



Melting of clean and debris-rich ice differentially affect nutrients, dissolved organic matter and bacteria respiration in the early ontogeny of the newly formed proglacial Ventisquero Negro Lake (Patagonia Argentina)

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Abstract

1. Climate change affects glaciers all over the world causing glacial recession with the formation of new lakes. Glaciers of Mount Tronador (41° S, Patagonia, Argentina) underwent an increase of more than 200 m in the equilibrium-line altitude (ELA), from 1994 to 2016. The proglacial Lake Ventisquero Negro showed a continuous increase in lake surface area since 2009, when a glacial outburst flood (GLOF) occurred. The Ventisquero Negro glacier is a debris-covered glacier located below the timberline; thus, the lake receives meltwater from both clean and debris-rich ice.
2. This study analyses the proglacial lake after the GLOF event, particularly the nutrient content, dissolved organic matter and bacterial respiration. Our main hypothesis was that the melting of debris-rich and clean ice would differentially affect nutrient inputs and bacterial respiration in the early ontogeny of the lake.
3. Sampling was conducted in austral spring–summer seasons (2012 to 2016) following the GLOF event. We carried out bacterial respiration experiments with lake water and two treatments enriched with clean or debris-rich ice from the glacier. Additionally, we carried out an another enrichment experiment with phosphate-P and glucose-C alone or in combination.
4. The lake exhibited high turbidity levels due to a high concentration of suspended solids. Vertical light profiles showed that almost the entire water column was aphotic. Phosphorus (P) concentration was high and was positively related to total suspended solids. Accordingly, P concentration was higher in debris-rich than in clean ice. However, the dissolved organic carbon concentrations in the lake were found to remain relatively constant through time (less than 50 $\mu\text{mol/L}$).
5. Analysing fluorescent excitation–emission matrices, we determined that the dissolved organic matter is very simple with only two peaks, one corresponding to protein-like compounds (C1) and the other to humic-like compounds (C2), coming from clean ice and debris-rich ice, respectively. C1 was present in all samples, while C2 was comparatively more important during summer, coinciding with higher temperatures and melting.

6. This study supports the hypothesis that melting of clean and debris-rich ice would affect DOM and P input at early stages of a proglacial lake formed by the recession of a debris-covered glacier. Bacterial respiration was observed to be positively affected by debris-rich ice melting and to be P limited. Thus, P is a major controlling factor for carbon dynamics in a newly formed proglacial lake.

KEYWORDS

bacterial respiration, dissolved nutrients, fluorescence matrices, glacial lake, glacial recession

1 | INTRODUCTION

Climate change affects glaciers all over the world, causing glacial recession with the formation of new lakes. In particular, the Alps, Greenland and the Central and Southern Andes are identified as vulnerable areas for glacial and ice sheet retreat (IPCC, 2014). As a consequence, the number of new lakes will increase in the areas affected by glacial recession, as for example, in the Swiss Alps where it has been predicted that more than 500 new lakes will be formed in future years (Linsbauer, Paul, & Haeberli, 2012). In the northern Patagonian Andes, glaciers have lost 25% of their total area since 1985, while the area of proglacial lakes has grown by 59% (Paul & Mölg, 2014). In addition, a glacial lake outburst flood (GLOF) episode recently occurred in North Patagonian Andes, which was associated with ongoing glacier retreat and glacier lake formation (Worni et al., 2012).

Proglacial lakes are characterised by heavy glacial clay inputs that cause turbidity-induced light attenuation, producing a light-limited environment for primary producers. Although turbid glacial lakes seem a rather rare ecosystem type, numerous new turbid lakes will be formed due to the ongoing glacial recession (Peter & Sommaruga, 2016). Ecological functioning of communities of glacial lakes during their early ontogeny is little known, particularly when turbidity levels are high (Sommaruga, 2015). However, these cold environments are colonised by a wide diversity of psychrophilic microorganisms, including bacteria, archaea, yeasts, filamentous fungi and algae (Margesin & Miteva, 2011), conforming a planktonic food web dominated by microbes with few metazoans (Sommaruga, 2015; Sommaruga & Kandolf, 2014). Along their ontogeny, lakes are expected to exhibit strong gradients in turbidity with potential changes in light availability affecting the distribution of producers, giving that meltwater discharge may protect primary producers from light stress including ultraviolet radiation (UVR) (Martyniuk, Modenutti, & Balseiro, 2014). Palaeolimnological evidence indicates that changes in algal pigments and species composition are associated with differences in sedimentation rates that can be related to periods of clear and turbid lake water (Guilizzoni et al., 2009).

In addition to light limitation imposed by glacial clay, proglacial lakes can exhibit fluctuations in nutrients driven by glacial meltwater inputs. Meltwaters can supply significant amounts of dissolved organic carbon (DOC) that is highly biologically available (Hood & Berner, 2009; Hood & Larson, 2015; Stibal, Šabacká, & Žárský,

2012). Snow and ice also play an important role in the nitrogen (N) cycle; thus, glacier meltwater may also supply nitrate or ammonium (Wolff, 2013). Finally, total phosphorus (TP) is high in glacial water (Chillrud, Pedrozo, Temporetti, Planas, & Froelich, 1994), although most of the phosphorus is adsorbed in the mineral clay phases and therefore its availability as reactive phosphorus is low (Chillrud et al., 1994; Hodson et al., 2008). Nevertheless, experimental addition of dry glacial clay has been shown to stimulate biological production, demonstrating that the adsorbed P is, at least partially, biologically accessible (Mindl et al., 2007).

Debris-covered glaciers are mountain glaciers covered by inorganic and organic debris fallen from the surroundings (Benn & Evans, 1996) and are common in different mountains around the world. The organic C is provided mainly by the continuous allochthonous deposition of organic matter (plant debris, animals, etc.) (Anesio et al., 2010). However, the final nutrient availability is likely influenced by bacterial activity that enriches supraglacial debris (Anesio, Lutz, Christmas, & Benning, 2017). Nevertheless, knowledge of the bacterial community and activity related to these debris-covered glaciers is very scarce (Darcy & Schmidt, 2016; Franzetti et al., 2013; Mertes, Thompson, Booth, Gulley, & Benn, 2017).

The Ventisquero Negro glacier (meaning “black” glacier) is located in Mountain Tronador (41° S, Patagonia, Argentina). The glacier is covered by a thick debris layer and is fed by snow, ice and debris avalanches from the steep slopes above. A recession of the glacier tongue was observed between the early 1990s and the present (Masiokas et al., 2008; Ruiz, Berthier, Viale, Pitte, & Masiokas, 2017; Worni, Huggel, Clague, Schaub, & Stoffel, 2014), with the concomitant formation of a new lake. After a moraine breach (GLOF) that occurred in 2009, the glacier valley was remodelled and lake size increased (Worni et al., 2012). The aim of the present study was to characterise this proglacial lake after the GLOF event, particularly nutrient content and bacterial respiration. Previous studies in an Antarctic glacier have shown that bacterial metabolic responses differed between clean and debris-rich layers (Montross et al., 2013). Based on this evidence and other studies carried out on debris-covered glaciers (Anesio et al., 2010; Franzetti et al., 2013; Reynolds, 2000), our main hypothesis was that the melting of “debris-rich” and “clean” ice would differentially affect nutrient inputs, dissolved organic matter and bacterial respiration in the early ontogeny process of the lake. Thus, the present study tested C or P limitation and determined the effect on bacterial respiration of the differential melting of

debris-rich and clean ice into the lake water. For this purpose, we carried out bacterial respiration experiments directly on lake water and in two experiments: one with lake water and two treatments enriched with “clean” or “debris-rich” ice from the glacier and the other with phosphate-P and glucose-C addition in a factorial design.

