Phytoplankton of Andean Patagonian lakes

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With 6 figures and 2 tables

Abstract: This article presents a review of the phytoplankton from the lakes of the Andean Patagonian region. This is one of the most important lake district of Argentina, which encompasses a large number and highly diverse unpolluted water bodies. Data from deep and shallow lakes within a trophic and latitudinal gradient are presented. The information focus on abundance, diversity, temporal and spatial dynamics, size and taxonomic structure, trophic interactions, functional groups, in most of the cases related to physical and chemical features.

The Andean lakes comprise deep and shallow basins of glacial origin. The phytoplankton abundance and biomass are usually low, and the assemblages are dominated by nanoflagellates (*Chrysochromulina parva* and *Plagioselmis lacustris*) and by microphytoplanktonic chrysophyceans and dinoflagellates like *Dinobryon* spp., *Peridinium* spp. and *Gymnodinium* spp., and the diatoms *Urosolenia eriensis*, *Cyclotella stelligera*, *Fragilaria* spp. and *Synedra* spp. The striking oligotrophy of the lakes in this region is regulated by nitrogen availability; despite the worldwide extend of phosphorus limitation in temperate lakes.

Deep Andean lakes have a very high transparency, and deep chlorophyll maxima (DCM) develop during the stratification period. These DCM are partially constituted by dinoflagellates, which usually dominate the total phytoplankton biomass in these environments. These results evidence the high impact of light and temperature in the phytoplankton vertical distribution in deep lakes.

On the other hand, the numerous shallow Andean lakes represent a varied group of environments with oligotrophic and in some cases mesotrophic conditions. The nanoplankton is also dominant, but the diversity of the microphytoplankton is higher than in deep lakes. They share a great number of species with deep lakes, however, some other groups like chlorococcals, desmids and euglenophytes (i.e. *Trachelomonas* spp.) usually dominate the phytoplankton assemblage.

**Keywords**: Phytoplankton, Andean lakes, Patagonia

Introduction

In the southern extreme of South America, Patagonia constitutes an extensive region shared by Argentina and Chile. The Andes Mountains, which comprise the limit between both coun-

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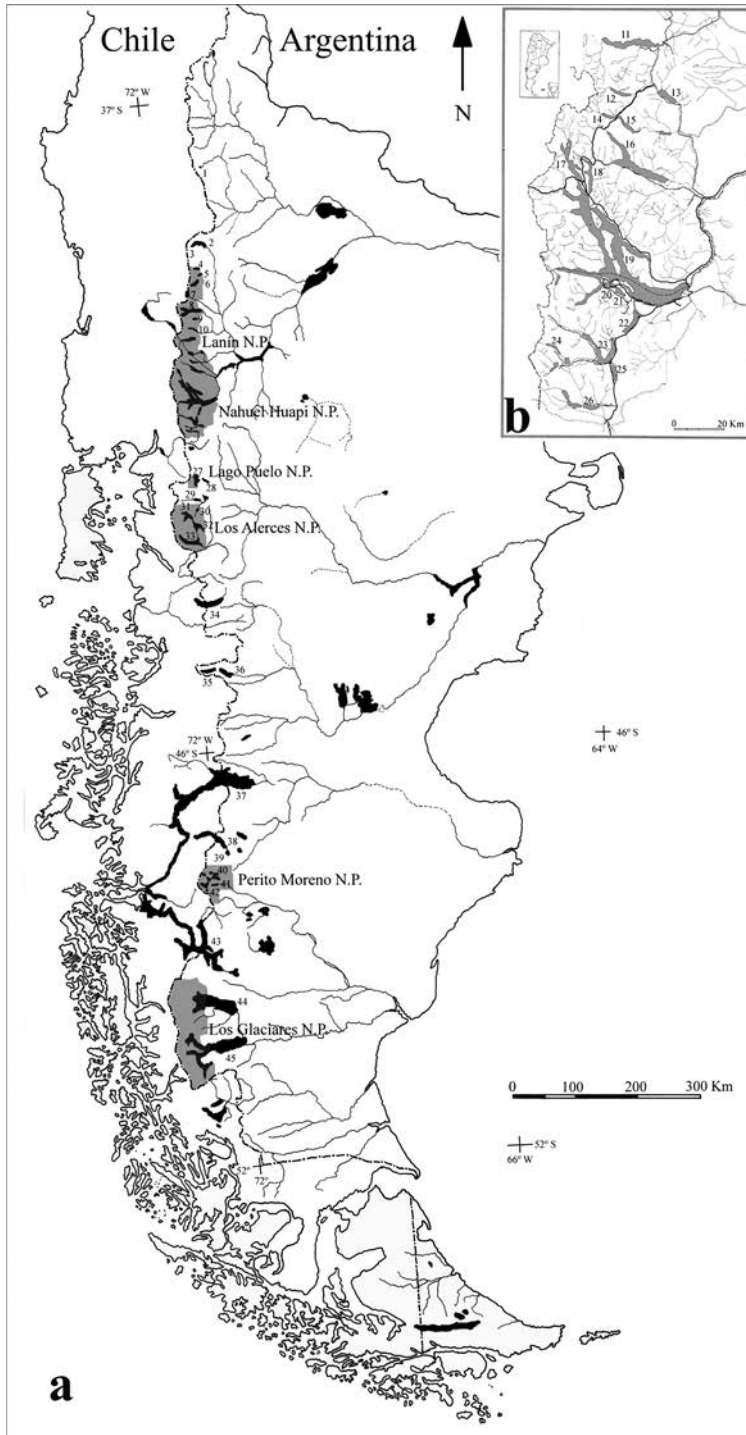
tries, represent a strong geographic feature in the region (Fig. 1a). At the east of the Andes, Argentine Patagonia is divided in the Andean-Patagonian region, and the Patagonian Plateau (Iriondo 1989). Both areas have a large number of water bodies, but only in the Andean region large and deep lakes are present. Between 37°S in the North Patagonia, to Tierra del Fuego (56°S) in the southernmost extreme, a large number of deep lakes of glacial origin characterize the region, and usually belong to National Parks (N.P.) or protected territories situated all along the latitudinal gradient (Table 1, Fig. 1a). The climate is cold-temperate with fall and winter as rainy seasons (Paruelo et al. 1998). These largest and deepest lakes of South America are situated in piedmont areas associated with the Andean Patagonian forests, and are accompanied by a profuse number of small and shallow lakes, comprising a lacustrine area of 9500 km^2 (Quirós & Drago 1999). Also, a few high mountain shallow lakes are present in the area. The very large and deep lakes of South Patagonia are still fed by active glaciers associated with the Southern Patagonian Ice Field (48°20´–51°30´S) (Los Glaciares N.P., Fig. 1a), the second largest extrapolar extension of ice in the world which is shared by Argentina and Chile, as well as a few lakes related with smaller glaciers in the Nahuel Huapi and Puelo N.P. (Fig. 1a, b). Most of the Andean Patagonian lakes drain their waters into the Atlantic watershed, while several lakes all along the South Andes Cordillera drain to the Pacific watershed (Table 1). According to their origin, the lakes are low productive and have very dilute waters (Pedrozo et al. 1993), providing particular scenarios for the development of aquatic organisms. This article summarizes the information about the phytoplankton communities of deep and shallow lakes of this large Andean region, emphasizing on the physical, chemical and biological factors which modulate their dynamics.

Previous research

The knowledge about the phytoplankton in this South Andean region began in the 50´s decade, when Thomasson studied the plankton communities of several deep and shallow lakes of Argentinean and Chilean Patagonia during the Swedish scientific expedition performed in 1953–1954. The main work was carried out within the Chilean Lake District; however, data obtained in the Nahuel Huapi National Park in Argentina (Fig. 1b) was also published (Thomasson 1959). Plankton samples from surface waters of the lakes Nahuel Huapi, Gutiérrez, Mascardi, Guillelmo, Frías and Hess, were obtained during summer (January–February 1954). These first records corresponded to the composition of the net phytoplankton fraction (as samples were collected with 25 μm mesh-sized plankton net), revealing the dominance of *Dinobryon divergens* and *Urosolenia eriensis*, the frequent presence of *Botryococcus braunii* and several species of desmids. The exception was constituted by the glacial Lake Frías, where the phytoplankton was less abundant and the diatoms *Diatoma elongatum* and *Synedra ulna* prevailed (Thomasson 1959). During a second survey, Thomasson (1963) included lakes from the Lanín and Los Alerces N.P., at the northern and southern of the Nahuel

Fig. 1. a) Map of the Patagonian region with the location of the deep Andean Patagonian lakes of Argentina, most of them included in National Parks (N.P.); **b**) Detailed map of the Nahuel Huapi National Park. Lakes are listed by numbers referenced in Table 1.

Table 1. Geographic location, altitude, lake area and maximum depth of the deep Andean Patagonian lakes, indicating their association to Provincial or National Parks and to the Atlantic or Pacific watersheds. The lakes are listed according to the North-South latitudinal gradient along the Andes. The *References on Phytoplankton* correspond to the lakes where limnological investigations on phytoplankton were performed. References: n.a., data not available.

