The effects of hydrology on plankton biomass in shallow lakes of the Pampa Plain

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Abstract

Climatic and hydrological variability is usually high in the Pampa Plain (Argentina). However it has not studied yet how this variability may affect the phytoplankton and zooplankton biomass and community structure in aquatic systems of this region. The main purpose of this study was to assess flushing effects on nutrient and plankton dynamics in two interconnected very shallow lakes of the Pampa Plain. In order to study the impact of hydrology on the plankton biomass and community structure, we compared the summer plankton community among three consecutive years with contrasting hydrological characteristics. Water residence time varied an order of magnitude among years and this variability was correlated to strong changes in physicochemical and biological lake characteristics. Depending on the water discharge level, the hydrological regime within the lakes ranged from lentic to more lotic conditions. Nutrient and phytoplankton biomass were positively related to water discharges. During high flushing periods, nutrients import from intensive agriculture lands leads to a dramatic increase in trophic conditions. On the other hand, macrozooplankton biomass was positively related to water residence time and showed a dramatic decrease during high flushing years. Rotifers biomass was not affected by interannual water discharge variability during the study period. Our results support that in case of lakes with high flushing rates, zooplankton development is dependent on water residence time and that hydrology may have stronger effects on macrozooplankton biomass than top-down control by planktivores.

Introduction

The comprehension of the factors that determine plankton biomass has been one of the main tasks in freshwater ecology since eutrophication debate started in early 1960s. Anthropogenic eutrophication is caused by using lakes and rivers as recipients for municipal, agricultural and industrial wastes. It has become clear that phosphorus can be usually considered the main limiting nutrient in freshwater systems and that phosphorus supply sets an upper bound on the phytoplankton bio-mass in lakes (Schindler, 1977; Schindler, 1978). But although total phosphorus explains more than 80% of the chlorophyll variability, the residual variance indicates that phytoplankton yield varies an order of magnitude among lakes with the same total phosphorus level (Andersen, 1997). In the 1980s, food web interactions appeared to explain phytoplankton biomass variability once nutrients concentration had been taken into account (Mc Queen et al., 1986; Quirós, 1990). Zooplankton grazing was identified as a strong modulator of the realized phytoplankton yield in lakes (Shapiro,

1980). The factors that affect the control of zooplankton over phytoplankton biomass were extensively studied during the last two decades (Bergquist, 1985; Vanni, 1987; Dawidowicz, 1990; Gliwicz, 1990).

Besides resource control and trophic interaction effects on plankton biomass, strong differences in plankton dynamic between shallow (polymictic) and deep (stratified) lakes were stated (see Wetzel, 2001). Shallow lakes can be colonized by macrophytes, which can prevent phytoplankton development if a critical nutrient loading level is not exceeded (Sheffer et al., 1993). Several mechanisms were proposed to explain low phytoplankton biomass in lakes dominated by macrophytes (shading, reduction of nutrient availability, excretion of allelopathic substances, reduction of resuspension and enhanced of grazing) (Sheffer, 1998). Another important difference between shallow and deep lakes is the strong influence of nutrients loading from the sediments in shallow lakes. Indeed, sediment release of phosphorus can be enhanced in shallow highly eutrophicated systems in which sediment has become anoxic because of intensive bacterial activity (Boström et al., 1982).

Variability in water residence time is another contrasting feature between shallow and deep lakes. Being of relatively small volume, the water residence time is lower and more variable in shallow than in deep lakes (Kalff, 2002). Dickman (1969) stated that in lakes with high flushing rates, all factors described above might be of secondary importance on plankton biomass if considerable plankton standing crop is removed by flushing. There is a growing number of studies on the effects of hydrological variability in the pelagic system of shallow lakes. Variation in water residence time is associated with changes in plankton biomass and community structure (Welker & Walz, 1999; Błędzki & Ellison, 2000; Olding et al., 2000; Baranyi et al., 2002).

Climatic and hydrological variability is usually high in the Pampa Plain. The effects of this variability in the aquatic systems of this region have been recently studied (Quirós et al. 2002a). However, it has not been studied yet how hydrological variability may affect the plankton biomass and community structure of the pampean shallow lakes. The main purpose of this study was to assess flushing effects on nutrients and plankton dynamics in two interconnected very shallow lakes of the Pampa Plain. If plankton community structure is affected by changes in water residence time we expect that both phytoplankton (Dickman, 1969) and zooplankton (Błędzki & Ellison, 2000; Baranyi et al., 2002) biomass will decrease during periods of high water discharge and that plankton species with high generation time will be replaced during flooding periods by species with shorter generation time (Walz, 1995; Olding et al., 2000).