2 | METHODS

2.1 | Study area and sampling

Mount Tronador (41° 10'S, 71° 52' W; 3,480 m above sea level, ASL) is the highest mountain in Nahuel Huapi National Park and straddles the border between Chile and Argentina in northern Patagonia (Figure 1). The upper part of the mountain is covered by a continuous ice cap with several outlet glaciers. The total glacier area is about 64 km² and the largest glaciers reach down to 950 m ASL, well below the local tree line of 1,700 m ASL (Villalba, Boninsegna, Veblen, Schmelter, & Rubulis, 1997). Ventisquero Negro is a debris-covered glacier located in the south-eastern flanks of Mount Tronador separated by a several hundred metres high steep cliff from the main ice cap. The glacier is fed by snow, ice and debris avalanches from the steep slopes above (Worni et al., 2012). All this material is processed, compacted and readhered giving the glacier a marbled appearance with clean and debris-rich ice (Figure 2b). During the Little Ice Age, the glacier partly overlapped the older (>2,000 year old) end moraine and subsequent glacier recession resulted in a debris-covered ice body bordering the inner slope of the end moraine (Masiokas et al., 2008). However, rapid thinning and recession of the glacier tongue were observed between the early 1990s and the present (Masiokas et al., 2008). The breach of the Ventisquero Negro

end moraine on May 21, 2009, produced a lake outburst flood. From that moment, the recession of Ventisquero Negro resulted in the formation of a proglacial lake that flows through the Negro River in the upper Rio Manso valley.

The Lake Ventisquero Negro (Figure 2a) was sampled during austral summer, spring and autumn, in 2012, 2013, 2014, 2015 and 2016 on 14 sampling occasions (Figure 3, see *). We measured turbidity (nephelometric turbidity units: NTU) using a portable turbidity meter (Lutron TU-2016, Taipei, Taiwan; Resolution: 0.01 NTU/1 NTU), pH with a pH meter (Hanna, Resolution: 0.01 pH) and temperature, conductivity and dissolved oxygen with an oximeter-conductimeter (YSI 85, Ohio, USA, accuracy: 1% temperature, 0.05% oxygen). We performed vertical light profiles (photosynthetically active radiation, PAR, 400–700 nm and UVR, 320 and 340 nm) with a PUV500-B radiometer (Biospherical Instrument) that collected data continuously (4 per second) while downloading it. Subsurface water samples (three replicates) were collected using sterile 2-L glass bottles and ice from the Ventisquero Negro glacier was collected in hermetically sealed sterile plastic bags (previously tested to ensure no DOC leaching by direct DOC concentration determinations and spectrofluorometric analysis, see detailed methods below). Samples were stored in a cooler until they could be processed for nutrient concentration determination and other laboratory procedures (generally 3 hr after collection).

2.2 | Chemical determinations

Total phosphorus (TP) was determined using unfiltered lake water, and total dissolved phosphorus (TDP) was determined using lake water filtered through GF/F filters. Samples for the TP and TDP determinations were digested with potassium persulphate at 125°C and 1.5 atm for 1 hr. Finally, P concentrations were obtained using the ascorbate-reduced molybdenum method (APHA, 2005) in 100-mm cuvettes with a Shimadzu UV2450 dual-beam spectrophotometer (detection limits: 0.5 µg/L = 0.016 µmol/L).

Dissolved organic carbon (DOC) concentration was determined in filtered lake water (precombusted GF/F filters) with a high-temperature combustion analyser (Shimadzu TOC V-CSH), using potassium hydrogen phthalate as the standard (detection limits: 0.5 µg/L = 0.04 µmol/L). Total dissolved nitrogen (TDN) was analysed in filtered lake water using a TN-M1 unit on the Shimadzu TOC V-CSH (detection limits: 10 µg/L = 0.7 µmol/L).

Chlorophyll *a* concentration (Chl *a*) was determined by filtration of 1 L of lake water onto GF/F filters and then extraction with 90% ethanol, according to Nusch (1980), using a fluorometer (Turner Designs, 10-AU, CA, USA, detection limits: 0.025 µg/L) which had been previously calibrated against spectrophotometric measurements.

2.3 | Dissolved organic matter characterisation

Spectrofluorometric optical analysis of dissolved organic matter (DOM) was achieved by single measurements at specific excitation/

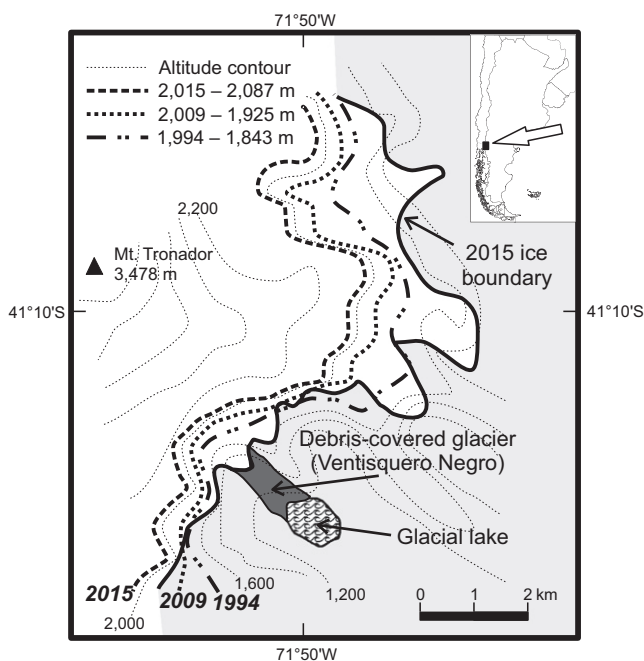


FIGURE 1 Map of the Mount Tronador ice cap with the equilibrium-line altitude (ELA) in 1994, 2009 and 2015

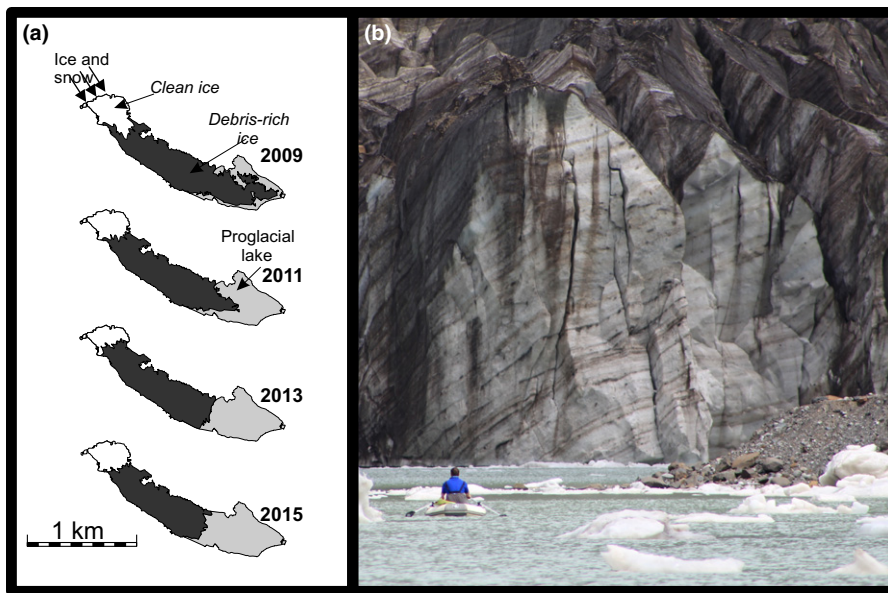


FIGURE 2 (a) Map of the newly formed Lake Ventisquero Negro showing the increment in surface area after the GLOF event in 2009 until 2015 extracted from Landsat images. (b) Photograph of the marble-like ice (clean and debris-rich) of Ventisquero Negro glacier and the proglacial lake

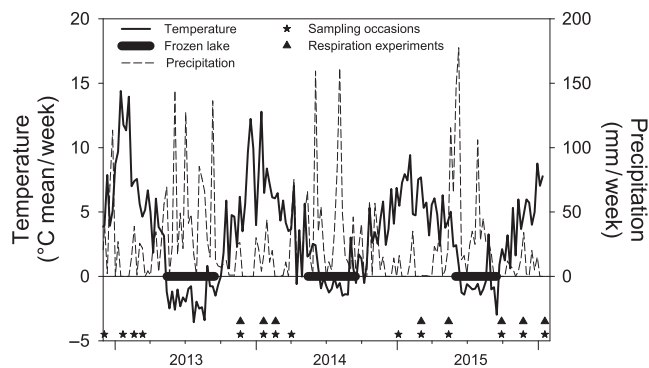


FIGURE 3 Temperature and precipitation during the studied period, indicating sampling occasions (*) and field respiration experiments (▲)

emission wavelengths, and excitation–emission matrices (EEMs) were performed with a PerkinElmer LS 45 fluorescence spectrometer (PerkinElmer, USA) equipped with a xenon discharge lamp. The excitation wavelength intervals were of 2 nm, between 240 and 450 nm, and the emission ranged between 300 and 550 nm with 5-nm increments. The measurements were performed at a constant room temperature of 20°C in a 1-cm quartz fluorescence cell; Raman scattering was corrected by subtracting the pure water (Milli-Q) EEM from the sample EEM obtained the same day.

