Structure changes in a planktonic food web: biotic and abiotic controls

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ABSTRACT

We examined the response of the plankton community to strong changes in the volume of oligotrophic Lake La Caldera through the ice-free period of 1995-1997. As consequence of the changes in the precipitation regime, the lake volume diminished to 2 m depth during the extremely dry year of 1995. The increase in phosphorus availability for this year caused the diversification of the plank-tonic community, and the autotrophic:heterotrophic (A/H) ratio was below 1. In spite of the sporadic dust loads associated to atmos-pheric events, the quick recovery of the lake volumen in 1996 led to a severe phosphorus limitation. Phytoplankton community was dominated by Chrysophyceae (>90% of abundance) and large zooplankters were very scarce (<1 ind l^{-1}). As a consequence, A/H ratio was over 1 and ciliates developed. Finally, towards the end of 1997, the zooplankton recovery led to a decrease of both A/H ra-tio and ciliates, and the lake returned to the conditions before drought. A decreasing tendency in both bacterial and phytoplankton densities, possibly as a consequence of top-down controls, was observed through the period of 1995-1997.

Key words: food web, taxonomic structure, seasonal and interannual variations

1. INTRODUCTION

High mountain oligotrophic lakes present simple planktonic communities which make them suitable to study complex interactions (Neill 1988). Oligotrophy promotes the existence of small sized phytoplankton species with high turnover rates (Reynolds 1984; Psen-ner & Zapf 1990) and large-bodied zooplankton with low metabolic rates (Taylor 1984). Direct competition between phytoplankton and bacteria for mineral re-sources sets up an important interaction in these nutri-ent-limited systems (Currie 1990; Thingstad *et al.* 1993). It is accepted that microzooplankton and mixo-trophic algae, through bacterivory, modulate the com-petition between algae and bacteria (Rothhaupt 1992; Nygaard & Tobiesen 1993; Thingstad & Rassoulzade-gan 1995). Furthermore, metazooplankton can alter al-gal and bacterial communities through grazing (Elser & Goldman 1991; Carrillo *et al.* 1995) or by increasing availability of limiting nutrients via excretion or sloppy feeding (Peduzzi & Herndl 1992; Sterner *et al.* 1995; Carrillo *et al.* 1996b).

It is known that the seasonal succession of phyto-plankton species involves complex interactions, where physical, chemical and biotic environmental factors play a basic role (Reynolds 1989). However there is contro-versy on how variations in the limiting nutrients affect phytoplankton succession. Meanwhile some studies evi-denced the important effect of external (climatic) proc-esses (Elser *et al.* 1995), other studies have considered that such forces exert negligible influence to phyto-plankton succession (Sarnelle 1993; Berman *et al.* 1995).

In this paper we describe inter-annual and seasonal variations in the structure of the planktonic community of the oligotrophic Lake La Caldera. We assess the re-lationships among biotic and abiotic components and the role of variations in the precipitation regime as key factor to understand changes in the planktonic structure.

2. MATERIALS AND METHODS

2.1. Sampling and laboratory procedure

Field samples were taken over the entire ice-free pe-riod, from late May to early November in 1995, and from July to early November in 1996 and 1997. A total of 27, 12 and 16 field samplings were carried out for the three consecutive years. Sampling was conducted weekly at one (1 m) and four (0.5, 5, 8 and 10.5 m) depths at a central deepest station during 1995 and 1996-97, respectively. Temperature and pH were meas-ured using a YSI probe. Organism samples were taken with a 6-L Van Dorn sampler. Chemical and biologic samples were processed following MOLAR Project protocols, including the recommended biomass conver-sion factors (Straškrabová *et al.* 1999, this issue).

Concentrate bacterial sub-samples were set on elec-tron microscopy grids (400-mesh Cu grids) with colloi-don film, stained with 1% uranyl acetate and examined at a magnification of ×20,000 in TEM equipment. Cells and calibration grids were pictured and the images were scanned. Length and width of >30 bacteria were meas-ured from scanned images using Corel Photo-Paint pro-gram. Cell volumes were calculated as $(W^2 L \pi)/6$, were W is the width and L is the length of the cell.

3. RESULTS

3.1. Abiotic characterization

During the study period La Caldera Lake showed strong inter-annual changes in its volume (depth) as a consequence of the severe drought of 1995. This was the driest year of a series of dry years (from 1988) and the driest year recorder for the last 4 decades (395 mm) and lake maximum depth reached only 2 m. In addition, the ice-free period was long and comprised from mid-May to early-November. The increase of precipitation during 1996 and 1997 was responsible for the recovery of the maximum lake depth (14 m), which was maintained within narrow limits for both years. The ice-free period for the wet years (1996-1997) was shorter than that registered in 1995.

La Caldera Lake exhibited weak thermal stratification in mid-summer, with maximum surface-bottom differences values ranging from 3.5 °C in 1996 to 6.7 °C in 1997. During the remaining of the season the lake had a uniform temperature profile and surface-bottom differences did not surpass 2 °C. Water temperature oscillated widely in 1995, but within a narrow range for the period of 1996-97.