Material and methods

Study area

The Pampa Plain is situated in the Subtropical Region (33°–39° S, 57°–64° W), in the central area of Argentina. The Pampa Plain lakes are shallow and their basins were usually formed by a combination of river and wind action (Tricart, 1973). These lakes have very high levels of nutrients (Quirós & Drago, 1999) and phytoplankton abundance is usually high (Quirós, 1988). Mean annual precipitation is 935 mm with marked interannual variability (Sierra et al., 1994). The study was carried out in Gómez and Carpincho lakes, which are located in the upper Salado River basin in a well-buffered calcareous sedimentary region (Fig. 1). Mean summer discharge of the Salado River is about 9.2 $m^3 s^{-1}$ with high interannual variability. Depending on the water discharge level of the Salado River, the hydrological regime within the lakes can range from lentic (low water renewal rate) to more lotic (very high water renewal rate) conditions. Gómez Lake area is 3600 ha and it has a mean depth of 1.2 m, while Carpincho Lake area is 400 ha and its mean depth is 1.1 m. Depth ratio, defined as the rate between mean depth and maximum depth, is 0.79 for Carpincho Lake and 0.63 for Gómez Lake. Both depth ratios fall into the range of ellipsoid forms, which characterizes shallow lakes with flat bottoms (Kalff, 2002). Lakes with this morphometry could be colonized by macrophytes and most probably Gómez and Carpincho lakes had been in a clear state dominated by macrophytes in historical times. However, both lakes have become
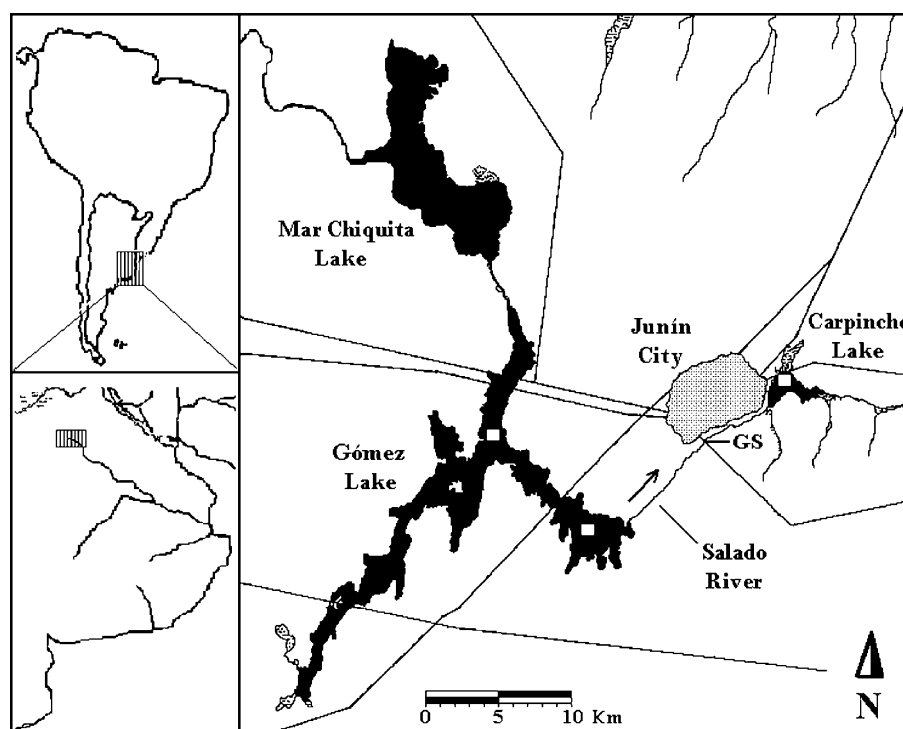
Figure 1. Study area, sampling sites for Gómez Lake and Carpincho Lake are shown as white squares. The arrow indicates the direction of flow. GS, the gauge station of water discharge of the Salado River.

hypertrophic because of intensive agriculture and urban discharges waste in Salado River basin (Quirós et al., 2002a). At present, Carpincho is actually more directly impacted by Junín city waste discharges.

