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Research Article

Spatial and temporal dynamics of virioplankton in a high-mountain tropical reservoir, El Neusa (Cundinamarca, Colombia)

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ABSTRACT. Temporal and spatial changes of virioplankton abundance (VLP), chlorophyll-*a* (Chl-*a*) concentration, and some environmental variables, were assessed from October 2004 to April 2005 at four sampling sites in a high-mountain reservoir in the Colombian Andes. VLP ranged from 2.4-10.5×10^7 and 3.6-6.5×10^7 VLP mL^{-1} in the samples from the photic zone and hypolimnion, respectively. Surface VLP showed a progressive increase from November to April in the limnetic zone, and until February in the littoral stations. This trend coincided with the gradual increase of the water column stratification, as well as the augment of the reservoir hydraulic volume. Principal components analysis showed a grouping of environmental (dissolved oxygen, pH, water temperature) and biological variables (VLP, Chl-*a*, bacterioplankton abundance and biomass) within the first component (26.4% of explained variance), associated to an increase of photosynthetic activity, as a potential supplement of organic substrates to heterotrophic viral hosts. High values of virus-to-prokaryote ratio (VPR), and a negative relationship between VLP and average biomass per prokaryotic cell, indicate strong viral control which is probably more intense on active and larger cells. These results provide a framework for understand the virioplankton responses to regional hydrological conditions and hydraulic behavior of this reservoir. The spatiotemporal scale of this study does not allow to confirm that viral dynamics is significantly affected by human activities causing potential alterations on nutrient cycling.

Keywords: virioplankton, virus-to-prokaryote ratio, temporal dynamics, high-mountain reservoir, El Neusa.

INTRODUCTION

In recent decades there has been increased interest in knowing the role of viruses in diverse aquatic environments (*e.g.*, Suttle, 2007; Anderson *et al.*, 2013). So far, it is known that viruses are the most abundant biological entities in the water column and sediment, both in freshwater and marine systems (Fuhrman, 1999; Bettarel *et al.*, 2003; Engelhardt *et al.*, 2014). They infect a wide spectrum of hosts ranging from prokaryotes (*e.g.*, bacteria and archaea) to unicellular and multicellular eukaryotes, and therefore are considered as a controlling factor of both the abundance and the genetic diversity of populations (Brussaard, 2004; Suttle, 2007; Fischer *et at.*, 2010). Studies in aquatic environments have implemented the concept of virioplankton to group all viral particles in suspension that are carried by currents or by turbulent motions (Wommack & Colwell, 2000). Because the virioplankton lacks the cellular machinery to replicate itself, its spatial and temporal dynamics is influenced by the number and activity of their host cells (Thingstad, 2000). Within the water column, the interaction between prokaryotic plankton (bacterio-plankton) and phytoplankton constitute the cornerstone of the aquatic microbial food web, and therefore the greatest amount of potential hosts for viral infection (Brussaard, 2004; Breitbart, 2012).

Nowadays, global estimates of mortality due to viral lysis and numerical modeling of the carbon flux within the microbial compartments indicate that between 20 to 40% of the prokaryotic production and between 6 to 26% of primary production in the oceanic pelagic zone is released in the form of dissolved organic matter

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(Jumars *et al.*, 1989; Fuhrman & Noble, 1996; Wilhelm & Suttle, 1999; Suttle, 2007). This short-circuit reduces the flow of carbon flow through the herbivorous food web, and promotes the production and recycling of dissolved organic matter toward microbial loop (Pomeroy *et al.*, 2007).

For tropical high Andes lentic ecosystems, there are few studies on the ecological role of virioplankton. Some studies in the region have been focused on the assessment of the total abundances of bacteriophages and its association with the presence of coliforms and other pathogenic bacteria, as an indicator of water quality in environments with different degrees of anthropogenic impact (Cárdenas-Guzmán & Guerrero, 2000; Lucena *et al.*, 2003; Sastoque-Salcedo, 2010; Venegas *et al.*, 2015). Given the potential importance of viruses as agents of phytoplankton and bacterio-plankton mortality, and the scarcity of information for high-mountain tropical ecosystems, such as those in Colombia, this study aims to examine the temporal and spatial dynamics of virioplankton abundance (evaluated as virus-like particles -VLP) in El Neusa reservoir (Cundinamarca, Colombia) and its covariance with environmental variables and the abundance of bacterioplankton and phytoplankton biomass (expressed as Chl-*a*), the latter as a possible indicator of viral control over these planktonic communities that contribute to the overall ecosystem production. In this region, human activities, such as subsistence agriculture, semi-intensive aquaculture, artisanal fishing and tourism, has being gradually impacting the water quality of lotic and lentic water environments (Larrahondo-Molina, 1992; Arce-Quintero, 2005). This promote several alterations in the nutrients loading, as well as the microbial food webs which has not been well recorded in the last decades. One of the assumptions of this work aims to evidence if part of the VLP dynamics and their potential viral control could be modulated, besides the hydrology of the region, by some gradient of environmental alteration as it would denoted by content of nutrients.

MATERIALS AND METHODS

The reservoir of El Neusa is located at 05°09'00"N and 73°59'00"W in the Department of Cundinamarca (Colombia) at an elevation of 3269 m.a.s.l. The monthly samplings were carried out between October 2004 and April 2005 in four fixed points. Two of these sites were located at the inner part of El Neusa (the dam or the deepest point and Chapinero or the middle of the reservoir); the other two sites corresponded to shallow littoral zones (<4 m) at Las Juntas and in river mouth of Cubillos River (Fig. 1). In the last two locations, measurements of temperature, dissolved oxygen (DO) and pH were performed at surface (0.5 m) by a pre-calibrated multiparameter Hydrolab sonde DS-4; in the remaining sites, continuous profiles of these variables were traced from surface until where the bottom depth allowed it (max. ~3 m).