16.3 µg P l^{-1}. PP accounted >74% of P fraction for this year.

Nitrogen was found mainly as inorganic forms in 1996 and during the first summer months of 1997 (DIN, dissolved inorganic nitrogen, represented more than 50% of TN, total nitrogen). However, DIN accounted *ca* 50% and <30% of TN, in 1995 and for the last months of 1997, respectively. DIN (and especially NO_3^-) slowly decreased over the summer of the wet years, although this tendency was not observed in 1995 (Tab. 1). According to Morris & Lewis (1988), DIN/PT (by weight) ratio values exceeding 12 implies a strong likelihood of P limitation, and in fact, this was the case of La Caldera for the study period except for the sporadic atmospheric loads of P. PN (particulate nitrogen) accounted for 20-30% of TN in 1995 (from late summer) and 1997 (almost all free ice period).

3.2. Phytoplankton

The autotrophic community was quite simple and composed of nanoplankton species, as is characteristic for oligotrophic systems (Rott 1984 & Carrillo 1995). Autotrophic picoplankton was absent.

During the dry year of 1995 (Fig. 1A) immediately

Tab. 1. Temperature and nutrients seasonal variation in La Caldera Lake for the study period. Values are monthly means for the water profile.

DATE	T (°C)	NO$_3$ (µg N l^{-1})	DIN (µg N l^{-1})	TN (µg N l^{-1})	PN (µg N l^{-1})	TP (µg P l^{-1})	PP (µg P l^{-1})	DIN:TP	NT:PT
May-95	12.0	166.3	259.9	473.2	30.9	6.7	5.1	48.6	74.0
June-95	12.5	122.8	133.3	311.1	16.2	4.9	3.6	37.1	62.8
July-95	15.4	142.1	151.8	328.6	11.9	5.9	3.7	80.8	57.7
August-95	14.0	233.4	238.2	575.0	128.7	9.9	8.0	31.0	58.1
September-95	7.5	297.2	301.0	620.2	64.7	12.7	8.5	35.9	50.2
October-95	6.9	277.5	282.6	665.8	85.8	5.2	4.7	68.3	165.9
November-95	4.2	286.5	289.2	612.3	129.5	2.3	2.3	123.9	262.4
July-96	1.6	381.0	393.9	617.2	26.4	4.6	2.1	87.3	135.7
August-96	6.5	271.9	280.5	480.1	8.9	5.4	3.4	53.6	90.5
September-96	7.7	228.0	239.3	456.7	18.4	11.4	4.1	40.9	77.6
October-96	6.0	214.6	229.8	383.0	31.1	3.6	2.5	64.4	107.3
June-97	1.2	231.5	255.9	308.9	31.1	1.9	1.0	139.5	181.9
July-97	5.5	205.6	213.5	325.4	45.2	4.2	3.0	52.8	80.8
August-97	11.5	128.6	136.0	361.8	130.3	6.5	4.1	21.8	56.9
September-97	11.6	103.7	108.0	233.8	78.6	3.8	3.0	29.9	62.8
October-97	7.7	83.4	90.9	284.7	129.1	4.1	2.8	23.1	71.9

During the wet years, total phosphorus (TP) usually ranged between 3.3 and 7.3 µg P l^{-1}. However, a strong increase was punctually registered in the lake in September of 1996, as a result of the Saharan dust input associated to atmospheric events, that resulted in an increase of about 10 fold the P of the lake (TP >32 µg P l^{-1}; TDP, total dissolved phosphorus, >25 µg P l^{-1}).

Particulate phosphorus (PP) was the dominant P fraction (>55%), except for the above mentioned increase, when PP accounted for less than 20%, and TDP over 80%. TP was (in average) higher in 1995 than during the wet years (Tab. 1) and ranged from 2.3 to

after thaw and till early-June, Chrysophyceae (*Chromulina nevadensis* and *Ochromonas* sp.) was the main developing group (>80% of phytoplankton abundance). From early-June, phytoplankton community was dominated by non-flagellated Chlorophyceae species (*Chlorella* sp.). In mid-summer, phytoplankton density reached the highest values (>75,600 cells ml^{-1}) and *Cyanarcus* sp. accounted for more than 40% of total cell abundance. By the end of the ice-free period phytoplankton abundance sharply decreased (<4000 cells ml^{-1}), and both *Chlorella* sp. and *Ochromonas* sp. dominated the autotrophic community. Other species, some