Sampling and laboratory analyses

In order to study the impact of hydrology on the plankton biomass and community structure, we compared the summer plankton community in Carpincho and Gómez lakes among three consecutive years with contrasting hydrological characteristics. During the periods December-March of the summer 1999, 2000 and 2001 both lakes were sampled monthly for total phosphorus (TP) and zooplankton. Chlorophyll-a was measured in summer 2000 and 2001. All sampling sites were in the pelagic zone; two sites were sampled in Gómez Lake (Gómez north, GN and Gómez east, GE) and one site in Carpincho Lake (Fig. 1).

For TP and chlorophyll-a analyses, water samples were taken at a depth of 50 cm bellow the water surface. TP concentrations were determined by the ascorbic acid method corrected for turbidity, following current APHA procedures (APHA, 1995). To determine the chlorophyll-a concentration, the water samples were filtered in the field through Whatman GF/F filters, using a hand vacuum pump. The filters were wrapped in aluminum foil, cooled and transported in dried silica gel to the laboratory. Chlorophyll-a concentrations were measured by spectrophotometry after extraction in 2:1 chloroform-methanol solution in the dark at 5 °C for at least 48 h (Wood, 1985). We used chlorophyll-a as an indicator of phytoplankton biomass and Secchi disk lecture (SDL) as a measure of water transparency. Water conductivity, corrected by temperature, was measured in the field with a YSI 85.

Zooplankton samples were collected with vertical net tows (15 cm diameter conical net; mesh width 69 μm) from 0.4 m above the lake bottom to the surface. Samples were immediately preserved in 4% sucrose-formalin solution (Haney & Hall, 1973). After thoroughly being

Table 1. Spring-summer rainfall and hydrological variables along the three sampling years. Mean values ($n = 4$) are given for summer period, standard deviations within parentheses. Means with the same letter (a or b) are not significantly different (paired *t*-test, $p < 0.05$). Tw, water residence time

Variable	1999	2000	2001
Spring-summer rainfall (mm)	773	535	1087
Water discharges (m^3 s^{-1})	10.8[a] (3)	6.0[a] (7)	42.2[b] (16)
Carpincho Tw (days)	4.9[a] (1.3)	28.7[a] (39.8)	1.6[b] (0.4)
Gómez Tw (days)	45.5[a] (12.9)	267.6[a] (377.3)	13.8[b] (3.5)

mixing, three 5-ml subsamples (representing up to 10% of the total sample) were counted and at least 100 specimens of cladocerans, copepods and rotifers were measured. Mean individual biomass, as dry weight, was calculated using length-weight regressions (Dumont et al., 1975; Bottrell et al., 1976). Standing crop biomass was estimated by multiplying the density of each group by mean individual dry weight values. Cladocerans were identified, where possible, to species level.

Calculation of water residence time

Water discharge data for the Salado River were obtained from the Department of Hydrology (Buenos Aires Province) based on monthly water gauge measurement. The water residence time (Tw) was calculated using lakes volumes based on measurements of surface area and mean depth (Quirós, 1990) and water discharge volume which was measured in Salado River between Carpincho and Gómez lakes; this measurement represents the into flow for Carpincho Lake and the out flow for Gómez Lake (Fig. 1). Besides the Salado River there is no other major into flow to Carpincho Lake.

Statistical analysis

Cladocerans biomass data were transformed into log $(x + 1)$ prior to analysis to meet statistical criteria for normality and stabilize variances. Paired *t*-test was employed for the detection of temporal and spatial differences. Spearman correlation analysis was carried out to relate TP concentrations to water discharges levels. Statistical analyses were performed using NCSS 2000 statistical software (Hintze, 1998).

