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Plankton and hydrochemistry of Lake Futalaufquen (Patagonia, Argentina) during the growing season

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Abstract

Plankton communities and hydrochemistry of an oligotrophic lake occupying a glacial valley in Argentinian Patagonia (42 °49′S; 71 °43′W) were studied. Monthly samples at three stations integrated from 0 to 50 m and stratified samples at the site of maximum depth, were taken during the growing season. Transparency was always controlled by glacial silt, and not by phytoplankton. Lake water belongs to the calcium-bicarbonate type, with low conductivity (24 μS cm^{-1}), and poor buffering capacity. Forty-five phytoplankton taxa were found. Mean phytoplankton density was 49 cells ml^{-1} and mean biomass 69 μg l^{-1}. N:P relationships, inorganic nitrogen exhaustion in the photic layer, and correlations between nutrients and phytoplankton density suggests nitrogen as the main limiting factor. Fifteen zooplankton species were found. Mean zooplankton density was 12.2 ind. l^{-1} and mean biomass 22.9 μg l^{-1}. Diatoms and Boeckellidae were the dominant planktonic groups. Morphometry and hydrological factors were responsible for horizontal heterogeneity in phytoplankton and chemical variables.

Introduction

This contribution deals with the plankton assemblages of Futalaufquen Lake in relation with hydrological and chemical variables and watershed features. The lake has been sampled sporadically, as part of extensive surveys (Thomasson, 1963; INALI, 1972; José de Paggi & Paggi, 1985; Quirós, 1988b, 1989; Izaguirre *et al.*, 1990). Futalaufquen is a temperate, monomictic, and oligotrophic lake (INALI, 1972) that lies in a pristine area of the Patagonian Andes. A spatial pattern expressed as horizontal heterogeneity *sensu* Margalef (1979) may be hypothesized due to the lake's complex morphology. Present results, obtained during a period of low anthropic impact, could be useful as baseline for the assessment of future perturbations in this watershed.

Table 1. Morphometrical parameters of Futalaufquen Lake.

Altitude	518 m a.s.l.
Surface area	44.6 km^2
Mean depth *	101 m
Maximum depth *	168 m
Volume *	4509 km^3
Total watershed area	2920 km^2

* From Quiros *et al.* (1988a).

Study site

Located on the east slope of the Andes (42 °49′S; 71 °43′W), Futalaufquen Lake, occupies an intermediate position in the lake chain of the Futaleufu River watershed (Fig. 1). Morphometrical parameters are shown in Table 1. The main inflow is Arrayanes River, next in importance are the rivers Desaguadero and Cen-