Secchi disk readings were performed to define thickness of the photic zone and the sampling depth according the percentage of surface irradiance (I_o). Water samples were collected manually at 0.5 m depth in all sites. Additionally, two water column samples were obtained for Chapinero at subsurface (between 10-40% I_o) and compensation depth (1% I_0), and two other for the dam about the compensation depth and bellow de photic layer (<1% I_0) at the hypolimnion. The photic layer was calculated by multiplying the Secchi depth by 2.7 (Cole, 1979). These samples were collected by J-Z sampler (ZoBell, 1946) and horizontal Van Dorn bottle, depending on whether they were destined for microbial counts and chlorophyll-*a* (Chl-*a*) analysis, respectively. The water samples for microbial counts were transported in sterile glass bottles (250 mL), protected of light and refrigerated (~4°C) until processing at the Laboratory of Aquatic Microbiology at the Universidad Jorge Tadeo Lozano of Bogota. For Chl-*a*, the suspended particles of water samples were collected directly in the field by filtration through 0.75 µm pore diameter Whatman GF/F; then were stored protected from light at -20°C until further extraction with a solution of 90% acetone. The analysis of extracts of Chl-*a* was conducted in the Laboratory of Limnology at the University Jorge Tadeo Lozano of Bogota through the fluorometric method according to the procedure proposed by Arar & Collins (1997) and Wetzel & Likens (1979) on a Turner Designs Fluorometer 10AU-072 (PMT Red 185-870 nm) equipped with a blue mercury vapor lamp, excitation filter 340-500 nm and emission filter >665 nm, which was calibrated against a Chl-*a* standard solution (Sigma-Aldrich Co.). Total concentrations of all dissolved inorganic nitrogen species (DIN: nitrite + nitrate + ammonia) and phosphate (DIP) were extracted from the results described in Hakspiel-Segura *et al.* (2015) to plot the vertical and monthly dynamics in the dam.

For VLP, small volumes (1-2 mL) of unfixed water sample were filtered through 25-mm diameter Anodisc membranes (Whatman International Ltd, Maidstone, England). These were stained with the DNA-specific fluorochrome SYBR Gold (Molecular Probes S-11494) at 2.5x final dilution during 15 min and subsequently air dried and mounted in glass slides with a drop of glycerol-PBS solution containing an anti-fading (Patel *et al.*, 2007). Quantification was performed post-proce-

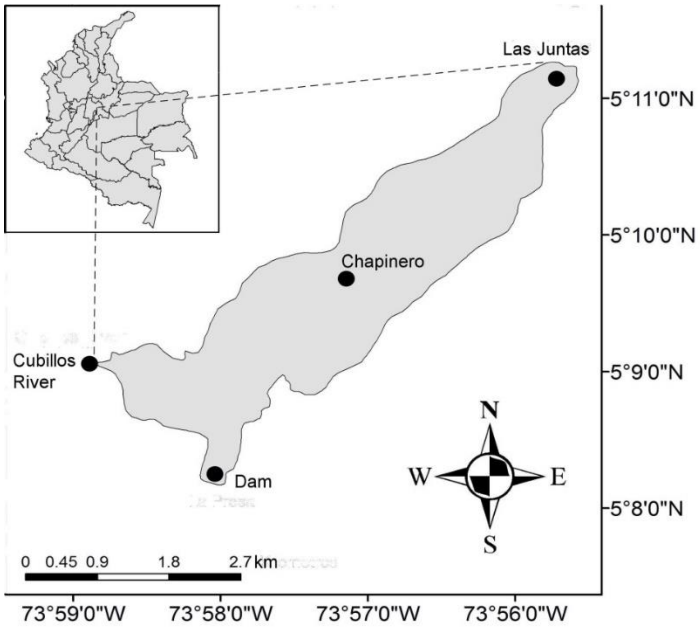

Figure 1. Study area and location of sampling sites (●) at El Neusa reservoir, Colombia.

ssing of the water sample on the day of sampling through a fluorescence microscope Olympus B Max 60 to a final magnification of 12000x and under blue light excitation (U-MWB filter, BP 450-480, barrier filter BA515 and dichromatic mirror DM500).

Non-parametric statistical tests were applied because the lack of homoscedasticity in the biological data. Kruskal-Wallis test, was used to determine temporal or spatial differences in the biological data (Zar, 1999). In order to establish possible interactions between virioplankton and environmental variability and some communities of potential host, nonparametric correlations (Spearman ρ test) were performed considering the data of VLP abundance, water temperature, pH, DO, inorganic nutrients (ammonia, nitrate and phosphate), Chl-*a* (as an indicator of phytoplankton biomass), and abundance (BA) and biomass (BB) of bacterioplankton. The virus-to-prokaryote abundance ratio (VPR) was calculated using the data set of bacterioplankton, previously published by Hakspiel-Segura *et al.* (2015), to infer the temporal and spatial variability of the degree of coupling and potential impact of viral lysis on the community of main potential host cells (Wommack & Colwell, 2000; Weinbauer, 2004), assuming that the increasing of this value indicate greater control over the bacterio-plankton. Environmental and biological data from all samples were analyzed using an ordination approach based on main principal component analysis (PCA), assuming that a multivariate normal distribution is not required (Johnson &Wichern, 1982). PCA computations were done with the PC-ORD software v6.0 (MjM Software, Gleneden Beach, Oregon, USA).

RESULTS

Physical, chemical and chlorophyll-*a* profiles

Part of the results of physical and chemical variables for the area of the dam during the study was previously described by Hakspiel-Segura *et al.* (2015). The vertical trend of the values of temperature, DO and pH generally showed a joint decrease with depth, which was reflected in the significant positive correlations among these variables (Spearman $\rho = 0.55$, 0.48, and 0.70 for the relationships between temperature and DO, temperature and pH, DO and pH, respectively; $P < 0.05$) except between temperature and pH in Chapinero. Temperature profiles showed a water column with relatively low values (13.6-16.5°C) from October to December 2004 and highest (14.9-18.2°C) from February to March 2005 with maxima restricted to a narrow layer between 0-5 m. In January and April 2005, temperatures were intermediate (14.8-16.7°C) and relatively more homogeneous than in other periods (Fig. 2a). Abrupt decreases in DO and pH between 5-10 m were observed in most samplings, except in February, which were shallower (2.5-4 m); however, all were consistent with the tracing of the thermocline (Figs. 2b-2c).