Results

Hydrology, nutrient and phytoplankton biomass

The mean summer water discharge of the Salado River seemed to be positively related to total spring-summer rainfall (Table 1). In 1999 and 2000 both precipitations and Salado River discharge were around the historical levels but in 2001 higher spring-summer rainfall leaded to a significantly increase in river discharge (Fig. 2, Table 1). Therefore, in both lakes Tw was significantly shorter in 2001 than in 1999 and 2000 (Table 1). High rainfall in 2001 determined more lotic conditions (roughly Tw < 15 days) in both lakes during the entire summer season of this year. Conversely, during summer 2000 lentic conditions prevailed (roughly Tw > 15 days) in both lakes. On the other hand, interannual variability in river discharge was reflected in the water conductivity of both lakes. Water conductivity was lower under lotic conditions in 2001 and maximum at lower discharge levels in 2000. In 1999, the river discharge and water conductivity achieved intermediate levels in all sites (Table 2).
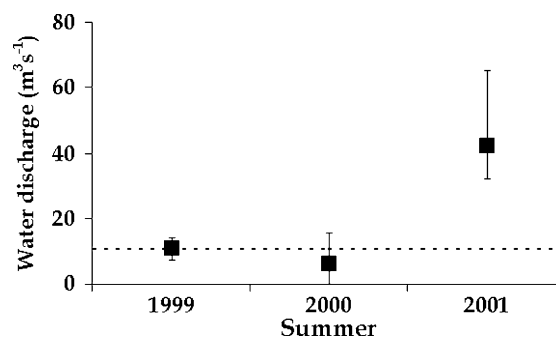

Figure 2. Mean and range of summer water discharges for Salado River during the three sampling summers ($n = 4$). Dashed line indicates the historical mean summer discharges (based on the measures of 12 summers periods).

Table 2. The physicochemical parameters and plankton biomasses for the three sampling sites. Mean values ($n = 4$) are given for summer period, standard deviations within parentheses. For a given site, means with the same letter (a, b or c) are not significantly different (paired t-test, $p < 0.05$). SDL, Secchi disk lecture; TP, total phosphorus concentration

	Gómez North			Gómez East			Carpincho		
	1999	2000	2001	1999	2000	2001	1999	2000	2001
Conductivity (μS cm^{-1})	4642 (51)	8255 (774)	3518 (47)	4415 (173)	7780 (694)	3513 (133)	3803 (948)	7060 (471)	3376 (95)
SDL (cm)	22$^{a\,b}$ (7)	26^a (5)	17^b (6)	33$^{a\,b}$ (13)	38^a (8)	20^b (6)	26^a (9)	38^b (8)	23^a (8)
TP (μg l^{-1})	1014$^{a\,b}$ (395)	643^a (280)	1263^b (79)	676^a (199)	473^b (66)	1321^c (164)	933^a (345)	463^b (69)	1333^c (304)
Chlorophyll-a (μg l^{-1})	–	78^a (17)	135^b (51)	–	56^a (25)	110^b (49)	–	61^a (28)	111^b (37)
Cladocera dw (μg l^{-1})	1062^a (760)	920^a (970)	84^b (165)	1472^a (1269)	1317^a (1331)	142^b (279)	219^a (162)	823^b (473)	53^c (106)
Cyclopoida dw (μg l^{-1})	648^a (254)	667$^{a\,b}$ (276)	77^b (46)	529$^{a\,b}$ (374)	440^a (108)	87^b (42)	246$^{a\,b}$ (203)	475^a (228)	35^b (42)
Calanoida dw (μg l^{-1})	165^a (158)	3^b (6)	9^b (17)	447^a (541)	4^b (9)	6^b (9)	219^a (159)	1^b (2)	0^b (0)
Nauplii dw (μg l^{-1})	64^a (37)	47$^{a\,b}$ (45)	9^b (9)	47^a (48)	10$^{a\,b}$ (5)	8^b (6)	15^a (8)	49$^{a\,b}$ (59)	3^b (4)
Rotifera dw (μg l^{-1})	345$^{a\,b}$ (469)	90^a (67)	29^b (29)	86^a (80)	63^a (52)	64^a (77)	92^a (124)	77^a (86)	58^a (43)

The water transparency and TP and chlorophyll-*a* concentrations revealed hypertrophic conditions for both lakes (Table 2). SDL was never higher than 50 cm in any sampling site and mean summer chlorophyll-*a* concentration was always higher than 50 μg/l (Table 2). During summer 2001, SDL was significantly lower than in summer 2000, when lentic conditions prevailed (Table 2). Furthermore, in all sites TP concentration was positively related to water discharge (Spearman correlation, Gómez North: $r = 0.61$, $p < 0.05$; Gómez East: $r = 0.88$, $p < 0.01$; Carpincho: $r = 0.73$, $p < 0.01$), in fact, the mean summer TP concentration was higher in 2001, intermediate in 1999 and lower in 2000 for all sampled sites (Table 2). Both TP and chlorophyll-*a* concentrations showed significant differences between 2000 and 2001 in all sites (Table 2). In 2001 chlorophyll-*a* levels were almost twice of those measured the previous year. Moreover, chlorophyll-*a*:TP ratio showed a decrease during 2001 but differences were not significant (Table 2).