of benthic origin, were also represented (e.g. *Amphidinium* sp.; *Navicula* sp.; filamentous green algae *Spirogyra* sp.).
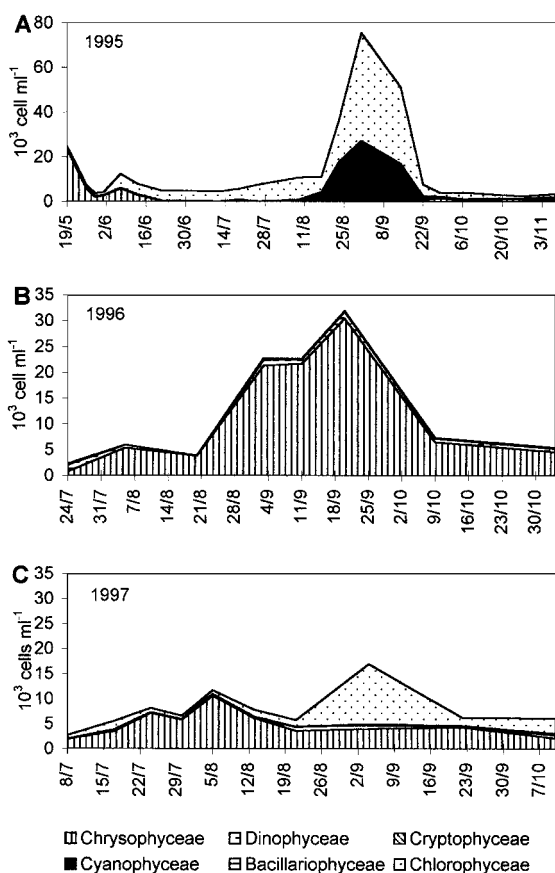

Fig. 1. Inter-annual and seasonal variation in the abundance of taxonomic phytoplankton groups. (A) 1995; (B) 1996; (C) 1997. Values are means for the water profile.

Phytoplankton community was dominated by *Chromulina nevadensis* for most of the ice-free period of 1996 (Fig. 1B), and from thaw to late August in 1997 (Fig. 1C), when it was replaced by *Chlorella* sp. which became the dominant species for a moderate period of time. Chrysophyceae reached its maximum density and biomass values in September of 1996: 21,000-30,400 cells ml^{-1} and >55 µg C l^{-1}, respectively (average values for the water column), immediately after a dust deposition event. Both Chrysophyceae and Chlorophyceae

reached lower densities (*ca* 12,000 cells ml^{-1}) and accounted >80% and >60% of total algal biomass, respectively, in 1997 (Fig. 1C).

Other less important species, such as *Amphidinium* sp. (Dinophyceae), *Rhodomonas minuta* (Cryptophyceae), *Ochromonas* sp. (Chrysophyceae) and *Cyanarcus* sp. (Cyanophyceae) developed during both wet years.

Phytoplankton seasonal succession showed the same basic pattern at all depths in 1996 and 1997. However, there were moderate differences on the water profile in both abundance and biomass of major phytoplankton groups. Highest values of abundance and biomass of the dominant algae species were reached after a dust event (September) and particularly at the surface of the water during the wet years. On the other hand, it is remarkable the high values of phytoplankton biomass (257 µg C l^{-1}) at the bottom depth immediately after thaw, in 1996. The development of a *Cryptomonas* sp. (Cryptophyceae) with a large cell volume (1730 ± 300 µm^3) was responsible for this situation, although abundance was less than 10%.

Chromulina nevadensis showed marked seasonal differences in size and morphology: after ice-out cells with big pyrenoids (mean cell volume 30-40 µm^3) developed, while cell volume gradually decreased to mean values of 5-8 µm^3 by the end of ice-free period. It is at this time when most of the cells (>70%) showed dendricules that increased surface of the cells.

3.3. Bacterioplankton

The heterotrophic bacterial community of La Caldera was composed of free small coccus-like (0.01 ± 0.004 µm^3) and rod shaped forms (0.05 ± 0.02 µm^3). Filamentous bacteria (0.18 ± 0.07 µm^3) were scarce. Most coccus-forms could be identified as virus like-particles because of their small size and poliedric shape, as similarly found for others lakes (Sommaruga *et al*. 1995; Pina *et al*. 1998).

Inter-annual changes in bacterial standing-stock variables for the period of 1995-1997 are shown in table 2. Overall, a decreasing tendency in these parameters is observed.

The seasonal dynamic of bacterial community showed limited inter-annual differences. Bacterial standing-stock parameters reached their highest values at mid-summer, with small oscillations towards the end of summer in 1995 (Fig. 2A). We observed a progres-

Tab. 2. Inter-annual changes in bacterial abundance and biomass observed during the period of 1995-1997. Values are annual means for the water profile.