	Lakes	Coordinates	Altitude (m a.s.l.)	Lake Area (km²)	Maximum Z (m)	National Park	Watershed	References on Phytoplankton
1	Caviahue	37°53′S 71°02′W	1620	9.2	95	Copahue (Prov.)	Atlantic	Beamud et al. 2007, 2010
2	Aluminé	38°55′S 71°08′W	1125	57.0	165	—	Atlantic	
3	Moquehue	38°54′S 71°16′W	1127	19.9	n.a.	—	Atlantic	
4	Ñorquinco	39°09′S 71°17′W	1025	5.4	89	Lanín	Atlantic	
5	Ruca Choroi	39°14′S 71°11′W	1232	3.3	n.a.	Lanín	Atlantic	
6	Quillén	39°25′S 71°19′W	975	23.0	155	Lanín	Atlantic	Thomasson 1963
7	Tromen	39°31′S 71°26′W	1049	125.0	n.a.	Lanín	Atlantic	
8	Huechulafquen	39°46′S 71°20′W	875	78.2	>150	Lanín	Atlantic	
9	Currhué	39°51′S 71°26′W	875	11.6	n.a.	Lanín	Atlantic	
10	Lolog	40°01′S 71°26′W	912	35.0	n.a.	Lanín	Atlantic	Díaz et al. 2007
11	Lácar	40°14′S 71°30′W	625	49.0	277	Lanín	Pacific	Thomasson 1963, Díaz (unpubl.)
12	Hermoso	40°21′S 71°31′W	1021	8.0	180	Lanín	Atlantic	
13	Meliquina	40°21′S 71°17′W	930	9.0	n.a.	Lanín	Atlantic	
14	Villarino	40°26′S 71°24′W	940	5.2	>100	Nahuel Huapi	Atlantic	Queimaliños (unpubl.)
15	Falkner	40°28′S 71°29′W	927	11.1	>100	Nahuel Huapi	Atlantic	Queimaliños (unpubl.)
16	Traful	40°36′S 71°28′W	804	76.0	300	Nahuel Huapi	Atlantic	Thomasson 1963, Díaz et al. 2000, 2007
17	Espejo	40°37′S 71°45′W	930	44.0	n.a.	Nahuel Huapi	Atlantic	Thomasson 1963, Queimaliños (unpubl.)
18	Correntoso	40°40′S 71°39′W	801	27.0	n.a.	Nahuel Huapi	Atlantic	Thomasson 1963, Queimaliños (unpubl.)
19	Nahuel Huapi	40°50′S 71°30′W	764	557.0	464	Nahuel Huapi	Atlantic	Thomasson 1959, 1963, Díaz et al. 1998
20	Moreno West	41°03′S 71°32′W	768	6.0	90	Nahuel Huapi	Atlantic	Queimaliños et al. 1999, 2002 Pérez et al. 2002, Balseiro et al. 2004
21	Moreno East	41°06′S 71°29′W	768	6.1	106	Nahuel Huapi	Atlantic	Thomasson 1963
22	Gutiérrez	41°12′S 71°26′W	750	16.4	111	Nahuel Huapi	Atlantic	Thomasson 1959, 1963 Díaz et al. 2000, 2007
23	Mascardi	41°17′S 71°34′W	750	39.2	218	Nahuel Huapi	Pacific	Thomasson 1959, 1963, Pérez et al. 2002 Díaz et al. 2000, 2007, Queimaliños (unpubl.)

Table 1. cont.

	Lakes	Coordinates	Altitude (m a.s.l.)	Lake Area (km²)	Maximum Z (m)	National Park	Watershed	References on Phytoplankton
24	Fonck	41°18´S 71°46´W	782	4.5	85	Nahuel Huapi	Pacific	Díaz et al. 2000, 2007
25	Guillelmo	41°23´S 71°23´W	826	5.4	107	Nahuel Huapi	Pacific	Thomasson 1963, Díaz et al. 2000, 2007 Pérez et al. 2002, Queimaliños (unpubl.)
26	Steffen	41°31´S 71°24´W	525	6.3	77	Nahuel Huapi	Pacific	
27	Puelo	42°10´S 71°40´W	150	44.0	180	Lago Puelo	Pacific	Pérez 2006, Queimaliños (unpubl.)
28	Epuyén	42°11´S 71°30´W	250	17.4	148	—	Pacific	
29	Cholila	42°28´S 71°40´W	547	17.5	108	—	Pacific	
30	Rivadavia	42°36´S 71°39´W	527	21.7	147	Los Alerces	Pacific	Balseiro et al. 2004, Reissig et al. 2004
31	Menéndez	42°40´S 71°50´W	800	55.7	287	Los Alerces	Pacific	Thomasson 1963
32	Futalaufquen	42°49´S 71°43´W	518	44.6	168	Los Alerces	Pacific	Thomasson 1963, Pizzolón et al. 1995 Queimaliños (unpubl.)
33	Amutui Quimei	43°03´S 71°42´W	485	86.7	300	Los Alerces	Pacific	
34	Vintter	43°59´S 71°33´W	936	144.2	290	—	Pacific	Díaz et al. 2000, 2007
35	La Plata	44°52´S 71°49´W	940	76.0	> 100	—	Pacific	
36	Fontana	44°56´S 71°30´W	925	81.5	> 90	—	Pacific	
37	Buenos Aires	46°29´S 71°29´W	235	1892.0	463	—	Pacific	Díaz et al. 2000, 2007
38	Pueyrredón	47°23´S 71°58´W	307	145.0	> 100	—	Atlantic	
39	Posadas	47°29´S 71°49´W	112	45.3	31	—	Atlantic	
40	Belgrano	47°51´S 71°08´W	807	59.9	n.a.	Perito Moreno	Atlantic	
41	Burmeister	47°57´S 72°11´W	954	12.8	n.a.	Perito Moreno	Atlantic	
42	Nansen	47°59´S 72°19´W	829	120.3	n.a.	Perito Moreno	Pacific	
43	San Martín	49°03´S 72°23´W	283	210.7	n.a.	Perito Moreno	Pacific	
44	Viedma	49°36´S 72°32´W	342	1211.1	> 100	Los Glaciares	Atlantic	
45	Argentino	50°20´S 72°45´W	187	1466.0	500	Los Glaciares	Atlantic	Díaz et al. 2000, 2007

Huapi N.P., respectively (Fig. 1a, b), and the sampling was performed in different seasons. The results revealed that in a seasonal trend the microphytoplankton was characterized by a rich development of *Dinobryon* sp., *Urosolenia* sp. and *Aulacoseira* sp., while during the rainy season, *Dictyosphaerium* prevailed. Other remarkably outcomes are related to the regular presence of *Fragilaria crotonensis* and of *Ceratium hirundinella* and *C. cornutum* which even in very low numbers, marked a difference with the phytoplankton of Chilean Patagonian lakes where this genus was absent.

In the 70´s decade, limnological investigations were carried out in Lake Mascardi, a deep V-shaped lake partially fed by a glacier of the Tronador Mountain, located in the Nahuel Huapi N.P. (Fig. 1b). The phytoplankton community was studied during an annual period from surface to 100 m depth by García de Emiliani & Schiaffino (1974). In this study, the nanoplanktonic fraction was analysed for the first time in a Patagonian lake, resulting the nanoflagellate *Plagioselmis lacustris* one of the four dominant species, together with *Selenastrum gracile*, *U. eriensis* and *Aulacoseira granulata*.

During a limnological survey carried out in an extensive Patagonian area during the summer of 1985, the phytoplankton fraction > 25 μm was comparatively analyzed between systems belonging to the Andean Patagonian region and the Patagonian Plateau by Izaguirre et al. (1990). The Andean lakes were included in the Nahuel Huapi, Puelo and Los Alerces N.P. (Fig. 1a, b), and the phytoplankton presented lower abundances and higher diversity values, in accordance to their oligotrophic condition. Moreover, the community was constituted by several diatom species (*Urosolenia* spp., *Fragilaria* spp., *Synedra* spp. and *Gomphonema* spp.), as well as by *Dinobryon* spp., *Peridinium* spp. and *Planctonema lauterbornii* Schm., characteristic of low productive environments. Moreover, the phytoplankton of Lake Futalaufquen (Los Alerces N.P., Fig. 1a) was analyzed during a spring-summer period from October 1988 to February 1989 by Pizzolón et al. (1995), who also found low abundance and biomass values, with *Synedra nana*, *Peridinium* spp., *Staurastrum tetracerum* and *Oocystis marssonii*, contributing with 74% of the total biomass.