Zooplankton biomass and community structure

Although rotifers were the most abundant among the zooplankton groups, cladocerans and cyclopoids dominated the zooplankton community in terms of biomass (Table 2). In Carpincho Lake, cladocerans biomass was higher in 2000 than in 1999, while no differences were found in the Gómez sites between these years (Table 2, Fig. 3). Cladocerans and cyclopoids biomass significantly decreased during more lotic conditions in 2001, achieving their lowest mean summer biomass in all sites during this year (Table 2). Moreover, in 1999 and 2000, both cladocerans and cyclopoids biomasses showed clear peaks during summer, whereas in the wet summer of 2001, the peaks disappeared and crustaceans biomass remained low throughout the entire season (Fig. 3).

Calanoids showed the same pattern in both lakes (Table 2). Their biomass was higher in 1999, when they also reached their highest relative biomass. Conversely, during 2000 and 2001 calanoids almost disappeared, their mean summer biomass decreased to less than 10 μg/l (Table 2) and their relative biomass did not exceed 5% of the total macrozooplankton biomass. Nauplii biomass was closely related to total copepod biomass, so it was also significantly lower in all sites during 2001,

when more lotic conditions prevailed (Table 2). Maximum levels of nauplii were reached in 1999 in Gómez Lake and in 2000 in Carpincho Lake.

In contrast to the crustaceans, there were almost no differences in rotifers biomass among years (Table 2, Fig. 3). Crustaceans dominated zooplankton biomass during the three sampled summers, however during high water discharges in 2001, an increase in rotifers representation was observed (Table 2). In 1999 and 2000 rotifers never contributed more than 15% to the total zooplankton biomass, while in 2001 the mean summer relative biomass of rotifers were 39% in Carpincho, 21% in GE and 13% in GN.

The temporal variations of cladocerans species compositions for both lakes are presented in Figure 4. The most frequently occurring species were found among the genus *Daphnia*, *Moina* and *Ceriodaphnia*. In GE, the genus *Daphnia* dominated during the entire summer season in 1999 and 2000. In GN *Daphnia* spp. prevailed during 1999, whereas both *Daphnia* spp. and *Moina* spp. were dominant in 2000. Finally, in Carpincho, *Daphnia* spp. dominated in 2000, while *Ceriodaphnia* spp. and *Moina* spp. were as abundant as *Daphnia* sp. during 1999. In early summer of 2001 *Daphnia* spp. was the most abundant cladoceran in all sites. However, in January *Daphnia* spp. populations declined and they were replaced by *Moina* spp. in Gómez Lake and by an assemblage of *Ceriodaphnia* spp., *Alona* spp., *Bosmina* spp. and *Leydigia* spp. in Carpincho Lake.

A comparison among lakes showed that there were no differences in zooplankton biomass during 2000 and 2001 (paired *t*-test $p > 0.05$). However, in 1999 cladocerans and cyclopoids biomass were lower in Carpincho than in Gómez Lake (paired *t*-test, $p < 0.05$ for both groups).