DO ranged from 4.0 to 8.8 mg L^{-1} in the euphotic layer. In the dam, most DO profiles recorded hypoxic

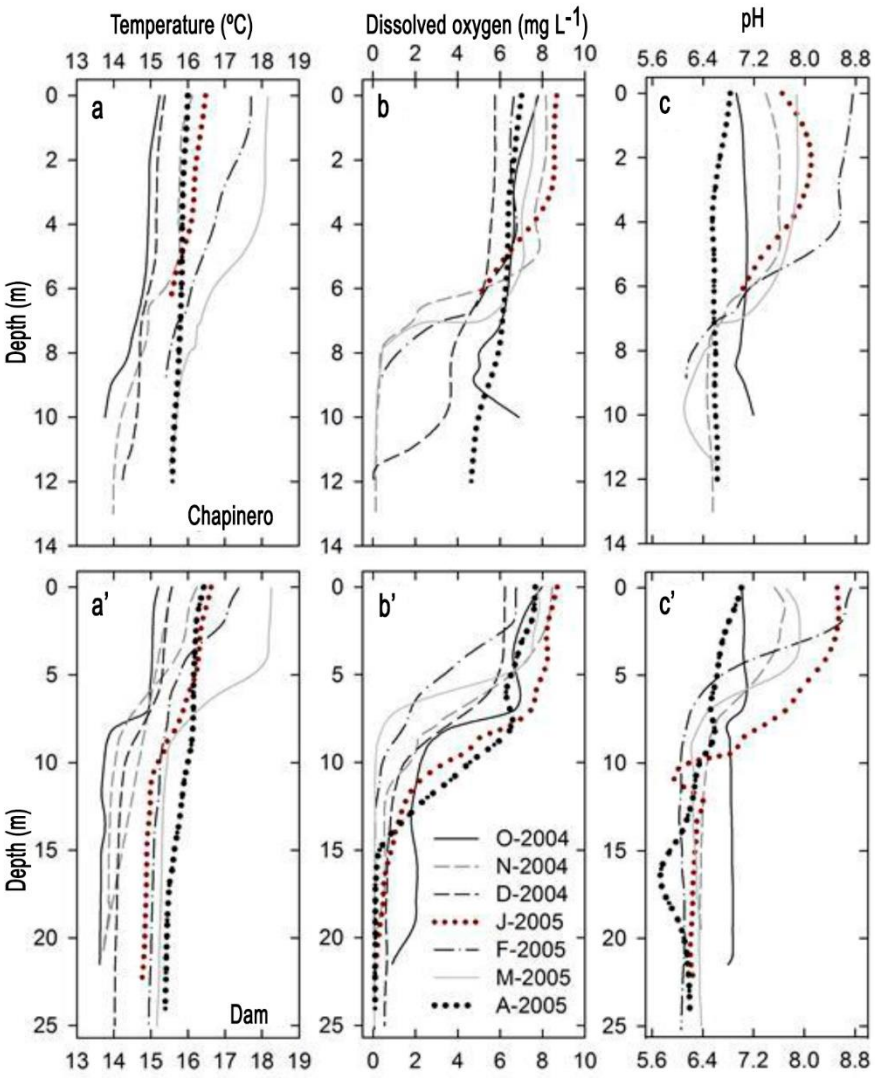

Figure 2. Vertical profiles of a) temperature, b) dissolved oxygen (DO), and c) pH at the inner sites of El Neusa reservoir. Letters with and without apostrophe correspond to Chapinero and Dam, respectively. O: October, N: November, D: December, J: January, F: February, M: March, A: April.

levels (<2 mg L^{-1}) below 13 m, and suboxic (<0.29 mg L^{-1}) below 20 m (hypolimnion) from January to April 2005. In Chapinero, suboxic values were detected from November to December 2004 and in March 2005 from 10 m above the layer near the bottom of the reservoir (Fig. 2b). The distribution of inorganic nutrients in the dam, as a proxy of the trophic conditions in the water column, showed predominantly low values for DIN (0.26 ± 0.16 mg N L^{-1}) and DIP (0.07 ± 0.04 mg P L^{-1}) in the first 10 m depth. DIP had its highest concentrations between 10-20 m, with a maximum value in March which also coincided with an increase in surface layer. DIN were highly variable in the hypolimnion (0.77 ± 0.84 mg N L^{-1}). Its maximum concentration was recorded in November 2004 at 18 m depth (2.78 mg N L^{-1}), but later it remained low onwards (Fig. 3b).

Chl-*a* values, as an indicator of phytoplankton biomass, ranged from 0.6-16.0 mg Chl-*a* m^{-3} (average: 5.2 mg Chl-*a* m^{-3}) and 0.7-2.4 mg Chl-*a* m^{-3} (average: 1.4 mg Chl-*a* m^{-3}) in the discrete sampled depths at the euphotic and aphotic layer, respectively (Fig. 4). Each sampling point, excepting the deepest samples from Chapinero and the dam, showed statistically significant differences among months (Kruskal-Wallis, d.f. = 6, $P < 0.05$). The vertical distribution of Chl-*a* showed a decrease with depth in the area of the dam, although this trend was not entirely clear at Chapinero that had a shallow water column.

