%)	BVM (%)
4 Jul	2.7 ± 0.1	22.5 ± 2.7	34.9 ± 11.2	41 ± 4	6.8 ± 5.6	23 ± 8.2	17.4 ± 6.8	19.9 ± 8.1
27 Jul	2.1 ± 0.3	16.7 ± 8.7	23.1 ± 5.7	30 ± 11	12.1 ± 10.2	16.2 ± 12.4	28.9 ± 13.7	33.5 ± 15.4
16 Aug	1.4 ± 0.6	10.1 ± 2.4	12.2 ± 3.4	32 ± 7	50.2 ± 23.8	66 ± 31.7	NS	18.3 ± 9.3
22 Sep	1.7 ± 0.2	12.9 ± 4.1	16.5 ± 2.6	44 ± 14	NS	35.7 ± 11.6	11.6 ± 3.7	19.8 ± 8.5
10 Oct	1.2 ± 0.1	8.2 ± 2.1	9.5 ± 3.3	28 ± 8	NS	19.1 ± 6.9	18.1 ± 5.9	23.5 ± 13.9
17 Nov	1.1 ± 0.2	7.2 ± 3.1	8.2 ± 1.9	28 ± 6	16.9 ± 9.5	NS	11 ± 4.6	21.1 ± 10.8

HESSD
10, 1–32, 2013

Dynamics of auto- and heterotrophic picoplankton in Lake Geneva

A. Parvathi et al.

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Table 3. Results of Pearson's correlation analysis to test for empiric correspondence among estimated variables. Abbreviations are explained in the text. Significant correlations are in bold at $p < 0.001$ at $n = 42$.

	Bact	PC	PP	VLP1	VLP2	VLP	Temp	NO_3	SiO_2	P_{tot}	N_{tot}	pH
PC	**0.78**											
PP	**0.79**	**0.82**										
VLP1	**0.83**	**0.74**	**0.65**									
VLP2	**0.79**	**0.81**	**0.66**	**0.88**								
VLP	**0.83**	**0.75**	**0.66**	**0.99**	**0.90**							
Temp	**0.56**	**0.79**	**0.60**	**0.61**	**0.67**	**0.63**						
NO_3	**−0.78**	**−0.88**	**−0.76**	**−0.81**	**−0.83**	**−0.82**	**−0.77**					
SiO2	**−0.72**	**−0.94**	**−0.80**	**−0.73**	**−0.75**	**−0.74**	**−0.79**	**0.86**				
P_{tot}	**0.62**	**0.54**	**0.60**	**0.57**	**0.42**	**0.56**	**0.44**	**−0.51**	**−0.61**			
N_{tot}	**−0.77**	**−0.78**	**−0.66**	**−0.70**	**−0.78**	**−0.72**	**−0.70**	**0.89**	**0.72**	**−0.44**		
pH	**0.72**	**0.84**	**0.76**	**0.69**	**0.66**	**0.69**	**0.77**	**−0.84**	**−0.87**	**0.59**	**−0.74**	
Chl *a*	0.17	0.32	0.20	0.14	0.09	0.13	0.34	−0.12	−0.31	0.32	−0.20	0.27

HESSD
10, 1–32, 2013

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Table 4. Results of the two-way ANOVA to test significant differences in the abundance of bacteria, picocyanobacteria, other phytoplankton and VLPs. Degrees of freedom are indicated as df. *S* = significant; NS = not significant.

Parameter	Difference	d*f*	*F* value	Significance
Bacteria	months	5, 30	31.2	S
	depth	6, 30	12.3	S
Picocyanobacteria	months	5, 30	4.5	S
	depth	6, 30	14.3	S
Other phytoplankton	months	5, 30	7.1	S
	depth	6, 30	2.3	NS
VLP1	months	5, 30	8.7	S
	depth	6, 30	8.7	S
VLP2	months	5, 30	13.7	S
	depth	6, 30	9.4	S
VLP	months	5, 30	9.2	S
	depth	6, 30	9.0	S