Discussion and conclusions

Hydrology, nutrient and phytoplankton biomass

Plankton dynamic in aquatic systems is governed by complex interactions between biotic and abiotic factors. For very shallow lakes it is accepted that nutrient resource, feeding, predation and macrophytes development have strong effects on both phytoplankton and zooplankton biomass and
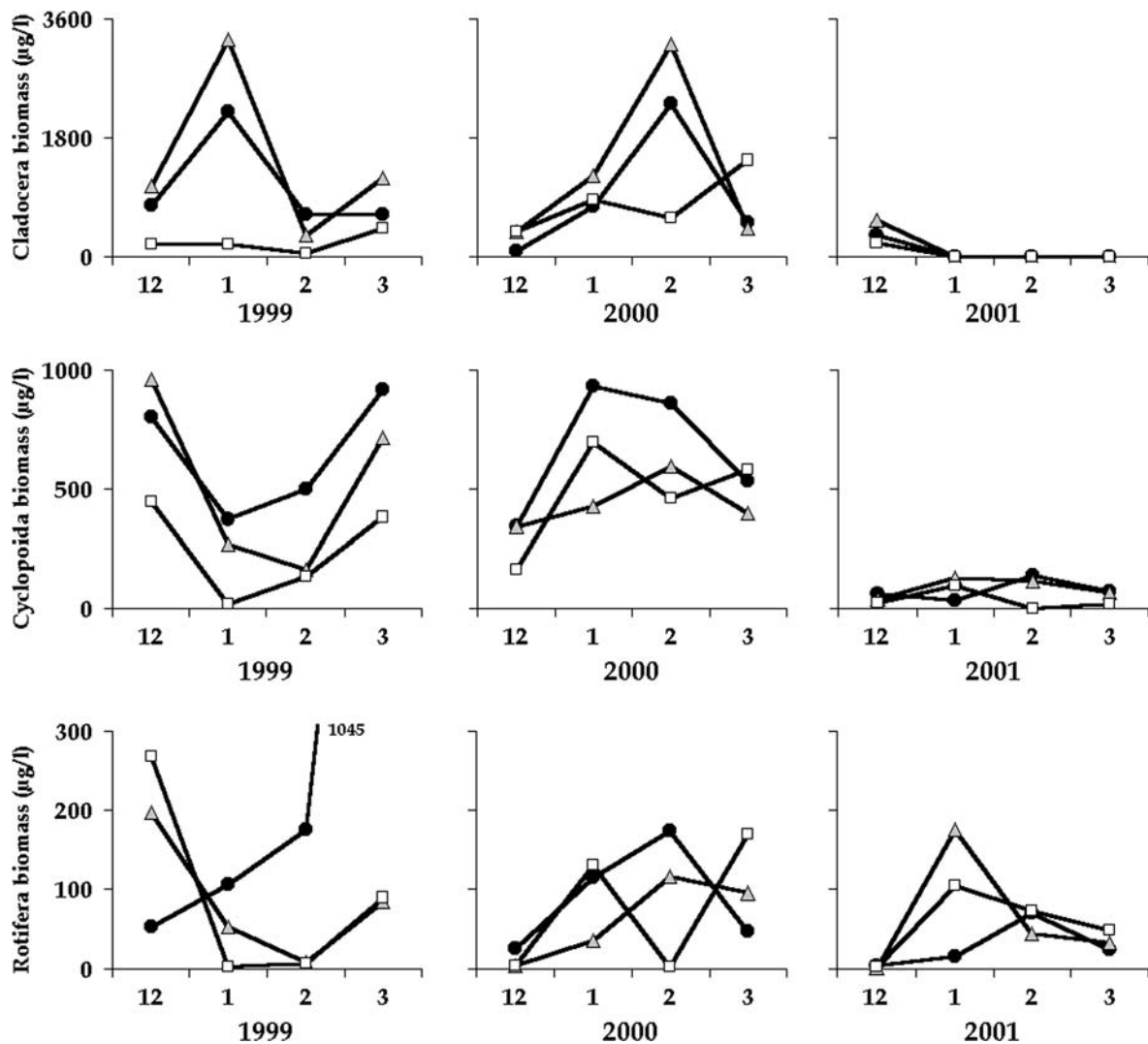
Figure 3. Variation in zooplankton biomass as dry weight along the three sampling summer for Carpincho lake (open square), Gómez North (black filled circle) and Gómez East (gray filled triangle). Note the change in scale of y-axis among different zooplankton groups.

community structure (Sheffer, 1998). With the exception of a few studies (Dickman, 1969; Søballe & Kimmel, 1987; Welker & Walz, 1999; Błędzki & Ellison, 2000; Olding et al., 2000; Baranyi et al., 2002), the effects of hydrology variability on plankton communities in very shallow systems have been less studied.