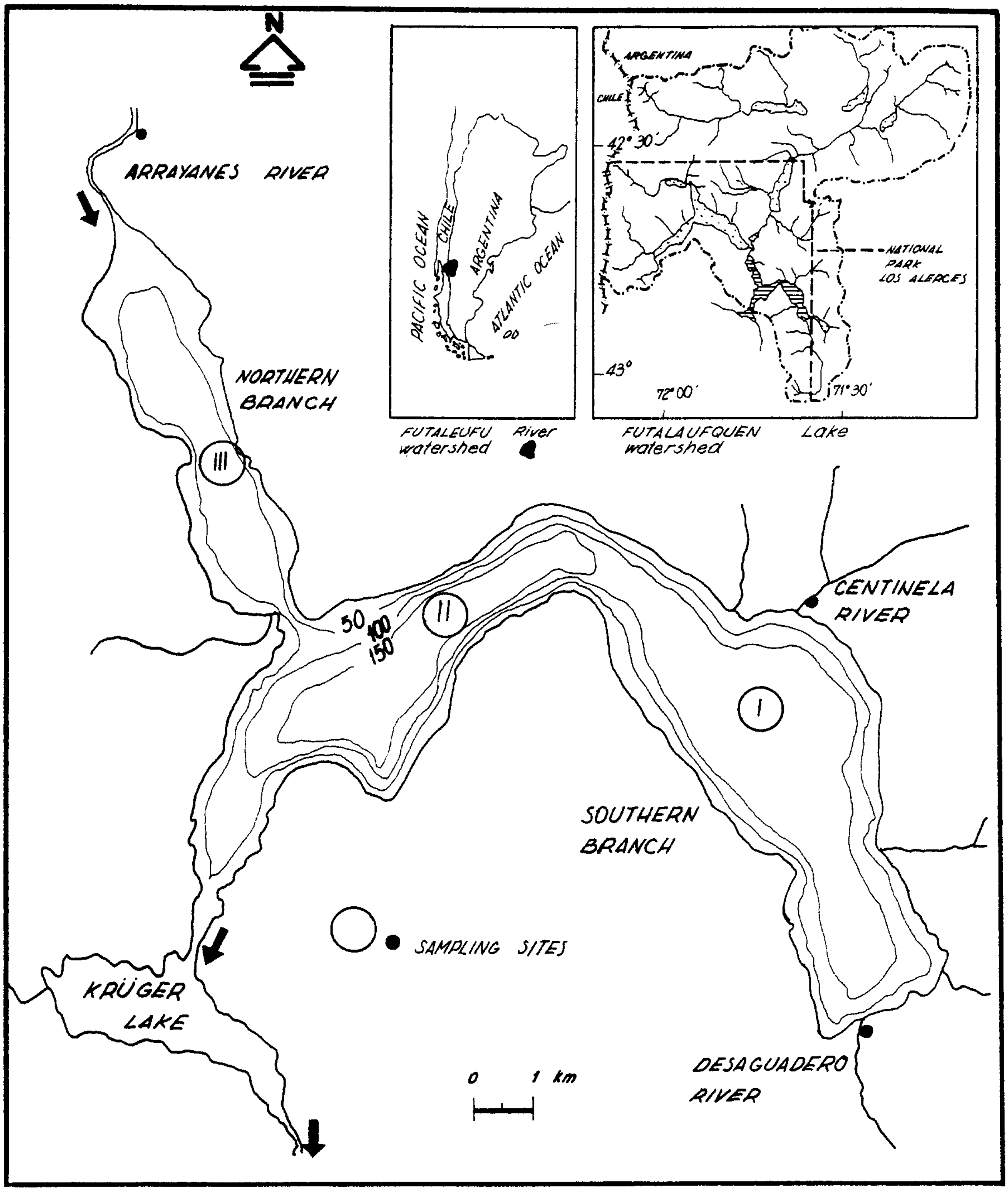

Fig. 1. Bathymetric map of Futalaufquen Lake (modified from Quirós 1988a) and lake watershed.

tinela. The southwestern arm discharges into Krügger Lake (Fig. 1). Rainfall shows a marked decrease from the Andes (1990 mm y^{-1}) towards the steppe. Intrusive and extrusive igneous rocks, composed by acid and intermediate materials, dominate the watershed lithology (Viera, pers. com.). The main human impacts are represented by 18 000 tourists each summer, cattle raising and lumbering. About 3000 inhabitants live in the watershed area.

Material and methods

Sampling sites I, II and III (Fig. 1), were monitored monthly from October 1988 to February 1989. Integrated samples for chemical and phytoplankton analyses were taken with a Van Dorn sampler by pooling water from 0, 15, 30 and 45 m. Stratified samples from 0, 50, 100 and 150 m for chemical analyses were taken at the deepest station (II). Main inflows were also sampled for chemical analyses. Transparency and surface temperature were measured with a Secchi disk and a mercury thermometer, respectively. Potentiometric total alkalinity and pH were measured with a VEGA V pH-meter, conductivity (25 °C) with an HORIBA U-27 water-checker, and dissolved oxygen using the Winkler method (A.P.H.A., 1978). Analyses were done within 24 hours after sampling. Unfiltered samples for nutrients and cations were frozen at −20 °C until analysis; samples for silicate-Si were kept at 4 °C. TIN (nitrate-N + nitrite-N) and SRP (soluble reactive phosphorus) were determined after Strickland & Parsons (1972). Silicate-Si was measured with a TECHNICON autoanalyzer (Technicon Instr., 1977). Calcium, magnesium, sodium and potassium were analyzed by atomic absorbance spectrophotometry. Hydrological data on daily water levels and the regression model to estimate water discharge were supplied by Agua y Energía Eléctrica (pers. com.).

Qualitative phytoplankton samples were taken with a 25 μm mesh net by vertical hauls from 50 m to the surface and fixed *in situ* with 5% formaldehyde. Quantitative samples were preserved with acetic lugol. Cell counting was done following the simple aliquot method (Semina, 1975). Between 100 and 200 cells of the most frequent species were counted to achieve a relative precision of 25–30% (Venrick, 1975). Diatoms were processed after Hasle & Syvertsen (1980). Cell biomass was estimated after Trevisan (1978) by measuring 15–20 individuals of each species.

Monthly zooplankton samples were obtained at II. Samples were collected by vertical hauls from 50 m to the surface, using a 75 μm mesh conical net, and preserved *in situ* with 5% formaldehyde. The number of subsamples for density estimations was determined according to Cassie (1971) (error under 10%). Macrozooplankton was subsampled with a Russell sampler and counted in 5 ml Bogorov chambers. Microzooplankton (rotifers and nauplii) was subsampled with a Hensen-Stempel pipette and counted in 1 ml Sedgwick-Rafter chambers. Thirty to 50 individuals of each category were measured. Crustacean dry weight was estimated according to Dumont *et al.* (1975) and Bottrell *et al.* (1976), and that of rotifers according to Ruttner-Kolisko (1977).