Year	Abundance (cells ml^{-1} × 10^5)			Biomass (µg C l^{-1})		
	Average	Maximum	Minimum	Average	Maximum	Minimum
1995	10.75	26.57	4.46	10.33	25.53	4.28
1996	5.17	7.50	1.82	5.08	7.44	1.84
1997	1.96	3.30	1.22	1.92	3.20	1.19

sive increase tendency of bacterial abundance at surface depths in 1996. Maximum bacterial densities were reached at bottom depths in late August for this year. Bacterial abundance varied slightly over the ice-free period of 1997 (Fig 2C). Bacteria showed a fairly homogeneous vertical distribution with slight inter-depth differences in abundance and biomass (Fig. 3).
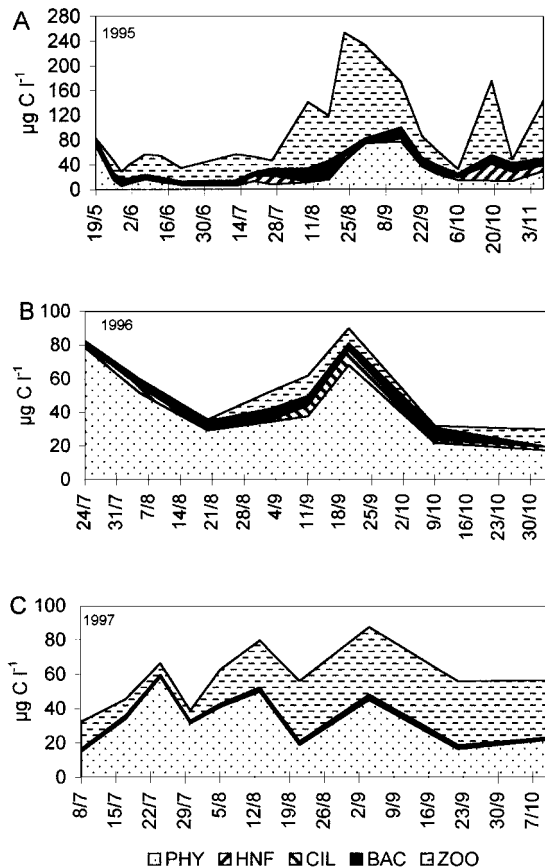

Fig. 2. Inter-annual and seasonal variation in the biomass of trophic groups. (A) 1995; (B) 1996; (C) 1997. Values are means for the water profile. PHY: Phytoplankton; HNF: Heterotrophic nanoflagellates; CIL: Ciliates; BAC: Bacteria; ZOO: Zooplankton.

3.4. Heterotrophic nanoflagellates and ciliates

The year of 1995 sets up a reference time with regard to the presence of heterotrophic nanoflagellates (HNF) and ciliates, not significantly represented in the lake before this year. Two distinct peaks of HNF were observed (Fig. 2A) during July (2000-5000 cells ml^{-1}) and by the end of the ice-free period (reaching values of up to 17,000 cells ml^{-1}).

Ciliates (*Oligotrichidae*) reached their highest density values immediately after the thaw (>4 cells ml^{-1}) and in August (>3 cells ml^{-1}) of 1995. Nevertheless, HNF populations were very scarce (<20 cells ml^{-1}) and ciliates increased considerably (>40 cells ml^{-1}) in mid-

September of 1996 (Fig. 2B). Finally, both groups were scarcely represented in 1997 (Fig. 2C).

3.5. Zooplankton

Zooplankton community composition was simple and we did not observe major inter-annual differences in composition. A calanoid copepod, *Mixodiaptomus laciniatus*, was the main zooplankton species. Rotifers (*Hexarthra bulgarica*) and cladocerans (*Daphnia pulicaria*) were usually present at low abundance.

Zooplankton abundance varied significantly among years, with lower densities (<1 ind l^{-1}) in 1996, in comparison to 1995 and 1997 (29 and 20 ind l^{-1}, respectively).

Seasonal biomass changes in zooplankton (mean values for the water column) ranged from 2.5 to 192.5 µg C l^{-1} (45.8 µg C l^{-1} on average) in 1995 (Fig. 2A). Although *H. bulgarica* contributed *ca* 10% on average to zooplankton biomass, this species dominated the zooplankton community (*ca* 50% biomass and >80% abundance) in early August and late September for the dry year of 1995. *D. pulicaria* was scarce and represented less than 10% of total zooplankton biomass by the end of summer (<5 µg C l^{-1}). Overall, *M. laciniatus* was the main species for the ice-free period and, in contrast to the wet years, it developed a bivoltine cycle with two hatching events that led towards two nauplii peaks during May-June (*ca* 70% total zooplankton abundance) and August-September (*ca* 10% total zooplankton abundance) in 1995. Nauplii were followed by subsequent adults peaks in mid-summer (*ca* 180 µg C l^{-1}) and by the end of the ice-free period (*ca* 120 µg C l^{-1}).

M. laciniatus comprised over 90% of zooplankton abundance and biomass in 1996 and 1997. Biomass (mean values for the water column) ranged from 0.002 to 12 µg C l^{-1} (approx. 4 µg C l^{-1} on average) in 1996 (Fig. 2B), and from 6 to 60µg C l^{-1} (approx. 29 µg C l^{-1} on average) in 1997 (Fig. 2C). *D. pulicaria* and *H. bulgarica* were scarce and accounted <5% of zooplankton abundance and biomass. The development of nauplii comprised the totality of zooplankton biomass from thaw until late August when copepods reached high abundance (maximum biomass value = 11.6 µg C l^{-1}) in 1996. A similar but earlier dynamic was observed for 1997, with the occurrence of naupliar stages replaced by adults of the dominant species *M. laciniatus* at the beginning of August. Other copepod species such us *Diaptomus cyaneus* or *Acanthocyclops vernalis* were very scarce for these wet years.