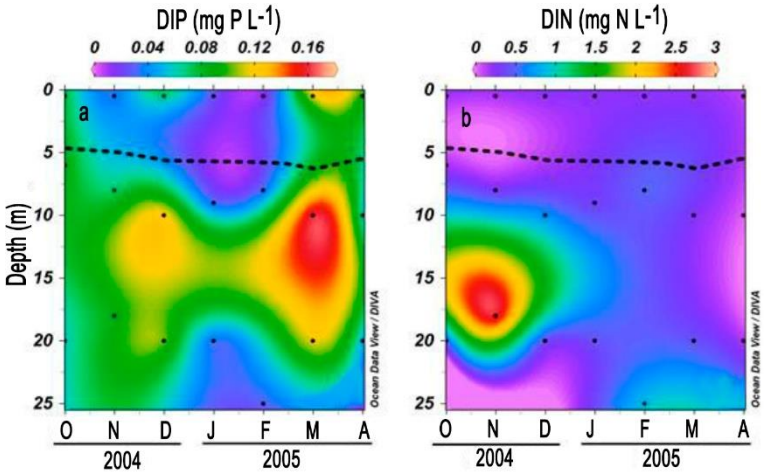

Figure 3. Temporal variability of vertical profiles of a) dissolved inorganic phosphorus (DIP), and b) dissolved inorganic nitrogen (DIN) in El Neusa reservoir. Dashed line corresponds to Secchi depth. O: October, N: November, D: December, J: January, F: February, M: March, A: April.

However, in this area, the largest Chl-*a* peaks could be detected at subsurface (Fig. 4a). In both sectors, lower discrete values were observed in March and April 2005, and the highest in October 2004 and from January to February 2005. Particularly, this pigment was always detected in the dam's hypolimnion (0.7-2.2 Chl-*a* m^{-3}). Surface values Chl-*a* describe a behavior more or less similar in the limnetic stations, characterized by two significant increases in October 2004 and February 2005, except for the latter in Chapinero that was slightly lower relative to last month. At the mouth of Cubillos River, Chl-*a* remained relatively high (5.7-9.8 mg Chl-*a* m^{-3}) in October and from December 2004 to March 2005 Fig. 4b). These relatively large surficial concentrations compared to the other sites were consistent with the increase in the hydraulic volume of reservoir and the subsequent flooding of the shores and the accumulations of sediment at the mouth (CAR, 2005). The temporal distribution of depth-integrated values was according with the magnitudes observed in the vertical profiles, excepting in January for Chapinero that was not comparable by having a smaller thickness of water column (Fig. 4c).

Virioplankton dynamics

Virioplankton abundance ranged from 2.4-10.5×10^7 VLP mL^{-1} (average: 6.0×10^7 VLP mL^{-1}) and 3.6-6.5 ×10^7 VLP mL^{-1} (average: 5.2×10^7 VLP mL^{-1}) in the euphotic and aphotic layer, respectively (Fig. 5). The temporal dynamics of the VLP abundance showed significant differences for each sampling point (Kruskal-Wallis, d.f. = 6, $P < 0.05$) except among the values of subsurface (1-7 m) in Chapinero and in the dam's hypolimnion. On the surface, the limnetic stations tended to increase slightly from November 2004 to April 2005 according with the increase in water column stratification, while in Las Juntas and Cubillos River, their peak occurred in February 2005 consistently with the augment in the hydraulic volume of the reservoir and flooding of the shores in the delta of the main tributaries (Fig. 5a). No significant differences were found among the water column VLP values of monthly vertical profiles for the sectors of Chapinero and the dam (Kruskal-Wallis, df = 6, $P > 0.05$), as well as a no clear pattern in the vertical distribution of VLP. The highest VLP values at Chapinero appeared between December and January in intermediate depths (3-7 m) and between March and April in surface, while at the Dam during the same periods, they were associated to the uppermost sampling levels (<10 m depth) excepting in April, when the intermediate and deepest samples (10 and 20 m, respectively) had also relatively large VLP (Fig. 5b).

Variability of virus-to-prokaryote abundance ratio (VPR)

The range of VPR for El Neusa fluctuated between 11.5 and 91.9 (mean = 38.6; Fig. 6), and significant temporal differences was noted (Kruskal-Wallis, df = 6, $P < 0.05$), but not among sampling stations. Littoral stations showed the highest VPR (39-51) in October 2004 and in April 2005, as well as sharp declines from November to December 2004 (11.5-13.2) and from January to February 2005 (18-24) at Las Juntas and the river mouth, respectively (Fig. 6a). In the limnetic stations and the hypolimnion, which also showed increases over the same periods than in littoral areas (41-92), additional