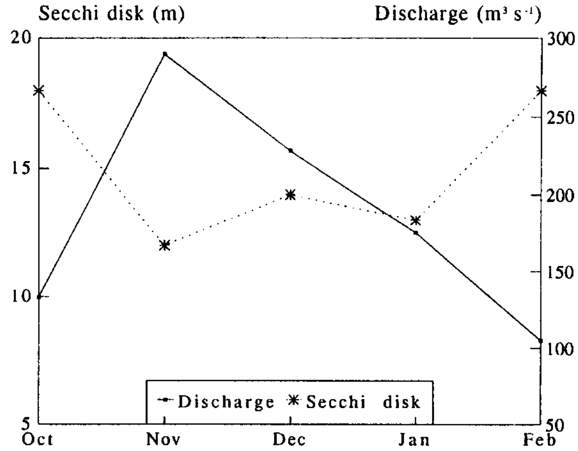

Fig. 2. Water discharge through Frey River and Secchi disk transparency of Futalaufquen Lake.

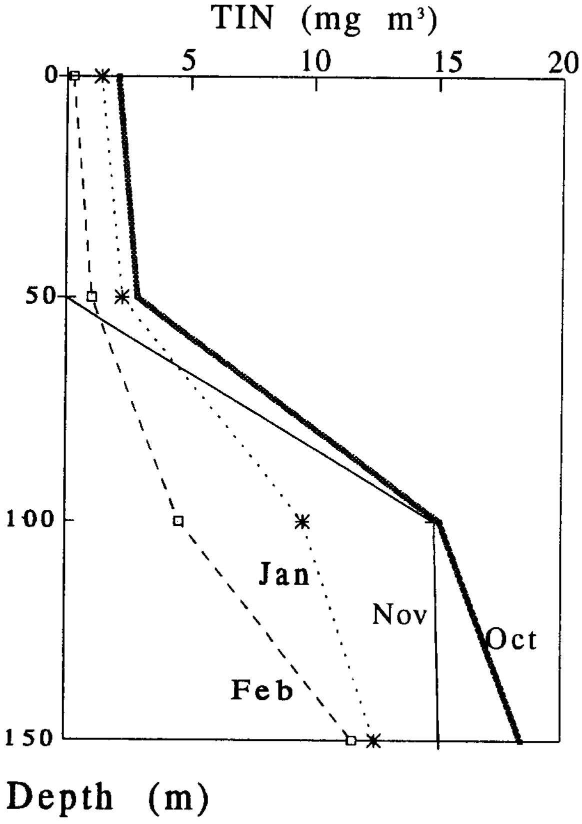

Fig. 3. Spring and summer vertical profiles of nitrate-N at station II in Futalaufquen Lake.

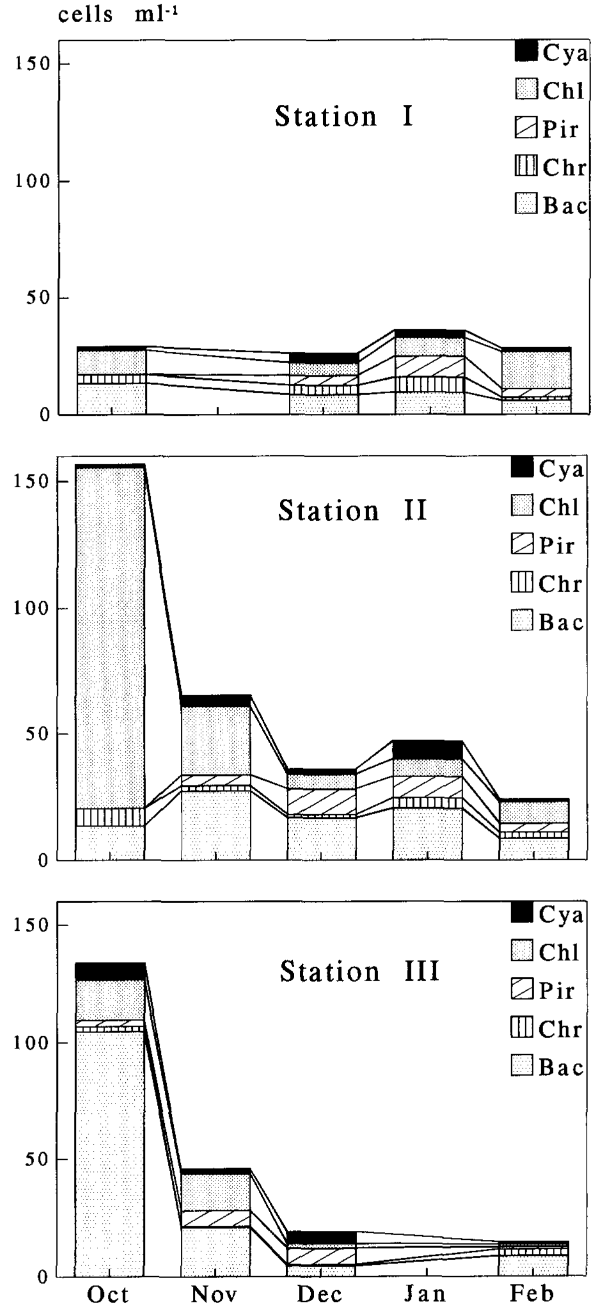

Fig. 4. Spring and summer sequence of the main phytoplankton groups at samplings sites I, II and III.