In addition, even though this topic falls outside the aim of this article, it is remarkable that numerous articles dealing with taxonomic aspects about the phytoplankton of the Andean Patagonian lakes of Argentina have been published, fundamentally describing and citing species of the microphytoplankton fraction (see Tell, 2014). In relation to nanoplanktonic species, the crucial citation of *Chrysochromulina parva* made for the first time for South America in 1990 by Diaz & Lorenzo (1990), improved significantly the analysis of the phytoplankton community as a whole in further studies performed in these lakes.

Even though there are numerous studies about phytoplankton in the Andean Patagonian region, it is noticeable that this community remains still unexplored in almost 50% of the deep Andean Patagonian lakes, fundamentally in those lakes located in the northern and southern extremes of the region (Table 1).

In the following sections, we present the main results from ecological research on the phytoplankton community of the Andean Patagonian region obtained since 1990.

Phytoplankton of deep lakes at the east of the Andes: a latitudinal analysis

The limnological variables and the phytoplankton summer structure of twenty-one cold temperate lakes from three National Parks of Patagonia were synthesized and analysed using a multivariate statistical tool by Diaz et al. (2000). The study suggests that the most important variables to define a trophic gradient are nutrients, conductivity and phytoplanktonic attributes. In this study the biomass (as biovolume) of each taxonomic group along the trophic gradient was examined. Although all Andean lakes appear to be similar as shown by their similar salt and nutrient concentration values, the phytoplankton biomass decomposed into different species composition allowed to distinguish clearly sub-groups along a latitudinal gradient: the deep Andean lakes set in Northern Patagonia (40 to 43°S), at Lanín, Nahuel Huapi and Los Alerces N.P. differed from the other group of lakes located in Southern Patagonia (46 to 50°S) (Fig. 1a, Table 1). The group of lakes set in Northern Patagonia was made-up by the oligotrophic (O) lakes: Guillelmo, Lolog, Nahuel Huapi, Moreno, Futalaufquen, Roca and Fonck (Diaz et al. 2000). These lakes share similar dissolved inorganic nitrogen (DIN), net phytoplankton and nanoplankton biomass values. Some characteristics are share by specific lakes: Prymnesiophyceae biomass included the Moreno and the Nahuel Huapi lakes, whereas a similar phytoplankton diatoms biomass allows to associate lakes Futalaufquen and Roca. Lake Fonck has a distinguish water temperatures and phosphorus content (soluble reactive phosphorus: SRP and total phosphorus: TP). The ultraoligotrophic (UO) lakes comprised a second group with two latitudinal sub-groups: the northern lakes (UO-N): Espejo, Espejo Chico, Mascardi and Traful and the southern lakes (UO-S): Argentino, Buenos Aires and Vintter. The first four lakes share similar specific diversity, phytoplankton biomass, water temperature and silica levels. Lake Espejo Chico though, has higher nitrate levels than the other three, whereas Lake Traful has higher silica levels. The last three lakes in this group (Argentino, Buenos Aires and Vintter) are all in Southern Patagonia and are still glacier fed. They have similar levels of total biomass, diatoms and diversity, whilst DIN, SRP and silica concentrations are also similar. Reports from southern temperate lakes revealed a different thermal regime to those in northern hemisphere (Campos et al. 1987, Geller 1992, Geller et al. 1997). The difference is a significantly lower stability of stratification and increased mixing depths. Summer maximum difference of temperature is about 12°C at 40°S against 20°C at 40°N, whereas this difference decreases to 5°C at 50°S (Geller et al. 1997). This may have consequences for the residence time of nutrients in the epilimnion (Baigún & Marinone 1995) and for nutrient supply from deep layers (Geller et al. 1997).

The contribution to the community assemblage by the species included in each of the seven morphologically based functional groups described by Kruk et al. (2009) is analyzed here using a reduced set of the original 231 identified species from Diaz et al. (2000). The most common species found in deep Andean lakes were: the nanoplanktonic *Chrysochromulina parva* and *Plagioselmis lacustris* (Group I); *Dinobryon divergens* (Group II); *Peridinium* spp. and *Gymnodinium* spp. (Group V) and the diatoms belonging to the Group VI: *Urosolenia eriensis*, *Cyclotella stelligera*, *Fragilaria* spp. and *Synedra* spp. The cell size of individual species varied widely, between 4 to 25000 μm³ and the total algal biomass of Andean lakes ranged between 70 and 7800 μg L^{-1}. Of this, 20–40% was classified as nanoplankton and the
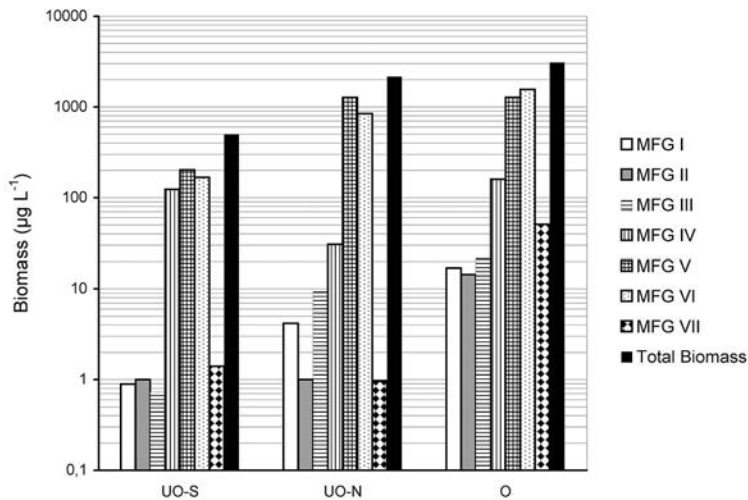
Fig. 2. Contribution (%) of individual Morpho-Functional Groups (MFG) to total summer biomass in Andean Patagonian lakes: Southern ultraoligotrophic (UO-S), Northern ultraoligotrophic (UO-N) and oligotrophic (O) waterbodies. Redrawn from Diaz et al. (2000).

total density values ranged between 40–8300 cells. ml^{-1}. Taking all the above into account, the deep temperate Andean lakes fitted into two trophic categories based on nutrients (mainly phosphorus), conductivity and phytoplanktonic attributes. However, single relationships fail to describe accurately the limnological spectrum of these lakes. For instance, the relationship between total phosphorus and chlorophyll (Chl-*a*) widely used in the other world regions showed overestimation of Chl-*a* concentrations for most of the lakes included in this set by Diaz et al. (2000, 2007). Recognizable summer associations based on the phytoplankton morpho-functional groups (MFG) in the deep Andean lakes, indicate the three trophic categories we discuss here (Fig. 2). In the ultra-oligotrophic lakes of the South three MFG were dominant: Group IV (mainly desmids and *Elakatothrix* spp.), Group V (*Gymnodinium* spp.) and Group VI (*Urosolenia eriensis*, *Aulacoseira granulata*). The ultra-oligotrophic Northern lakes have a total biomass similar to the oligotrophic lakes and one order of magnitude higher than the ultra-oligotrophic from the South. The UO-N lakes were dominated by Group V (*Peridinium willei* and other dinoflagellates), Group VI (*Urosolenia eriensis*, *Fragilaria crotonensis*, *Synedra ulna*, *Aulacoseira granulata*) and Group IV (*Staurodesmus triangularis*). The groups III (*Dolichospermum spiroides* and *Anabaena* spp.) and I (*Chrysochromulina parva* and *Plagioselmis lacustris*, *Cryptomonas erosa*) were also present in these lakes. In the oligotrophic lakes the biomass was mainly represented by Group VI (*Urosolenia eriensis* and other diatoms), Group V (*Gymnodinium* and *Peridinium* species), Group II (*D. divergens*, *Mallomonas* spp. and *Chrysosphaerella* sp.), Group IV (*Sphaerocystis schroeteri* Chodat, *Monoraphidium* spp.) and nanoplanktonic species of Group I (Diaz et al. 2000).

North Patagonian Andes

Spatial and temporal dynamics in phytoplankton assemblages in deep and shallow lakes

The physical environment

Light and temperature effects on the vertical distribution of phytoplankton: a case study about dinoflagellates in a deep lake

Deep lakes of the North Patagonia have very transparent waters which create a good scenario for the development of deep chlorophyll maxima (DCM) during the stratification period (Queimaliños et al. 1999, Pérez et al. 2002). Interestingly, these DCM are generally constituted by the mixotrophic ciliate *Ophrydium naumanni* Pejler and the dinoflagellate *Gymnodinium paradoxum* Schilling, together with picoplanktonic algae (Queimaliños et al. 1999). In contrast, the shallow lakes of this region do not present such vertical heterogeneity (Pérez et al. 2002).