HESSD
10, 1–32, 2013

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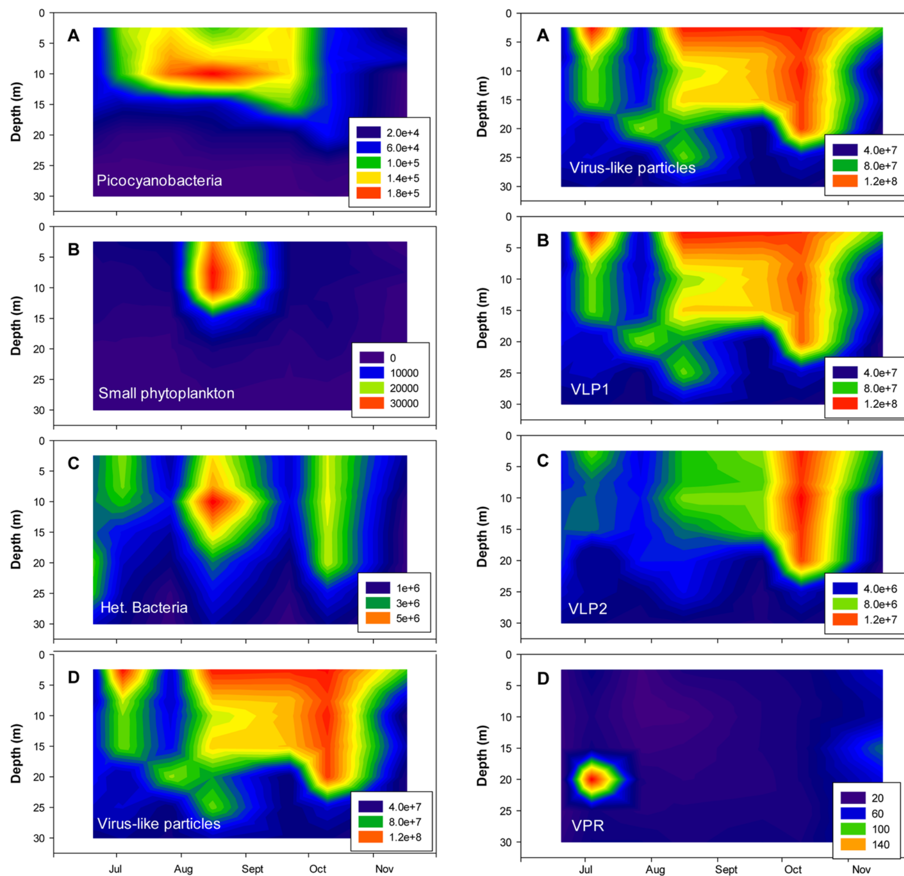

Fig. 1. Vertical distribution of picocyanobacteria, small phytoplankton populations (as detected using FCM), heterotrophic bacteria, virus-like particles (also discriminated as VLP1 and VLP2) and the virus to prokaryote ratio (VPR) from July to November 2011.

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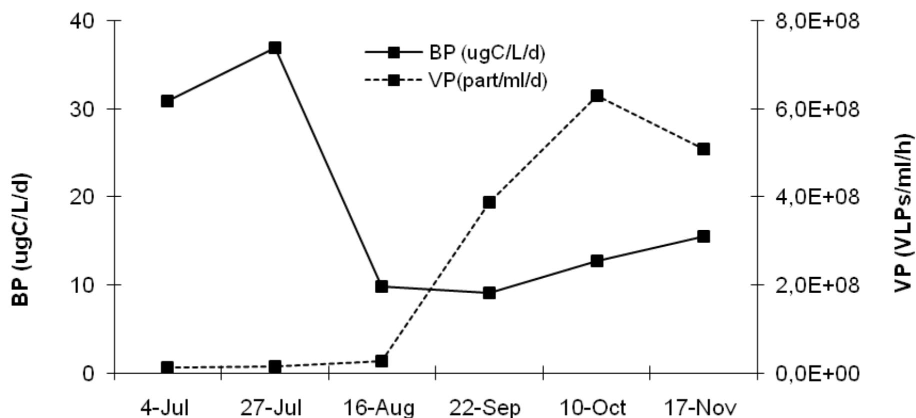

Fig. 2. Bacterial production (BP) and viral production (VP) measured from July to November 2011.

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10, 1–32, 2013

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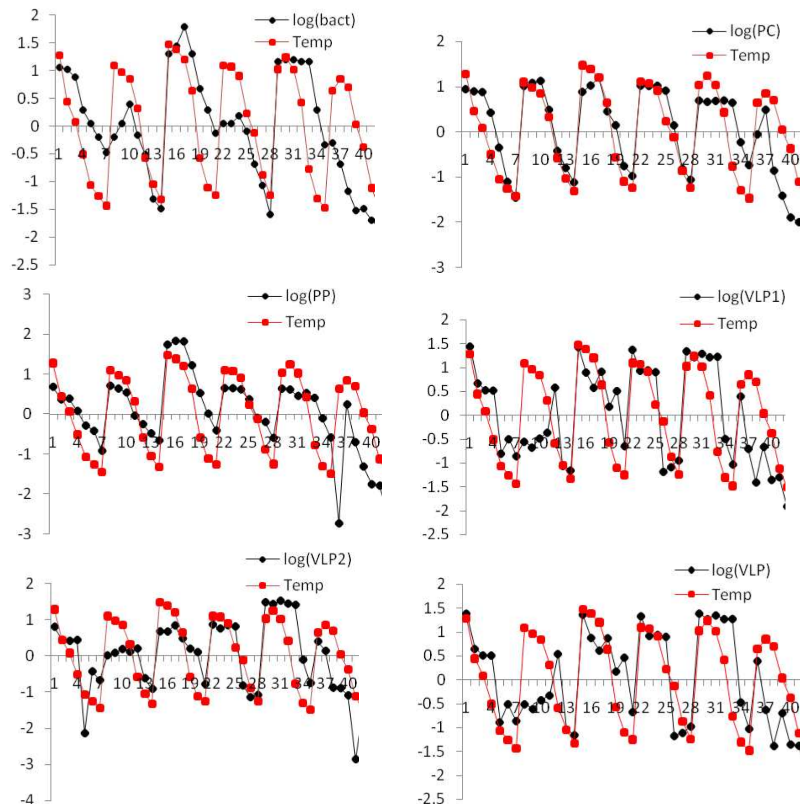