2.4 | Bacterial abundance and respiration experiments

Bacterial abundance was determined using 50 ml of lake water fixed with filtered formaldehyde at a final concentration of 2% v/v. The bacterial cells were stained with 4',6'-diamidino-2-phenylindole (DAPI) at a final concentration of 0.2% w/v (Porter & Feig, 1980). Counting was performed on polycarbonate black membrane filters (0.2 µm pore size, Osmonics) at 1250X magnification in an

Olympus BX50 epifluorescence microscope using UV light (U-MWU filter).

Short-term (48 hr) bacterial respiration experiments (Guillemette & del Giorgio, 2011) were performed in triplicate using 500-ml ground-stoppered Erlenmeyer flasks in an incubation chamber in the dark at 10°C. The concentration of dissolved oxygen was measured every 6 hr over a period of 48 hr using an optical-oximeter (ODO) with noninvasive oxygen fluorescent sensors (PreSens, Germany) located inside the flasks. The O₂ consumption rates were estimated as the least-squares regression slope of the O₂ concentration over time. All glassware used during these experiments was carefully sterilised prior to starting each procedure.

On eight samplings dates (Figure 3, triangles), we carried out respiration measurements with water from Lake Ventisquero Negro. Experiments consisted of incubating lake water after filtering through sterile polycarbonate (2-µm Nucleopore) filters to exclude larger eukaryotic cells. The potential loss of bacteria was tested by counting before and after filtration and the bacteria loss was less than 5% on average.

To test differences in bacterial respiration caused by melting of debris-rich and clean ice, we carried out another laboratory experiment (January 2015). The experiment consisted of control (filtered lake water unamended), treatment 1: clean ice; treatment 2: debris-rich ice (3 replicates each) (Supporting Information Figure S1). For this purpose, we sampled clean and debris-rich ice directly from the Ventisquero Negro glacier using a clean geological hammer. The different ice samples were stored separately in hermetically sealed sterile plastic bags. We also sampled 10 L of lake water. All samples were immediately transported to the laboratory (3 hr after collection). In the laboratory, the melting water from the debris-rich and clean ice was filtered through a 0.2-µm pore filter (Nucleopore). Lake water was divided into two 5-L subsamples, one was filtered through a 0.2-µm pore filter, and the other 5 L was used to prepare the bacterial inoculum by filtering it through 2-µm polycarbonate filter. The

flasks were filled (80% of flask volume) with the different water treatments (400 ml of 0.2- μm filtered water of lake, debris-rich or clean ice) and 20% of bacterial lake inoculum (100 ml of 2- μm filtered lake water) (Supporting Information Figure S1).

To test C, and P as limiting factors for bacterial respiration, we carried out a laboratory experiment (February 2015) in a fully factorial design, with filtered lake water (2- μm) in four treatments (three replicates each): control (filtered lake water unamended), phosphorus (+P), glucose (+G), and glucose plus phosphorus (+G+P) additions. Glucose (333 $\mu\text{mol C/L}$) or phosphate (1.61 $\mu\text{mol P/L}$ as KH_2PO_4) or both were added to the replicates (final concentration 375 $\mu\text{mol C/L}$ and 1.8 $\mu\text{mol P/L}$, concentrations based on previous study (Bertoni, Callieri, Balseiro, & Modenutti, 2008)), in order to obtain a C: P ratio of 215 (lake unamended), 1,973 (+G), 23 (+P) and 207 (+G+P).

2.5 | Bacterial assemblage DNA

In December 2012, March 2013 and January and March 2014, we collected samples for bacterial assemblage identification. 200 ml of lake water was filtered through Nucleopore[®] filters (0.2- μm pore size, 25 mm diameter). The Nucleopore filters were then collected and stored at -80°C . DNA was extracted from the filters using a MoBio Soil DNA Isolation kit (MoBio Laboratories, Carlsbad, CA, USA) following the manufacturer's protocol. Purity of DNA was determined by PCR amplification with universal bacterial primers (8 F/1492R) and quantified using Take 3 on a microplate reader Synergy HTX (Bio Tek, Vermont, USA). Purified DNA samples were sent to INDEAR (Rosario University, Argentina). Amplicon sequencing libraries were constructed by PCR amplification of the V1–V3 variable region in the 16S rRNA gene. Amplicon and shotgun libraries were sequenced using 454-FLXPlus-Titanium chemistry (Roche, Switzerland). Raw data processing was performed following standard procedures suggested by the manufacturer. The amplicon dataset was analysed using QIIME v1.5 software package (97% similarity) (Caporaso et al., 2010). A total of 169,496 readings with a mean size of 534.48 bp were obtained. Identification was carried out with the database GreenGenes V13.8. Raw sequences were deposited in NCBI accession number SRP131488 under Bioproject PRJNA431735 (<https://www.ncbi.nlm.nih.gov/sra/SRP131488>).

2.6 | Data analysis

The evolution of Ventisquero Negro glacier and the newly formed proglacial lake was manually digitalised and extracted from Landsat images. We used Landsat LT5 sensor for December 2009 and February 2011, LE7 sensor for February 2013 and LC8 sensor for February 2015.

We estimated the equilibrium-line altitude (ELA) following Benn and Hulton (2010), using the Excel[®] spreadsheet developed by these authors. The amount of ice/snow melt was obtained following the temperature-index approach described by Hock (2003). Ablation was calculated by multiplying positive temperatures by a factor that relates temperature and ablation, the degree-day factor (DDF). The

DDF corresponds to the amount of melting (of ice and snow) per day, which occurs when temperatures are above 0°C . Daily meteorological data were collected from a meteorological station in Los Alerces (774 m) from the COHIFE (Consejo Federal Hídrico Argentino). The DDF values (ice, snow and debris), the lapse rate of precipitation and the temperature lapse rate were obtained from a high-resolution surface velocity work of Monte Tronador glaciers (Ruiz, Berthier, Masiokas, Pitte, & Villalba, 2015). By applying this model at 5 different glacier elevations (1,000, 1,600, 2,000, 2,100 and 2,200 m), we obtained a glacier mass balance curve (specific mass balance with altitude).

Light attenuation coefficients were calculated as the absolute value of the regression slope of the \log_e -transformed light intensity with depth.

The analysis of the EEMs was performed using the PARAFAC analysis with the DOMFluor 1.7 Module (Stedmon & Bro, 2008) on MATLAB R2015a. Each EEM matrix was corrected with the EEM of Milli-Q water on the same day, and the matrices were then expressed as Raman units.

The relationships between TP, TDP, TDN and TSS were analysed by Pearson correlation coefficient and least-squares regression analysis. Relationships were considered significant at $\alpha = 0.05$.

Respiration rates were obtained as the absolute value of the regression slope of O_2 concentration with time and expressed as $\mu\text{mol O}_2 \text{ L}^{-1} \text{ hr}^{-1}$. In both experiments, comparison between treatments was carried out with an ANOVA, comparing treatments with three replicates per treatment. Normality and homoscedasticity were confirmed prior to the ANOVA. When differences were significant a posteriori, Tukey test was applied.