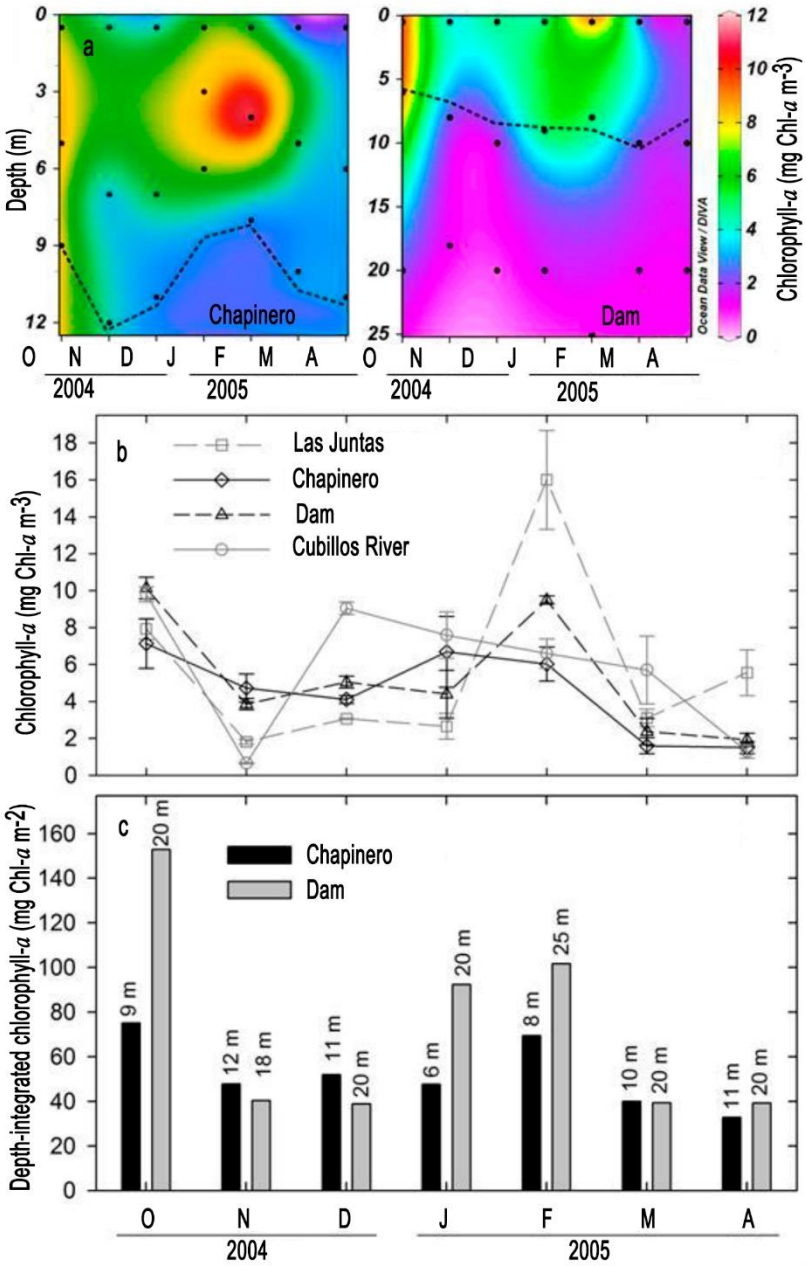

Figure 4. Temporal variability of chlorophyll-*a* (Chl-*a*) concentrations in a) vertical profiles, b) surficial stations, and the c) depth-integrated water column in El Neusa reservoir. Error bars represent the standard error. Dashed line corresponds to the depth of the photic layer. The vertical values over the bars indicate the depth of integration in meters. O: October, N: November, D: December, J: January, F: February, M: March, A: April.

peaks were detected in December 2004 (49-63), subsequent to the largest diminishing for both sites (18-24), and one more at the surface layer of Chapinero (52.4) in March. The vertical profiles of VPR were relatively more homogeneous in Chapinero than in the dam. Large VPR values (>60) were noted in October (5 m), December (7 m) and April (0.5 m) at Chapinero, and along the three sampling depths (0.5, 10 and 20 m) in December and subsurface in April (10 m) at the dam. In the latter location, the lowest VPR (18-32) were detected mainly from the samples of November 2004 and March 2005 (Fig. 6b).

Relationships among environmental and biological variables

PCA plot done with all available data set simplified the interpretation of those related environmental and biological variables through the magnitude and direc-

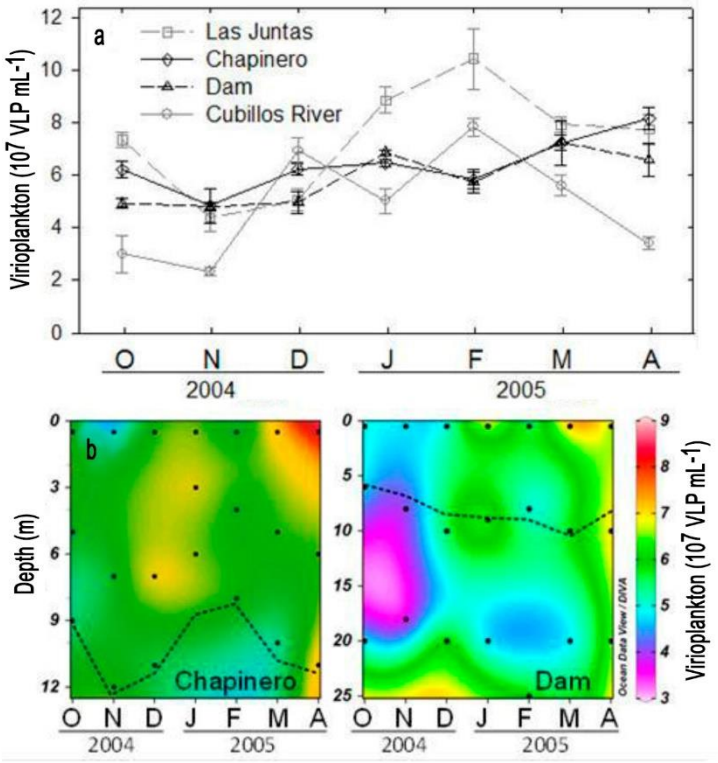

Figure 5. Temporal variability of virioplankton abundance (VLP) in a) surface samples at the sites and b) vertical profiles in El Neusa reservoir. Error bars represent the standard error. Dashed line corresponds to the depth of the photic layer. O: October, N: November, D: December, J: January, F: February, M: March, A: April.