Considering the conspicuous contribution of dinoflagellates (Group V) to the phytoplankton in the Andean Patagonian lakes (Queimaliños et al. 1999, Diaz et al. 2000, Pérez et al. 2002), a detailed study analyzing their diurnal vertical distribution was performed in Lake Moreno West (Northern Patagonia, Table 2, Fig. 1a, b). This study based on nine sampling occasions during a period between mid-spring and early autumn (Queimaliños et al. 2002). Seven unarmored and armored dinoflagellate species were registered, including four species of *Gymnodinium*, which were reported for Argentina and South America for the first time. Four species belong to the microphytoplankton fraction (*Gymnodinium paradoxum*, *G. uberrimum*, *Peridinium willei* and *Ceratium hirundinella*), and the other two are nanoplanktonic species (*G. varians* and *Peridinium* sp.). *G. helveticum* is considered as a planktic protist since it is colourless (Queimaliños et al. 2002). During the study period, the lake was thermally stratified, with an epilimnion fluctuating between 24 and 33 m depth, and presented an euphotic zone which varied between 30 to 38 m depth (Fig. 3). Interestingly, the illuminated zone always included the epilimnetic and metalimnetic layers, excepting in early autumn (Fig. 3, April 7). On the other hand, the phytoplankton biomass of Lake Moreno West was clearly dominated by dinoflagellates (Fig. 3), particularly by *G. paradoxum*, the prevailing species of the larger fraction (Queimaliños et al. 2002). The epilimnetic phytoplankton biomass fluctuated between 100 and 250 µg L^{-1}, and was always lower than that observed at the metalimnetic layers, which reached up to 500 µg L^{-1} (Fig. 3). In this particular scenario of light and temperature conditions, the dinoflagellates preferred the illuminated metalimnetic waters to develop their maximum, producing the DCM. This strategy reveals their ability to exploit dim light conditions and seems to be a mechanism to avoid the exposition to high levels of both visible and UV lights, characteristic of the surface layers of these deep Patagonian lakes (Pérez et al. 2002, Queimaliños et al. 2002).

Table 2. Morphometric, physical and chemical variables of the North Patagonian Andean lakes quoted in this article. References, TP: Total Phosphorus, SRP: Soluble Reactive Phosphorus, TN: Total Nitrogen; DIN: Dissolved Inorganic Nitrogen, Chla: Chlorophyll a, DOC: Dissolved Organic Carbon, n.a.: data not available; n.d.: not detectable. References: [1]Diaz et al. (1998), [2]Queimaliños et al. (1999), [3]Diaz et al. (2007), [4]Queimaliños et al. (2012), [5]Diaz & Pedrozo (1993), [6]Bastidas Navarro et al. (2009), [7]Pérez et al. (2010), [8]Gerea (2013), [9]Modenutti et al. (2000), [10]Queimaliños (1997), [11]Queimaliños et al. (1998).

|	Deep lakes			Shallow lakes			
	Nahuel Huapi[1]	Moreno West[2,3,4]	Verde[1]	Escondido[3,5,6,7,8]	Morenito[6,8,9]	Ezquerra[7,10]	El Trébol[3,6,7,11]
Coordinates	40°50'S 71°30'W	41°03'S 71°32'W	40°50'S 71°50'W	41°02'S 71°29'W	41°03'S 71°31'W	41°03'S 71°30'W	41°04'S 71°29'W
Area (Ha)	52900	610	1.0	8.0	83.1	6.0–9.0	31.6
Mean Z (m)	157.0	33.5	2.6	5.5	5.3	1.8	n.a.
Maximum Z (m)	438.0	90.0	9.5	8.0	12.0	3.0–4.0	12.0
Mixing frequency	Monomictic temperate	Monomictic temperate	Monomictic temperate	Monomictic temperate or Dimictic	Monomictic temperate or Dimictic	Cold polymictic	Monomictic temperate or Dimictic
Sd (m)	14–20	15–18	4.0	4–8	7–10	2–3	4–5
pH	6.2–7.7	6.7–7.2	6.4–7.3	6.9–7.6	6.7–7.4	6.9–7.5	7.3–7.6
Cond. (μS cm^{-1})	21	40–44	57	50–65	59–75	45–80	65–77
TP (range) (μg P L^{-1})	3–9	4–7	1–74	3–11	12–14	7–11	11.0
SRP (range) (μg P L^{-1})	3.0–6.9	nd–2	nd–21.7	nd–7	1–7	nd–4	nd–4
TN (range) (μg N L^{-1})	34–245	45–240	n.a.	150–400	220–405	n.a.	150–350
DIN (range) (μg N L^{-1})	nd–5	nd–5	0.4–28.6	3–142	7–75	n.a.	3–10
Alkalinity (mg L^{-1})	19	15	17–28	4–8	n.a.	50–54	4–7
Chl a (range) (mg m^{-3})	0.10–1.20	0.5–1.5	0.05–2.70	0.5–1.8	0.8–5.5	0.5–2.1	0.9–4.5
DOC (mg/L^{-1})	0.7	0.4–0.8	n.a.	2.7–5.4	1.8–3.3	4.3	1.4–2.5
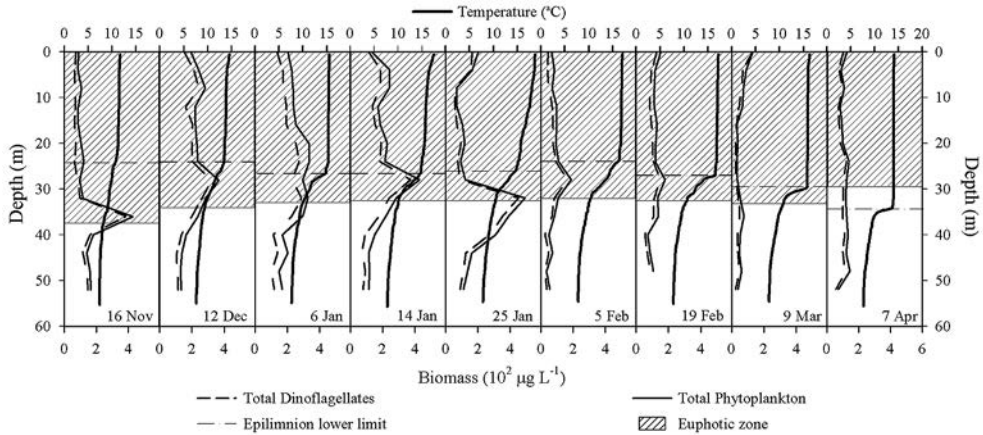
Fig. 3. Vertical distribution of light, temperature, total phytoplankton and total dinoflagellate biomass in Lake Moreno West during the spring-early autumn 1998–1999. Redrawn from Queimaliños et al. (2002).

Effects of temperature, wind exposure and water level fluctuations on the phytoplankton of a shallow lake

In a small and shallow lake belonging to the Nahuel Huapi system (Laguna Ezquerra, Table 2), strong effects of physical variables on the phytoplankton structure and succession were analysed during a spring-summer period (Queimaliños 1997). This study, performed on the basis of a high frequency sampling (every 3–4 days during 6 months), revealed a marked seasonality in phytoplankton biomass and composition associated to variations in temperature, wind exposure and water level. During spring and early summer, when the fluctuating water temperature averaged 13.5°C, the community assemblage was alternatively dominated by the nanoflagellates *Plagioselmis lacustris*, *Trachelomonas intermedia* (both belonging to Group I), and the aflagellate *Stichogloea doederleinii* (Group IV) with a total biomass fluctuating around 500 µg L^{-1}. Afterwards, during the last two summer months when the mean water temperature was 17°C, the total biomass steadily increased to a maximum of 32,000 µg L^{-1}, due to an exponential growth of *Asterionella formosa* (Group VI). The greatest change in the community produced during the transition between seasons and coincided with a flooding period caused by the snowmelt in late spring. The wind was homogeneously irregular and rather high during the whole study period; therefore, owing to the lake shallowness and wind exposure, phytoplankton of Laguna Ezquerra was stressed during both seasons. These altered conditions for the phytoplankton development were strengthened by the fluctuating temperature and the water level variation. The phytoplankton responses were reflected in high succession rate values, characteristic of communities with abrupt changes and exposed to critical environmental conditions, and by the evolution towards a plagioclimatic stage dominated by the ruderal species *A. formosa* (Reynolds 1984, Queimaliños 1997).

The chemical environment

Nutrient deficiency

Phytoplankton production and biomass in lakes are primarily constrained by the nutrient supply and especially by phosphorus (Schindler 2006). The extreme oligotrophy characterising many Andean Patagonian lakes owes more to a direct nitrogen deficiency than to a shortage of phosphorus and that it is scarcely compensated by dinitrogen fixation (Diaz et al. 2007). The low SRP and DIN contents of the Andean lakes where the bioavailable P levels are generally < 10 μg L^{-1} and, in many instances, < 3 μg L^{-1}, which are typical of oligotrophic (OECD 1982) and unpolluted lakes of the world (Meybeck 1983). However, it is the DIN levels in these lakes that are most remarkable; they are quite ten times below the average of world fresh waters. The molecular ratios of N/P are frequently < 1 and far below the value of 16, said to distinguish nitrogen-limited systems from those constrained by phosphorus (Rhee & Gotham 1980). The reason for this nitrogen poverty in the Andean lakes owes, presumably, to deficiencies in the leachates from mountainous catchments dominated by an assortment of igneous, volcanic and plutonic rocks, all highly eroded by glaciations. The forest cover of the Andes at this latitude is effective in sequestering and retaining much of the available N, in a near-closed cycle that leaves little to overspill into the drainage. Thus, the low levels of phytoplankton biomass observed to be well within the supportive capacity of the bioavailable phosphorus but to be, instead, correlated with nitrogen availability, in proportions predicted from stoichiometry by Diaz et al. (2007).