When data did not fulfil normality and/or homoscedasticity (i.e., nutrient concentrations in the lake), nonparametric Kruskal–Wallis (K-W) was applied. DOC concentrations from ice and lake were compared with a Mann–Whitney *U* test. All statistical analyses were performed using the SigmaStat 12.5 statistical package.

3 | RESULTS

3.1 | The lake and the melting ice

During the last decades, Mount Tronador suffered a change in the equilibrium-line altitude (ELA). In 1994, this line was observed at 1,843 m ASL, while by 2009 (GLOF event), the equilibrium line was located at 1,925 m ASL and continued rising reaching in 2015, 2,087 m ASL, resulting in an increase of more than 200 m in 20 years. Accordingly, the evolution of Ventisquero Negro glacier and the proglacial lake extracted from Landsat images showed a continuous increase in lake surface from 2009 (GLOF event) onwards, particularly in the years in which this study was performed (Figure 2).

The lake was sampled in the period with highest temperature and lowest precipitation (Figure 3). In the subsurface samples of the lake, total suspended solid averaged 36 mg/L with a range between 17 and 91 mg/L, and this showed a significant relationship with

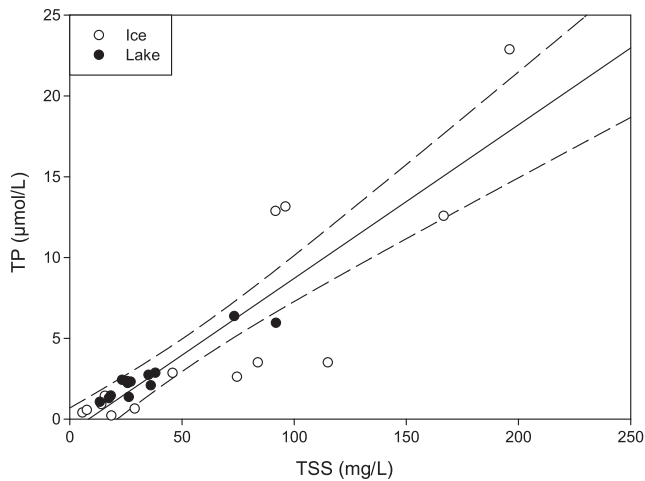


FIGURE 4 Total suspended solids (TSS) and total phosphorus (TP) relationship in the lake and in the ice ($r^2 = 0.774$ $n = 27$, $p < 0.0001$)

turbidity levels (21 to 125 NTU) ($r^2 = 0.96$, $n = 14$, $p < 0.001$). Based on vertical light profiles obtained in the lake, we calculated that the attenuation coefficient of photosynthetically active radiation, (K_{dPAR}) ranged between 1.96 and 2.91 m^{-1} and the euphotic zone depth ($Z_{1\%PAR}$) was approximately 1.5 m depth. Thus, almost the entire water column (up to 60 m) was observed to be aphotic. Accordingly, subsurface chlorophyll *a* concentration in the lake was always low (on average 0.49 ± 0.05 $\mu g/L$).

Phosphorus concentration (TP) was positively correlated with TSS (Figure 4) ($r^2 = 0.774$ $n = 27$, $p < 0.0001$). In the ice, we observed a gradient in TSS concentration (from clean to debris-rich) and thus in TP (Figure 4 open circles). Accordingly, clean ice exhibited comparatively low phosphorus concentration (Figure 4: ice with TSS values less than 50 mg/L has less than 3 $\mu mol/L$). TDP in the ice also showed an increase with TSS, but weaker than TP ($r^2 = 0.26$ $n = 27$, $p = 0.048$). In the lake, we observed that TP concentration increased in January and February (Figure 5) (K-W: $H = 8.813$, $df = 3$, $p = 0.032$) in coincidence with highest temperature and lowest precipitation values (Figure 3). In comparison, total dissolved phosphorus was low (less than 1 $\mu mol/L$) and lacked any seasonality (K-W: $H = 3.791$, $df = 3$, $p = 0.342$) (Figure 5).

We found no relationship between TSS and TDN concentration in neither the lake nor in the ice ($r^2 = 0.011$ $n = 21$, $p = 0.066$). In addition, there were no significant differences among different sampling dates in the lake (K-W: $H = 0.111$, $df = 3$; $p = 0.997$) (Figure 5).

Concentrations of DOC in the lake were always very low (around 46 $\mu mol/L$) (Figure 5) with no significant differences among sampled seasons (K-W, $H = 0.873$, $df = 3$; $p = 0.863$). Compared to the lake, ice was richer in carbon ranging from 166 to 4,500 $\mu mol/L$ (10- to 100-fold higher than lake values) (Mann-Whitney $U = 11$, $df = 27$, $p < 0.001$).

The PARAFAC analysis of DOM showed the presence of two components: based on Coble (1996), one component corresponded to protein-like (C1) and the other humic-like (C2) substances

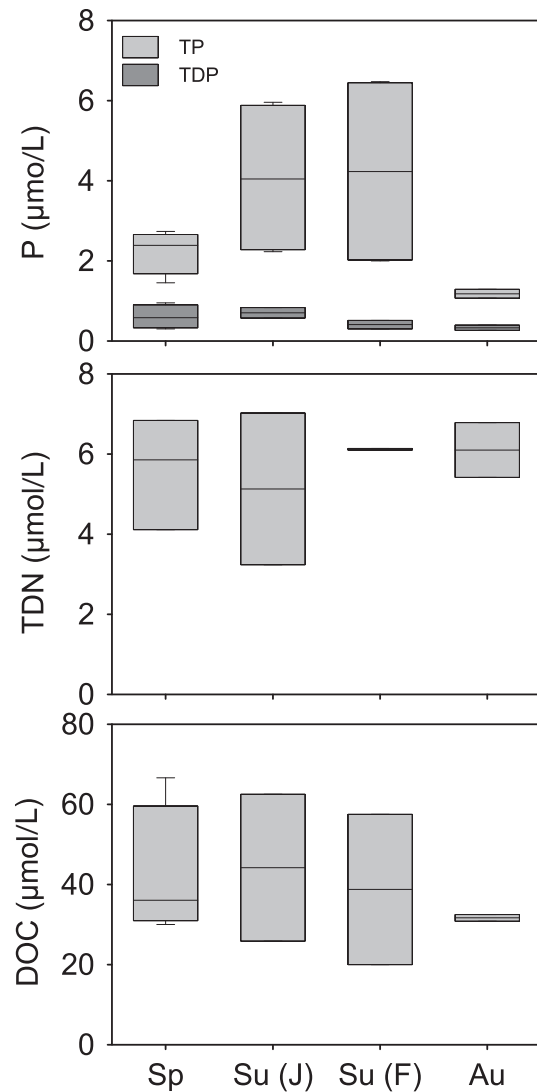


FIGURE 5 Box-plot of the nutrient concentrations in Lake Ventisquero Negro: TP: total phosphorus, TDP: total dissolved phosphorus, TDN: total dissolved nitrogen, DOC: dissolved organic carbon. References: Sp: Spring, Su (J): Summer (January), Su (F): Summer (February), Au: autumn

(Figure 6a). Analysing the fluorescence spectra, we found a predominance of C1 in the clean ice while both C1 and C2 were observed in debris-rich ice and in the lake (Figure 6b,c). In the lake, we observed seasonality in the appearance of the two peaks: while C1 was present in all samples, C2 was comparatively more important during summer (Figure 6c), coinciding with higher temperatures and melting.