Zooplankton showed a heterogeneous vertical distribution. Overall, species concentrated at bottom depths during the time of sampling (mid-day), and especially during sunny days when zooplankton biomass at the bottom exceeded over three times that of surface (Fig. 3).
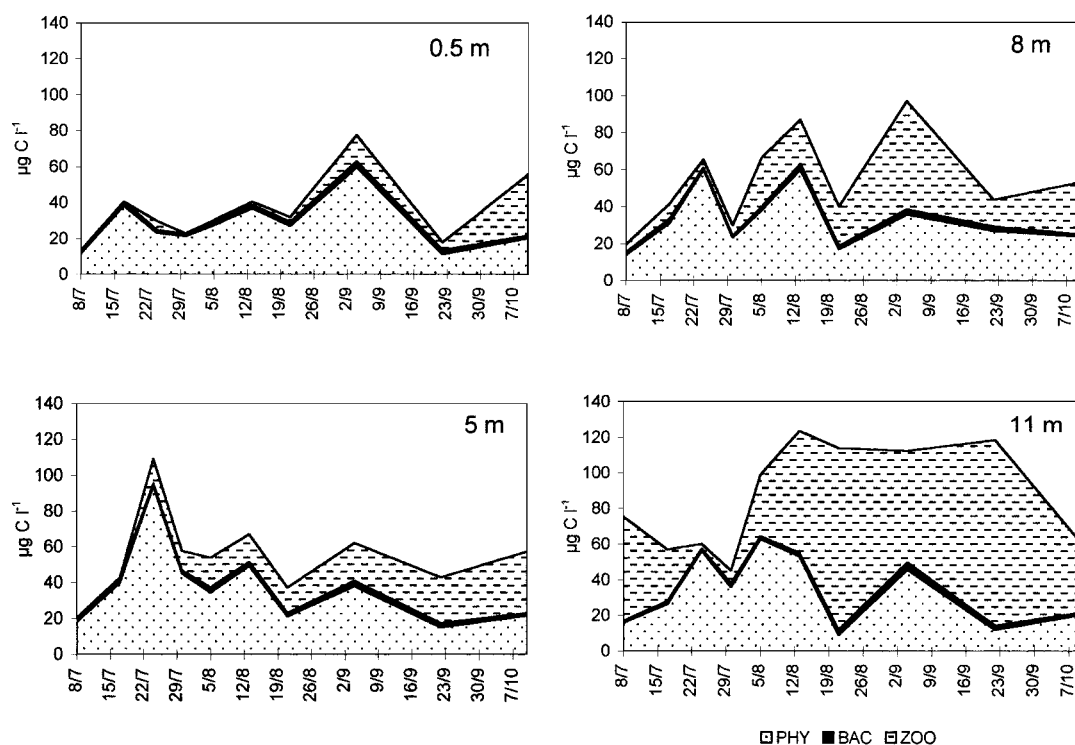
Fig. 3. Seasonal variation in the biomass of the main trophic groups during 1997 at 0.5, 5, 8, and 11 m depth. Legend as in figure 2.

3.6. Biotic and non-biotic components relationship

The autotrophic/heterotrophic (A/H) ratio showed significant differences between the dry and the wet years. Thus, values under 1 were registered during 1995, whereas this ratio averaged 5.7 and 2.2 for 1996 and 1997, respectively. The A/H ratio was always over 1 (from 1.5 to 20.3) in 1996, and under 1 (ranging from 0.4 to 0.6) towards the end of the ice-free period of 1997. A/H ratio was always over 1 after thaw.

Inter-annual changes in the contribution of trophic groups to total plankton biomass (water column average values) are summarized in table 3. Bacteria constituted a minor proportion of plankton biomass, especially for the wet years. On the other hand, phytoplankton was the main group for the wet years, but it only contributed 28% on average in 1995, as suggested by the A/H ratio <1. Zooplankton contributed significantly to the overall biological community, although being a non important fraction during 1996. HNF were only significant in 1995. Finally, and as a consequence of zooplankton scarcity, ciliates significantly contributed to the biological pool in 1996.

Our results showed that a tight relationship exists between nutrients (mainly P and N) and phytoplankton standing-stock parameters in 1995 (Tab. 4). Heterotrophic bacteria was negatively related to phytoplankton (r = -0.94, p <0.01) in 1996 (Tab. 4). In 1997 (Tab. 4)

algae were negatively related to *TN:TP* ratio (r = -0.92, p <0.001), and ciliates showed an inverse relationship with zooplankton (r = -0.80, p <0.01). Zooplankton and temperature showed a positive relationship in wet years (Tab. 4).

