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Geothermal Diatoms: Seasonal Variability in the El Tatio Geothermal Field (Altiplano, Chile)

Alejandro Angel[1*], Irma Vila[1], Carolina Díaz[1], Ximena Molina[1], Paola Sepúlveda[2]

[1]Faculty of Science, Universidad de Chile, Santiago, Chile
[2]Laboratorio Ambiental Centro de Ecología Aplicada, Santiago, Chile
Email: *alejandro.angel@ug.uchile.cl, limnolog@uchile.cl, cardiaz@uchile.cl, mxmolinap@gmail.cl, paula.munoz@uchile.cl

Abstract

Diatom floras were examined in a high-altitude geothermal field, 4200 - 4500 m (29˚19'S 68˚W'), located in the Central Andean dry Puna ecoregion or southern Altiplano. These locations include hostile environments subjecting living organisms to extreme conditions. The aim of the present study was to investigate the spatial patterns and describe the response of diatom assemblages to differences in physical and chemical variables. Different shallow (<10 cm) aquatic systems with variable chemical and physical conditions (fumaroles, freshwater-saline rivers and swamps) were studied seasonally during 2011-2012. The conductivity exhibited high variability (360 to 18340 µS cm^{-1}) among the systems studied, temperature was lower in rivers and swamps (6.8˚C - 10˚C) and high in fumaroles stations (30˚C - 37.5˚C), and pH was lower in fumaroles than freshwater systems (3.25 to 8.97). Statistical analyses suggest that the diatoms cluster into three major groups. The most common taxa include: *Achnanthidium exiguum* (Grunow) Czarnecki, *Cocconeis placentula* var. *lineata* (Ehrenberg) Van Heurck, *Eolimna minima* (Grunow) Lange-Bertalot, *Staurosirella pinnata* (Ehrenberg) Williams and Round, *Navicula gregaria* Donkin, *Nitzschia inconspicua* Grunow, *Nitzschia palea* (Kützing) Smith, *Nitzschia perminuta* (Grunow) Peragallo, and *Planothidium lanceolatum* (Brébisson ex Kützing) Lange-Bertalot. As expected, the 20 to 200 µm-size fraction contained the highest numbers of diatom taxa (53 species), although an unexpectedly high number (47 species) were also found in the smaller 5 to 20 µm-size fraction, more associated to fumaroles and saline systems. The 180 to 2000 µm size fraction contained only two species, including rosette-forming diatom *Ulnaria ulna* (Nitzsch) Compère, and the unicellular species *Surirella chilensis* Janisch, both species exclusively reported in freshwater systems. Canonical correspondence analysis (CCA) and Monte Carlo permutation tests showed clear correlations between species, conductivity, TP (total phosphorous), NO_3^-, HCO_3^-, Mg^{2+}, temperature and dissolved

oxygen (DO). The gradient of ionic composition values explaining most variation in diatom assemblages ranged from waters dominated by Ca^{2+} and SO_4^{2-} to waters with higher proportions of Na^+, K^+, F^-, Li^+, Mg^{2+} and Cl^-. Other factors include substrate type, presence of macrophytes, current velocity and other local environmental conditions. The results presented here enhance our understanding of diatom richness/composition in hostile environments from a high-altitude arid and semi-arid geothermal region.

1. Introduction

El Tatio geothermal field, one of the least known major geothermal systems in the southern hemisphere, comprise an area that contains a high heterogeneity of aquatic micro-habitats with unique physiographic conditions, high altitude 4200 - 4600 m, low latitude 22'8˚S, high surface solar radiation (280 W/m²), lower water boiling point (86˚C), and the influence of high contents of potentially toxic elements in the water [1]. These features make these systems particularly interesting in order to interpret the factors that could influence the diatom richness/composition, and the origin of diagenetic evolution of hot-spring silica deposits [2]. El Tatio is the largest known geyser field in the southern hemisphere, and the third larger field in the world after Yellowstone, USA, and Dolina Geizerov, Russia. The geothermal systems are concentrated in three main zones encompassing an area of ~10 km². Other thermal manifestations, such as small hot springs, fumaroles, and steaming soils, extend over an area of some 30 km² at elevations from 4200 to 4600 meters [2].

The surface water discharges at a maximum temperature of 86˚C, which is the boiling point for an altitude of 4200 m [3]. Deep dilution of a predominant, primary high chloride (5500 mg/l) supply water derived from precipitation some 15 km east of El Tatio and local groundwater produces a secondary chloride water type (4750 mg/l), feeding springs over a limited area [4]. Absorption of this separated steam and carbon dioxide into local ground water and mixing with chloride waters at shallow levels produce a series of intermediate temperature (40˚C - 70˚C), low chloride, and high bicarbonate waters [2]. These conditions in chemistry water types from different geothermal microhabitats represent an interest model to be evaluated in relation to diatom richness/composition, dispersal limitation and metapopulation theories.

Several investigations of diatom floras have been carried out at individual hot springs type, or for multiple springs within a single geological setting [5] [6]. Studies of warm-spring diatoms have also been published for New Zealand [7]

and the East African rifts [8] [9] [10]. Other diatom floras were described in hot-spring systems of Iceland, New Zealand, and Kenya [6]. Some of the common taxa described in these systems were *Achnanthidium exiguum* var. *heterovalvum* (Krasske) Czarnecki, *Anomoeoneis sphaerophora* Pfitzer, *Brachysira brebissonii* f. *thermalis* (Grunow) R. Ross, *Diadesmis confervacea* Kützing, *Epithemia argus* (Ehrenberg) Kützing, *Nitzschia amphibia* Grunow, *Nitzschia inconspicua*, *Staurosira construens* var. *venter* (Ehrenberg) P. B. Hamilton and *Staurosirella pinnata*. The historical diatom register from the Yellowstone National Park, described an extensive diatom beds of recent origin covering many square miles in the vicinity of the geyser and hot spring basins [5]. However, to compare and estimate distribution patterns, there are few available studies of diatom floras from geothermal systems in South America [11] [12], and there is no information of diatom richness/composition from the El Tatio geothermal field, considering that contain a high heterogeneity of microhabitat with unique environmental conditions.

Affinities of some freshwater diatoms with certain ions can be found in widely known richness composition [13]. For instance, a number of taxa have been characterized as preferring calcium rich or calcium poor waters [14]. It is difficult, however, to compile this information for water quality monitoring purposes in the Altiplano because the local floras studies have been scattered. It is highly probable that optima and tolerance values estimated for conductivity and major ions for common taxa among Europe, Africa and the Dry Puna ecoregion (Altiplano) would be very different, especially for aspects such as salinity, geothermal activity and mineral water dissolution.

In this study the main objectives were to: 1) describe the diatom assemblages associated with each system and to examine their spatial variability; 2) examine the degree of floral similarity/dissimilarity and size classes distribution among the systems studied; 3) use the resulting data to relate species to environmental variables; and 4) use the models to characterize the optima and tolerance values for the most common diatom taxa. Given that environmental heterogeneity can demonstrate varying and significant impacts on diatom floras, this research project emphasizes to study not only species richness/composition, but how local communities vary across seasonal changes, including chemical and physical conditions.

2. Materials and Methods

2.1. Study Area

El Tatio is a geothermal field located in northern Chile (29°19'S 68°W', 4200 - 4500 m) at the Central Andean dry Puna ecoregion (**Figure 1**), a montane grassland with three main types of thermal springs [1]: springs discharging high chloride waters (8000 mg/l) located along a SW-NE trending line in the northern part of the main thermal area, more dilute, intermediate chloride pools (5000 mg/l) in the south-western part, and low chloride, high sulfate pools along the
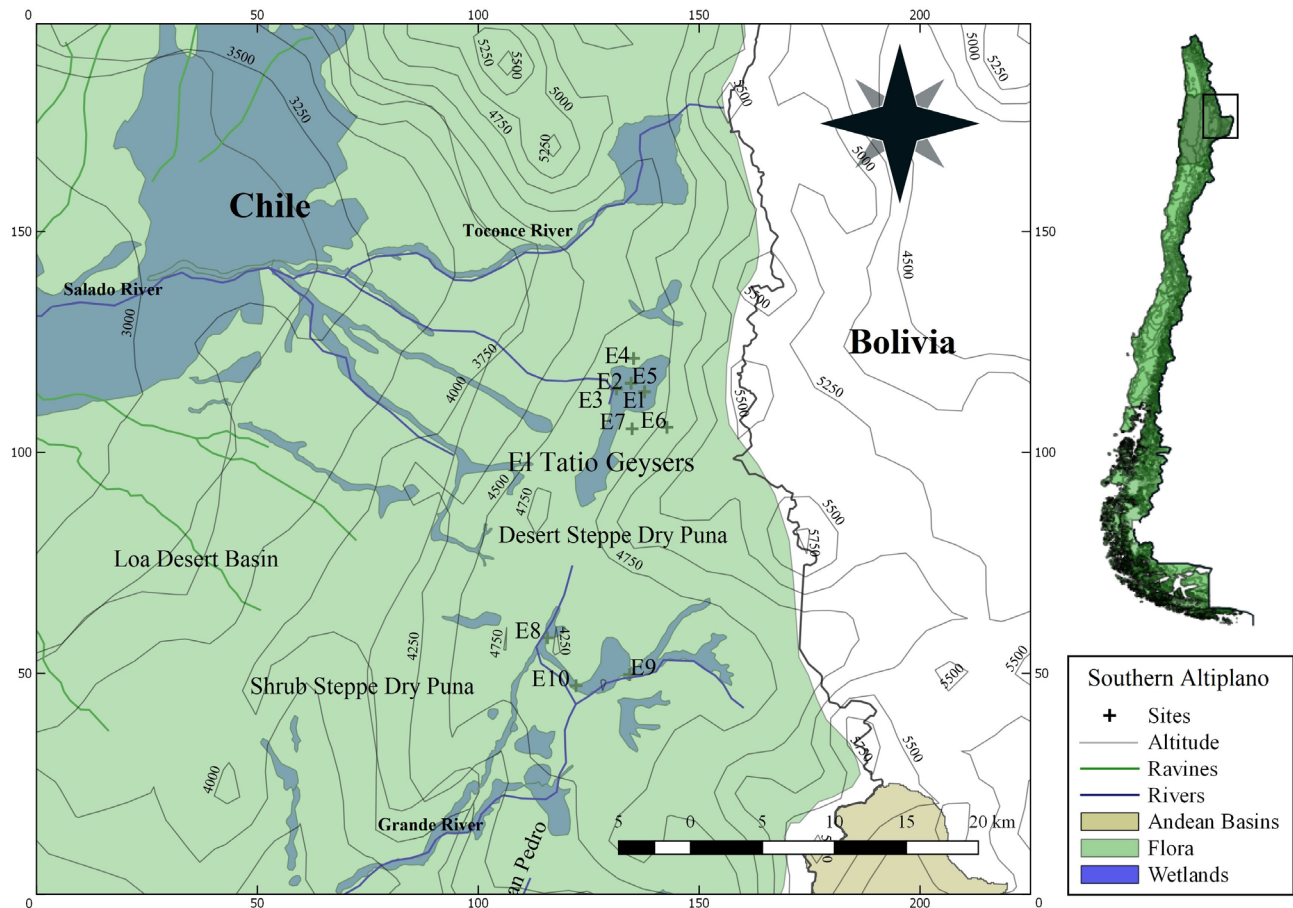
Figure 1. Location of the study sites in El Tatio Geothermal field (Altiplano, Chile).