An ultraoligotrophic extreme of the gradient is constituted by high mountain lakes located at or above the treeline. These shallow lakes are extremely transparent with very low levels of nutrients and dissolved organic carbon, due to the unproductive water basins deprived of forests (Zagarese et al. 2000).

The phytoplankton community structure and dynamics on two piedmont water-bodies, one large (Nahuel Huapi) and one shallow (Verde), were related to the physical and nutrient characteristics. The first lake was monitored along a year on the basis of a monthly frequency sampling and the second one biweekly (Diaz et al. 1998). Besides, the summer phytoplankton of the high mountain lakes Toncek and Schmoll was described by Zagarese et al. (2000).

Lake Nahuel Huapi

In this lake, which is the largest in the North Patagonian region, the pattern of dissolved nutrients available for phytoplankton showed the maximum values during the winter (Table 2, Fig. 4a). The relationship DIN/SRP was always below 10 (Diaz et al. 1998). Forty phytoplankton species were identified and the density values were between 129 and 831 cell. ml^{-1},

Fig. 4. Variation of some chemical and biological variables in Lake Nahuel Huapi, during 1995–1996: **a**) dissolved inorganic nutrients: DIN, PRS and N/P relationship; **b**) fresh-weight phytoplankton biomass; **c**) composition of MFG during the studied period in % of the total biomass; **d**) Variation of the Diversity (Shannon index) along the year. Redrawn from Diaz et al. (1998).
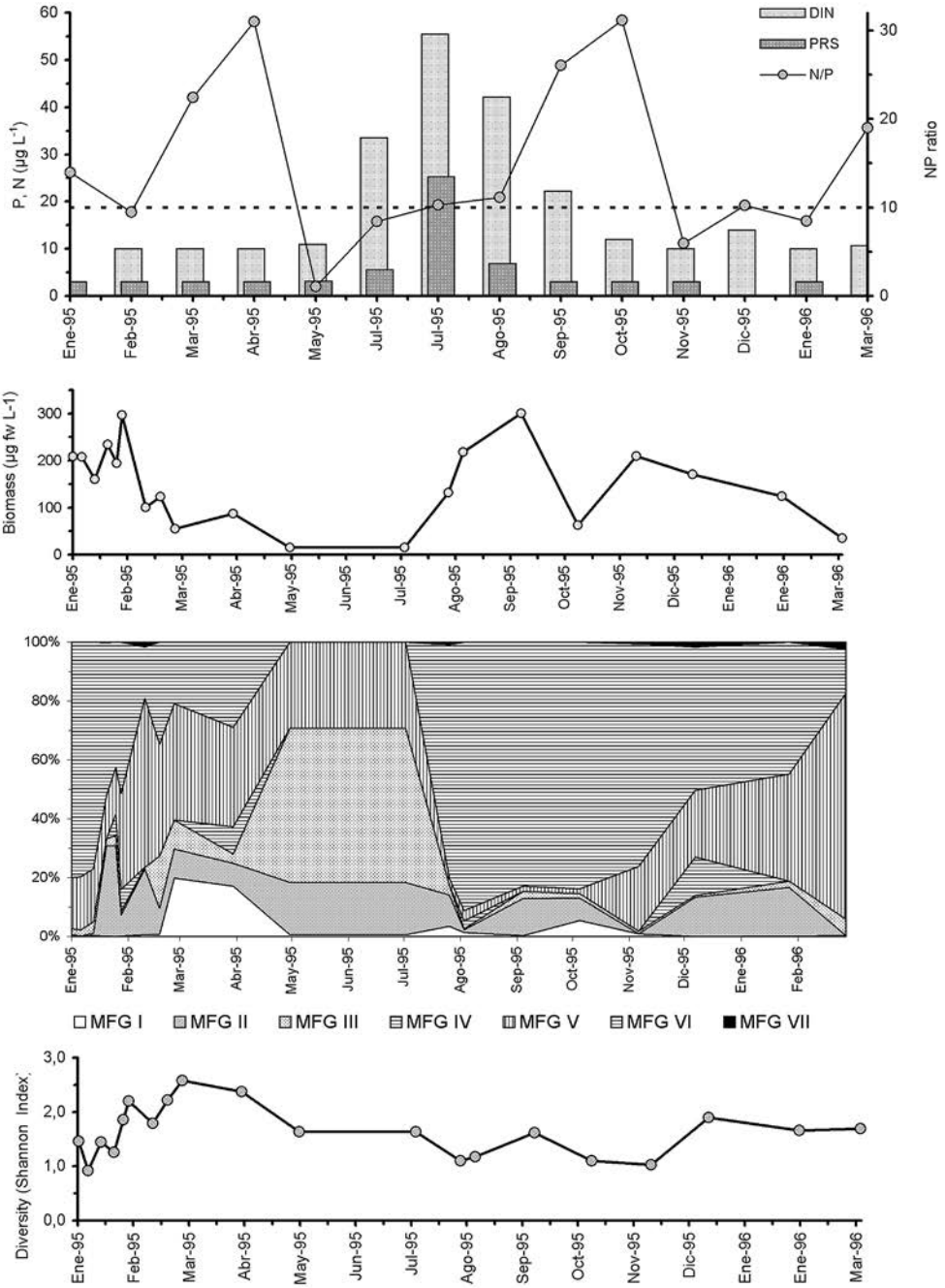
with a minimum in late summer and maxima in autumn and early spring. The groups of phytoplankton that contributed more than 50% to the total density were Prymnesiophyceae during winter and summer, Cyanobacteria during fall, and Bacillariophyceae in spring. The phytoplankton biomass ranged between 15 and 300 μg L^{-1} (Fig. 4b) and the mean annual biomass was 147 μg L^{-1}. Total biomass showed two maxima: one in summer and another in spring. In the deep ultra-oligotrophic lake Nahuel Huapi, the phytoplankton biomass was strongly dominated by Group VI (*Aulacoseira granulata*, *Urosolenia eriensis* and *Cyclotella stelligera*), Group I (*Chrysochromulina parva* and *Plagioselmis lacustris)* and Group V (*Gymnodinium* and *Peridinium* spp.) (Fig. 4c). The temporal dynamic in phytoplankton assemblages started during early spring when the lake was mixed and the levels of TP and SRP were low. Group VI (*U. eriensis*, *A. granulata* and *S. ulna*) dominated in biomass. During spring (October to December) *U. eriensis* was the most important species in terms of biomass, a situation that continued during summer with the development of *Dinobryon divergens* and *Gymnodinium* sp. populations. During summer, the specific diversity ranged between 1 and 2 (Fig. 4d). By fall there was a species replacement and *Chrysochromulina parva* and *Plagioselmis lacustris* became dominant both in terms of biomass and density. Simultaneously, there was an increase in the levels of DIN and a more pronounced increase in SRP and a decrease in the DIN/SRP ratio, which were coincident with the species replacement and the beginning of the mixing period. In winter, when values of phosphorus and nitrogen were higher, *U. eriensis* was the dominant species in terms of biomass and *C. parva* in terms of density. The Diversity (Shannon index) showed the minimum values (0.3; Fig. 4d) in the middle of the winter.

Lake Verde

This small mesotrophic shallow lake, located within the Nahuel Huapi system, near Villa La Angostura city (Table 2), showed a total of 74 phytoplankton taxa. The dominant algae were Group V (*Trachelomonas* spp.) and Group IV (*Cosmarium punctulatum*) during the summer biomass maximum. Group I (*Plagioselmis lacustris*, *Chrysochromulina parva*) and Group VI (*Synedra ulna* and *Navicula* spp.) were important contributors to the biomass during the autumn. The maximum biomass value was 7800 μg L^{-1} in summer (Fig. 5b). The pattern of variation of the phytoplankton biomass showed a minimum (96 μg L^{-1}) in spring and a maximum (7800 μg L^{-1}) in summer. By the end of winter, the availability of DIN and silica, associated with the increase in light intensity and photoperiod, caused a change in the phytoplankton community: Group II, which was the most abundant during the winter, was replaced by nanoplanktonic Group I (Fig. 5c). Low biomass and density levels were observed during spring. Group V represented 50% of the total biomass by early spring and were replaced again by the Group II (75–90% of total biomass) in late spring. This replacement occurred simultaneously with the decrease in SRP, nitrites and ammonia.