Tab. 3. Annual percentage biomass for each trophic group. BAC: Bacteria; CIL: Ciliates; HNF: Heterotrophic nanoflagellates; PHY: Phytoplankton; ZOO: Zooplankton.

Year	PHY	HNF	CIL	BAC	ZOO
1995	28.2	7.5	0.5	14.4	49.5
1996	73.9	0.2	5.4	9.3	11.2
1997	57.1	0.1	0.0	3.4	39.3

4. DISCUSSION

We have included data not only from 1996 and 1997 (study years of MOLAR Project) but also from 1995. We considered of basic relevance the analysis of the period spanning these three years because of the strong changes in precipitation regime from 1995. These changes caused variations in the physical and chemical features of the lake, since inputs of allochthonous nutrients (mainly *P*) occur with the thaw (Carrillo *et al.* 1996a), but also with the sporadic atmospheric depositions events associated to massive dust outbreaks from Sahara desert (Talbot *et al.* 1986; Guerzoni *et al.* 1997; Moulin *et al.* 1997a, 1997b). The peculiar water regime plus the influence of the atmospheric external forces

might be fundamental to plankton structure and dynamics.

Tab. 4. Results of the intra-annual correlation analysis among abiotic and biotic components (r values). ns: not significative. BAC: Bacteria; BIO: Biotic components; CIL: Ciliates; HNF: Heterotrophic nanoflagellates; MVB: Micro-bacterivorous; PHY: Phytoplankton; ZOO: Zooplankton. A: Abundance; B: Biomass. TP: Total phosphorus; PP: Particulate phosphorus; TN: Total nitrogen; T: Temperature. * p < 0.05, ** p < 0.01, *** p < 0.001.

| | 1995 | | | |
	PHY B	CIL B	ZOO A	BIO B
HNF A	ns	- 0.61*	- 0.62**	-
TP	0.73***	0.55*	ns	0.58**
PP	0.75***	0.68**	ns	0.61**
TN	0.75***	ns	ns	0.63**
	1996			
	BAC B	BAC A	MVB A	ZOO A
PHY B	- 0.94**	- 0.94**	ns	ns
PHY A	ns	ns	0.79*	ns
PN	0.90*	0.90*	ns	ns
T	ns	ns	ns	0.85*
	1997			
	PHY B	MBV A	ZOO A	ZOO B
PHY B	ns	0.79**	ns	ns
CIL A	ns	ns	- 0.78*	- 0.80**
TN:TP	- 0.92***	- 0.85**	ns	ns
T	ns	ns	0.87**	ns

4.1. Phytoplankton

Until 1995, phytoplankton seasonal succession showed a quite definite pattern: after thaw, flagellates (Chrysophyceae: *Chromulina nevadensis*; Dinophyceae: *Amphidinium* sp.) dominated, and were replaced by a large population of non colonial Cyanophyceae (*Cyanarcus s*p.) during mid-summer. At this time (August), the abundance of phytoplankton was maximum with values ranging 1700-5000 cells ml^{-1} in 1986 (Carrillo *et al*. 1995), 8000-14,000 cells ml^{-1} in 1992-93 (Carrillo *et al*. 1996a), *Cyanarcus* sp. accounting for more than 60-90% of phytoplankton biomass (Carrillo *et al*. 1995, 1996a). At the end of the summer, flagellates (*C. nevadensis, Amphidinium* sp.) were predominant again. Other species were less important (Chlorophyceae: *Oocystis lacustris*; Bacillariophyceae: *Cyclotella* sp.). The consistency of this pattern over the years is well documented for this lake (Martínez 1977; Carrillo 1989; Reche 1995).

Total algal abundance increased about 7.5 fold in 1995 with respect to previous years. Chrysophyceae was replaced by non-flagellate Chlorophyceae species (*Chlorella* sp.), even though *Cyanarcus* sp. accounted for about 40% of total algal abundance at mid-summer (Fig. 1A). We believe that this shift could be related to the high *P* levels (Tab. 1) in a year (1995) when resuspension processes were significant due to the small lake volume. As already suggested by Currie (1990), the positive correlation found between either TP or PP with algal biomass (Tab. 4) indicates the increase of P avail-

ability to algae. Such an increase could favour the competitive development of *Chlorella* sp. over Chrysophyceae species, as the first thrive in relatively rich phosphorus habitats (Reynolds 1984, 1998). Moreover, the increased phosphorus levels can surpass a critical threshold above which P would not be limiting to maximum algal growth rates, in spite of the high N/P ratio (Reynolds 1992, 1998).

We found that temperature is a second key factor that could explain the development of *Chlorella* sp. The results of the stepwise regression analysis showed that about 16% (p <0.05) of the variance in Chlorophyceae abundance was explained by temperature only (TP and temperature together explained 56% of variance, p <0.01) in 1995. In this context, we found that *Chlorella* sp. developed when water temperature surpass 10 ºC on average (1995 and second half of 1997).