eastern margins [1] [3] [4]. The Dry Puna ecoregion is oligothermic (mean annual temperature range: 8˚C to 11˚C). Daily temperature variation reaches 35˚C in summer and fall to 30˚C in winter, lower night temperature fall to 5˚C in summer and −10˚C in winter [1] [2] [3]. Only flora and fauna highly adapted to the extreme daily temperature variability and high-altitude live in this ecoregion.

The negative water balance is characterized by low precipitation (100 mm/year), very seasonal rainfall between December to March and an eight month-long dry season [3]. In this context, a variety of five aquatic systems associated to the hot springs, saline fumaroles, freshwater fumaroles, saline rivers, freshwater rivers and swamps, were sampled within two sub-basin areas (**Table 1**). The study sites included the Loa River basin (north area) and Salado River sub-basin (south area). The stations studied are located in two areas approximately 30 kilometers apart and were selected based on proximity and important environmental dissimilarities (**Figure 2**).

2.2. Water Chemistry and Environmental Variables

Water temperature, pH, and conductivity were measured with portable instruments, calibrated in the field. For our study we collected 40 samples during four seasons from April, 2011 to January, 2012. The samples were collected at 10

Table 1. Stations coordinates and altitude.

Sample	Location	Coordinates UTM-WGS (N-E)		Altitude (m)
E1	Fumarole-warm spring (saline system)	7529058	600390	4248
E2	Fumarole-warm spring (saline system)	7529058	600386	4248
E3	Fumarole-war spring (saline system)	7529023	600385	4250
E4	La Concha River (saline system)	7529475	601391	4245
E5	Fumarole-warm spring (freshwater system)	7526506	603998	4480
E6	Loa River (freshwater system)	7529478	601390	4245
E7	Loa River (freshwater system)	7526314	601583	4350
E8	Juana Swamp-Tocorpuri (swamps)	7511566	596292	4202
E9	Putana Swamp high water level (swamps)	7509247	602100	4270
E10	Putana Swamp low water level (swamps)	7508319	598407	4271

Figure 2. Habitat description. Fumaroles and active geysers ejecting water and steam through a vent (a), laminated structures, saline rivers and fumaroles associated to the geothermal field (b), Tocorpuri swamps and common Juncacae peat bogs (c), Putana swamps and common arid mountains (d).

designated sampling stations along transects selected. The analyses for individual cations Li$^+$, Ca^{2+}, K$^+$, Na$^+$, and Mg^{2+} were performed by ionic chromatography [15]. The analysis for Cl$^-$ was performed by the argentometric method, SO$_4^{2-}$ by the gravimetric method and residual drying [15], and F$^-$ by a specific electrode with Coupled Plasma Induction/Mass spectrophotometry (ICP/MS). The analyses for nutrients, carbonates, and bicarbonate were performed by standardized APHA 2005 methods [16].

2.3. Collection of Algal Communities

At each site, algal communities were obtained in submerged open and unshaded areas by scraping muddy substrates or rocky riffle from epipelic sections within

a 10 m study reach. Algal samples were taken from 6 randomly selected golden-brown patches that were scraped for diatoms or collected by syringe suction into dark bottles and immediately preserved with formalin (10% final concentration). Then, two golden–brown patches from different riffles or muddy substrates were subsequently pooled into a single sample (*i.e.* n = 3) to minimize the anticipated within-reach variation of algal assemblages, because the emphasis in the study was to examine broad (between-site) spatial patterns in benthic algal communities. Where necessary, diatom smear slides were made after carbonates were dissolved with HCl and organics were removed with H_2O_2. Cleaned diatom samples were mounted in Naphrax, before examination with a light microscope 1000×. Identifications were based in morphological characters according to [8] [11] [13] [17] [18] [19]. Three hundred diatoms were counted per smear slide, except where diatoms were rare, in which case all diatoms were counted.

2.4. Statistical Analyses

Multivariate techniques were used to examine the environmental factors associated with diatom and their distributions. Detrended correspondence analysis (DCA) suggested that a unimodal model was suitable and the data were then explored using Canonical correspondence analysis (CCA) using CANOCO 4.5 [20]. All diatoms were included in these analyses. A subset of 39 species (conditional to 0.01% to 0.33% of the total variance) was selected to simplify diagrams. Inference models were developed for pH, Dissolved oxygen, temperature, and major ions, using the data analysis program (C2, version 1.4) and techniques according to [6]. Floral communities and sampling sites were distinguished based on percentage diatom data (forming 5% of the flora in at least one sample), using Agglomerative Hierarchical Cluster Analyses (AHC) and Heat Maps (removing all species with interquartile range lower than 0.25) carried out with XLSTAT Version 2016 (Addinsoft).

3. Results

3.1. Environmental Characteristics

The soil structure in fumaroles stations was irregular and variable with different mineral formations (Figure 2(a)), presence of laminated structures (Figure 2(b)), and salt crust layers without macrophytes. Hydrological conditions were variables among the systems studied, high conductivity and low sulfates concentration were reported in saline rivers, La Concha River station (E4), contrasting with low conductivity and high sulfates levels in the Loa River stations (E6 and E7). To the south area, is common the presence of peatland bogs (e.g. Bofedales) located in the Atacama sub-basin (stations E8, E9 and E10, Figure 2(c) & Figure 2(d)) and aquatic systems with very low current velocity, these condition determined low and middle values in conductivity and high levels in nutrient concentration. The largest step in the samples dendrogram occurs at 0.76 level of dissimilarity and produced five clusters, corresponding with the five type of sys-

tems studied (Figure 3(a)).

The rivers sampled were characterized by two different types saline and freshwater systems, conductivity varied from 10 to 18,340 μS cm^{-1}. Median and interquartile range values for conductivity and concentration of individual ions indicated that the Loa River stations had moderate levels of salt content and were classified as sulfate calcium bicarbonate type (Figure 3(b)). However, La Concha River station showed low seasonal variability and high conductivity (range from 16,680 to 18,340 μS cm^{-1}), this station was classified as sodium chloride type (Figure 3(b)). The conductivity in saline fumaroles varied from 4860 to 12,150 μS cm^{-1}, corresponding to waters highly variable in ionic composition, with the exception of the freshwater fumarole station (E5) where conductivity showed the lowest values (range from 440 to 810 μS cm^{-1}). Conductivity in swamps varied from 540 to 8020 μS cm^{-1}, with moderate levels of electrolytes and high concentrations of Ca^{2+}, HCO_3^- and SO_4^{2-}. The total concentration of Ca^{2+} and Na^+ was, however, maximum in waters with the highest proportion of Cl^- among anions, mostly in saline fumaroles and saline rivers. The highest concentrations of Li^+, K^+, F^- and Cl^- were also observed in these sites (Figure 4). For instance, the total concentration of Mg^{2+} was maximum in waters with the highest proportion of SO_4^{2-} among anions; this condition was observed in the Loa River and Swamps stations (Figure 5). Table 2 details chemical and physical characteristics of the stations studied.

3.2. Diatom Community Composition

A total of 102 species and 41 genera were identified (Table 3), diatom preservation was generally good or excellent with little corrosion and minimal fragmentation, however, teratological forms were common in fumaroles stations. The Shannon-Wiener diversity index for the diatom communities ranged from 1.02
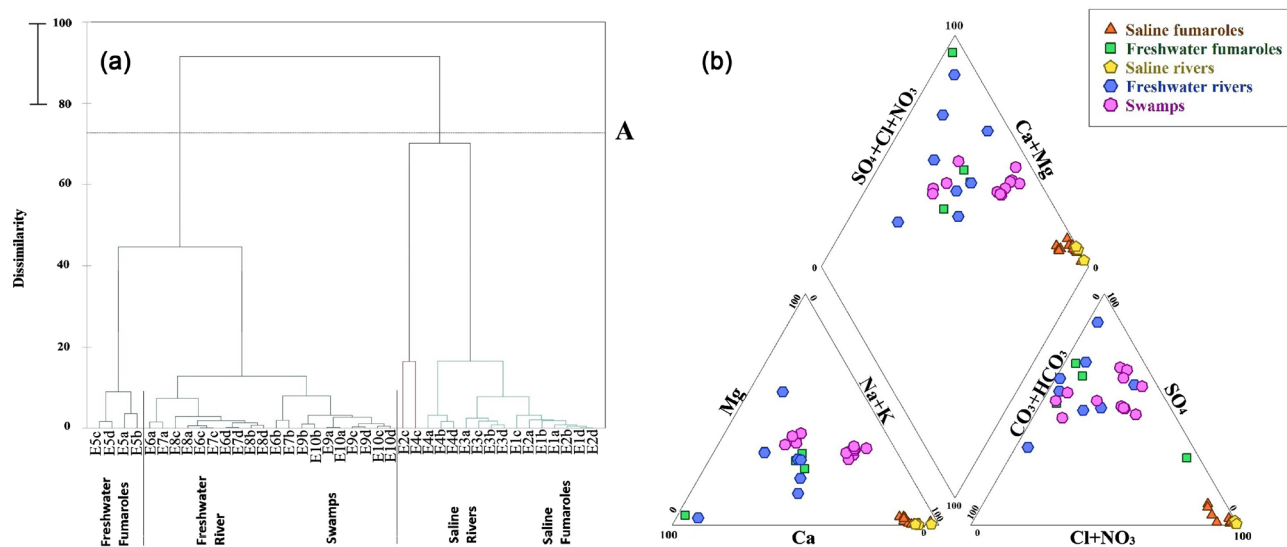