3.2 | Bacterial abundance and respiration experiments

Bacterial abundance was on average 0.76×10^6 cell/ml (range 0.5 to 1×10^6 cell/ml) and bacterial respiration rates in the lake varied between 0.3 and 1.2 $\mu mol O_2 L^{-1} hr^{-1}$ (Supporting Information Table S1). We did not find a significant relationship between

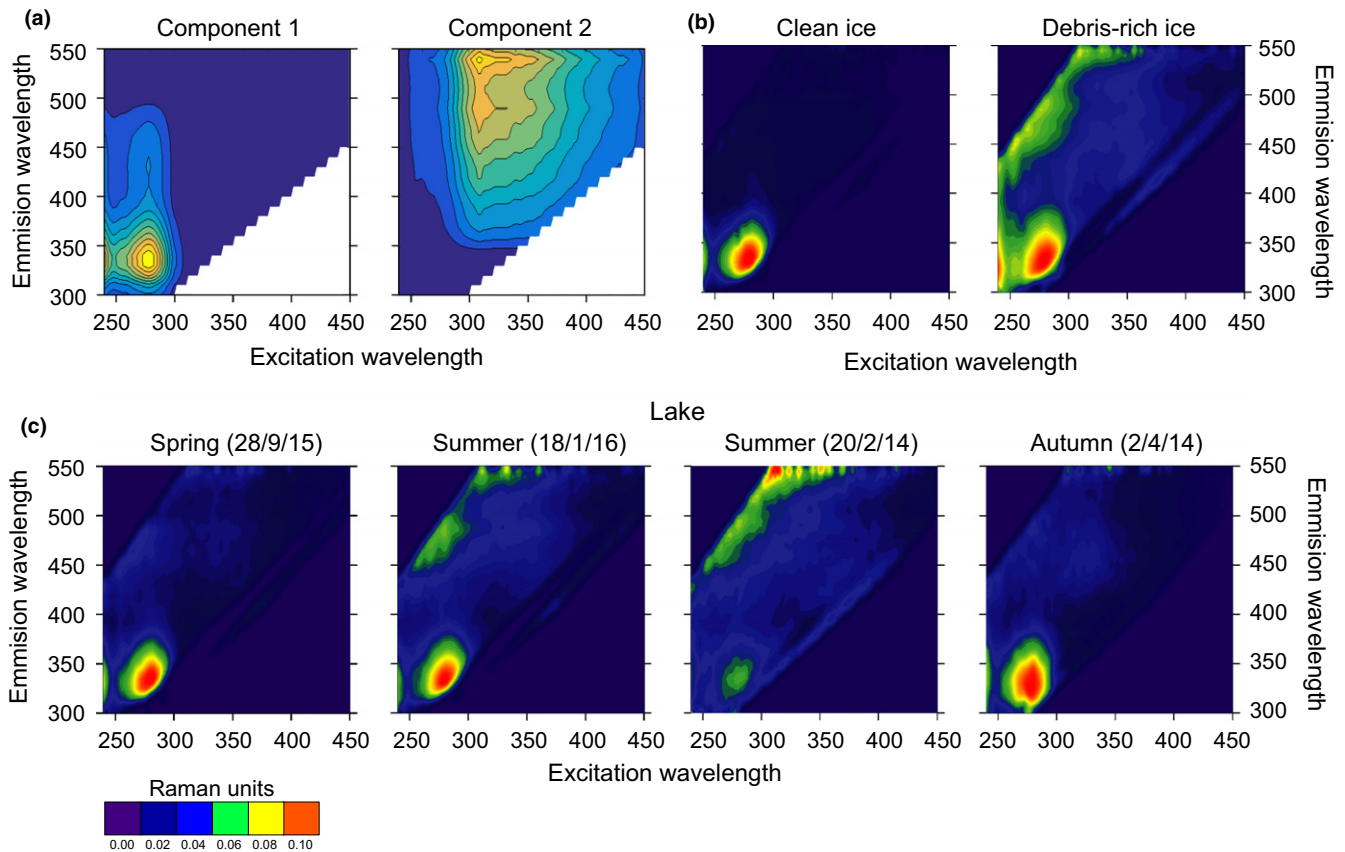


FIGURE 6 Dissolved organic matter analysis: EEMs (excitation–emission Matrices) of water of Lake Ventisquero Negro and ice and peaks identified with PARAFAC. (a) Identified peaks with the PARAFAC analysis. Component 1: protein-like peak, component 2: humic-like peak. (b) Data from debris-rich and clean ice. (c) Data from selected samples (spring, early summer, late summer and autumn) from Lake Ventisquero Negro. The fluorescence intensity is in Raman units

bacterial respiration in the field with DOC nor TDP concentrations (TDP: $r^2 = 0.0007$, $n = 8$, $p = 0.919$; DOC: $r^2 = 0.007$, $n = 8$, $p = 0.750$).

In contrast, our experiments showed significant differences between treatments. In our first laboratory experiment, we tested the effect of debris-rich and clean ice enrichment on bacterial respiration (Control: lake, Treatment 1: clean ice, Treatment 2: debris-rich ice) (Figure 7a). We observed that the higher respiration rates were attained in the incubations with debris-rich ice ($1.82 \mu\text{mol O}_2 \text{ L}^{-1} \text{ hr}^{-1}$) and the lowest ones in the control lake water ($0.5 \mu\text{mol O}_2 \text{ L}^{-1} \text{ hr}^{-1}$). Statistical analysis showed significant differences between treatments (ANOVA $F_{(2,8)} = 75.78$, $p < 0.001$), and the a posteriori test showed that all treatments differed (Tukey test, $p < 0.001$ for all three combinations, Figure 7a, lower case letters indicated significant differences).

In our second experiment, we tested the effect of the addition of glucose and phosphorus to lake water. The treatments with P (+P) or the +G+P) resulted in significant increase in bacterial respiration (Figure 7b, lower case letters indicated significant differences in the “a posteriori” Tukey test) (two-way ANOVA, + P treatment, $F_{(1,8)} = 13.23$, $p = 0.007$), while +G alone produced no significant increases (Figure 7b).

3.3 | Bacterial community

In Lake Ventisquero Negro, analyses of the four samples of bacterial communities using the 16S rRNA gene identified a total of 2,135 OTUs consisting mainly of Proteobacteria, Bacteroidetes, Actinobacteria and Cyanobacteria (Supporting Information Figure S2). Two phylotypes were identified each representing more than 20% of the community: *Polaromonas* and *Limnohabitans* (Comamonadaceae, Betaproteobacteria) and unclassified Cytophagaceae (Supporting Information Figure S3). *Polaromonas* and unclassified Cytophagaceae were dominant on three sampling occasions, while *Limnohabitans* dominated in January 2014. Cyanobacterial cells were represented in all samples by Nostocaceae (*Nostoc*) and Gomphosphaeriaceae.

4 | DISCUSSION

These first data for the early ontogeny of Lake Ventisquero Negro in the North Patagonian Andes were obtained after the glacial lake outburst flood (GLOF) that occurred in autumn 2009. In this case, the event produced a sudden discharge in which the lake reduced its volume and afterwards refilled (Worni et al., 2012). Thus, newly