Fig. 5. Variation of some chemical and biological variables in Lake Verde, during 1990–1991: **a**) Dissolved inorganic nutrients: DIN, PRS and N/P relationship; **b**) Fresh-weight phytoplankton biomass; **c**) Composition of MFG during the studied period in % of the total biomass; **d**) Variation of the Diversity (Shannon index) along the year. Redrawn from Diaz et al. (1998).
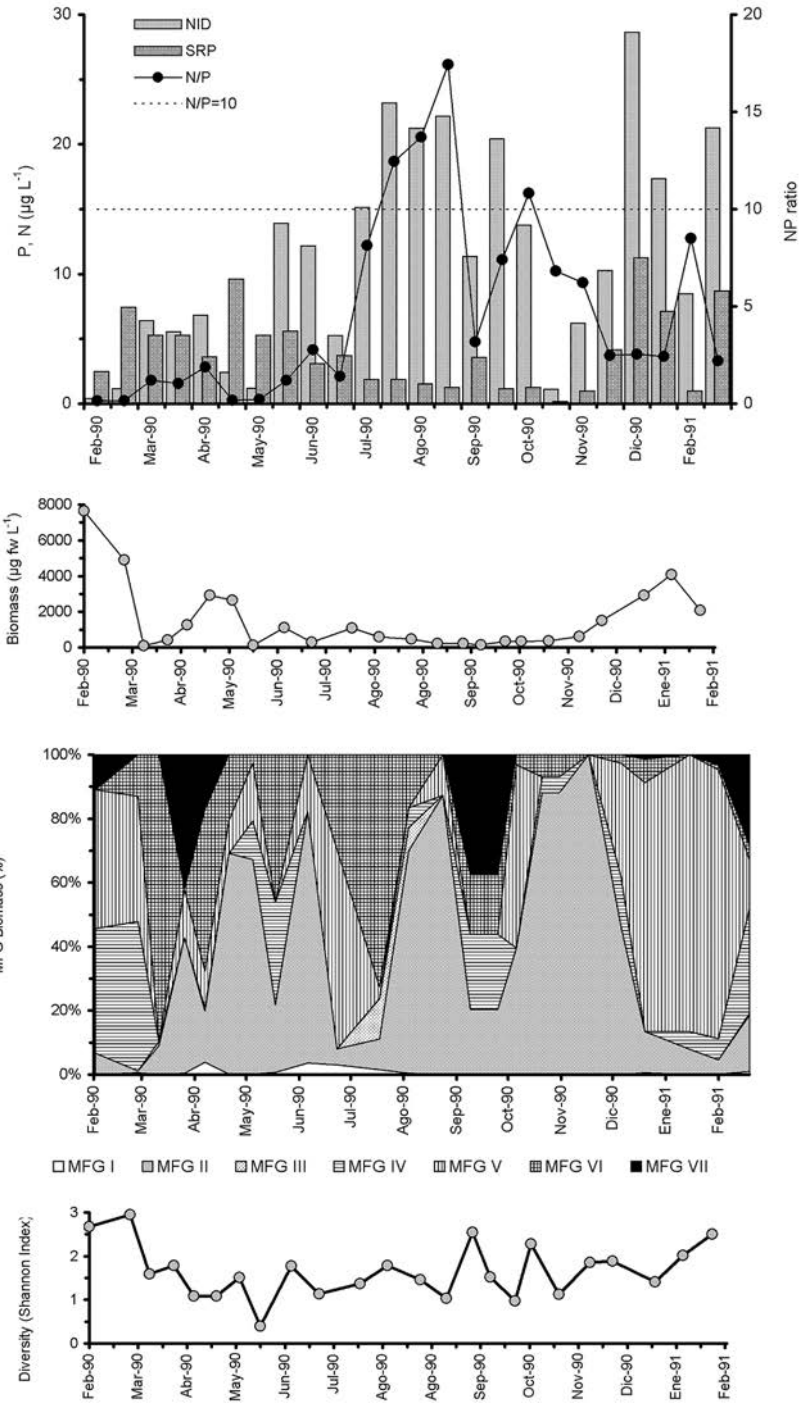
In summer, the warmer temperatures and higher nutrient concentrations favoured the maximum annual biomass. The diversity not only showed an increase in richness, but also a higher complexity and functional diversification of the phytoplankton structure, evidenced by the coexistence of species of small and large size. Small species (Group I) occurred together with medium size non-flagellated organisms of the Group IV and flagellated of Group V. The high biomass caused decreases in phosphorus and depletion of nitrogen followed by a drastic decrease in biomass and in the development of the diatoms of the Group VI during the late summer. As the fall progressed, the shortening of the photoperiod and the continuous circulation of the water column caused the increase in the concentration of nutrients, and a new increase in biomass, with co-dominance of Group I, II, and VII. The winter biomass minimum was characterized by the presence of species of Groups VI and V. As winter progressed, the diatoms were replaced by Chrysophyceae of Group II. During this period an increase of the different forms of nitrogen was observed. The species diversity varied in a seemingly random fashion during the year (Fig. 5d). It showed two maxima, one in summer (2.95) and another in spring (2.28) and a very apparent minimum in autumn (0.40). Similar contribution of the MFG was registered in the phytoplankton seasonal dynamic in relation of the steps of the PEG model studied in the Lake Escondido by Diaz & Pedrozo (1993).

High mountain lakes

Mountain lakes differ from piedmont lakes in their thermal structure, remaining frozen for about 6–8 months every year, while during summer a weak thermocline develops. The phytoplankton was studied during a summer period in two of these high altitude lakes (> 1700 m a.s.l.). The community was mainly dominated by nanoplanktonic flagellates (Group I), and in general the species found in mountain lakes also occur in piedmont lakes. The main difference between forest and mountain lakes is a matter of degree: species richness, diversity, abundance and biomass are lower at higher altitudes (Zagarese et al. 2000).

Trophic interactions

Interactions with zooplankton

During the decades of 1980s and 1990s, a notable interest on the phytoplankton-zooplankton coupling arose in numerous investigations, recognizing that the herbivorous zooplankton affect phytoplankton directly by grazing, but also indirectly by increasing the nutrient availability through recycling processes (Sterner 1986). The importance of the zooplankton regenerating effect was increasingly recognised in relation to the trophic status of the system (McQueen et al. 1986, Carrillo et al. 1996). Rates of turnover of N and P are faster in oligotrophic than in eutrophic waters as the nutrient pool sizes are smaller, and thus, oligotrophic waters appear to be more dependent on internal recycling (Harris 1986). In North Patagonian lakes, Balseiro et al. (1997) found a positive relationship between released nutrients (N and P) and zooplankton biomass, and this situation was enhanced when the zooplankton was dominated by crustacean species rather than rotifers. Moreover, other studies have shown

that the small flagellated algae, which dominate the nanoplankton of these Andean lakes, are heavily selected by cladoceran species like *Bosmina longirostris*, largely abundant in these waters (Balseiro et al. 1992, Queimaliños 1993). In this context, three series of field experiments with different zooplankton species composition and biomass were performed in order to measure the responses of phytoplankton species to grazing mortality and to stimulation of growth by nutrient recycling (Queimaliños et al. 1998). The experiments were set up in Lake El Trébol, a small Andean lake of the Nahuel Huapi system (Table 2, Fig. 1b), on three dates: late spring, early and mid-summer. The design included treatments without zooplankton (Filtered water), and three others with increasing zooplankton biomass (1X, 2X, and 3X). In terms of trophic interactions, the community was analysed according to its size fractions, since the nanoplankton represents the edible fraction, while the microphytoplankton is not or less accessible to zooplankton feeding. The prymnesiophycean *Chrysochromulina parva* (Group I), dominated the small fraction, and *Aulacoseira granulata* (Group VI) prevailed in the inedible microphytoplankton (Queimaliños et al. 1998). The main results of these experiments revealed that zooplankton manipulation caused increased nutrient availability within the experimental units, due to the nutrient recycling enhanced by the increasing zooplankton biomass. At the same time, the small phytoplankton fraction was reduced in all treatments evidencing that the mortality rates caused by grazing were not compensated by the growth favoured by higher nutrient availability. On the contrary, a significant positive relationship between *A. granulata* and nutrient concentration was obtained, indicating that the ungrazed diatom was able to capitalise on the increase of nutrient availability. As a net result, a change
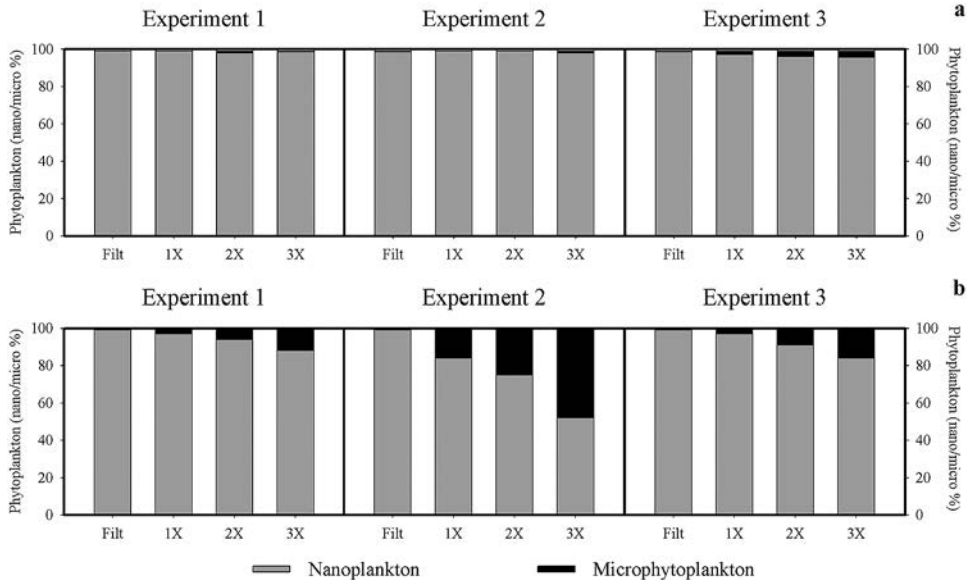