Figure 3. Herarchical analysis (a) using environmental variables (cutoff line "A" occurs at 0.76 dissimilarity and produces five clusters) and ternary diagram (b) showing major ion composition.
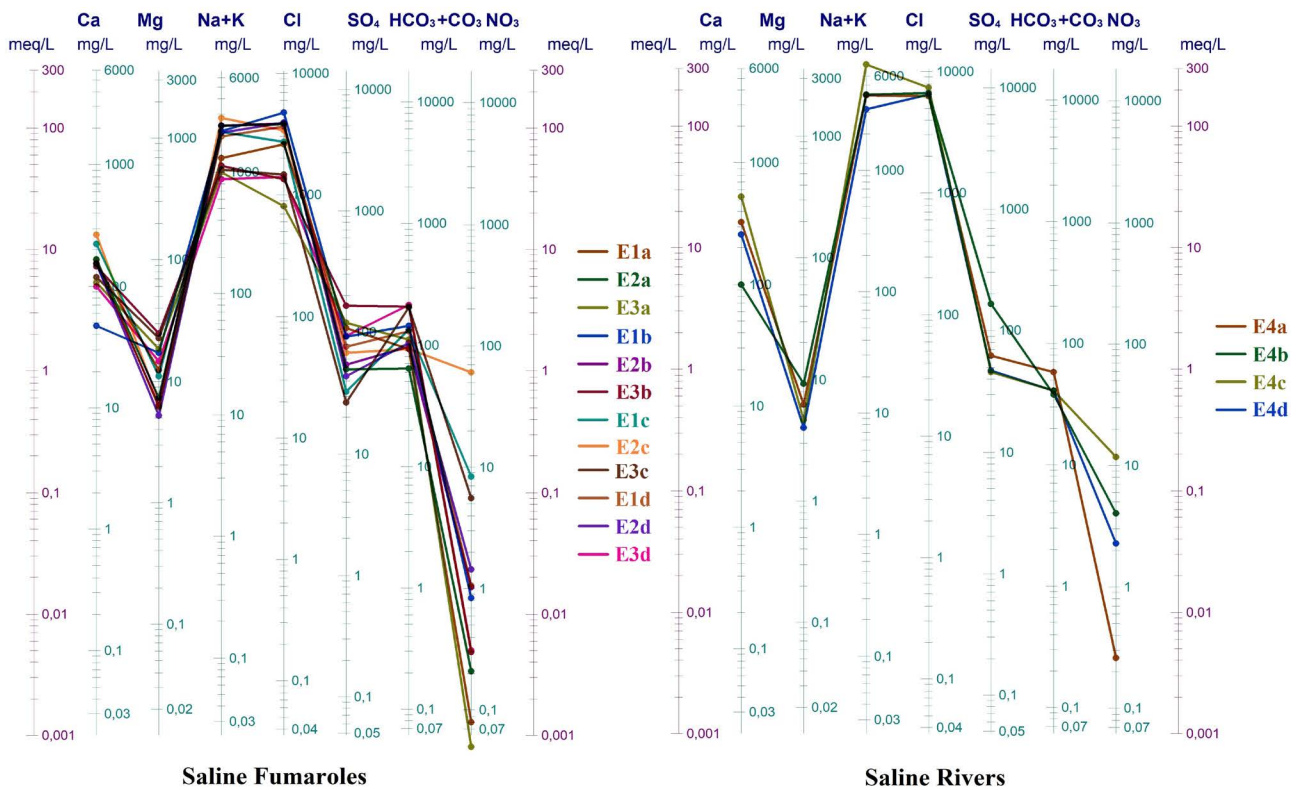
Figure 4. Vertical diagrams (Schoeller–Berkaloff) of surface water in the El tatio geothermal field. Data from this work (2010-2011) showing seasonal ion concentration (a: autumn, b: winter, c: spring, d: summer) and saline water types.
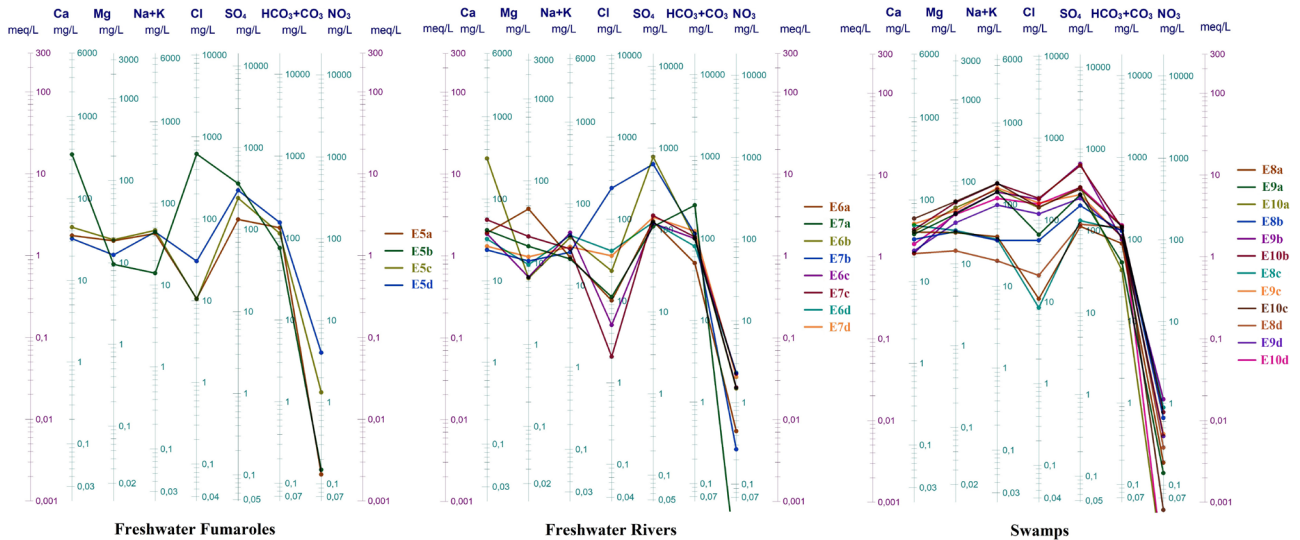
Figure 5. Vertical diagrams (Schoeller–Berkaloff) of surface water in the El tatio geothermal field. Data from this work (2010-2011) showing seasonal ion concentration (a: autumn, b: winter, c: spring, d: summer) and freshwater types.

to 2.9 with the lowest diversity at proximal hot spring locations. The most common species, forming 5% of the flora in at least one sample, for all sites were described in **Figure 6**. Cluster analyses using the whole dataset produced similar species patterns. The samples dendrogram produces five clusters, meanwhile, species dendrogram produces three clusters. Placing a cutoff at this point tends

to be supported by a levelling off of the subsequent fusion points in the histogram of dissimilarity vs. agglomeration stage (Figure 6). This also has the advantage of distinguishing clusters and their associations, which is similar in CCA plot discussed below, and the floras of which have contrasting ecological requirements. Some of the most common species photographs are described in Figure 7 and Figure 8. Using the latter approach, three groups are recognized.

Group I was only formed by three species that included: *Achnanthidium exiguum* (Figure 7(a)), *Nitzschia perminuta* (Figure 8(s)), and *Staurosirella leptostauron* (Ehrenberg) Williams and Round. These species were most common in slightly alkaline (pH 7.5 - 8) low-conductivity fumaroles, freshwater rivers and margins of warm (30°C - 35°C) springs.

Group II was more varied and included: *Halamphora acutiuscula* (Kützing) Levkov, *Pseudostaurosira brevistriata* (Grunow) Williams and Round, *Nitzschia valdecostata* Lange-Bertalot and Simonsen, *Navicula gregaria* (Figure 7(j)), *Planothidium delicatulum* (Kützing) Round and Bukhtiyarova (Figure 8(t)),

Table 2. Physical and chemical variables of freshwater and saline stations studied in the El Tatio geothermal field.