Results

Hydrology and water chemistry

Maximum discharge took place during the thaw and correlated exponentially with transparency ($r = -0.91$; $p < 0.05$) (Fig. 2). The euphotic zone estimated from the Secchi disk transparency (Lemoalle, 1981) varied from 30 to 50 m. Surface water temperature rose from 4.4 °C up to 16 °C from October to February.

A theoretical retention time (T_w) of 0.94 y^{-1} for the whole lake was estimated using historical records (Agua y Energía Eléctrica, 1983). However, the northern branch has 0.48 km^3 while the southern branch has a volume of 2.14 km^3. The first receives 80% of the lake inflow from Arrayanes River. Therefore, T_w of northern and southern branches differs markedly, being 0.11 and 4.5 y^{-1} respectively.

Average and standard deviations of chemical variables at I, II and III, are shown in Table 2. Mean conductivity was 24 $\mu S\ cm^{-1}$; an exceptional value of 56 $\mu S\ cm^{-1}$ at III, in January, was coincident with high values of Ca, Mg and alkalinity. pH values were always below seven. Cationic relationships (equivalents) were Ca>Mg = Na>K. Silicate-Si showed similar concentrations at all stations, with a maximum of 4.44 mg l^{-1} (station III, January). Vertical profiles of pH, alkalinity, conductivity, silicate-Si and cations were orthograde or close to that type. Oxygen profiles at II always showed good oxygenation even at the bottom. From October to December, oxygen saturation oscillated around 90%. The minimum saturation (86%) was detected at a depth of 150 m, in November. Total inorganic nitrogen was similar at all sampling sites. All TIN vertical profiles (Fig. 3) were negative clinogrades. SRP vertical profiles were irregular. Molar N:P relationship (TIN/SRP) showed a mean ratio of 0.65 in the euphotic zone, being lowest at III. The rivers Arrayanes, Desaguadero and Centinela presented similar ratios (0.39, 0.58 and 0.59, respectively).

Phytoplankton

Mean phytoplankton density was 50 cells ml^{-1} (range: 15–155 cells ml^{-1}), with a mean biomass of 69 $\mu g\ l^{-1}$ (range: 16–261 $\mu g\ l^{-1}$). Forty-five phytoplankton taxa were found (Table 3), with a mean of 18 taxa per sample. Four taxa contributed 74% of the total biomass, *Synedra nana*, *Peridinium* spp., *Staurastrum tetracerum* and *Oocystis marssonii.*

Bacillariophyceae accounted for the highest relative cell density (41%), followed by Chlorophyceae (35%), Cryptophyceae (10%), Chrysophyceae (7%), and Xanthophyceae (0.5%). The five most frequent species at each station are shown in Table 4. Thirty-two, 39 and 36 taxa were found at I, II and III, respectively. The spring maximum took place in Octo-

Table 2. Seasonal mean (X) and standard deviation (SD) values of physical and chemical variables measured in the euphotic zone of sampling sites I, II, and III in Futalaufquen Lake and its main inflows.

		X SD	X SD	X SD
Lake station		I	II	III
pH		6.69-0.27	6.75-0.21	6.71-0.17
Alkalinity	(meq l^{-1})	0.26-0.005	0.25-0.03	0.29-0.15
Conductivity	(μS cm^{-1})	23.80-2.90	23.60-1.82	29.00-15.3
TIN	(μg l^{-1})	1.40-1.07	1.68-0.96	1.48-1.94
SRP	(μg l^{-1})	4.45-2.92	4.76-2.58	7.16-3.32
SiO_3-Si	(mg l^{-1})	3.41-0.10	3.43-0.13	3.54-0.52
Ca	(mg l^{-1})	3.52-1.22	3.82-1.18	6.54-4.14
Mg	(mg l^{-1})	0.85-0.31	0.94-0.41	0.90-0.44
Na	(mg l^{-1})	1.48-0.08	1.39-0.17	1.48-0.22
K	(mg l^{-1})	0.42-0.06	0.42-0.11	0.39-0.04
Rivers		Arrayanes	Desaguadero	Centinela
pH		6.72-0.37	7.32-0.33	6.83-0.28
Alkalinity	(meq l^{-1})	0.26-0.03	0.55-0.01	0.40-0.02
Conductivity	(μS cm^{-1})	21.50-2.69	55.50-8.50	59.00-21.0
TIN	(μg l^{-1})	0.77-0.61	2.80-0.56	1.35-1.14
SRP	(μg l^{-1})	5.83-2.12	15.35-7.65	23.77-21.1
SiO_3-Si	(mg l^{-1})	3.15-0.09	4.40-0.19	5.12-0.25
Ca	(mg l^{-1})	3.50-1.49	4.80-1.53	3.91-1.10
Mg	(mg l^{-1})	0.76-0.30	1.22-0.09	0.98-0.28
Na	(mg l^{-1})	1.23-0.11	2.64-0.67	2.83-0.46
K	(mg l^{-1})	0.36-0.06	0.51-0.13	0.40-0.09