The typical interannual variability of hydrology in the Pampa Plain was clearly observed during the study period. Water residence time varied an order of magnitude among years and this variability was correlated to strong changes in physicochemical and biological lake characteristics. Depending on the water discharge level, the hydrological regime within the lakes ranged from lentic to more lotic conditions. The summer 2000 was the driest one and it was characterized by clear lentic conditions. Water residence time was higher and water conductivity and transparency were maximum in both lakes. High water conductivity revealed that evapotranspiration process prevailed over precipitation during this year. Conversely, in 2001 high spring-summer rainfall leaded to higher discharges in the Salado River and then more lotic
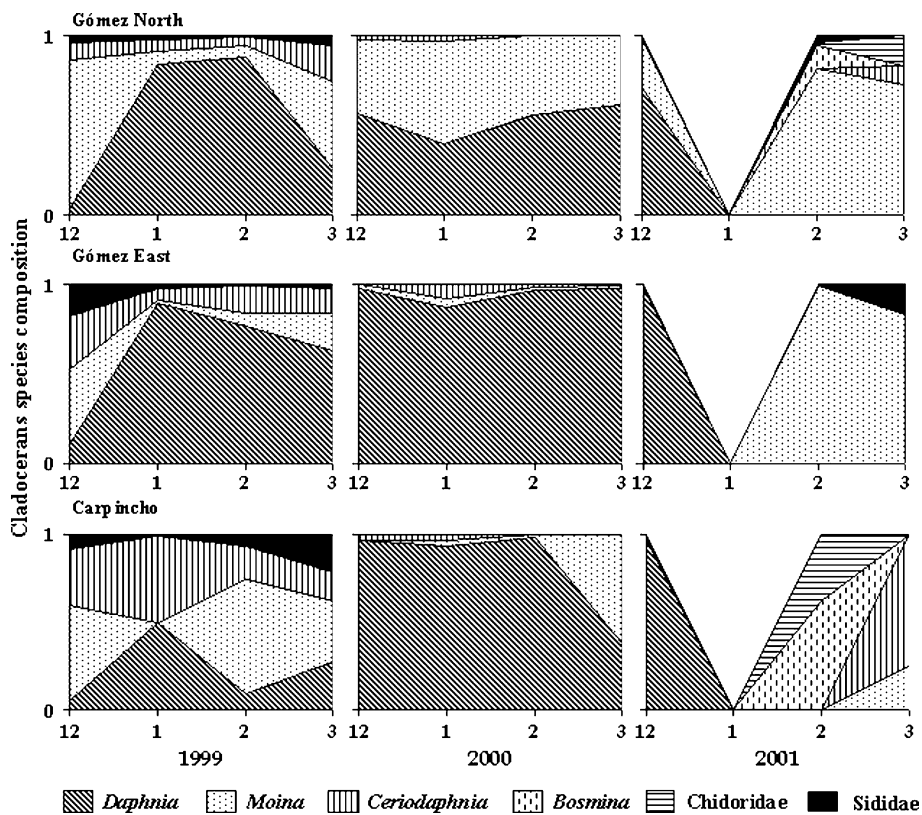
Figure 4. Variation in cladocerans species composition along the three sampling summers.

characteristics were observed in both lakes. Therefore, water residence time reached the lowest levels, turbidity increased during this summer and dilution effects were reflected by lower water salinity.

It is generally accepted that both phytoplankton and zooplankton biomass are negatively affected by low water residence time (Søballe & Kimmel, 1987). However, in both study lakes phytoplankton biomass reached its highest levels when water residence time was shorter. Potentially, this increase of phytoplankton biomass during the wet summer of 2001 could be related either to the increase of the TP concentration (Dillon & Rigler, 1974) or to the decrease in the zooplankton grazing pressure owing to the decline of large cladocerans (Pace, 1984). If grazing by large cladocerans had been the main factor limiting phytoplankton development during high water residence time periods, chlorophyll-TP ratios should have increased during high flushing years. However, the chlorophyll-a:TP ratios were lower in 2001 than in 2000, thus strong bottom-up effects should be inferred for very shallow pampean lakes during high flushing periods.

Total phosphorus concentrations for pampean lakes are positively related to the intensity of land use in its drainage basins (Quirós et al., 2002b). Agriculture and urban wastes are the main sources of nutrient enrichment in the upper Salado River basin and both Gómez and Carpincho are among the most hypertrophic lakes in the world (Quirós, 2003). In this study, we present empirical evidence that an increase in water discharges levels can lead to an increase of threefold in total phosphorus concentration and twofold in phytoplankton biomass for these lakes. Eutrophication process could have been enhanced during wet conditions in 2001 as a consequence of nutrient import from intensive agriculture lands. Nutrient enrichment and phytoplankton biomass increase during flooding events have been reported previously in other shallow systems (Van den Brink et al., 1994;

Quintana et al., 1998; Walz & Welker, 1998; Zalewski, et al. 2000).