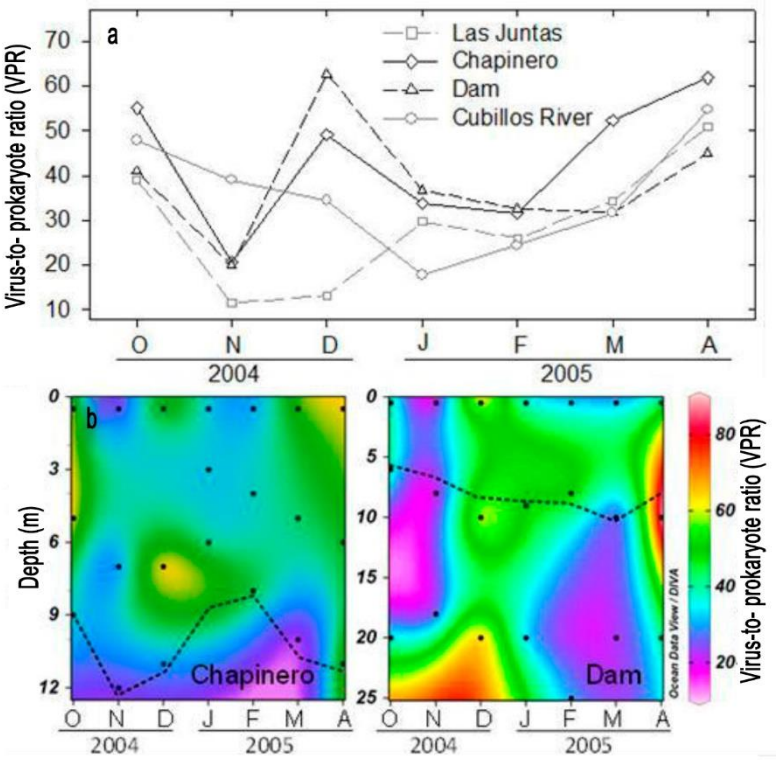

Figure 6. Temporal variability of virus-to-prokaryote abundance ratio (VPR) in a) surface stations at the sites and b) vertical profiles in El Neusa reservoir. Dashed line corresponds to the depth of the photic layer. O: October, N: November, D: December, J: January, F: February, M: March, A: April.

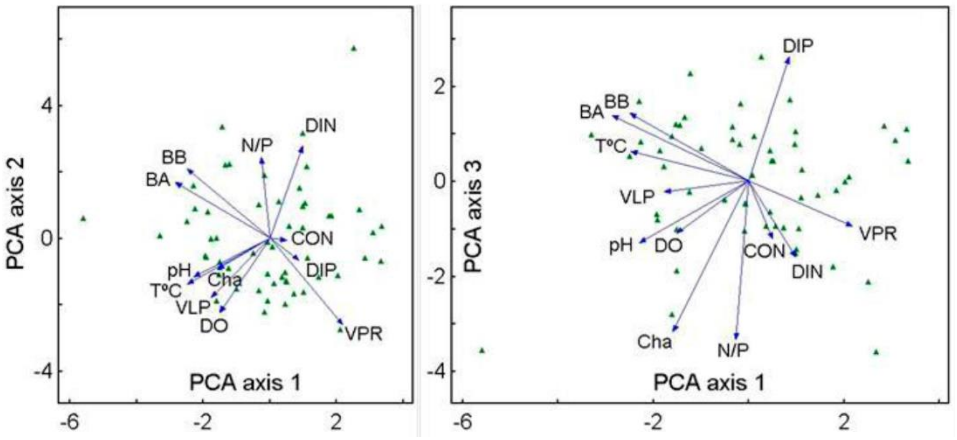

Figure 7. Projections of environmental and biological variables onto the biplot defined by the combination of the a) first versus second and b) first versus third principal components of CPA. TºC: water temperature, DO: dissolved oxygen, CON: conductivity, DIN: dissolved inorganic nitrogen, PO4: phosphate, N/P: nitrogen to phosphorus ratio, Cha: chlorophyll-*a*, BA: bacterioplankton abundance, BB: bacterioplankton biomass and VPR: virus-to-prokaryote abundance ratio. The green triangles represent all stations sampling.

tion of their orthogonal projections along the axes. The distribution of samplings according to the eigenvectors of the covariance among these variables was primarily explained by the first three axes with an accumulative variance of 61.4%. The first component, which accounted for 26.4% of the total variance, showed a positive and noticeable correlation with VBR, and negative correlations with BA, BB, water temperature, pH, PSV, OD and Chl-*a*, where the first four were the most influential in the distribution of samplings. Based results of second axis (20.5% of explained variance) showed a group of variables integrated by NID, nitrogen to phosphorus ratio (N/P), BB and BA that were positively correlated, and another group in which the VBR, DO and VLP were the most negatively correlated with this component (Fig. 7a). The third axis of PCA was negatively correlated to N/P and Chl-*a* and positively with DIP (Fig. 7b).

DISCUSSION

The temporal dynamics of the physical and chemical variables suggested a gradual increase in the stratification of the water column between October 2004 and March 2005. This is consistent with the weakening of the winds from the southeastern (CAR, 2003), which blow stronger between June and August, inducing a partial mixing system (Rivera, 1997). This condition has been previously observed in this and other tropical reservoirs (Márquez, 1996; Márquez & Guillot, 2001; Campuzano *et al.*, 2012), where the decreasing of DO and pH with depth is associated with the establishment of reducing conditions, as a result of aerobic and anaerobic respiration (*e.g.*, denitrification, reduction of sulfate to sulfide, etc.) and remineralization processes (*e.g.*, nitrification) of organic matter that is produced in the euphotic zone and transported efficiently to the bottom of the reservoir (Niño & Guillot, 2004; O'Sullivan & Reynolds 2005; Boehrer & Schultze, 2008). Moreover, the incidence of relatively high pH values (>7.8) in surface from January to March coincide well with the observed by Rivera (1997), which it was associated to increased stratification and subsequent decrease of dissolved inorganic phosphorus, and low phytoplankton production mainly represented by populations of Chlrophyceae and Desmidiaceae, that are typical of oligotrophic environments.

The registered values of Chl-*a* at El Neusa reservoir fluctuated within a range that goes from oligo to mesotrophic condition according to concentrations established for trophic status indices (TSIs) from lentic ecosystems (Carlson & Simpson, 1996; Brown & Simpson, 2001). This is consistent with the previously described for this reservoir through microbiological indicators and nutrient concentrations (Canosa & Pinilla, 1999a, 1999b, 2001, 2007; Hakspiel-Segura, 2005). Due to the low vertical resolution of sampling, we cannot ensure the presence of thin layers of greater accumulation of phytoplankton populations in both deep sampling sites, Chapinero and the dam, which might be stimulated by the particular combination of adequate conditions of nutrient and solar irradiance, or other physical and chemical gradients under stratified conditions (Camacho, 2006; Hamilton *et al.*, 2010). In the reservoir, the Chl-*a* dynamics were inversely correlated with phosphates (Spearman ρ = -0.36, P < 0.05; see also the inverse behavior of these variables in the first and third axis of PCA), indicating a positive

response of phytoplankton when this nutrient is being exhausted by their respective consumption. These results confirm some of the previously mentioned assumptions about the property of reactive phosphorus to regulate the photosynthetic production in El Neusa and other lentic high mountain ecosystems from the Andean region (Ramírez & Machado, 1982; Rivera, 1997; Pinilla *et al.*, 2002; Barrios, 2005; Vásquez *et al.*, 2006).