Fig. 3. Covariance between the temperature and all the biological variables. All the biological variables were converted to logarithmic scale and is represented in the y-axis. Abbreviations include bact: Bacteria, PC: picocyanobacteria, PP: picoplankton, VLP: Viral like particles. Temperature is represented in the x-axis.

HESSD
10, 1–32, 2013

Dynamics of auto- and heterotrophic picoplankton in Lake Geneva

A. Parvathi et al.

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
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Printer-friendly Version
Interactive Discussion

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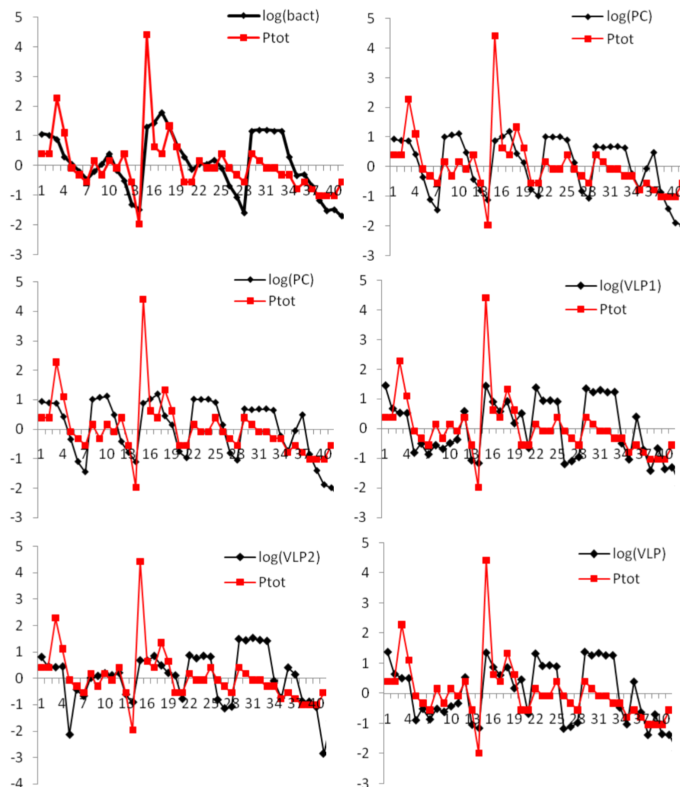

Fig. 4. Covariance between total phosphorus and all the biological variables. This shows that the variation in total phosphorus has a lesser impact on the biological variables. All the biological variables were converted to logarithmic scale and is represented in the y-axis. Abbreviations include bact: Bacteria, PC: picocyanobacteria, PP: picoplankton, VLP: Viral like particles. Total Phosphorus (P_{tot}) is represented in the x-axis.

HESSD
10, 1–32, 2013

Dynamics of auto- and heterotrophic picoplankton in Lake Geneva

A. Parvathi et al.

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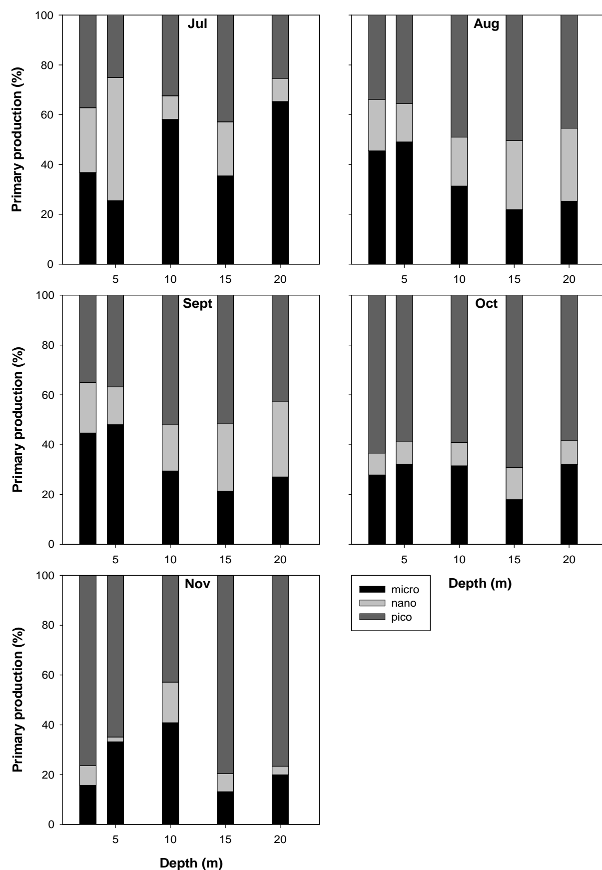