Variables	Saline Fumaroles	Freshwater Fumaroles	Saline Rivers	Freshwater River	Swamps
Conductivity	9.3 ± 3.1	0.6 ± 0.2	17.6 ± 0.7	0.4 ± 0.1	2.3 ± 2.1
pH	7.5 ± 0.3	3.5 ± 0.2	7.3 ± 0.4	8.1 ± 0.7	7.3 ± 0.6
T	30.7 ± 4.4	34.8 ± 2.3	14.8 ± 8.4	9.9 ± 0.7	9.5 ± 3.5
DO	5.2 ± 0.6	4.3 ± 0.5	7.1 ± 0.9	8.8 ± 0.5	7.6 ± 2.4
Ca^{2+}	149.7 ± 56.6	104.6 ± 107.1	301.1 ± 176.6	75.5 ± 109.4	37.4 ± 11.8
K^+	155.7 ± 39.1	13.4 ± 4.4	203.4 ± 17.1	9.4 ± 5.1	14.3 ± 6.3
Na^+	1618.6 ± 631.8	23.1 ± 6.2	4537.5 ± 1876.6	22.1 ± 8.2	95.3 ± 54.5
Li^+	13.5 ± 4.9	0.8 ± 0.5	30.1 ± 2.2	0.2 ± 0.2	0.4 ± 0.2
Mg^{2+}	12.7 ± 6.8	17.5 ± 9.2	6.5 ± 2.3	14.8 ± 4.3	37.4 ± 13.5
Cl^-	2820.8 ± 1290.9	19.8 ± 9.5	6698.5 ± 472.4	120.1 ± 117.1	103.9 ± 67.1
NO_2	139.4 ± 242.2	0.8 ± 0.4	237.1 ± 202.5	1.8 ± 1.3	4.1 ± 3.4
NO_3^-	6.6 ± 17.1	1.62 ± 0.9	4.6 ± 5.1	1.9 ± 1.4	0.4 ± 0.3
SO_4^{2-}	77.4 ± 40.4	260.7 ± 99.5	80.1 ± 57.8	274.6 ± 73.2	304.1 ± 176.8
F^-	1.3 ± 0.9	0.4 ± 0.1	2.8 ± 2.7	0.2 ± 0.1	0.3 ± 0.1
TKN	2.9 ± 1.8	10.2 ± 7.1	1.8 ± 1.6	1.9 ± 1.1	1.2 ± 0.7
TP	1.1 ± 0.8	0.9 ± 0.6	2.1 ± 2.8	0.7 ± 0.4	0.5 ± 0.4
PO_4^{2-}	0.5 ± 0.2	0.2 ± 0.1	1.4 ± 2.1	0.3 ± 0.2	0.2 ± 0.1
HCO_3^-	132.5 ± 50.3	82.5 ± 23.6	44.5 ± 9.1	134.1 ± 54.2	109.9 ± 35.1
$CaCO_3$	0.9 ± 0.5	0.9 ± 0.5	0.5 ± 0.7	0.9 ± 0.5	0.5 ± 0.3

Conductivity (mS/cm), Temperature (°C), Dissolved Oxygen (DO), Total phosphorous (TP), Total Kjeldahl Nitrogen (TKN) and Ionic Composition values in (mg/L).

Table 3. Diatom species, occurrence and ecology in aquatic systems from the El Tatio geothermal field. Occurrence: number of presence in stations during all the seasons. The algae were classified as: abundant (>10^3 cells/mm^3); common (10^3 - 10^2 cells/mm^3), occasional (10^2 - 10 cells/mm^3) or rare (<10 cells/mm^3).

Taxa	Code	Saline Fumaroles	Saline Rivers	Freshwater Fumaroles	Freshwater Rivers	Swamps	Occurrence	Ecology
Achnanthes atacamae Hustedt	*Ac at*	R	N	N	N	R	2	E
Achnanthes sp1	*Ac sp*	N	N	N	N	R	1	B
Achnanthes thermalis var. *rumrichorum* Lange-Bertalot	*Ac th*	N	R	N	N	N	1	B
Achnanthidium exiguum (Grunow) Czarnecki	*Ac ex*	C	O	A	A	R	21	E
Achnanthidium minutissimum (Kützing) Czarnecki	*Ac mi*	O	C	C	O	O	3	T
Adlafia minuscula (Grunow) Lange-Bertalot	*Ad mi*	N	N	C	O	O	8	A
Amphora pediculus (Kützing) Grunow	*Am pe*	N	N	N	N	O	2	T
Amphora sp1	*Am sp*1	C	C	N	N	N	10	B
Amphora sp2	*Am sp*2	C	O	N	R	N	6	B
Amphora sp3	*Am sp*3	R	N	N	N	R	2	B
Brachysira aponina Kützing	*Br ap*	O	O	N	N	N	3	E
Caloneis bacillum (Grunow) Cleve	*Ca ba*	N	N	O	R	R	3	T
Caloneis sp1	*Ca sp*	N	N	N	N	O	1	T
Cocconeis placentula var. *euglypta* (Ehrenberg) Grunow	*Co pl*	N	N	N	O	N	1	T
Cocconeis placentula var. *lineata* (Ehrenberg) Van Heurck	*Co li*	O	A	N	A	A	28	T
Cymbellonitzschia sp1	*Cy sp*1	O	N	N	N	N	1	E
Denticula elegans Kützing	*De el*	N	O	N	N	N	1	A
Denticula kuetzingii Grunow	*De ku*	O	N	N	N	N	2	A
Denticula subtilis Grunow	*De su*	A	O	N	N	N	11	A
Denticula thermalis Kützing	*De th*	O	R	N	N	N	4	A
Denticula valida (Pedicino) Grunow	*De va*	N	O	N	N	N	1	A
Diadesmis confervacea Kützing	*Di co*	R	N	N	N	N	5	E
Encyonema chilense Krammer	*En ch*	N	N	N	N	R	1	N
Encyonopsis microcephala (Grunow) Krammer	*En mi*	N	N	O	N	N	1	A
Eolimna minima (Grunow) Lange-Bertalot	*Eo mi*	R	R	C	C	C	16	P
Epithemia adnata (Kützing) Brébisson	*Ep ad*	N	N	N	R	N	1	B
Eunotia incisa W.Smith ex W. Gregory	*Eu in*	N	N	N	N	R	1	A
Fragilaria capucina Desmazières	*Fr ca*	R	N	C	C	O	10	T
Fragilaria capucina var. *vaucheriae* (Kützing) Lange-Bertalot	*Fr va*	R	N	N	C	C	16	A
Fragilaria construens (Ehrenberg) Grunow	*Fr co*	O	N	N	O	R	1	T
Fragilaria fasciculata (C. Agardh) Lange-Bertalot	*Fr fa*	O	N	N	N	R	8	T
Geissleria sp1	*Ge sp*	N	N	N	R	R	2	P
Gomphonema angustatum (Kützing) Rabenhorst	*Go ag*	N	N	N	O	R	5	B

Continued

Gomphonema angustum C. Agardh	*Go an*	N	N	O	N	N	1	B
Gomphonema gracile Ehrenberg	*Go gr*	N	N	N	O	N	1	E
Gomphonema parvulum (Kützing) Kützing	*Go pa*	N	N	N	O	R	3	E
Gomphonema pseudoaugur Lange-Bertalot	*Go ps*	N	N	C	C	R	5	E
Gomphonema sp1	*Go sp*	N	N	N	N	R	1	E
Gomphonema tristigmatum Metzeltin & Lange-Bertalot	*Go tr*	N	N	N	N	R	1	E
Halamphora acutiuscula (Kützing) Levkov	*Ha ac*	C	C	N	N	N	12	A
Halamphora atacamae (Frenguelli) Levkov (fossil)	*Ha at*	R	O	N	N	N	3	B
Halamphora coffeiformis (C. Agardh) Levkov	*Ha co*	O	N	N	N	N	3	B
Halamphora veneta (Kützing) Levkov	*Ha ve*	R	O	N	N	O	6	T
Hippodonta hungarica Lange-Bertalot	*Hi hg*	N	N	N	N	R	1	E
Lemnicola hungarica (Grunow) Round & Basson	*Le hg*	N	N	N	N	O	5	B
Luticola mollis Lange-Bertalot & U.Rumrich	*Lu mo*	N	N	N	N	R	1	A
Mastogloia elliptica (C. Agardh) Cleve	*Ma el*	R	N	N	N	N	3	E
Mayamaea atomus (Kützing) Lange-Bertalot	*My at*	N	N	C	O	O	7	E
Navicula cincta (Ehrenberg) Ralfs	*Na ci*	O	N	O	C	C	11	A
Navicula cryptocephala Kützing	*Na cr*	N	N	O	N	N	1	T
Navicula cryptotenella Lange-Bertalot	*Na ct*	O	O	N	N	N	4	B
Navicula gregaria Donkin	*Na gr*	N	N	N	N	C	7	E
Navicula lauca U. Rumrich & Lange-Bertalot	*Na la*	O	R	N	O	O	15	B
Navicula microdigitoradiata Lange-Bertalot	*Na mi*	R	N	N	N	N	1	B
Navicula parinacota U. Rumrich & Lange-Bertalot	*Na pa*	O	R	N	N	R	4	B
Navicula pseudogracilis Hustedt	*Na ps*	R	N	N	N	N	1	N
Navicula salinicola Hustedt	*Na sa*	C	C	N	N	N	13	B
Navicula sp1	*Na sp*1	O	O	N	N	N	3	B
Navicula tripunctata (O. F. Müller) Bory	*Na tr*	N	N	N	N	C	4	B
Navicula veneta Kützing	*Na ve*	O	O	N	N	N	5	B
Navicula viridula (Kützing) Ehrenberg	*Na vi*	N	N	N	R	R	2	B
Naviculadicta chilensis (Krasske) Lange-Bertalot	*Nv ch*	N	N	N	O	R	3	B
Navicymbula pusilla (Grunow) Krammer	*Nc pu*	R	N	N	N	N	2	A
Nitzschia accedens var. *chilensis* R.M.Patrick	*Nt ac*	R	N	N	N	N	1	B
Nitzschia amphibia Grunow	*Nt am*	N	N	C	N	N	1	A
Nitzschia bacillum Hustedt	*Nt ba*	O	O	C	O	N	10	B
Nitzschia fonticola (Grunow) Grunow	*Nt fo*	O	N	C	C	C	9	B
Nitzschia gracilis Hantzsch	*Nt gr*	N	O	N	N	O	4	P
Nitzschia halloyii N. I. Maidana & N. Herbst	*Nt ha*	R	N	N	N	O	6	B
Nitzschia inconspicua Grunow	*Nt in*	C	O	O	N	A	17	B