The detection of Chl-*a* values in the Dam's hypolimnion under low-light conditions (<1% I_0) was consistent with the simultaneous counts of autofluorescent cells in the size of nanoplankton (Hakspiel-Segura, 2005; Hakspiel-Segura *et al*., 2015). This suggests a broad range of possibilities ranging from the collapse and sinking of senescent phytoplankton populations to the incidence of active cells adapted to low irradiances and/or to consume organic matter as carbon and energy sources (Kiefer *et al.*, 1972; Yacobi & Ostrovsky, 2010, 2012; Rottberger *et al.*, 2013). However, the above requires more field observations and conducting experimental studies which corroborate these assumptions and incorporate these alternative pathways to the biogeochemical cycles of carbon and other nutrients in aquatic ecosystems in the high Andes.

The VLP values from El Neusa reservoir were within the same order of magnitude as those observed in lentic ecosystems of temperate and tropical latitudes with different trophic states, especially those with moderate to high levels of nutrients and biological productivity (Wilhelm & Smith, 2000; Bettarel *et al.*, 2003; Liu *et al.*, 2006; De Araújo & Godinho, 2009; Ram *et al.*, 2011; Hardbower *et al.*, 2012; Almeida *et al.*, 2015). However, the variability of this study was relatively higher than in other studies, probably due to differences in temporal and spatial scales of the sampling design. This levels of viral abundance contrasts slightly with the mentioned about the trophic status of the system, which could apparently be attributed to the progressive impact of nearest anthropogenic activities in the region (production of domestic water, cutting and burning of forests for agriculture and animal breeding) and practices within the same reservoir (fish farming and tourism) on the structuring of food webs (Salas, 1989; Arce-Quintero, 2005; Roldán & Ramírez, 2008). However, it is still not clear when the viral dynamics is more prone to fluctuate due indirectly to the additional nutrient supplement that may stimulate their assembly through biomass production at all trophic levels than by the effect of other pollutants derived from these human activities that directly may induce to the lytic phase in hosts (Weinbauer *et al.*, 2003; Choi *et al.*, 2010).

The absence of a clear trend in the vertical profiles of viral abundances was also previously observed in temperate lentic systems. (Pina *et al.*, 1998; Colombet *et al.*, 2012; Zhong *et al.*, 2014). According component loadings in the first axis from PCA analysis, the increase of VLP was relatively coupled within the behavior of a group of environmental and biological variables associated to a high primary production (Fig. 7). Some of these variables that contributed the most in PCA, such as DO and pH, independently showed a strong positive relationship with PSV (Spearman ρ = 0.44 and 0.42, respectively, $P < 0.05$). This association could be indirect through stimulation of the photosynthetic production which is then used by the heterotrophic component, mainly in the surface and subsurface layer, where aerobic conditions still prevail. In tropical and highland regions, solar ultraviolet radiation (UV), among other environmental variables, tends to have a larger forcing on environmental and biological components compared to areas of temperate latitudes and lower elevations above the sea level (Madronich, 1993; Piazena, 1996; Cabrol *et al.*, 2014; Häder *et al.*, 2015). This factor influences directly and indirectly on the distribution and activity of microorganisms due to induced damage to the integrity of viral structures (capsids, envelopes, nucleic acid, etc.) and cellular components (membrane system, organelles, nucleic acids, etc.) of potential hosts, as well as transformations inflicted on the organic substances that serve as substrates for some of these microorganisms (Visser *et al.*, 1999; Fernández-Zenoff *et al.*, 2006; Ruiz-González *et al.*, 2013). Certain studies suggest that the degree of infectivity and phage production tends to decrease with the increasing of exposure time and the received amount of UV-B radiation (Jeffrey *et al.*, 1996; Noble & Fuhrman, 1997; Weinbauer *et al.*, 1997; Wilhelm *et al.*, 1998, 2003; Cheng *et al.*, 2007). For the study area, a time series of monthly average solar radiation from 1960 to 1999 indicates that higher average levels occur commonly between January and March (548-607 cal cm^{-2}; CAR, 2005). This suggests that sunlight, more than affect the structural integrity of the virus, might indirectly favor its surficial abundance through the growth stimulation of other planktonic components. In surface samples incubated *in situ* (some of them without protozoa grazers >0.8 μm) from Lac Cromwell (Canada) and from Raunefjorden Bay (Western Norway), showed that high densities of virus was attributed to the induction the lytic cycle in lysogenic prokaryotes by solar UV radiation (Heldal & Bratbak, 1991; Maranger *et al.*, 2002). This hypothesis has been experimentally corroborated in marine samples, but with a smaller phage production when is compared with other inducers to the lytic cycle such as mitomycin C (Ackermann & DuBow, 1987; Weinbauer & Suttle, 1996, 1999; Jiang & Paul, 1998). Moreover, Suttle & Chen (1992) argue that the negative effect of

solar radiation on rates of viral infectivity is independent of its removal in the water column, and therefore a large proportion of virus that remain and are detected in counts by epifluorescence method may be non-infective or inactive.