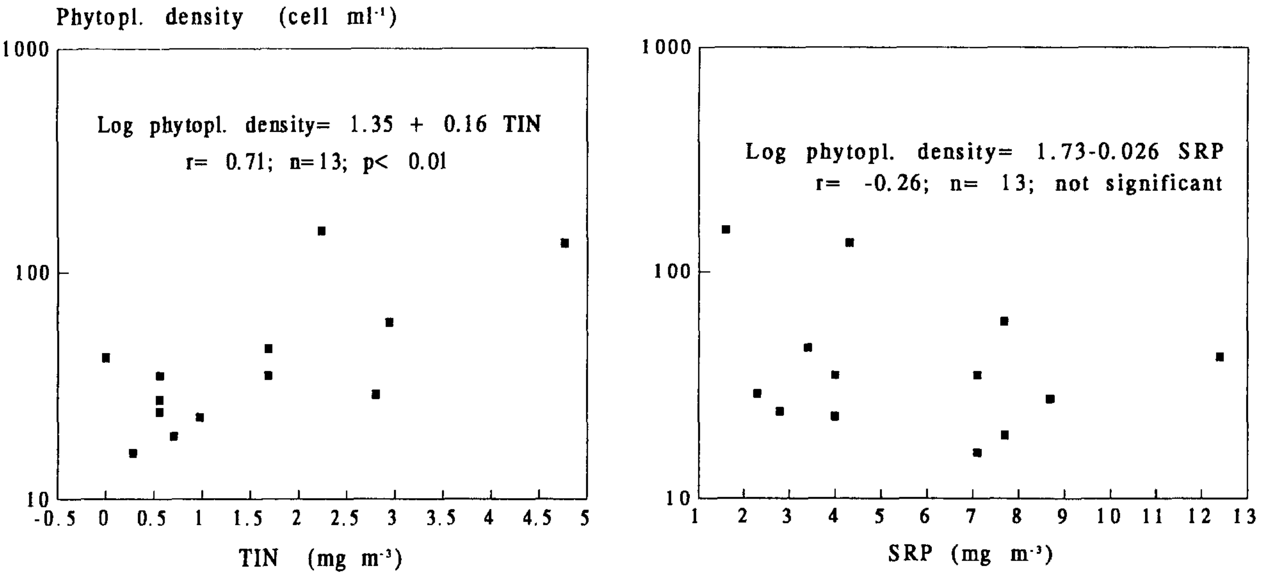

Fig. 5. Relationships between phytoplankton density and nutrients in Futalaufquen Lake from October 1988 to February 1989.

Table 3. Phytoplankton taxa identified during the growing season in Futalaufquen Lake.

BACILLARIOPHYCEAE
Asterionella formosa Hass.
Ceratoneis arcus Kutzing
Cyclotella stelligera Cl. u. Grun.
Cymbella affinis Kutzing
Cymbella cistula (Hemprich) Grun.
Epitemia sorex Kutzing
Fragilaria sp.
Gomphonema olivaceum (Lyngbye) Kutzing
Melosira sp.
Navicula spp.
Nitzchia acicularis W. Smith
Nitzchia frustulum (Kutzing) Grun.
Nitzchia pseudoamphyoxis Husted
Rhizosolenia eriensis H.L. Smith
Synedra nana Meister
Synedra ulna (Nitzch.) Ehr.
CHRYSOPHYCEAE
Dinobryon divergens Imhof.
Dinobryon sociale Ehrenberg
Malomonas sp.
cyst of Chrysophyceae
CRYPTOPHYCEAE
Chroomonas sp.
Rhodomonas lacustris Pascher et Ruttner
DYNOPHYCEAE
Peridinium spp.
XANTOPHYECEAE
Gloeochloris sp.
CHLOROPHYCEAE
Chlamydomonas spp.
Coccomyxa lacustris (Chod.) Pasch. 1915
Coenocystis subcylindrica Kors 1953
Cosmarium sp.
Cruciginiella lunaris Lemn.
Elakatothrix genevensis (Reverd.) Hindak
Eudorina elegans Ehr. 1832
Desmatractum sp.
Dicthyosphaerium simplex Korchikoff
Neprocytium limneticum (G.M. Smith) G.M. Smith
Oocystis marssonii Lemm. 1878
Paulschulzia pseudovolvox (Schulz.) Skuja
Pandorina smithii Chodat
Sphaerocystis schroeteri Chodat
Staurastrum tetracerum Ralfs
Staurodesmus triangularis v. subparalellus (G.M. Smith) Teiling
CYANOPHYCEAE
Anabaena sp.
Aphanocapsa elachista v. conferta West et West
Coelosphaerium kutzingianum Nageli
Oscillatoria sp.