Continued

Nitzschia latens Hustedt	*Nt la*	R	O	N	N	N	4	B
Nitzschia liebetruthii Rabenhorst	*Nt li*	O	N	N	N	R	7	B
Nitzschia linearis W. Smith	*Nt ln*	N	N	O	N	R	2	T
Nitzschia palea (Kützing) W. Smith	*Nt pa*	C	O	A	C	C	20	T
Nitzschia perminuta (Grunow) M. Peragallo	*Nt pe*	O	N	O	C	C	16	B
Nitzschia pusilla Grunow	*Nt pu*	O	C	N	N	R	7	E
Nitzschia sp1	*Nt sp*	O	A	A	A	A	26	B
Nitzschia subrostratoides Cholnoky	*Nt su*	N	N	N	N	R	1	B
Nitzschia valdecostata Lange-Bertalot & Simonsen	*Nt va*	O	C	O	O	C	21	B
Pinnularia subrostrata (A. Cleve) Cleve-Euler	*Pi su*	N	N	O	O	R	3	B
Planothidium chilense (Hustedt) Lange-Bertalot	*Pl ch*	N	N	N	O	R	2	B
Planothidium delicatulum (Kützing) Round & Bukhtiyarova	*Pl de*	R	N	N	R	C	10	T
Planothidium frecuentissimum (Lange-Bertalot) Lange-Bertalot	*Pl fr*	N	N	O	C	O	12	B
Planothidium lanceolatum (Brébisson ex Kützing) Lange-Bertalot	*Pl la*	N	R	O	O	A	13	T
Planothidium renei (Lange-Bertalot & Rol.Schmidt) Van de Vijver	*Pl re*	N	N	N	N	R	5	B
Planothidium sp1	*Pl sp*	R	C	N	N	N	4	B
Psamothidium subatomoides (Hustedt) Bukhtiyrova & Round	*Ps su*	N	N	N	O	N	2	B
Pseudostaurosira brevistriata (Grunow) D.M. Williams & Round	*Ps br*	O	C	N	N	O	7	T
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot	*Rh ab*	N	N	N	N	O	4	T
Rhopalodia acuminata Krammer	*Rh ac*	N	N	N	R	N	1	B
Rhopalodia gibba (Ehrenberg) Otto Müller	*Rh gi*	N	N	N	N	R	1	T
Staurosira aventralis Lange-Bertalot & Rumrich	*St av*	N	N	N	N	R	1	B
Staurosira brevistriata (Grunow) Grunow	*St br*	C	O	N	N	O	8	T
Staurosira subsalina (Hustedt) Lange-Bertalot	*St su*	O	C	N	O	O	7	T
Staurosirella leptostauron (Ehrenberg)	*St le*	C	O	N	O	C	13	T
Staurosirella pinnata (Ehrenberg) D. M. Williams & Round	*St pi*	R	R	N	N	O	10	T
Stephanodiscus sp1	*St sp*	N	N	N	N	R	1	P
Surirella angusta Kützing	*Su an*	N	N	O	N	N	1	T
Surirella chilensis C. Janisch	*Su ch*	R	N	N	N	N	1	E
Synedra goulardii Brébisson ex Cleve & Grunow	*Sy go*	N	N	N	N	R	2	E
Tryblionella hungarica (Grunow) Frenguelli	*Tr hu*	N	N	O	N	N	3	B
Ulnaria ulna (Nitzsch) Compère	*Ul ul*	N	N	C	C	R	12	E

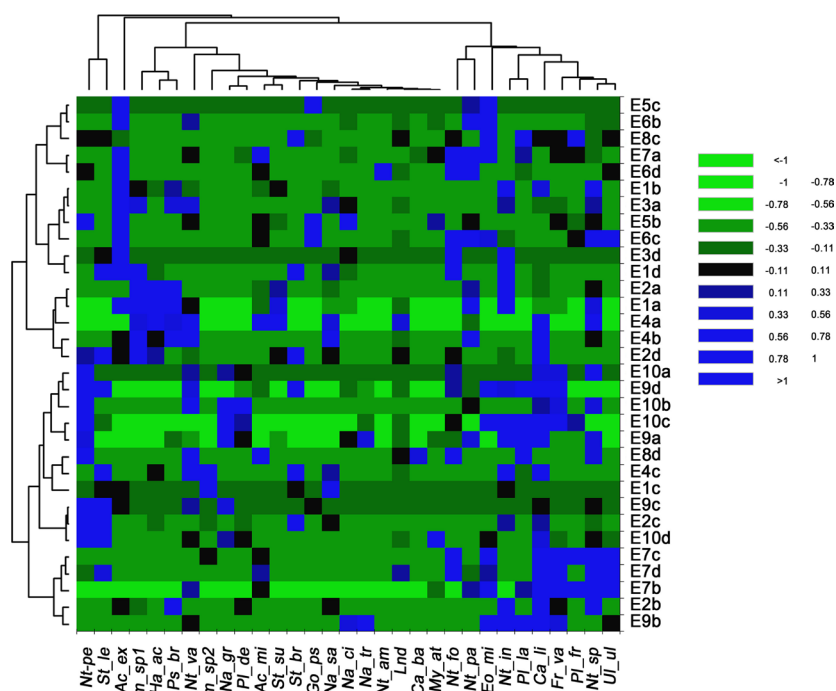Aerophilic (A): Benthic (B): Epiphytic (E): Planktonic (P): Tychoplanktonic (T): Non presence (N).

Figure 6. Heat map of diatom taxa forming 5% of the flora in at least one sample. The colors key is shown to the right (red color represent low association, green color represent high association and black color represent intermediate association), histograms are shown upper and to the left. All associations were determined by saline and freshwater conditions for both species and samples respectively (sample codes and species acronyms are described in Table 1 and Table 3).
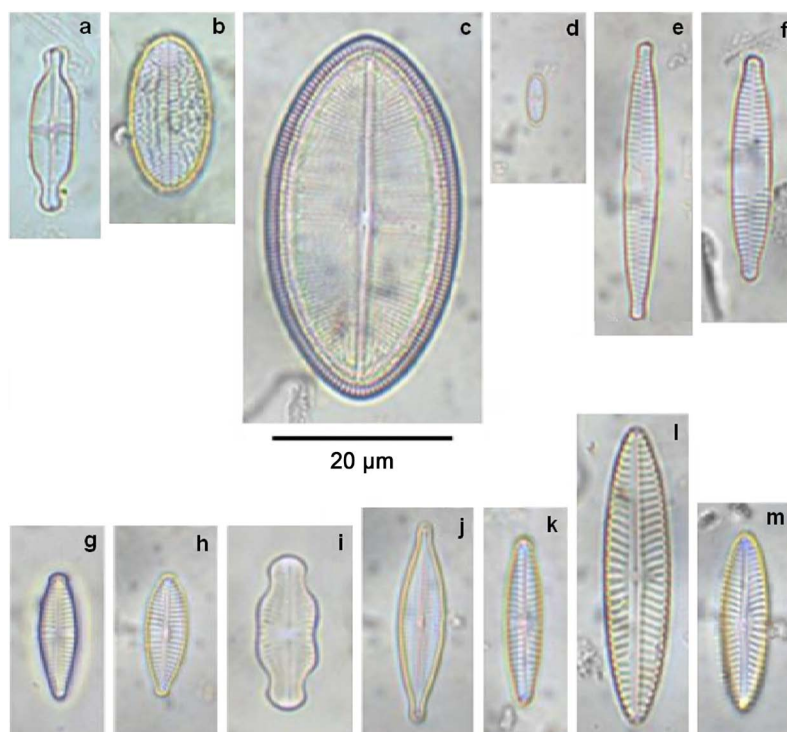

Figure 7. Light microscopy photographs of diatoms from the El Tatio geothermal field. *Achnanthidium exiguum* (a), *Cocconeis placentula* var. *euglypta* (b), *Cocconeis placentula* var. *lineata* (c), *Eolimna minima* (d), *Fragilaria capucina* (e), *Fragilaria capucina* var. *vaucheriae* (f), *Gomphonema angustum* (g), *Gomphonema parvulum* (h). *Luticola mollis* (i). *Navicula gregaria* (j), *Navicula lauca* (k), *Navicula parinacota* ((l), (m)).
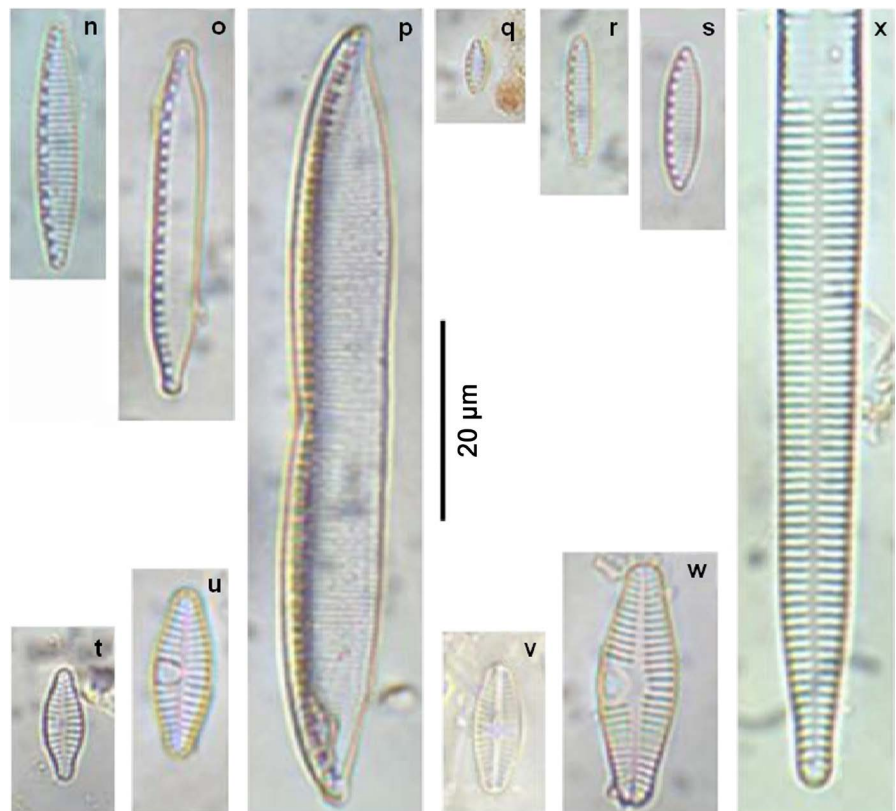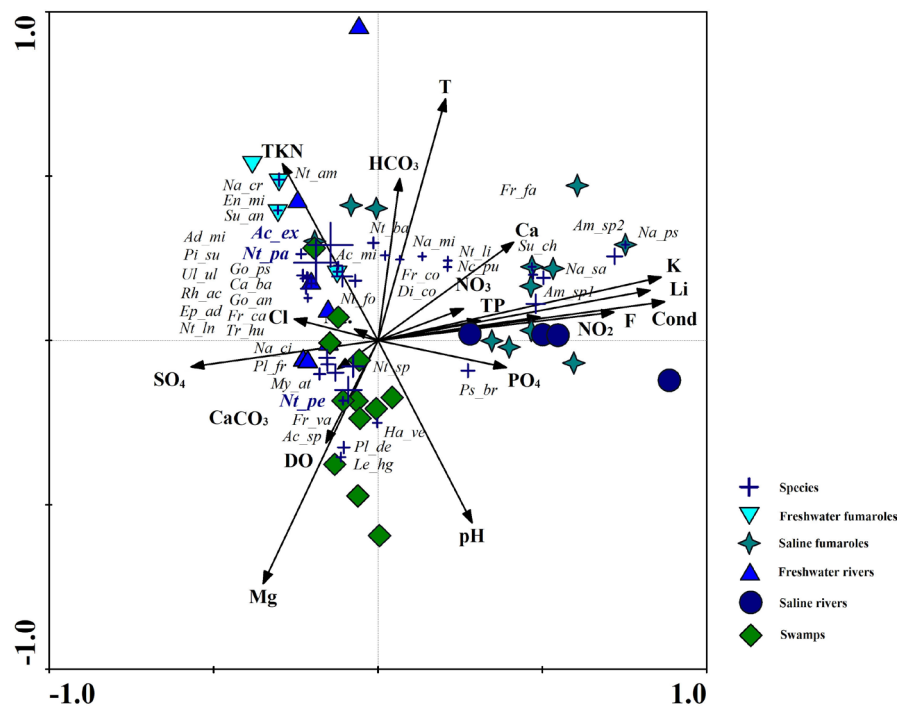
Figure 8. Light microscopy photographs of diatoms from the El Tatio geothermal field. *Nitzschia amphibia* (n), *Nitzschia halloyi* (o), *Nitzschia hungarica* (p), *Nitzschia inconspicua* ((q), (r)), *Nitzschia perminuta* (s), *Planothidium delicatulum* (t), *Planothidium frecuentissimum* (u), *Planothidium lanceolatum* ((v), (w)), *Ulnaria ulna* (x).