The recovery of the lake volume led towards *C. nevadensis* (Chrysophyceae) domination of the phytoplankton community during 1996 (Fig. 1B) and the first half of 1997 (Fig. 1C). The absence of a significant relationship between TP or TDP with any biological parameter suggests the insignificant role played by phosphorus in controlling plankton seasonal dynamics and hence the weakness of bottom-up forces during this period. Furthermore, most of the phosphorus associated to external loads was presumably not taken up by plankton but lost to the sediment (Tab. 1), since much of this phosphorus is adsorbed to grain particles (Avila *et al*. 1997; Perry *et al*. 1997). The scarce zooplankton during this period favoured *C. nevadensis* growth because of zooplankton effectiveness in controlling phytoplankton via grazing (Carrillo *et al*. 1990, 1991b, 1995).

When Chrysophyceae dominated the phytoplankton community of La Caldera, Reche *et al*. (1997) found that phosphorus released by zooplankton, could satisfy between 74 and 316% of the sestonic minimum *P* demands. Due to the extremely low zooplankton abundance and biomass values during 1996, zooplankton could only satisfy between 1.24 and 41% of the *P* algae demands (Villar-Argaiz *et al*. submitted). It is reported that aquatic bacteria are rich in phosphorus and show low *N:P* ratio (Andersen *et al*. 1986; Elser *et al*. 1995; Fagerbakke *et al*. 1996). As a consequence, much of algae phosphorus demands might be satisfied by bacterial phosphorus through the possible bacterivory shown by *C. nevadensis* (Carrillo *et al*. 1991a), as previously reported for other Chrysophyceae species (Porter 1988, Salonem & Jokinen 1988, Nygaard & Tobiesen 1993). The negative relationship found between algal biomass and bacterial abundance or biomass (r = -0.94, p <0.01, Tab. 4) and the morphologic pattern showed by *C. nevadensis* further support this hypothesis. Besides, the positive relationship between algal standing-stock parameters and heterotrophic micro-bacterivorous (HNF plus ciliates) abundance (1996: r = 0.79, p <0.05; 1997: r = 0.79, p <0.01, Tab. 4), suggests that two potential

bacterivorous communities covariate with respect to a common factor, which we hypothesize as bacteria.

The *Cryptomonas* sp. population developed at the bottom just after thaw, what is consistent with its ability to growth during vernal conditions (Reynolds 1984). Moreover, the growth of *Cryptomonas* sp. occurred at a period of zooplankton scarcity, due to the high grazing susceptibility of this species. (Reynolds 1998).

Maximum phytoplankton densities dropped during 1997 (approx. 10000-15000 cells ml^{-1}), and was consistent with the recovery of zooplankton populations (mainly calanoids), and consequently with the increase of the zooplankton grazing pressure (Carrillo *et al.* 1990, 1991b, 1995).

C. nevadensis was the dominating species from thaw to mid-August, when *Chorella* sp. began to replace it, coinciding with water temperature values above 10 ºC and the recovery of the zooplankton community. Algal biomass was negatively related to TN/TP ratio (r = -0.92 p <0.001, Tab. 4) suggesting a seasonal growth pattern controlled by phosphorus. Since allochthonous phosphorus inputs were low in 1997, much of the *P* availability in the pelagic zone should originate from zooplankton recycling which could satisfied about 335% of algal minimum P requirements (Villar-Argaiz *et al.* submitted) Moreover, from mid-summer, the DIN/TP ratio reached similar values to those registered in 1995, indicating a fall in the severity of P limitation, what could support Chlorophyceae development.

During the wet years, the usual development of *Cyanarcus* sp. at mid-summer (Carrillo *et al.* 1995) was absent. It is well known that Cyanophyceae thrive in relatively warm waters (Smith 1985; Reynolds 1984, 1998). The water temperature in mid-summer of years before 1996 reached values above 14 ºC (Carrillo *et al.* 1996a), whereas water was always below 12 ºC for the same period of 1996 and 1997. For this reason, we interpreted that the relatively low water temperature values (<14 ºC) registered at any time during 1996 and 1997 could explain the absence of *Cyanarcus*, meanwhile other more temperature tolerant taxonomic group (Chrysophyceae, Chlorophyceae) could successfully growth.

4.2. Bacterioplankton

Because of the small cell size, bacterial contribution to overall planktonic biomass was low, specially during the wet years (<10% on average). A clear diminishing pattern in bacterial standing-stock parameters is observed (Tab. 2) from 1995, with values in the lowest limit of the range characteristic for oligotrophic lakes (Thomas *et al.* 1991a, 1991b; Reche *et al.* 1994; Ochs *et al.* 1995).

The net results of bottom-up (mainly P-availability) and top-down (grazing) forces determine the variation in bacterioplankton parameters (Pace & Cole 1994).