ber except in I (Fig. 4). *S. nana* and *A. formosa* codominated at III while *Coccomyxa lacustris* and *O. marssonii* codominated at II. From November onwards no relevant differences were observed among sampling sites. The Shannon-Weaver diversity index was minimum in October (-1.69 bits ind^{-1}) and maximum in November (4.5 bits ind^{-1}). Mean diversity for all samples was 3.34 bits ind- $^{-1}$, without significant differences among sampling sites. Phytoplankton

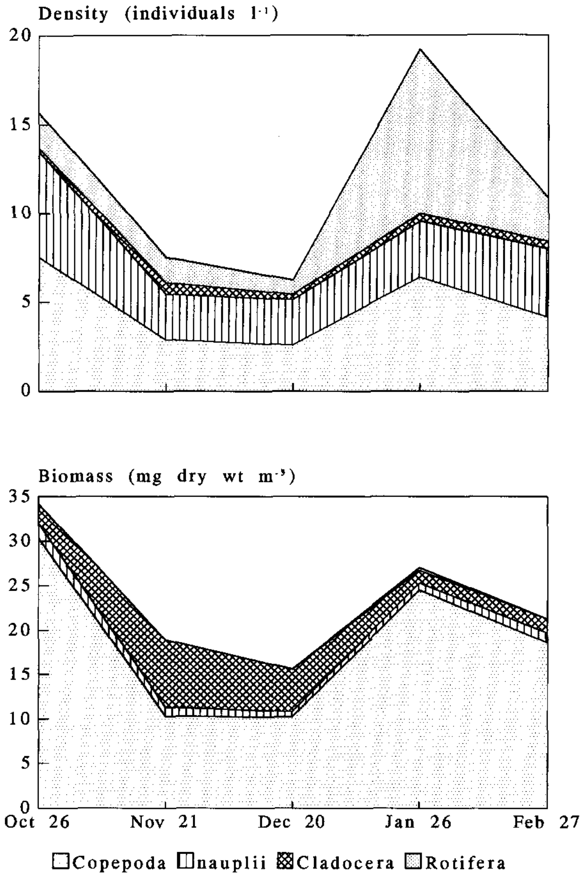

Fig. 6. Temporal sequence of density and biomass of the main zooplankton groups at station II in Futalaufquen Lake. Rotifer biomass is almost undetectable at this scale.

biomass was well correlated with phytoplankton density (r = 0.63; n = 15). Variance of phytoplankton density was explained (50.4%) by TIN and not by SRP (Fig. 5a and 5b).

Zooplankton

Fifteen zooplankton species were recorded: 3 cladocerans, 4 copepods and 8 rotifers (Table 6). *Boeckella michaelseni* was always dominant both in density and biomass (Fig. 6). *Mesocyclops araucanus* and *Parabotreas sarsi* were the only predator species, representing on average a very low proportion of the whole community. Cladocerans were uniformly scarce (Fig. 6). The most important species were *Daphnia middendorffiana* (*sensu* Paggi, 1973) in November and December, and *Bosmina chilensis* during the rest of the season. *Conochilus unicornis* was the dominant rotifer in all sampling dates, probably owing to its colonial habit. Mean density was 12.2 ind l^{-1}, with a biomass of 22.9 $\mu g\ l^{-1}$. The community composition showed a great constancy, with smooth fluctuations in density and biomass (Fig. 6). Total species number varied between 8 and 13, and crustaceans between 5 and 7. Zooplankton minima were recorded in November and December, while maxima corresponded to early spring and midsummer. The summer density peak was mainly determined by rotifers. Mean macrozooplankton size (762 μm) tracked the changes in *Daphnia* density. Phytoplankton biomass explained 52% of zooplankton biomass variance ($r = 0.72$; $p < 0.05$) (Fig. 7).

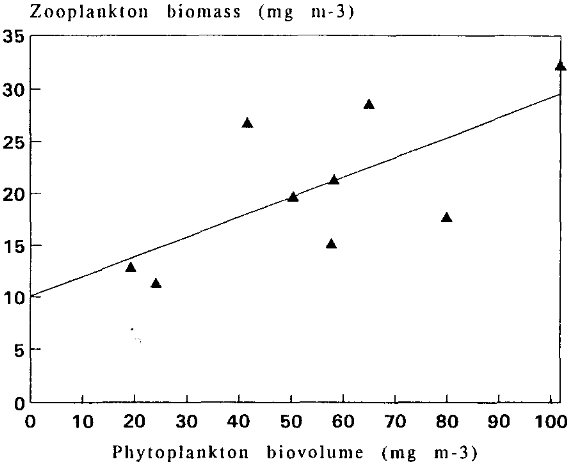

Fig. 7. Relationships between phytoplankton and zooplankton total biomass in Futalaufquen Lake during the growing season.