Achnanthidium minutissimum (Kützing) Czarnecki, *Staurosira subsalina* (Hustedt) Lange-Bertalot, *Staurosira brevistriata* (Grunow) Grunow, *Gomphonema pseudoaugur* Lange-Bertalot, *Navicula salinicola* Hustedt, *Navicula cincta* (Ehrenberg) Ralfs, *Navicula tripunctata* (Müller) Bory, *Nitzschia amphibia* (**Figure 8(n)**), *Caloneis bacillum* (Grunow) Cleve, and *Mayamaea atomus* (Kützing) Lange-Bertalot. These taxa were mostly observed in water flow across the north discharge area (e.g. fumaroles and saline systems), and through stream channels until it arrives at the Salado River.

Group III included: *Nitzschia fonticola* (Grunow) Grunow, *Nitzschia palea*, *Cocconeis placentula* var. *lineata* (Ehrenberg) Van Heurck (**Figure 7(c)**), *Eolimna minima* (**Figure 7(d)**), *Fragilaria capucina* var. *vaucheriae* (Kützing) Lange-Bertalot (**Figure 7(f)**), *Nitzschia inconspicua* (**Figure 8(q)** & **Figure 8(r)**), *Planothidium lanceolatum* (**Figure 8(v)** & **Figure 8(w)**), *Planothidium frecuentissimum* (Lange-Bertalot) Lange-Bertalot (**Figure 8(u)**) and *Ulnaria ulna* (**Figure 8(x)**). These diatoms were not exclusive at south area, however a high number of taxa were clearly associated to freshwater systems, rivers and the margins of swamp stations. They were dominant in the sparse flora that occurs on both discharge areas (north and south), and formed part of the common flora in freshwater systems at El Tatio geothermal field.

3.3. Statistical Model

Monte Carlo test (999 permutations, p < 0.05) showed that physical and chemical variables were important diatom predictor ([Figure 9](#)). The best species response to significant environmental variables were observed in 39 taxa including all the samples in the CCA analysis. Permutation under the reduced model indicated conductivity, dissolved oxygen and composition of major ions (TP, HCO_3, TKN and Mg) as the most important variables with relation to diatom species assemblages (p < 0.05, 999 permutations). Some taxa were associated to saline systems, the most common were: *Fragilaria fasciculata* (C.Agardh) Lange-Bertalot, *Surirella chilensis, Navicula salinicola, Navicula pseudogracilis* Hustedt, *Navicula microdigitoradiata* Lange-Bertalot, *Nitzschia liebetruthii* Rabenhorst, *Navicymbula pusilla* (Grunow) Krammer, *Pseudostaurosira brevistriata*. These species were correlated with high conductivity and temperature, and concentration of nitrogen and phosphorous. The second group was associated to swamp stations separated from the other freshwater systems. This group included: *Navicula cincta, Planothidium frecuentissimum, Mayamaea atomus, Fragilaria capucina* var. *vaucheriae, Planothidium delicatulum, Lemnicola hungarica* (Grunow) Round and Basson, and *Halamphora veneta* (Kützing) Levkov. Other species associated to this group was *Nitzschia perminuta*, and reported the highest statistical weight, this species was only observed in swamps and was highly correlated with SO_4^{2-} and $CaCO_3^-$ water types. The third assemblage was associated

Figure 9. CCA ordination plot of diatom assemblages (using only species that explain 0.1 to 0.33 of the total variance) against selected environmental variables, including weighted average for each species plot (showing in blue bold the species that represent the higher values, species acronyms are described in [Table 3](#)).

to freshwater fumaroles and freshwater rivers. This group was more diverse and include: *Nitzschia amphibia, Navicula cryptocephala* Kützing, *Encyonopsis microcephala* (Grunow) Krammer, *Surirella angusta* Kützing, *Adlafia minuscula* (Grunow) Lange-Bertalot, *Pinnularia subrostrata* (A. Cleve) Cleve-Euler, *Ulnaria ulna, Rhopalodia acuminata* Krammer, *Epithemia adnata* (Kützing) Brébisson*, Nitzschia linearis* W. Smith, *Tryblionella hungarica, Fragilaria capucina* Desmazières (Figure 7(e)), *Gomphonema angustum* C.Agardh (Figure 7(g)), *Caloneis bacillum*, and *Gomphonema pseudoaugur*. Other two species were also associated to these systems, *Achnanthidium exiguum* and *Nitzschia palea* (Figure 9), and reported the highest statistical weight highly correlated with nitrogen contained in organic substances plus the nitrogen in inorganic ammonia and ammonium (NH_3/ NH_4^+).

3.4. Species Indicator Values

Multiple sensitive species for significant variables ($p < 0.05$) were determined using Generalized Additive Model (GAM) and Poisson distribution. Using maximum values and stepwise selection with Akaike Index Criterion (AIC), only 30 species pass the restrictions (the rest of the species were no candidate for additive model because had AIC values lower than null model) and where used to species curve fitted (Table 4). The optima and tolerance was estimate using restrictions (species with statistical weight among 0.01 and 0.33 of the total variance); they were explained by significant variables ($p < 0.05$). Conductivity optima for those diatoms ranged from 960 to 15,310 µS cm^{-1}. Mostly, diatoms that exhibited the highest affinity to $Ca(HCO_3)_2$ rich waters had high to moderate conductivity optima. In this aspect, the most common taxa were *Halamphora acutiuscula, Halamphora atacamae* Hustedt, *Diadesmis confervacea, Fragilaria fasciculata, Nitzschia lateens* Hustedt, *Nitzschia palea, Staurosira brevistriata*, and *Cocconeis placentula* var. *lineata*. Other species indicator values for the most significant variables were described in Table 4.

4. Discussion

High seasonal variation both in thermal and chemical properties have been described, and those variables tend to alter diatom assemblages, alternately favoring one species than another. Seasonal rains keep the diatom assemblages in an early successional state, composed of fluctuating 'opportunistic' species (e.g. rare or occasional, Table 3). Initial colonization usually produces a variety of species, none in great abundance but in high diversity [5]-[21]. Gradually, with longer exposure to the strongest dryness a few species are capable of rapid growth, gaining dominance and stability. For example, *A. exiguum* and *S. pinnata* were the most abundant species found in fumaroles and saline rivers, with maximal abundance reported during the dry season. In contrast, *N. palea* had maximal abundance at summer during the seasonal rains. The maximal values for the dominant species in swamps, *C. placentula* var. *euglypta, N. gregaria, N. inconspicua, N. perminuta*, and *P. lanceolatum*, were after seasonal rains.

Table 4. Optima and tolerance values for common thermal/non-thermal associated diatoms, and peak maximum (Cells/mm^3) based on a weighted averaging model.