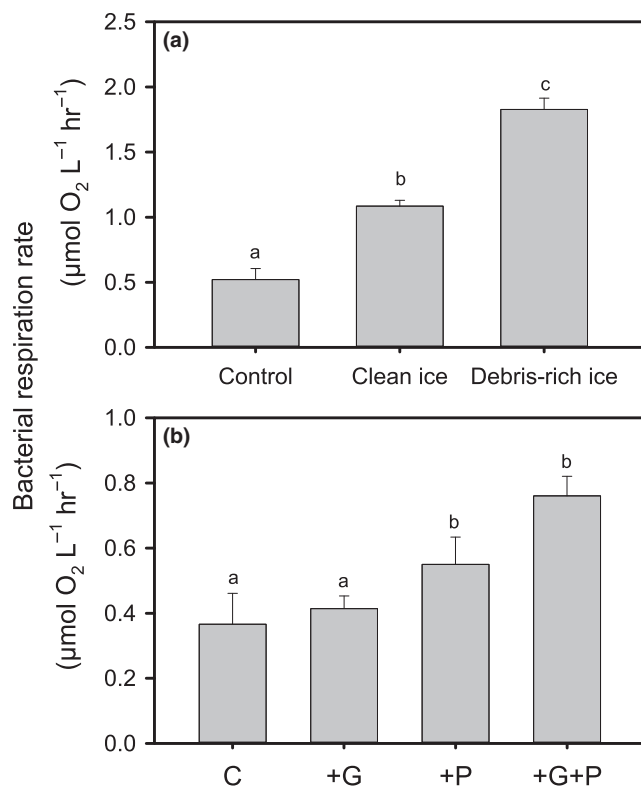


FIGURE 7 (a) Bacteria respiration in the experiment with clean and debris-rich ice. Control (lake unamended), clean ice and debris-rich ice. (b) Bacteria respiration in the experiment with glucose and phosphate addition. C: Control: lake unamended, +G glucose addition, +P phosphate addition, +G +P: glucose and phosphate addition. Reference: Lowercase letters indicated homogeneous group in the “a posteriori” Tukey test. Values are expressed as mean \pm standard error

created proglacial lakes, such as Lake Ventisquero Negro, are unstable and can be emptied and refilled (Mertes et al., 2017). The break of the frontal moraine occurs in part because of the presence of ice inside the moraine (Worni et al., 2012) that thaws with increases in temperature. In the last 20 years, the equilibrium altitude (ELA) in Mount Tronador increased more than 200 m. The ELA represents a limit where accumulation and ablation are equal and is very closely related to the local climate, particularly winter precipitation and summer air temperature (Benn & Lehmkuhl, 2000). This increase in the altitude of the equilibrium line, not only explains the rapid glacier recession that has occurred in recent decades in the area (Masiokas et al., 2008), but also weakens ice-bearing dams and indicates that such a recession will continue, since this line is located between 200 and 400 m above the current ice limit in Tronador Mountain (Figure 1). Accordingly, during the study period (2012–2016), the Landsat images indicate that the whole Ventisquero Negro glacier is becoming smaller while the lake is increasing in size.

Patagonia is a cool-temperate region and precipitation is mainly concentrated in winter (Paruelo, Beltran, Jobbágy, Sala, & Golluscio, 1998). The studied period included summer data when mean weekly air temperature was higher than 5°C and precipitation was

lower than 25 mm per week. Thus, our study corresponds to dry and warm periods in which ice melt increases and causes high turbidity levels as observed in other proglacial lakes (Sommaruga, 2015). Melting increases sediment input, including glacial clay, that causes the increase in phosphorus (TP) in the new lake particularly in mid-summer. In the same period, we also observed in the DOM of lake water the presence of two fluorescence peaks C1 and C2. According to Coble (1996), C1 is associated with a labile protein-like component. In glacier surface meltwater, microbial communities are the primary driver for labile dissolved organic carbon production (Anesio et al., 2017; Musilova et al., 2017). In the clean ice, this microbial activity may have generated the presence of labile protein-like component (C1). Although we did not quantify the concentration of the C1 component, this is the only one observed in the EEM analysis in the clean ice; thus, most of the DOC corresponds to this component. The second peak (C2) corresponds to a humic-like component (Coble, 1996). The Ventisquero Negro glacier is covered by a thick sediment layer of debris coming from the terrestrial environment, including inorganic sediments but also organic ones from the surrounding *Nothofagus* forest. It is likely that these sediments are the main source of this second component that is present also in the lake in mid-summer (January and February), the months of higher temperatures and hence, more rapid melting. During that period, bacterial communities have more diverse carbon resources.

Glacial environments can have phosphorus deficiency, and thus, microbial growth and activity have the potential to be P limited (Mindl et al., 2007; Säwström, Laybourn-Parry, Granéli, & Anesio, 2007; Stibal, Tranter, Telling, & Benning, 2008). Our experiments with the addition of glucose and phosphate showed that the bacterial respiration is P limited. In addition, some aspects of P-cycling on glacier environments have been largely overlooked, including P adsorption and readsorption onto mineral surfaces and the role of dissolved phosphorus (Mueller, Vincent, & Jeffries, 2006; Stibal et al., 2008). In the Ventisquero Negro lake, we observed that total phosphorus concentration was high and related to suspended solids while dissolved phosphorus concentration was comparatively low. However, the concentration of dissolved phosphorus was higher in debris-rich ice suggesting that sediments coming from the terrestrial environment might also be a source of dissolved phosphorus. The tree line imposes a boundary for DOM and P input in high altitude lakes, where lakes below this limit receive a more complex DOM and higher P for bacterial metabolism (Bastidas Navarro, Balseiro, & Modenutti, 2014). The location of Ventisquero Negro Lake below the tree line (*Nothofagus* forest) would also increase nutrient input from terrestrial sources (i.e., phosphorus). Such an input would be of particular relevance for bacterial respiration which would increase with increasing P concentration, as observed in our experiments.

In Ventisquero Negro lake, we were able to analyse just 4 samples for bacterial community composition. However, the four samples showed a very similar bacterial composition with predominance of Betaproteobacteria (Comamonadaceae) with two

phylotypes: *Polaromonas* and *Limnohabitans*. *Polaromonas* is considered to be a psychrophile and has been reported in glacial ice and glacial sediments worldwide, including polar and high elevation environments and debris-covered glaciers (Darcy, Lynch, King, Robeson, & Schmidt, 2011; Franzetti et al., 2013). *Polaromonas* has been found to be one of the dominant groups together with *Flavobacterium* (also present in Lake Ventisquero Negro) in shallow freshwater lakes in northern Victoria Land, East Antarctica (Michaud, Sabacka, & Priscu, 2012). In contrast, *Limnohabitans* is a planktonic bacteria very common in the water column of freshwater lakes (Simek, Kasalicky, Zapomelova, & Hornak, 2011) and can be abundant in many habitats (Kasalicky, Jezbera, Hahn, & Simek, 2013; Newton, Jones, Eiler, McMahon, & Bertilsson, 2011). The photosynthetic organisms observed in our samples were cyanobacteria with Nostocaceae (*Nostoc*) and Gomphosphaeriaceae present in the four samples. Cyanobacteria have a wide range of adaptive mechanisms that allow them to survive frozen conditions and grow under low irradiances with periodic exposure to UV radiation and bright PAR (Quesada & Vincent, 2012; Vincent, 2007). Due to the turbidity imposed by sediments, Ventisquero Negro Lake has very low transparency and a narrow euphotic zone. Under these conditions, we observed that chlorophyll concentration was always low (on average $0.49 \pm 0.05 \mu\text{g/L}$) suggesting that autotrophs are light-limited, as was indicated previously for turbid glacial lakes (Sommaruga, 2015).

Large North Patagonian Andean lakes are transparent, oligotrophic and characterised by very low DOC concentrations (Corno et al., 2009; Morris et al., 1995). Interestingly, DOC concentration in Lake Ventisquero Negro remained always within a range of very low values (less than $0.6 \text{ mg/L} = 50 \mu\text{mol/L}$), very similar to the large lakes in the area (Corno et al., 2009; Morris et al., 1995). Values observed in the lake are half those observed in the proglacial lakes of Svalbard glacier (Mindl et al., 2007) and in the same range or slightly lower than those observed in Leverett Glacier (Antarctica) (Musilova et al., 2017). In spite of the differences in C concentrations, bacterial metabolism is strongly dependent on phosphorus availability rather than total carbon availability (Smith & Prairie, 2004; Vidal, Granéli, Daniel, Heiberg, & Roland, 2011). The present study supports the hypothesis that melting of clean and debris-rich ice would affect DOM and P input at early stages of a proglacial lake formed by the recession of a debris-covered glacier. Bacterial respiration was observed to be positively affected by debris-rich ice melting and to be P limited. Thus, P is a major controlling factor for carbon dynamics in a newly formed proglacial lake.