The enumeration technique of microorganism by epifluorescence microscopy cannot distinguish between algal viruses and bacteriophages, so we use the PCA, simple correlation analysis and the VPR to elucidate the degree of interaction between VLP and these potential hosts. No significant relationship between the VLP abundance and Chl-*a* was detected (Spearman $\rho = 0.14$, $P > 0.05$). For a longer time period since July 2004 to April 2005, this pigment was weakly but positively correlated with the abundance and biomass of bacterioplankton (Spearman $\rho = 0.24$ and 0.27, respectively, $P < 0.05$). This relationship is consistent to that observed between counts of nanophytoplankton and bacterioplankton abundance and biomass for the same system (Hakspiel-Segura *et al*., 2015), confirming some of the assumptions about the substantial contribution of phytoplankton biomass to supplement organic substrates that require heterotrophic prokaryotes (*e.g.*, Reche *et al.*, 1996; Vrede, 1996; Laybourn & Walton, 1998).

Through the reduction of data dimensionality by PCA, it was noted that bacterioplankton variables and VLP were positively associated to the axis of first component, despite a simple linear correlation between these variables were no clearly observed. A positive association would be explained by a direct dependence of the phages by the density of its main host, as previously described in a large number of ecosystems (*e.g.*, De Araújo & Godinho, 2009; Barros *et al.*, 2010; Ram *et al.*, 2011; Ben Rhomdame *et al.*, 2014; Parvathi *et al.*, 2014). However, this relationship could be partially darkened by the interaction of other biological components, such as mixotrophic and heterotrophic nanoflagellates, which have been detected as important agents of bacterioplankton mortality (Hakspiel-Segura, 2005). However, a weak negative correlation between VLP and average biomass per prokaryotic cell was also identified (Spearman $\rho = -0.31$, $P < 0.05$), possibly indicating a strong viral control over prokaryotic populations in active growth and/or with relatively larger cell sizes (Bouvier & del Giorgio, 2007; Bonilla-Findji *et al.*, 2009; Winter *et al.*, 2010). This agrees well with that observed for El Neusa reservoir, where it was estimated that between 16% and 43% (on average: ~34% = ~10 mg C L^{-1}) of the total biomass prokaryotic is provided by a relatively low number of cells (4-10% of the total bacterioplankton abundance) with a larger biovolume (>0.24 μm^3; Hakspiel-Segura *et al*., 2015).

The dynamics of VPR showed high spatial and temporal heterogeneity of the virus to infect and control the abundance of prokaryotic community. The VPR values observed here were slightly higher than the average range described for continental environments (20-25; Maranger & Bird, 1995; Wommack & Colwell, 2000), and possibly similar to those reported in some systems with mesotrophic to eutrophic conditions, where a strong viral control has been attributed by a high rate of contact between viral particles and hosts (Bettarel *et al.*, 2003; Weinbauer, 2004; Liu *et al.*, 2006; Almeida *et al.*, 2015). Thus, the trophic status or sporadic events of enrichment may promote the growth rates and/or the increase in biovolume of the host cell community, which in turn influence positively the assembly of viral particles and the burst size (Weinbauer & Höfle, 1998; Middelboe, 2000; Choi *et al.*, 2003).

In general, VPR dynamic had no significant single correlation with the environmental variables of the water column and Chl-*a* (Spearman $\rho = 0.01$, $P > 0.05$), suggesting that the interaction between virioplankton and bacterioplankton is more complex and may be influenced by other factors not tested here or a combination, of several of these variables. VPR values from surficial littoral locations showed significant correspondences with the hydraulic volume of reservoir and precipitation levels (Spearman $\rho = -0.68$ and 0.55, respectively, $P < 0.05$). We believe that during the strongest rainfall levels (91-195 mm $month^{-1}$) since September to November 2004 and April 2005, the entrance of allochthonous substrates by run-off or river discharges might stimulate the induction of lytic cycle in lysogenic prokaryotes or favor the exportation of certain allochthonous populations from land (*e.g.*, Bergström & Jansson, 2000; Hewson *et al.*, 2012; Williamson *et al.*, 2014). In the limnetic locations, some high VPR peaks seem to be non-statistically related to rainfall and also with conditions of low water column stability, but an unexpected high value in December could be attributed possibly to the permanence of low temperatures (<16°C) in the water column (Fig. 2a). An alternative explanation for the high VPR in the subsurface and the hypolimnion may result from a low viral decay due to a high preservation of VLPs under conditions of lower temperature and DO, and/or by adsorption to organic matrices composed of humic substances (Weinbauer & Höfle, 1998; Vrede *et al*., 2003).

CONCLUSIONS

The data provided by this research about the dynamics of virioplankton and Chl-*a*, as well as the previous

reports of abundance and biomass of bacterioplankton, and abundance of nanoplankton (Hakspiel-Segura *et al*., 2015), suggest that the planktonic microbial community is an active component of aquatic food webs that modulate the fate of carbon and other nutrients at El Neusa reservoir. A rough calculation of viral carbon, by applying a conversion factor of 0.2 fg C VLP^{-1} in marine viruses (Suttle, 2005), indicates that this biological entity may contribute on average with ~72 % (~20-174%) of the estimated biomass of bacterioplankton for this system, which means a considerable reservoir of carbon. This coupled with the cell mortality caused by viral lysis promotes enrichment in the dissolved organic matter pools that could be incorporated again through the microbial loop, and therefore an inefficient transfer of this carbon toward higher trophic levels (Wilhelm & Suttle, 1999); however, our data are not enough to prove these assumptions. Future efforts should be focused on quantifying rates of viral infection, the prevalence of phage in cells, and virus-induced mortality, and particular attributes of the viral community (richness, diversity, host specificity, etc.) to get a better understanding of its impact on the dynamics of planktonic populations in high Andes aquatic ecosystems.

At the spatial and temporal scales of this study, we cannot confirm that the dynamics of VLP and its viral control are more largely affected by human activities causing potential alterations on nutrient loading and cycling processes than the modulation exerted indirectly by regional hydrological conditions and the hydraulic behavior of the reservoir. This is possibly due the poor spatial and temporal resolution of this research to detect sites with potential sources of nutrient pollution as well as the lack of environmental and limnological data in high mountain aquatic systems.

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