Zooplankton biomass and community structure

As expected, hydrological variability was correlated to strong changes in zooplankton biomass and community structure in both study lakes. Macrozooplankton biomass was negatively affected by higher water renewal time. On the other hand, a clear effect of hydrology on rotifers biomass was not observed. Low densities of cladocerans and cyclopoids were related to high flushing rates (summer 2001). Conversely under lentic conditions, the biomasses of both groups reached maximum levels. Calanoids biomass also decreased under lotic conditions, but they showed the highest biomass at intermediate discharges levels (summer 1999). The negative effects of low water residence time on macrozooplankton biomass were particularly reflected in *Daphnia* biomass.

The low relative abundance of *Daphnia* in Carpincho in 1999 and in Gómez North in 2000 was previously related to the high abundance of visual planktivores (Rennella & Quirós, 2002). However, visual planktivores almost disappeared in both lakes during summer 2001 (Rosso, personal communication). Therefore, the *Daphnia* decline in summer 2001 cannot be explained by size selective predation by planktivores. Dickman (1969) proposed that flushing rate might be a dominant selective pressure in determining the species composition of the plankton community during high flushing rate periods. Species which reproduce fast enough to offset their removal by flushing will dominate the plankton community. Our results are in agreement with this idea. A clear shift toward small species occurred in summer 2001 when flushing rate was high. Not only rotifers increased its representation but also small cladocerans species replaced *Daphnia* populations in both lakes. Rotifers and small cladocerans may be positively selected under high water discharges periods probably owing to its shorter generation time (Walz, 1995). On the other hand, *Daphnia* decrease under lotic conditions has previously been related to high water velocity (Rzoska, 1978) and to an increase of inorganic suspended particles (Kirk & Gilbert, 1990). Both circumstances occurred during summer 2001 in Gómez and Carpincho lakes and it probably also contributed to the decline of *Daphnia*.

The zooplankton community of small shallow lakes could be more vulnerable to flushing effects than the zooplankton of larger shallow lakes. When both studied lakes were compared at intermediate discharge levels (summer 1999) the macrozooplankton biomass of the smaller lake (Carpincho) was significantly lower than the one of the larger lake (Gómez lake). In fact, due to its lower volume, water residence time in Carpincho was tenfold less than in Gómez Lake. Therefore, flushing effects on zooplankton biomass and species composition should be observed at lower discharges levels of Salado River in Carpincho Lake than in Gómez Lake. In 1999, in contrast to Gómez sites, water residence time in Carpincho was short enough to significantly diminish macrozooplankton biomass.

For the very shallow lakes of the Pampa Plain, it was previously stated that biomass in different trophic levels are related to total nutrient concentrations (Quirós et al., 2002b). On the other hand, planktivores may affect zooplankton community structure but not zooplankton biomass in these lakes (Rennella & Quirós, 2002). Our results support that in case of lakes with high flushing rates, zooplankton development is dependent on water residence time and that hydrology may have stronger effects on macrozooplankton biomass than top-down control by planktivores.

A continuum may exist between what is defined as a stream or a lake (Brook & Woodward, 1956). It has been recognized that it is a useful strategy to view aquatic systems as occupying positions along a continuum ordered by water residence time (Søballe & Kimmel, 1987). Along this continuum, very shallow lakes situated in semi-arid climates would oscillate from lentic conditions during dry years to more lotic characteristics during wet years. This is a strong difference compared to deeper lakes. Reynolds et al. (1994) emphasized that the selection of species in rivers and shallow lakes is not as different as that between deep and shallow lakes. It was accepted that hydrology contributes to determine the plankton biomass and species composition in rivers (Basu & Pick, 1996; Viroux, 2002). Nevertheless, hydrological effects in shallow lakes were

less studied. Hydrology may potentially explain a large amount of zooplankton biomass variability in shallow lakes; however water flushing is rarely measured in comparative surveys of such lakes. In particular, *Daphnia* populations seem to be extremely vulnerable to high flushing rates (Baranyi et al., 2002; this study). As *Daphnia* plays a critical role in matter and energy flows in aquatic systems, our results supports that water renewal time variability would have important effects on ecology of shallow systems.

Acknowledgements

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