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REFERENCES

- Anesio, A. M., Lutz, S., Christmas, N. A. M., & Benning, L. G. (2017). The microbiome of glaciers and ice sheets. *NPJ Biofilms Microbiomes*, 3, 10. <https://doi.org/10.1038/s41522-017-0019-0>
- Anesio, A. M., Sattler, B., Foreman, C., Telling, J., Hodson, A., Tranter, M., & Psenner, R. (2010). Carbon fluxes through bacterial communities on glacier surfaces. *Annals of Glaciology*, 51, 32–40. <https://doi.org/10.3189/172756411795932092>
- APHA (2005). *Standard methods for the examination of water and wastewater*. Washington, DC: American Public Health Association, AWWA.
- Bastidas Navarro, M., Balseiro, E., & Modenutti, B. (2014). Bacterial community structure in Patagonian Andean Lakes above and below timberline: From community composition to community function. *Microbial Ecology*, 68, 528–541. <https://doi.org/10.1007/s00248-014-0439-9>
- Benn, D. I., & Evans, D. J. A. (1996). The interpretation and classification of subglacially-deformed materials. *Quaternary Science Reviews*, 15, 23–52. [https://doi.org/10.1016/0277-3791\(95\)00082-8](https://doi.org/10.1016/0277-3791(95)00082-8)
- Benn, D. I., & Hulton, N. R. J. (2010). An Excel™ spreadsheet program for reconstructing the surface profile of former mountain glaciers and ice caps. *Computers & Geosciences*, 36, 605–610. <https://doi.org/10.1016/j.cageo.2009.09.016>
- Benn, D. I., & Lehmkuhl, F. (2000). Mass balance and equilibrium-line altitudes of glaciers in high-mountain environments. *Quaternary International*, 65–66, 15–29. [https://doi.org/10.1016/S1040-6182\(99\)00034-8](https://doi.org/10.1016/S1040-6182(99)00034-8)
- Bertoni, R., Callieri, C., Balseiro, E. G., & Modenutti, B. E. (2008). Susceptibility of bacterioplankton to nutrient enrichment of oligotrophic and ultraoligotrophic lake waters. *Journal of Limnology*, 67, 120–127. <https://doi.org/10.4081/jlimnol.2008.120>
- Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., ... Knight, R. (2010). QIIME allows analysis of high-throughput community sequencing data. *Nature Methods*, 7, 335. <https://doi.org/10.1038/nmeth.f.303>
- Chillrud, S. N., Pedrozo, F. L., Temporetti, P. F., Planas, F. H., & Froelich, P. N. (1994). Chemical weathering of phosphate and germanium in glacial meltwater streams: Effects of subglacial pyrite oxidation. *Limnology and Oceanography*, 39, 1130–1140. <https://doi.org/10.4319/lo.1994.39.5.1130>
- Coble, P. G. (1996). Characterization of marine and terrestrial DOM in seawater using excitation-emission matrix spectroscopy. *Marine Chemistry*, 51, 325–346. [https://doi.org/10.1016/0304-4203\(95\)00062-3](https://doi.org/10.1016/0304-4203(95)00062-3)
- Corno, G., Modenutti, B. E., Callieri, C., Balseiro, E. G., Bertoni, R., & Caravati, E. (2009). Bacterial diversity and morphology in deep ultraoligotrophic Andean lakes: The role of UVR on vertical distribution. *Limnology and Oceanography*, 54, 1098–1112. <https://doi.org/10.4319/lo.2009.54.4.1098>
- Darcy, J. L., Lynch, R. C., King, A. J., Robeson, M. S., & Schmidt, S. K. (2011). Global distribution of *Polaromonas* phylotypes—evidence for a highly successful dispersal capacity. *PLoS ONE*, 6, e23742. <https://doi.org/10.1371/journal.pone.0023742>
- Darcy, J. L., & Schmidt, S. K. (2016). Nutrient limitation of microbial phototrophs on a debris-covered glacier. *Soil Biology and Biochemistry*, 95, 156–163. <https://doi.org/10.1016/j.soilbio.2015.12.019>
- Franzetti, A., Tatangelo, V., Gandolfi, I., Bertolini, V., Bestetti, G., Diolaiuti, G., ... Ambrosini, R. (2013). Bacterial community structure on two alpine debris-covered glaciers and biogeography of *Polaromonas* phylotypes. *ISME Journal*, 7, 1483–1492. <https://doi.org/10.1038/ismej.2013.48>