Species	Cond. Opt.	Cond. Tol.	Peak max.	D.O. Opt.	D.O. Tol.	Peak max.	pH Opt.	pH Tol.	Peak max.	T.P. Opt.	T.P. Tol.	Peak max.
Achnanthes thermalis var. *rumrichorum*	7.1 ± 0.8	3.8 ± 0.8	35.9	4.3 ± 2.7	0.7 ± 0.1	13.4	5.2 ± 0.9	1.5 ± 0.3	4.3	0.4 ± 0.1	0.1 ± 0.1	15.9
Achnanthidium exiguum	8.5 ± 2.8	3.6 ± 0.6	110.4	6.8 ± 0.5	2.7 ± 1.2	120.5	5.8 ± 0.7	1.8 ± 0.5	103.7	0.5 ± 0.2	0.6 ± 0.2	152.8
Achnanthidium minutissimum	5.2 ± 0.1	0.9 ± 0.3	20.1	5.6 ± 0.2	2.9 ± 0.2	18.2	5.3 ± 0.5	1.9 ± 0.5	58.5	0.2 ± 0.1	0.1 ± 0.1	18.2
Adlafia minuscula	2.1 ± 0.2	2.2 ± 0.2	11.5	8.4 ± 0.5	2.7 ± 0.5	28.7	5.1 ± 0.6	0.7 ± 0.2	18.4	0.9 ± 0.4	0.1 ± 0.1	20.7
Amphora pediculus	1.1 ± 0.1	0.4 ± 0.2	114.1	6.8 ± 0.2	0.4 ± 0.2	49.7	7.7 ± 1.1	0.9 ± 0.1	51.9	0.6 ± 0.3	0.2 ± 0.1	15.9
Cocconeis placentula var. *euglypta*	7.1 ± 2.5	3.5 ± 0.8	49.7	7.8 ± 0.2	2.9 ± 0.1	65.9	7.3 ± 1.8	2.3 ± 0.8	10.8	0.6 ± 0.1	0.7 ± 0.1	22.8
Diadesmis confervacea	11.9 ± 0.6	4.7 ± 1.1	22.7	5.9 ± 0.8	0.6 ± 0.1	23.8	7.9 ± 1.9	0.5 ± 0.1	15.5	0.3 ± 0.1	0.2 ± 0.1	22.9
Fragilaria capucina	3.4 ± 1.2	5.8 ± 4.4	15.5	11.5 ± 0.1	2.4 ± 0.2	46.5	7.3 ± 1.7	0.8 ± 0.4	20.2	0.8 ± 0.3	0.2 ± 0.1	11.8
Fragilaria capucina var. *vaucheriae*	2.3 ± 0.1	2.8 ± 0.9	51.6	8.8 ± 0.4	2.3 ± 0.6	34.8	7.8 ± 1.2	1.2 ± 0.3	15.0	0.2 ± 0.1	0.1 ± 0.1	150.1
Fragilaria fasciculata	9.2 ± 0.2	3.8 ± 0.2	23.2	4.7 ± 0.2	0.7 ± 0.3	16.2	7.5 ± 1.1	1.6 ± 0.5	18.2	0.2 ± 0.1	0.4 ± 0.1	6.5
Halamphora acutiuscula	13.5 ± 0.8	3.5 ± 0.1	130.9	5.4 ± 0.6	1.5 ± 0.4	45.2	9.9 ± 2.7	2.4 ± 0.7	598.3	0.2 ± 0.1	0.3 ± 0.1	18.3
Halamphora atacamae	13.2 ± 0.9	5.1 ± 1.6	32.2	5.6 ± 0.9	1.6 ± 0.4	11.2	7.7 ± 1.5	0.8 ± 0.2	11.7	0.2 ± 0.1	0.2 ± 0.1	7.1
Halamphora veneta	11.2 ± 0.8	4.5 ± 1.3	20.5	7.5 ± 0.2	2.8 ± 0.3	28.7	7.3 ± 1.8	0.8 ± 0.1	11.5	0.2 ± 0.1	0.1 ± 0.1	11.8
Lemnicola hungarica	3.3 ± 0.1	1.6 ± 0.1	17.2	6.5 ± 0.1	0.8 ± 0.1	13.1	7.7 ± 1.3	0.7 ± 0.4	10.5	0.1 ± 0.1	0.1 ± 0.1	14.7
*Mayamaea atomus*m	2.3 ± 0.5	1.3 ± 0.3	51.2	4.9 ± 0.2	0.5 ± 0.1	23.2	5.5 ± 1.1	1.7 ± 0.5	42.5	0.3 ± 0.1	0.3 ± 0.1	34.4
Navicula cincta	2.4 ± 0.2	1.4 ± 0.2	36.4	4.4 ± 0.7	1.2 ± 0.1	46.5	5.8 ± 1.2	1.9 ± 0.6	293.3	0.1 ± 0.1	0.2 ± 0.1	45.3
Navicula gregaria	1.8 ± 0.4	0.3 ± 0.1	270.2	6.8 ± 0.5	1.6 ± 0.3	75.2	8.5 ± 2.6	1.7 ± 0.5	293.3	0.4 ± 0.1	0.2 ± 0.1	353.6
Navicula tripunctata	1.7 ± 0.3	0.2 ± 0.1	224.4	6.8 ± 0.2	0.7 ± 0.3	53.1	7.8 ± 2.7	2.5 ± 1.2	183.8	0.3 ± 0.1	0.2 ± 0.1	58.2
Nitzschia amphibia	8.1 ± 0.5	3.9 ± 1.5	192.3	5.7 ± 0.1	1.8 ± 0.2	2242.6	4.7 ± 1.3	0.8 ± 0.3	3440.3	1.8 ± 0.3	0.8 ± 0.5	935.2
Nitzschia fonticola	0.8 ± 0.3	0.6 ± 0.1	1183.8	8.2 ± 0.5	1.6 ± 0.3	153.4	4.6 ± 0.8	1.4 ± 0.5	182.2	0.7 ± 0.1	0.8 ± 0.2	565.5
Nitzschia lateens	15.3 ± 0.9	5.2 ± 1.3	26.5	5.7 ± 0.3	0.9 ± 0.1	22.4	6.8 ± 1.5	0.7 ± 0.2	92.5	0.5 ± 0.1	0.6 ± 0.1	12.1
Nitzschia palea	14.7 ± 2.4	4.9 ± 3.1	276.7	5.4 ± 0.2	1.8 ± 0.4	212.6	4.8 ± 0.7	1.9 ± 0.9	87.5	1.8 ± 0.5	0.9 ± 0.4	135.2
Nitzschia perminuta	2.8 ± 0.1	1.8 ± 0.2	469.5	7.6 ± 0.5	1.4 ± 0.6	92.1	6.8 ± 1.2	1.8 ± 0.5	98.8	0.3 ± 0.1	0.6 ± 0.1	150.5
Nitzschia pusilla	11.8 ± 0.2	4.8 ± 1.1	55.2	5.4 ± 0.5	1.5 ± 0.3	102.6	5.8 ± 1.2	0.5 ± 0.2	14.4	0.7 ± 0.4	0.6 ± 0.2	12.8
Planothidium delicatulum	2.1 ± 0.3	0.9 ± 0.2	60.7	7.8 ± 0.3	0.8 ± 0.4	54.2	7.2 ± 1.6	1.8 ± 0.5	611.7	2.1 ± 0.5	1.1 ± 0.5	116.4
Planothidium lanceolatum	2.7 ± 0.8	0.8 ± 0.1	1093.3	7.7 ± 0.2	1.1 ± 0.2	175.0	5.9 ± 1.5	1.3 ± 0.5	120.2	1.2 ± 0.5	0.7 ± 0.3	105.2
Rhoicosphenia abbreviata	2.9 ± 0.4	0.8 ± 0.1	32.7	7.5 ± 0.4	0.8 ± 0.3	13.4	7.9 ± 1.2	0.8 ± 0.1	24.8	1.6 ± 0.5	0.9 ± 0.5	28.6
Staurosira brevistriata	6.5 ± 0.8	2.9 ± 0.1	53.4	4.1 ± 0.5	1.7 ± 0.5	35.1	7.8 ± 1.5	1.8 ± 0.5	28.5	1.8 ± 0.5	0.7 ± 0.2	33.2
Ulnaria ulna	3.6 ± 0.2	1.1 ± 0.5	17.6	8.6 ± 0.9	2.2 ± 0.4	33.7	5.6 ± 1.1	2.5 ± 0.7	24.4	0.9 ± 0.1	0.4 ± 0.1	18.5

Dissolved Oxygen (DO) and Total Phosphorous (TP) values in (mg/L); Conductivity (mS/cm).

The epiphytic *Cocconeis placentula* (and varieties) is considered a euryhaline and tychonoplanktonic species [22]. In Bolivia, it has been recorded in saline systems (44 - 80 g l⁻¹), and diatom stratigraphy works by [22] and [23]. It now occurs in a large range of salinity, in large permanent freshwater water bodies colonized by macrophytes (essentially Isoetes) and also reported in the glacial valley of Hichu Kkota in a shallow salt lake (e.g. 15 g l⁻¹ salinity), and in the Lake Poopó (40 g l⁻¹ salinity). In Chile, this species have been described in a large range of salinity, from sediments and littoral habitat of the Chungará Lake [24], to variable saline systems in the Salar de Atacama [25]. *C. placentula* var. *euglypta* (Figure 7(b)) and *C. placentula* var. *lineata* (Ehrenberg) Van Heurck (Figure 7(c)) are widespread in a variety of environments, from clean to enriched streams [6], described commonly as epiphytic (Patrick and Reimer 1966), but also appear to have an important ecological function in a variety of aquatic environments, especially in littoral water bodies colonized by macrophytes. *N. cincta* (Ehrenberg) Ralfs, an aerophilous species according to [26], lives at around 10 g l⁻¹ salinity in Bolivia. This species was more associated with fumaroles and saline rivers (>10³ cells/mm³) than freshwater systems studied.

Some studies have focused on assessing the impact of environmental and spatial drivers in explaining the differences in diatom species richness and composition patterns. However, these aspects in microbial communities are poorly know especially in extreme environments. In New Zealand, according to [7] 144 taxa in thermal and mixed thermal/non-thermal waters were dominated by the genera *Nitzschia* (24), *Pinnularia* (16), *Navicula* (10), and *Surirella* (7). In this work, we reported 102 taxa in thermal and mixed thermal/non-thermal waters dominated by the genera *Nitzschia* (16), *Navicula* (13), *Gomphonema* (7), *Planothidium* (6), and *Denticula* (5). In Iceland 178 taxa were identified in hot springs, where *Diploneis elliptica* (Kützing) Cleve, *N. amphibia*, *Pinnularia borealis* Ehrenberg, and *E. adnata* occurred in 50% of the samples [27]. However, other authors suggested that nine species were found only in hot springs in Iceland [28]. In contrast, other report [29] argued that exclusive geothermal diatoms do not exist and pointed out that other studies [27] [30] had detected these taxa in other habitats as well. In this context, we found only 18 taxa exclusive of warm-fumarole springs.