However, the absence of a significant relationship between bacterial standing-stock parameters and other biotic or abiotic components does not clarify for the relative strength of the above controls in 1995. Nevertheless, several facts might support for top-down control on bacteria for the wet years. First, we found a strong negative relationship between algal biomass (mainly Chrysophyceae) and bacteria (r = -0.94, p <0.01, Tab. 4) in 1996; second, the low bacterial densities registered during 1997 (Fig. 2C), coincides with a phytoplankton community dominated by *C. nevadensis* (at least during the first half of the ice-free period) and with high zooplankton densities. In this context, Reche (1995) found that *M. laciniatus* indeed grazed on bacteria. Finally, the mean bacterial cell size (*ca* 0.03 µm^3) was among the lowest found for natural bacterioplankton (Ammerman *et al.* 1984; Lee & Fuhrman 1987; Ochs *et al.* 1995). This low bacterial cell size might be the result of an intense grazing pressure, since phagotrophic nanoflagellates and ciliates can graze selectively on larger bacterioplankton cells (Anderson *et al.* 1986; González *et al.* 1990; González 1996; Pernthaler 1996). In addition, it has been reported the presence of large filamentous bacteria resistant to protistan grazing (Jürgens & Güde 1994; Sommaruga & Psenner 1995). Our results indicate the presence of such filamentous bacteria, but in low densities (<2% of total bacteria abundance), which could suggest zooplankton selective predation (Güde 1988; Jürgens *et al.* 1994).

4.3. Heterotrophic nanoflagellates and ciliates

HNF populations were significantly present only in 1995 (Fig. 2A) when the increase in *P* led to a higher diversification of the plankton community. The negative relationship between HNF and ciliates on a seasonal scale (r = -0.61, p <0.05) suggests a competitive exclusion for a common resource (bacteria). Also, HNF populations could be controlled by zooplankton (potential HNF grazer) as suggested by the negative relationship between both groups abundance (r = -0.62, p <0.01).

In Lake La Caldera, ciliate populations might be subject to strong top-down control by zooplankton. This view agrees well with the negative relationship found (1997) between ciliates abundance and zooplankton biomass (r = -0.80, p <0.01) and abundance (r = -0.78, p <0.05). This could explain the large ciliate development registered in 1996 coinciding with the extremely low zooplankton densities. Furthermore, in most previous papers ciliates have been very scarce in La Caldera, whereas zooplankton have been well represented (Carrillo *et al.* 1995; Reche *et al.* 1997). Several studies showed that protozoans are excellent preys with high nutritional value exploited by zooplankton (Porter *et al.* 1979; Stoecker & Capuzzo 1990; DeBiase *et al.* 1990; Gifford 1991; Cruz-Pizarro *et al.* 1994).

4.4. Zooplankton

The *P*-limitation conditions in this system can help to explain the dominance of calanoids copepods over cladocerans, since the latter are expected to dominate in fishless systems (Gliwicz 1985; Cruz-Pizarro *et al.* 1994). Calanoid copepods show higher *N:P* ratios and lower *P* requirements than cladocerans (Andersen & Hessen 1991; Villar-Argaiz *et al.* in press), so they would be better adapted to live in *P*-limited environments. On the other hand, *H. bulgarica* (Rotifers), with lower *N:P* ratios (Villar-Argaiz *et al.* submitted), developed significantly only during 1995, since phosphorus availability was higher than measured in wet years and the bacterioplankton community (their potential preys) showed the highest density values for the three years of the study period. It is likely that the increase in both *P* availability and ice-free season duration were responsible for *M. laciniatus* bivoltine cycle, since nauplii show higher *P*-requirements than copepodites or adults (Carrillo *et al.* 1996a, 1996b; Villar-Argaiz *et al.* in press).

The low specific growth rates of *M. laciniatus* (Cruz-Pizarro 1981a), as expected from the relatively high *N:P* ratio (Sterner 1995; Elser *et al.* 1996), led towards the slow recovery process until "normal" zooplankton abundance in 1997. Moreover, since temperature and zooplankton standing-stock parameters covaried positively (Tab. 4) it is possible that the low water temperature values registered during wet years might have conditioned this slow recovery process. Thus, during 1997, zooplankton densities and biomass values were similar to those registered before 1995 (Cruz-Pizarro 1981b; Carrillo 1989; Reche 1995, Carrillo *et al.* 1995).

The heterogeneous vertical distribution shown by zooplankton, in a large proportion at bottom depths during mid-day (Fig. 3), is consistent with the direct migratory behaviour pattern characteristic of zooplankton in La Caldera (Carrillo *et al.* 1991b).

4.5. Autotrophic:Heterotrophic ratio

Input of allochthonous organic carbon into the Lake are negligible (Reche *et al.* 1996) and, therefore, the system is considered autotrophic. Interestingly, the A/H ratio showed values under 1 during the dry year of 1995, indicating the presence of relatively lower phytoplankton standing stock but with a fairly high production, which ultimately could support a complex heterotrophic community (Reynolds 1984; Stegmenn & Peinert 1984). In contrast, A/H ratios over 1 were found after thaw during the wet years, except for late summer of 1997 coinciding with zooplankton recovery.

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