Fig. 5. Fractionated primary production representing the contribution of the various size fractions of the phytoplankton (i.e. the pico-, nano and microphytoplankton) at the different periods sampled.

HESSD
10, 1–32, 2013

Dynamics of auto- and heterotrophic picoplankton in Lake Geneva

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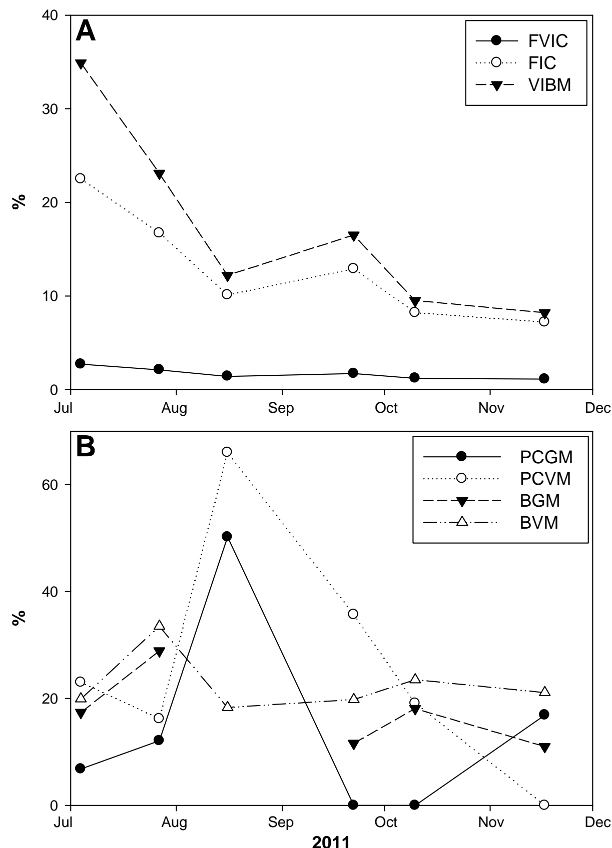

Fig. 6. Patterns of the frequency of viral infected cells (FVIC), the frequency of infected cells (FIC), the viral induced bacterial mortality (VIBM) and the burst size estimated using transmission electron microscopy **(A)**. Grazing mortality and viral lysis on picocyanobacteria (PCGM and PCVM respectively) and on heterotrophic bacteria (BGM and BVM) estimated using the modified dilution technique **(B)**.

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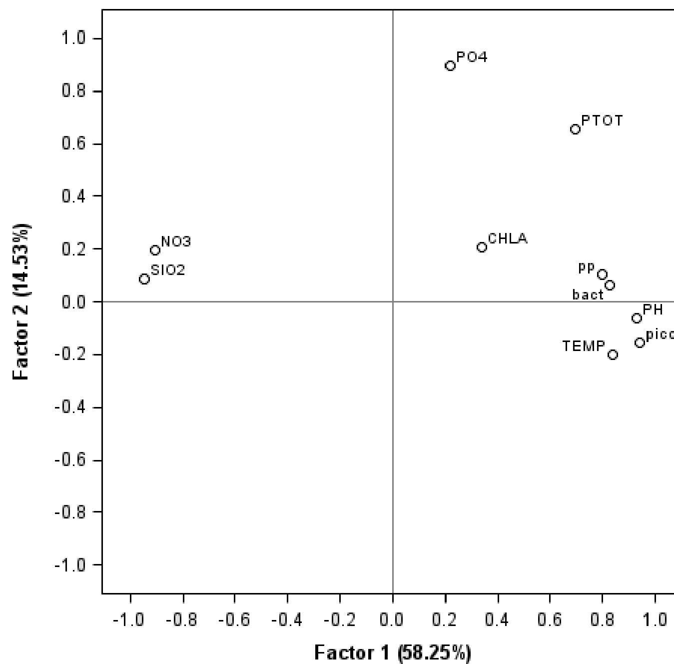

Fig. 7. PCR analysis for bacteria, picocyanobacteria and other phytoplankton with the rest of the environmental variables.

HESSD
10, 1–32, 2013

Dynamics of auto- and heterotrophic picoplankton in Lake Geneva

A. Parvathi et al.

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