Fig. 6. Nano-microphytoplankton relationship during the three experiments. Upper panel: initial conditions (day 0), lower panel: final conditions (day 3). Treatments: Filt, filtered water (without zooplankton); 1X; 2X and 3X (1-, 2- and 3-fold increase in zooplankton biomass). Redrawn from Queimaliños et al. (1998).

in the nano:microphytoplankton relationship was obtained in the three treatments, with increasing importance of the microphytoplankton as a response to increased zooplankton biomass (Fig. 6) (Queimaliños et al. 1998).

In other study conducted in Lake Ezquerra (Table 2, Fig. 1b), where an extraordinary growth of *Asterionella formosa* developed, a peculiar phyto-zooplankton interaction was observed. The large numbers of the diatom provoked the starvation of the cladoceran *Bosmina longirostris* (Balseiro et al. 1991). This situation was explained by two reasons: i) the nanoflagellates which constitute the food for this zooplankter were heavily decreased during the diatom peak due to the self shading of the diatom; ii) the particular morphology of *A. formosa* created a "virtual" volume which made more inaccessible the low numbers of flagellates to the grazers. In this context, Balseiro et al. (1991) proposed that the flagellate:diatom ratio has a direct effect on cladoceran demography in these shallow lakes of North Patagonia.

Interactions with fishes

Planktivorous fish can increase phytoplankton biomass indirectly by reducing zooplankton grazing, as it was stated by Carpenter et al. (1985), and directly through fish excretion and egestion processes, as a direct source of nutrient for phytoplankton, stimulating algal production (Attayde & Hansson 1999, among others). In Lake Escondido, other small and shallow lake of the Nahuel Huapi system (Table 2, Fig. 1b), the effects of *Galaxias maculatus* Jenyns (a landlocked small fish species) on nutrient dynamics, and the consequent effects on phytoplankton biomass were analysed through field and laboratory experiments by Reissig et al. (2003). The nutrients released by *G. maculatus* were explored with increasing fish biomass and body size, analysing the phytoplankton responses. The results showed that phytoplankton biomass was strongly enhanced in the presence of fish, and that enhancement was greater with increasing fish biomass. These algal increments were associated with higher nutrient concentrations, due to the excretion/egestion processes of fish. As was expected, mass-specific nutrient release rates were higher in smaller fish than in larger ones. So, the amount of nutrients supplied to phytoplankton would be influenced by the size structure of fish population as well. As a consequence of different N and P release rates, an increase in the $N-NH_4$:P-TDP ratio was observed in the presence of fish. The fact that *G. maculatus* is a species that moves in schools would determine spatial heterogeneity in nutrient release, with important effects of reducing nutrient limitation and shifting $N-NH_4$:P-TDP ratios (Reissig et al. 2003).

The role of mixotrophic algae in Andean Patagonian lakes

In the Andean Patagonian lakes, several phytoplanktonic species show mixotrophic behaviour. In particular, in Lake Caviahue, where the inorganic carbon is limiting due to the very low pH values, it has been demonstrated that *Keratococcus rhaphidioides*, *Euglena mutabilis* and *Watanabea* sp. are osmotrophic, since they utilize dissolved organic matter as source of carbon and nutrients (see Diaz & Beamud, 2014).

Moreover, other dominant species of the North Patagonian lakes, such as *Chrysochromulina parva*, *Gymnodinium varians*, *Cryptomonas marssonii* and *Dinobryon divergens* show

bacterivorous behaviour (Queimaliños 2002). These species play an important role in the energy flow and in nutrient cycling in these oligotrophic environments, since one potential advantage of mixotrophy is the acquisition of nitrogen and phosphorus from bacteria when concentrations of dissolved nutrients are low (Jones 2000). This topic is particularly developed in the article Modenutti (2014).

General remarks

This extended lacustrine region of the Southern Andes holds the largest and deepest lakes of South America of glacial origin. These deep ultraoligotrophic and oligotrophic environments represent a particular scenario for the growth of phytoplankton, which usually develops in low abundance and biomass. The community is largely dominated by diatoms, dinoflagellates and chrysophycean species, together with several species of nanoflagellates, mainly mixotrophic. The North Patagonian lakes, fundamentally those belonging to the Nahuel Huapi National Park, are the best studied. In these lakes, nitrogen instead of phosphorus limitation has been demonstrated, while silica is never restrictive for the phytoplankton community. In relation to the physical conditions, the high transparency together with the direct thermal stratification, create the necessary conditions for the occurrence of Deep Chlorophyll Maxima (DCM) during the spring-summer periods. These DCM develop in metalimnetic layers, in coincidence with the lower limit of the euphotic zone, and are dominated by dinoflagellates together with mixotrophic ciliates.

The numerous shallow lakes of the region are characterised by a slightly higher trophic conditions, which stand higher phytoplankton biomass during the growing season. The analysis of the trophic interactions with zooplankton revealed that the nutrient recycling performed by the grazers diminishes the nutrient limitation usually observed in these lakes, resulting sometimes in the enhancement of diatom populations during summer.

Acknowledgements

References

Attayde, J. L. & Hansson, L. A. (1999): Effects of nutrient recycling by zooplankton and fish on phytoplankton communities. – Oecologia **121**: 47–54.

Baigún, C. & Marinone, M. C. (1995): Cold-temperate lakes of South America: do they fit northern hemisphere models? – Arch. Hydrobiol. **135**: 23–51.

Balseiro, E. G., Modenutti, B. E. & Queimaliños, C. P. (1992): The coexistence of *Bosmina* and *Ceriodaphnia* in a South Andes lake: an analysis of the demographic responses. – Freshwat. Biol. **28**: 93–101.

Balseiro, E. G., Modenutti, B. E. & Queimaliños, C. P. (1997): Nutrient recycling and shifts in N.P. ratio by different zooplankton structures in a South Andes lake. – J. Plankton Res. **19**: 805–817.

Balseiro, E. G., Queimaliños, C. P. & Modenutti, B. E. (1991): Evidence of interference of *Asterionella formosa* with the feeding of *Bosmina longirostris*: a field study in a south Andes lake. – Hydrobiologia **224**: 111–116.

Balseiro, E. G., Queimaliños, C. P. & Modenutti, B. E. (2004): Grazing impact on autotrophic picoplankton in two south Andean lakes (Patagonia, Argentina) with different light:nutrient ratios. – Rev. Chil. Hist. Nat. **77**: 73–85.

Bastidas Navarro, M., Modenutti, B. E., Callieri, C., Bertoni, R. & Balseiro, E. G. (2009): Balance between primary and bacterial production in North Patagonian shallow lakes. – Aquat. Ecol. **43**: 867–878. DOI 10.1007/s10452-008-9220-9.

Beamud, S. G., Diaz, M. M. & Pedrozo, F. L. (2007): Summer phytoplankton composition and nitrogen limitation of the deep, naturally-acidic (pH~2.2) Lake Caviahue, Patagonia, Argentina. – Limnologica **37**: 37–48.

Beamud, S. G., Diaz, M. M. & Pedrozo, F. L. (2010): Nutrient limitation of phytoplankton in a naturally acidic lake (Lake Caviahue, Argentina). – Limnology **11**: 103–113.

Campos, H., Steffen, W., Agüero, G., Parra, O. & Zuñiga, L. (1987): Limnology of lake Riñihue. – Limnologica **18**: 339–357.

Carpenter, S. R., Kitchell, J. F. & Hodgson, J. R. (1985): Cascading trophic interactions and lake productivity. – BioScience **35**: 634–639.

Carrillo, P., Reche, I., Sánchez Castillo, P. & Cruz-Pizarro, L. (1995): Direct and indirect effects of grazing on the phytoplankton seasonal succession in an oligotrophic lake. – J. Plankton Res. **17**: 1363–1379.