- Guilizzoni, P., Massaferro, J., Lami, A., Piovano, E. L., Guevara, S. R., Formica, S. M., ... Gerli, S. (2009). Palaeolimnology of Lake Hess (Patagonia, Argentina): Multi-proxy analyses of short sediment cores. *Hydrobiologia*, 631, 289–302. <https://doi.org/10.1007/s10750-009-9818-5>
- Guillemette, F., & del Giorgio, P. A. (2011). Reconstructing the various facets of dissolved organic carbon bioavailability in freshwater ecosystems. *Limnology and Oceanography*, 56, 734–748. <https://doi.org/10.4319/lo.2011.56.2.0734>
- Hock, R. (2003). Temperature index melt modelling in mountain areas. *Journal of Hydrology*, 282, 104–115. [https://doi.org/10.1016/S0022-1694\(03\)00257-9](https://doi.org/10.1016/S0022-1694(03)00257-9)
- Hodson, A. J., Anesio, A. M., Tranter, M., Fountain, A., Osborn, M., Priscu, J., ... Sattler, B. (2008). Glacial ecosystems. *Ecological Monographs*, 78, 41–67. <https://doi.org/10.1890/07-0187.1>
- Hood, E., & Berner, L. (2009). Effects of changing glacial coverage on the physical and biogeochemical properties of coastal streams in south-eastern Alaska. *Journal of Geophysical Research*, 114, G03001.
- Hood, G. A., & Larson, D. G. (2015). Ecological engineering and aquatic connectivity: A new perspective from beaver-modified wetlands. *Freshwater Biology*, 60, 198–208. <https://doi.org/10.1111/fwb.12487>
- IPCC (2014). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. R.K.P.a.L.a.M.E. Core Writing Team, p. 151 pp. IPCC.
- Kasalicky, V., Jezbera, J., Hahn, M. W., & Simek, K. (2013). The diversity of the *Limnohabitans* genus, an important group of freshwater bacterioplankton, by characterization of 35 isolated strains. *PLoS ONE*, 8, e58209. <https://doi.org/10.1371/journal.pone.0058209>
- Linsbauer, A., Paul, F., & Haeberli, W. (2012). Modeling glacier thickness distribution and bed topography over entire mountain ranges with GlabTop: Application of a fast and robust approach. *Journal of Geophysical Research: Earth Surface*, 117, F03007.
- Margesin, R., & Miteva, V. (2011). Diversity and ecology of psychrophilic microorganisms. *Research in Microbiology*, 162, 346–361. <https://doi.org/10.1016/j.resmic.2010.12.004>
- Martyniuk, N., Modenutti, B., & Balseiro, E. G. (2014). Can increased glacial melting resulting from global change provide attached algae with transient protection against high irradiance? *Freshwater Biology*, 59, 2290–2302. <https://doi.org/10.1111/fwb.12431>
- Masiokas, M. H., Villalba, R., Luckman, B. H., Lascano, M. E., Delgado, S., & Stepanek, P. (2008). 20th-century glacier recession and regional hydroclimatic changes in northwestern Patagonia. *Global and Planetary Change*, 60, 85–100. <https://doi.org/10.1016/j.gloplacha.2006.07.031>
- Mertes, J. R., Thompson, S. S., Booth, A. D., Gulley, J. D., & Benn, D. I. (2017). A conceptual model of supra-glacial lake formation on debris-covered glaciers based on GPR facies analysis. *Earth Surface Processes and Landforms*, 42, 903–914. <https://doi.org/10.1002/esp.4068>
- Michaud, A. B., Sabacka, M., & Priscu, J. C. (2012). Cyanobacterial diversity across landscape units in a polar desert: Taylor Valley, Antarctica. *FEMS Microbiology Ecology*, 82, 268–278. <https://doi.org/10.1111/j.1574-6941.2012.01297.x>
- Mindl, B., Anesio, A. M., Meirer, K., Hodson, A. J., Laybourn-Parry, J., Sommaruga, R., & Sattler, B. (2007). Factors influencing bacterial dynamics along a transect from supraglacial runoff to proglacial lakes of a high Arctic glacier [corrected]. *FEMS Microbiology Ecology*, 59, 307–317. <https://doi.org/10.1111/j.1574-6941.2006.00262.x>
- Montross, S., Skidmore, M., Christner, B., Samyn, D., Tison, J.-L., Lorrain, R., ... Fitzsimons, S. (2013). Debris-rich basal ice as a microbial habitat, Taylor Glacier, Antarctica. *Geomicrobiology Journal*, 31, 76–81.
- Morris, D. P., Zagarese, H., Williamson, C. E., Balseiro, E. G., Hargreaves, B. R., Modenutti, B. E., ... Queimaliños, C. (1995). The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography*, 40, 1381–1391. <https://doi.org/10.4319/lo.1995.40.8.1381>
- Mueller, D. R., Vincent, W. F., & Jeffries, M. O. (2006). Environmental gradients, fragmented habitats, and microbiota of a northern ice shelf cryoecosystem, Ellesmere Island, Canada. *Arctic, Antarctic, and Alpine Research*, 38, 593–607. [https://doi.org/10.1657/1523-0430\(2006\)38\[593:EGFHAM\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2006)38[593:EGFHAM]2.0.CO;2)
- Musilova, M., Tranter, M., Wadham, J., Telling, J., Tedstone, A., & Anesio Alexandre, M. (2017). Microbially driven export of labile organic carbon from the Greenland ice sheet. *Nature Geoscience*, 10, 360–365. <https://doi.org/10.1038/ngeo2920>
- Newton, R. J., Jones, S. E., Eiler, A., McMahon, K. D., & Bertilsson, S. (2011). A guide to the natural history of freshwater lake bacteria. *Microbiology and Molecular Biology Reviews*, 75, 14–49. <https://doi.org/10.1128/MMBR.00028-10>
- Nusch, E. A. (1980). Comparison of different methods for chlorophyll and phaeopigment determination. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie*, 14, 14–36.
- Paruelo, J. M., Beltran, A., Jobbágy, E., Sala, O., & Golluscio, R. (1998). The climate of Patagonia: General patterns and controls on biotic processes. *Ecologia Austral*, 8, 85–101.
- Paul, F., & Mölg, N. (2014). Hasty retreat of glaciers in northern Patagonia from 1985 to 2011. *Journal of Glaciology*, 60, 1033–1043. <https://doi.org/10.3189/2014JoG14J104>
- Peter, H., & Sommaruga, R. (2016). Shifts in diversity and function of lake bacterial communities upon glacier retreat. *ISME Journal*, 10, 1545–1554. <https://doi.org/10.1038/ismej.2015.245>
- Porter, K. G., & Feig, Y. S. (1980). The use of DAPI for identifying and counting aquatic microflora. *Limnology and Oceanography*, 25, 943–948. <https://doi.org/10.4319/lo.1980.25.5.0943>
- Quesada, A., & Vincent, W. F. (2012). Cyanobacteria in the cryosphere: Snow, ice and extreme cold. In B. A. Whitton (Ed.), *Ecology of cyanobacteria II* (pp. 387–399). Springer: Dordrecht. <https://doi.org/10.1007/978-94-007-3855-3>
- Reynolds, J. M. (2000). On the formation of supraglacial lakes on debris-covered glaciers. *IAHS Publication*, 264, 153–161.
- Ruiz, L., Berthier, E., Masiokas, H. M., Pitte, P., & Villalba, R. (2015). First surface velocity maps for glaciers of Monte Tronador, North Patagonian Andes, derived from sequential Pléiades satellite images. *Journal of Glaciology*, 61, 908–922. <https://doi.org/10.3189/2015JoG14J134>
- Ruiz, L., Berthier, E., Viale, M., Pitte, P., & Masiokas, M. H. (2017). Recent geodetic mass balance of Monte Tronador glaciers, northern Patagonian Andes. *The Cryosphere*, 11, 619–634. <https://doi.org/10.5194/tc-11-619-2017>
- Sävström, C., Laybourn-Parry, J., Granéli, W., & Anesio, A. M. (2007). Heterotrophic bacterial and viral dynamics in Arctic freshwaters: Results from a field study and nutrient-temperature manipulation experiments. *Polar Biology*, 30, 1407–1415. <https://doi.org/10.1007/s00300-007-0301-3>
- Simek, K., Kasalicky, V., Zapomelova, E., & Hornak, K. (2011). Alga-derived substrates select for distinct Betaproteobacterial lineages and contribute to niche separation in *Limnohabitans* strains. *Applied and Environmental Microbiology*, 77, 7307–7315. <https://doi.org/10.1128/AEM.05107-11>
- Smith, E. M., & Prairie, Y. T. (2004). Bacterial metabolism and growth efficiency in lakes: The importance of phosphorus availability. *Limnology and Oceanography*, 49, 137–147. <https://doi.org/10.4319/lo.2004.49.1.0137>
- Sommaruga, R. (2015). When glaciers and ice sheets melt: Consequences for planktonic organisms. *Journal of Plankton Research*, 37, 509–518. <https://doi.org/10.1093/plankt/fbv027>
- Sommaruga, R., & Kandolf, G. (2014). Negative consequences of glacial turbidity for the survival of freshwater planktonic heterotrophic flagellates. *Scientific Reports*, 4, 4113.

- Stedmon, C. A., & Bro, R. (2008). Characterizing dissolved organic matter fluorescence with parallel factor analysis: A tutorial. *Limnology and Oceanography: Methods*, 6, 572–579.
- Stibal, M., Šabacká, M., & Žárský, J. (2012). Biological processes on glacier and ice sheet surfaces. *Nature Geoscience*, 5, 771–774. <https://doi.org/10.1038/ngeo1611>
- Stibal, M., Tranter, M., Telling, J., & Benning, L. G. (2008). Speciation, phase association and potential bioavailability of phosphorus on a Svalbard glacier. *Biogeochemistry*, 90, 1–13. <https://doi.org/10.1007/s10533-008-9226-3>
- Vidal, L. O., Granéli, W., Daniel, C. B., Heiberg, L., & Roland, F. (2011). Carbon and phosphorus regulating bacterial metabolism in oligotrophic boreal lakes. *Journal of Plankton Research*, 33, 1747–1756. <https://doi.org/10.1093/plankt/fbr059>
- Villalba, R., Boninsegna, J. A., Veblen, T. T., Schmelter, A., & Rubulis, S. (1997). Recent trends in tree-ring records from high elevation sites in the Andes of northern Patagonia. *Climatic Change*, 36, 425–454. <https://doi.org/10.1023/A:1005366317996>
- Vincent, W. F. (2007). Cold tolerance in cyanobacteria and life in the cryosphere. In J. Seckbach (Ed.), *Algae and cyanobacteria in extreme environments* (pp. 289–304). Heidelberg, Germany: Springer.
- Wolff, E. W. (2013). Ice sheets and nitrogen. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 368, 20130127. <https://doi.org/10.1098/rstb.2013.0127>
- Worni, R., Huggel, C., Clague, J. J., Schaub, Y., & Stoffel, M. (2014). Coupling glacial lake impact, dam breach, and flood processes: A modeling perspective. *Geomorphology*, 224, 161–176. <https://doi.org/10.1016/j.geomorph.2014.06.031>
- Worni, R., Stoffel, M., Huggel, C., Volz, C., Casteller, A., & Luckman, B. (2012). Analysis and dynamic modeling of a moraine failure and glacier lake outburst flood at Ventisquero Negro, Patagonian Andes (Argentina). *Journal of Hydrology*, 444–445, 134–145. <https://doi.org/10.1016/j.jhydrol.2012.04.013>

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