Many of the taxa reported in the El Tatio geothermal field were described by many authors in a wide range of thermal/non-thermal environments. For example, *A. exiguum* has a worldwide distribution in hot springs [31]. *S. pinnata* predominated in shallow arctic lakes and is more competitive in lakes with long periods of ice cover [32] [33]. *P. lanceolatum* is common and widespread in the hot springs of New Zealand and can be found in a variety of water chemistries [6]. It typically prefers oxygen-rich waters of neutral to slightly alkaline pH [13]. This condition was similar to this report, especially in freshwater systems. In this case it was very restrictive to pore-water electrolytes. *N. palea* is common in many environments worldwide and described as a sensitive taxon in New Zealand [6] and variable environments in Alaska [34]. We reported the maximal

abundance for this taxa in fumaroles and saline rivers (Table 3). The distribution of *H. atacamae*, *H. coffeaeformis* (C. Agardh) Levkov, *Denticula elegans* Kützing, *Denticula thermalis* Kützing, and *S. chilensis* were coincident with the photosynthetic microbial communities described in a near local high-altitude saline basin [35].

According to [22] species of the genus *Fragilaria* were dominant in the freshwater environments of the Hichu Kkota glacial valley in Bolivia. It is rare in aerophilic habitats, but particularly abundant (always more than 50%) in flowing streams (50 - 100 cm deep) which are scattered in the Juncacae peat bogs (bofedales). *Fragilaria* are here assigned as tychoplanktonic; some species are considered as benthic in lakes and ponds [11]. They prefer low conductivity in lotic environments [32]. However, we described four taxa, *F. capucina* (Figure 7(e)), *F. capucina* var. *vaucheriae* (Figure 7(f)), *Fragilaria construens*, and *F. fasciculata* above 10,000 μS cm⁻¹ conductivity in some rivers and swamps from the El Tatio geothermal field. In Bolivia, *F. fasciculata* and *F. capucina* were observed in mixed saline and freshwaters. *F. fasciculata* was also described in the Salar of Uyuni (0.9 - 30 g l⁻¹ salinity), and Lake Poopó (14 - 30 g l⁻¹ salinity, 50 - 200 cm water depth). Moreover, *F. capucina* and *F. construens* was reported in the streams of the Hichu Kkota valley in Bolivia.

The fossil benthic species composition in core sediment from Lake Titicaca [23], indicated abundant taxa in common with the El Tatio such as *C. placentula*, *N. veneta*, *Navicula lauca* Rumrich and Lange-Bertalot (Figure 7(k)), *P. lanceolatum* (Figure 8(v) & Figure 8(w)) and *S. pinnata*. High percentage values of fossil periphytic diatoms, mainly epiphytes, were described in the Quillagua formation (Atacama Desert); indicating permanent palustrine conditions with abundance of macrophytes and very shallow mesohaline water bodies [36]. The most relevant species including saline forms were similar to the species described in the El Tatio, *Achnanthes atacamae* Hustedt, *Brachysira aponina* Kützing, *Cocconeis placentula* Ehrenberg, *Denticula valida* (Pedicino) Grunow, *N. amphibia*, *N. inconspicua*, *N. valdecostata*, and *Denticula kuetzingii* Grunow. The freshwater species described in common with the El Tatio were *U. ulna* and *N. palea*, which tolerate great variation in oxygen and moderate to low electrolyte concentration [17] [18] [19]. Another freshwater species described was *Achnanthes lanceolata* Smith, and two peaks of *F. brevistriata* and *S. subsalina*, interpreted as indicators of freshwater inputs. Moreover, a peak in *Achnanthes thermalis* (Rabenhorst) Schönfeldt was indicated as the influence of water discharges from nearby hot springs [13] [36]. The presence of *Cymbella pusilla* Grunow, described as an indicator of CaSO₄-rich water type [8], suggests a similar condition with the actual diatom flora described in the El Tatio geothermal field.

Recently, interesting patterns related with diatom size fractions has been evaluated to interpret their relations to environmental variables in a global scale [37]. The maximum growth factor can vary by a factor of two, even within a given species of diatom, increasing with size as cells are transformed from pre to

post-auxospore cells. Similarly, when mean size cell decreases in diatom because of the reduction of the frustule size over succeeding generations, growth rates decrease [38]. These aspects can influence the diatom size-fraction in hostile environments. As expected, the 20 to 200 μm-size fraction in El Tatio contained the highest numbers of diatom taxa (53 species) although an unexpectedly high number (47 species) were also found in the smaller size fraction, belonging to smaller species (e.g., *Achnanthidium*, *Eolimna*, and *Planothidium*). The 5 to 20 μm-size fraction was an important component more associated to brackish (except for stations E1-E3 during winter season) and saline systems (**Figure 10**). Apparently, the aquatic systems in El tatio geothermal field are highly restrictive for larger size-fraction 180 - 2000 μm, only two species, including rosette-forming diatom *U. ulna* and the unicellular species *S. chilensis*, were found exclusively in freshwater systems.

As indicated by various studies, some habitats are highly stressful and so few
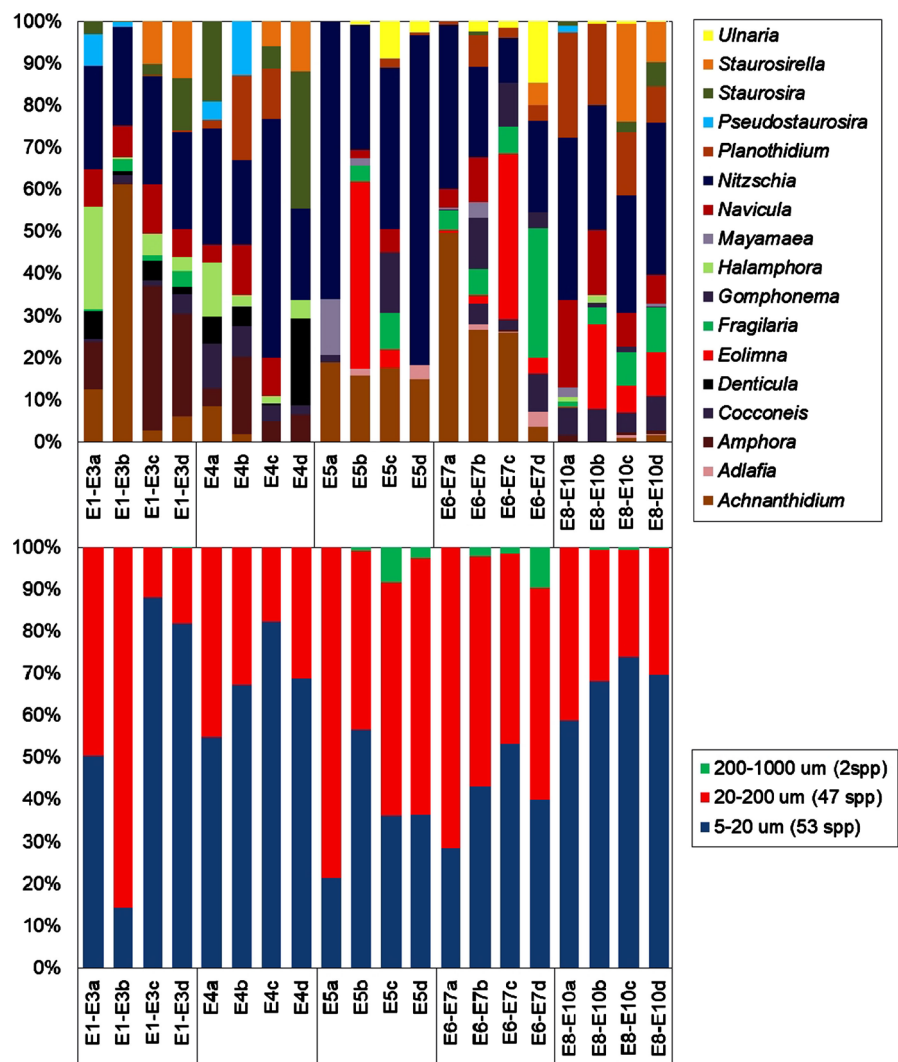

Figure 10. Seasonal change of the most representative genera (>1% total abundance per sample) and size fractions variability.

microorganisms are adapted for life there, this result in many of them are unique or rare [35] [39] [40]. Water bodies in different geographic regions often show considerable variability with regard to their diatom richness/composition patterns. These patterns would response to altitude and latitudinal variations (solar radiation, cloudiness, temperature, desiccation and seasonality) superimposed on local habitat controls (current velocity, water chemistry, and substrate types). In many studies, cosmopolitan diatom taxa are described, suggesting easy dispersal mechanisms [37]. However, regional studies of geothermal diatoms have shown taxonomic variability between thermal/non-thermal waters at varied local to regional scales [6]. Our study clearly shown exclusive diatom taxa related to thermal waters, however, salinity and other local environmental condition appear to have a major influence in the structure of diatom assemblages. In contrast, cosmopolitan taxa are widespread, but only some occurs in specialized settings such as the hot springs.

5. Conclusion

Diatom floras in the El Tatio geothermal field vary in terms of beta diversity and abundance, and several taxa were found in all the systems studied. Nevertheless, the study areas could still be distinguished by: 1) the dominance of *A. exiguum*, *A. minutissimum*, *D. subtilis*, *D. thermalis*, *H. acutiuscula*, *N. salinicola*, *N. amphibia* and *N. bacillum* in fumaroles, with the common occurrence of teratological forms; 2) the common occurrence of *A. exiguum*, *C. placentula var. lineata* and *N. palea* in rivers; 3) the common occurrence of *C. placentula* var. *euglypta*, *N. gregaria*, *N. tripunctata*, *N. inconspicua* and *P. lanceolatum* in swamps. These variations probably reflect the combined influence of heterogeneity and differences in temperature, water chemistry brought about by contrasts in lithologies, and flow paths of water courses. Stations were distinguished from saline to freshwater systems; cluster analyses indicate three distinct floral groups, and CCAs indicate that the diatoms can be related to a variety of environmental variables. Inference models show strong correlations between diatoms and conductivity, TP (total phosphorous), NO_3^-, HCO_3^-, Mg^{2+} and DO (dissolved oxygen). Other factors such as substrate type and current velocity are probably important factors in the local community structures. The diatoms were well preserved in the El Tatio and would potentially provide valuable information on groundwater chemistry in studies of similar spring systems. However, their use in such investigations would also depend on the important preservation of these unique environments.

Acknowledgements

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