Diaz, M. M. & Beamud, G. (2014): Acidophilic phytoplankton in Argentina: the case study of Lake Caviahue (Patagonia). – Adv. Limnol. **65**: 257–271.

Diaz, M. M. & Lorenzo, L. (1990): *Chrysochromulina parva* Lackey (Prymnesiophyceae) new for South America. – Algol. Stud. **60**: 19–24.

Diaz, M. M. & Pedrozo, F. L. (1993): Seasonal succession of phytoplankton in a small Andean Patagonian lake (Rep. Argentina) and some considerations about the PEG Model. – Arch. Hydrobiol. **127**: 167–184.

Diaz, M. M., Pedrozo, F. L. & Baccalá, N. (2000): Summer classification of Southern Hemisphere temperate lakes (Patagonia, Argentina). – Lakes & Reserv.: Res. Manage. **5**: 213–229.

Diaz, M. M., Pedrozo, F. L., Reynolds, C. & Temporetti, P. (2007): Chemical composition and nitrogen-regulated trophic state of Patagonian lakes. – Limnologica **37**: 17–27.

Diaz, M. M., Pedrozo, F. L. & Temporetti, P. (1998): Phytoplankton of two Araucanian lakes of differing trophic status (Argentina). – Hydrobiologia **369/370**: 45–57.

García de Emiliani, M. O. & Schiaffino, M. (1974): Fitoplancton del Lago Mascardi (Río Negro, Argentina). – Bol. Soc. Arg. Bot. **15**: 411–426.

Geller, W. (1992): The temperature stratification and related characteristics of Chilean lakes in midsummer. – Aquat. Sci. **54**: 39–57.

Geller, W., Hannappel, S. & Campos, H. (1997): Temperature and stratification of southern hemisphere temperate lakes in Patagonia (Chile, Argentina). – Verh. Internat. Ver. Limnol. **26**: 243–247.

Gerea, M. (2013): La implicancia de las algas mixotróficas en la trama trófica microbianda de ambientes someros de Patagonia Norte y Antárdia (Argentina). –Doctoral Thesis, Univ. Nac. Comahue.

Harris, G. P. (1986): Phytoplankton Ecology. Structure, function and fluctuation. – Chapman and Hall, London.

Iriondo, M. (1990): Quaternary lakes of Argentina. – Palaeogeogr. Palaeoclimat. Palaeoecol. **70**: 81–88.

Izaguirre, I., del Giorgio, P., O'Farrell, I. & Tell, G. (1990): Clasificación de 20 cuerpos de agua andino-patagónicos (Argentina) en base a la estructura del fitoplancton estival. – Cryptog. Algol. **11**: 31–46.

Jones, R. I. (2000): Mixotrophy in planktonic protists: an overview. – Freshwat. Biol. **45**: 219–226.

Kruk, C., Huszar, V. L. M., Peeters, E. T., Bonilla, S., Costa, L., Lürling, M., Reynolds, C. & Scheffer, M. (2009): A morphological classification capturing functional variation in phytoplankton. – Freshwat. Biol. **55**: 614–627.

McQueen, D. J., Post, J. R. & Mills, E. L. (1986): Trophic relationships in freshwater pelagic ecosystems. – Can. J. Fish. Aquat. Sci. **43**: 1571–1581.

Meybeck, M. (1983): Carbon, Nitrogen and Phosphorus transport by world rivers. – Am. J. Sci. **282**: 401–450.

Modenutti, B. (2014): Mixotrophy in Argentina freshwaters. – Adv. Limnol. **65**: 359–374.

Modenutti, B. E., Balseiro, E. G. & Queimaliños, C. P. (2000): Ciliate community structure in two South Andean lakes: the effect of lake water on *Ophrydium naumanni* distribution. – Aquat. Microb. Ecol. **21**: 299–307.

OECD (1982): Eutrophication of waters: monitoring, assessment and control. – Organisation for Economic Co-operation and Development, Paris.

Paruelo, J. M., Beltrán, A., Jobággy, E., Sala, O. E. & Golluscio, R. A. (1998): The climate of Patagonia: general patterns and controls on biotic processes. – Ecol. Austral **8**: 85–101.

Pedrozo, F. L., Chillrud, S., Temporetti, P. & Díaz, M. M. (1993): Chemical composition and nutrient limitation in rivers and lakes of northern Patagonian Andes (39.5°-42°S; 71°W) (Rep. Argentina). – Verh. Internat. Ver. Limnol. **25**: 207–214.

Pérez, G. L. (2006): Distribución vertical de organismos autotróficos y mixotróficos y su relación con extinciones diferenciales de la luz en lagos andinos. – Doctoral Thesis, Univ. Nac. Comahue, Bariloche.

Pérez, G. L., Queimaliños, C. P. & Modenutti, B. E. (2002): Light climate at the Deep Chlorophyll Maxima in North Patagonian Andean lakes (Argentina). – J. Plankton Res. **24**: 591–599.

Pérez, G. L., Torremorell, A., Bustingorry, J., Escaray, R., Pérez, P., Diéguez, M. & Zagarese, H. (2010): Optical characteristics of shallow lakes from the Pampa and Patagonia. – Limnologica **40**: 30–39.

Pizzolón, L., Santinelli, N., Marinone, M. C. & Menú-Marque, S. A. (1995): Plankton and hydrochemistry of Lake Futalaufquen (Patagonia, Argentina). – Hydrobiologia **316**: 63–73.

Queimaliños, C. P. (1993): Efectos del zooplancton sobre la dinámica sucesional del fitoplancton en un ambiente lacustre andino. – Doctoral Thesis, Univ. Buenos Aires.

Queimaliños, C. P. (1997): Some physical and biological factors affecting a spring-summer phytoplankton dynamics in a shallow, temperate lake of South Andes (Argentina). – Internat. Rev. Hydrobiol. **82**: 147–160.

Queimaliños, C. P. (2002): The role of phytoplanktonic size fractions in the microbial food webs in two north Patagonian lakes (Argentina). – Verh. Internat. Ver. Limnol. **28**: 1236–1240.

Queimaliños, C. P., Modenutti, B. E. & Balseiro, E. G. (1998): Phytoplankton responses to experimental enhancement of grazing pressure and nutrient recycling in a small Andean lake. – Freshwat. Biol. **40**: 41–49.

Queimaliños, C. P., Modenutti, B. E. & Balseiro, E. G. (1999): Symbiotic association of the ciliate *Ophrydium naumanni* with *Chlorella* causing a deep chlorophyll *a* in an oligotrophic South Andean lake. – J. Plankton Res. **21**: 167–178.

Queimaliños, C. P., Pérez, G. L. & Modenutti, B. E. (2002): Summer population development and diurnal vertical distribution of dinoflagellates in an ultraoligotrophic Andean lake (Patagonia, Argentina). – Arch. Hydrobiol. **145**: 117–129.

Queimaliños, C. P., Reissig, M., Diéguez, M. C., Arcagni, M., Ribeiro-Guevara, S., Campbell, L., Soto Cárdenas, E. C., Rapacioli, R. & Arribére, M. A. (2012): Influence of precipitation, landscape and hydrogeomorphic lake features on pelagic allochthonous indicators in two connected ultraoligotrophic lakes of North Patagonia. – Sci. Total Environ. **427/428**: 219–228.

Quirós, R. & Drago, E. (1985): Relaciones entre variables, físicas, morfométricas y climáticas en lagos patagónicos. – Rev. Asoc. Cs. Nat. Lit. **16**: 181–189.

Reissig, M., Queimaliños, C. P. & Balseiro, E. G. (2003): Effects of *Galaxias maculatus* on nutrient dynamics and phytoplankton biomass in a North Patagonian oligotrophic lake. – Environ. Biol. Fishes **68**: 15–24.

Reynolds, C. S. (1984): Phytoplankton periodicity: the interactions of form, function and environmental variability. – Freshwat. Biol. **14**: 111–142.

Rhee, G.-Y. & Gotham, I. J. (1980): Optimum N:P ratios and co-existence of planktonic algae. – J. Phycol. **16**: 486–489.

Schindler, D. W. (2006): Recent advances in the understanding and management of eutrophication. – Limnol. Oceanogr. **51**: 351–355.

Sterner, R. W. (1986): Herbivores' direct and indirect effects on algal populations. – Science 231: 605–607.

Tell, G. (2014): Phytoplankton diversity. – Adv. Limnol. **65**: 5–20.

Thomasson, K. (1959): Nahuel Huapi. Plankton of some lakes in an Argentine National Park, with some notes on terrestrial vegetation. – Acta Phytogeogr. Suec. **42**: 1–83.

Thomasson, K. (1963): Araucanian Lakes. Plankton studies in North Patagonia, with notes on terrestrial vegetation. – Acta Phytogeogr. Suec. **47**: 1–139.

Zagarese, H. E., Diaz, M., Pedrozo, F. & Úbeda, C. (2000): Mountain lakes in Northwestern Patagonia. – Verh. Internat. Ver. Limnol. **27**: 533–538.