Discussion

Futalaufquen Lake waters are calcium-bicarbonate type, with low conductivity and poor buffering capacity. This is explained by the watershed geochemistry, dominated by igneous rocks, a feature shared with other lakes and rivers of the Patagonian Andes (Campos, 1984; Pedrozo *et al.*, 1993). Cationic relationships and absolute values were the same found during the summer of 1984 (Quiros, 1989). Maxima of alkalinity, conductivity, and Ca found in January at III, may be due to rain and land washout four days before sampling. Concentrations of SRP, Ca and K were higher at III. Variances were also particularly high at III (Table 2), indicating that it was the most unstable station. This finding confirms the riverine characteristics of the northern branch, also evidenced by the short

Table 4. Relative frequency (%) of the five most frequent phytoplankton species at sampling sites I, II and III in Futalaufquen Lake.

Station I	%	Station II	%	Station III	%
R. eriensis	11.9	*C. lacustris*	32.6	*S. nana*	30.8
D. divergens	11.9	*O. marssonii*	9.6	*A. formosa*	8.4
R. lacustris	10.5	*R. eriensis*	8.2	*S. schroeteri*	7.9
Chlamydomonas sp.	8.6	*R. lacustris*	6.7	*R. eriensis*	7.5
S. schroeteri	8.1	*A. formosa*	5.1	*R. lacustris*	5.8

Table 5. Zooplankton species identified during the growing season in Futalaufquen Lake.

CLADOCERA

- *Bosmina chilensis* Daday, 1902
- *Bosmina longirostris* (O.F. Muller, 1785)
- *Daphnia middendorffiana* Fischer, 1851

COPEPODA

Calanoida

- *Boeckella michaelseni* (Mrazek, 1901)
- *Parabroteas sarsi* (Daday, 1901)

Cyclopoida

- *Mesocyclops araucanus* Löffler, 1961
- *Tropocyclops prasinus v. meridionalis* (Kiefer, 1931)

ROTIFERA

Bdelloidea

- *Collotheca mutabilis* (Hudson, 1885)
- *Collotheca pelagica* (Rousselet, 1893)
- *Conochilus unicornis* (Rousselet, 1892)
- *Euchlanis dilatata* Ehrenberg, 1832
- *Keratella thomassoni* Thomasson, 1957
- *Polyarthra vulgaris* Carlin, 1943
- *Synchaeta pectinata* Ehrenberg, 1832

retention time (40 days). The chemical composition of the main inflow (Table 2) was determinant of lake water chemistry.

We have found several evidences of N-limitation. The spring phytoplankton maximum seems to decay due to nitrate-N exhaustion in photic layers, as shown by TIN vertical profiles (Fig. 3). This is a common feature shared by many lakes on the western slope of the Andes (Campos, 1984). On the other hand, the N:P molar ratios of all lake arms and the main inflows, were always below 1 after October, being 1.4 the maximum value observed. These values are far from the colimitation range of 11–26.5 (Thayer, 1974; Fricker, 1980; Ram & Plotkin, 1983), considering N:P as $(NO_3 + NO_2 + NH_4)$-N/SRP. Ammonia-N was undetectable in a preliminary survey of the Lake. The maximum N:P ratio was 1.4, being always lower than unit after October. *Nostoc* sp. colonies (2–4 cm diameter), a biological indicator of N-limitation (Margalef, 1983), were recorded at the bottom of coastal waters. Regression-correlation analysis (Figs 5a, 5b) also highlights the importance of nitrogen instead of phosphorus in explaining phytoplankton density variance. All approaches used suggest nitrogen as the main limiting factor in Futalaufquen Lake. This feature could also be shared by upstream lakes of the watershed, as suggest the low N:P ratio of the Arrayanes River (0.39). However, Quirós (1989) using a different methodology, found in a single survey at the end of summer a TN:TP ratio of 242, indicating P-limitation. Phytoplankton communities evolve in a non-equilibrium dynamic (Harris, 1986; Sommer, 1989b) and therefore, could be limited by more than one factor at the same time (Dodds *et al.*, 1989), or by different factors along the year (Pizzolon, unpublished data; Pedrozo *et al.*, 1993; Diaz *et al.*, 1994). Despite the worldwide extend of phosphorus limitation in temperate lakes proposed by Schindler (1978), recent data on Patagonia

Table 6. Mean seasonal density (ind l^{-1}) and biomass ($\mu g\ l^{-1}$) for the main zooplankton groups at Station II in Futalaufquen Lake. Calanoida and Cyclopoida include adults and copepodites.

	Calanoida	Cyclopoida	nauplii	Cladocera	Rotifera
Density	4.22	0.48	3.60	0.30	3.62
(range)	1.68-7.17	0.03-0.88	1.37-6.66	0.07-0.57	0.72-9.27
Biomass	16.02	2.72	1.13	2.92	0.16
(range)	7.0-27.82	0.24-5.87	0.41-2.05	0.55-7.45	0.04-0.42

(Pedrozo *et al.*, 1993; Soto *et al.*, 1994; Diaz & Pedrozo, 1994) and the present results, suggest the existence of a greater number of N-limited lakes than expected, in temperate South America.

Silicate-Si concentration was high, although lower than in Chilean and New Zealand lakes (Campos, 1984; Duthie & Stout, 1986). Silicate-Si vertical profiles were always orthograde and its concentration did not change over time. Correlation with diatoms was not significant. Compared with published data (Werner, 1977; Tilman *et al.*, 1982; Sommer, 1989b; Diaz, 1994), the values recorded in Futalaufquen Lake do not seem to be limiting for diatoms growth.

The most surprising feature of phytoplankton succession was the simultaneous dominance in October of the large diatom *Synedra nana* (3127 μm^3) at III, and of the small Chlorophyceae *Coccomyxa lacustris* (20.7 μm^3) at II. This event does not agree with the general theory of phytoplankton succession, which states a sequence that begins in spring with a bloom of small cells that grow fast in turbulent waters (Sommer, 1989a). Margalef (1983) reported *Synedra acus* as a frequent species in potamoseston, while Duthie & Stout (1986) also found the suspension of heavy cells without floating mechanisms in a New Zealand lake exposed to strong winds. The northern branch is characterized by winds frequently over 18 m s^{-1}, and a retention time typical of rivers. Both are synergic factors of turbulence, which can explain the dominance of *S. nana* at III. We cannot explain the dominance of the chlorophyceans *C. lacustris* and *O. marssonii* at II in October instead of the small diatoms expected in this time of the year (Tilman *et al.*, 1982; Harris, 1986; Sommer, 1989a; Diaz *et al.*, 1994).

Decreased water transparency after the spring maximum was explained by glacial silt inflow, as shown by the highly significant correlation between water discharge and transparency (Fig. 2), and not by phytoplankton growth. Phytoplankton biovolume has proved to be an element of lake eutrophication assessment at least as valuable as chlorophyll *a* (Rott, 1984). Maximum (0.26 mg l^{-1}) and mean phytoplankton biomass (0.069 mg l^{-1}) allow us to consider this lake as oligotrophic (Fricker, 1980; Rott, 1984; Margalef, 1983).

The zooplankters present in the lake are widely distributed in Andean Patagonia, where calanoid copepods are dominant, cladocerans scarce and diversity low (Soto & Zúñiga, 1991; Marinone & Menu-Marque, unpublished data). Crustacean density and biomass in February (8.6 ind l^{-1} or 22.8 $\mu g\ l^{-1}$) were in good agreement with records of March 1984 (13.9 ind l^{-1} or 27.5 $\mu g\ l^{-1}$) by Marinone & Menu-Marque (unpublished data). Biomass values were comparable to those published for oligotrophic, deep, stratified lakes of Europe (Herzig, 1979). Mean macrozooplankton biomass (21.7 $\mu g\ l^{-1}$) is among the lowest levels recorded in the world's literature (Ivanova, 1987). Spring and summer zooplankton maxima have been recorded in Chilean Araucanian lakes (Campos, 1984; Campos *et al.*, 1987), when the community experiences strong changes (Zúñiga & Domínguez, 1978). Other coincidences with these lakes are the dominance of centropagid copepods over cladocerans, which indicates oligotrophy (Campos *et al.*, 1987), and the parallel oscillations of phyto and zooplankton which would suggest that there is no top-down control of phytoplankton (Campos, 1984). The presence of a large cladoceran such as *Daphnia* denotes low predation pressure by larval or planktivorous fish, while the reduction in *Daphnia* size in January could be related to the fish recruitment season. Chilean lakes seem to have higher zooplankton densities and higher proportions of cladocerans and cyclopoids (Domńguez & Zúñiga, 1979) than lakes east of the Andes (Marinone & Menu-Marque, unpublished). These features are probably related to the lower elevation and higher temperature of Chilean lakes, that render them slightly more productive than Argentine lakes (Quirós & Drago, 1985). Sporadic records on phyto and zooplankton (Thomasson, 1963; INALI, 1972; José de Paggi & Paggi, 1985) indicate that the dominant species remain the same, thus failing to show water quality changes during the last decades.

The hypothesis on lake horizontal heterogeneity was supported by chemical and phytoplankton community results. Phytoplankton periodicity in these lakes could be influenced by the rainfall regime, as suggested by Thomasson (1963). Not only vertical mixing is important to explain phytoplankton succession, but also horizontal transport from the watershed. Pulses of nutrients can reach the lake through Arrayanes River, generating a spatial pattern expressed as horizontal heterogeneity (Margalef, 1979). A gradient of perturbations, *sensu* Margalef (1975), decreasing from the northern branch to the southern one can be hypothesized and partially evidenced in the present study. The northern branch is the most directly exposed to chemical and biological perturbations induced by Arrayanes River, while the southern branch is the most protected. On the other hand, during hydrologically stable periods the differences among stations would be minimum.

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