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Plankton relationships under small water level fluctuations in a subtropical reservoir

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Abstract In reservoirs, variations in water level may affect plankton biomass and species composition. Studies on the effect of water-level fluctuations are scarce and restricted to Europe and Australia. In the Río Tercero Reservoir (Argentina), the management policies of a nuclear-power plant require a minimum depth of 650 m. During periods of excessive rainfall, however, the input is such that the excess passes over the spillway, thus causing a high turnover of water. Phytoplankton, zooplankton, and physicochemical variables were monitored over 2 years at three sampling stations during a period with annual precipitation higher than the historical annual mean. Different hydrological situations occurred based on precipitation, spillway outflow, and water-renewal rate. At high renewal rates, phyto- and zoo-plankton diversities peaked. During high outflow periods phytoplankton biomass peaked through the contribution of *Ceratium hirundinella*. Once the spillway outflow ceased, stable conditions (low renewal rates) were achieved, thus allowing the onset of biological interactions. Maximum phytoplankton density (mainly *Actinocyclus normanii*) was reached at such times, and efficient grazers (*Daphnia laevis*) with long life cycles dominated in terms of biomass. The structure and dynamics of the plankton community could be altered by changes in hydrological conditions (renewal rate and spillway outflow) that act to compromise the apparent stability imposed by steady water levels. These variables must be considered to identify disturbance conditions and improve knowledge of reservoir environments, so as to implement appropriate management practices.

Keywords Phytoplankton · Zooplankton · Reservoir management · Spillway outflow · Water-level stability

Abbreviations

CNE	Central Nuclear Embalse
CHFS	Central Hidroeléctrica Fitz Simons
MRR	Monthly renewal rate
MP	Monthly precipitation
PP_{10}	Precipitation occurring during the previous ten days
SPO_{10}	Spillway outflow occurring during the previous ten days
ND	Number of days with continuous outflow
SOCO	Spillway outflow occurring during the continuous outflow
CHFSO	CHFS outflow

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Introduction

Although both internal and external variables determine the structure of the plankton community in reservoirs, physical variables generally predominate (Wilk-Wożniak and Pociecha 2007). The greater stability of these latter variables, however, allows biotic variables to become the principal factors in the regulation of community structure (Marzolf 1990; Naselli-Flores and Barone 1997).

In reservoirs, fluctuations in water level might affect the species composition and biomass of phyto- and zoo-plankton through changes in both the underwater light climate (Naselli-Flores and Barone 1997) and nutrient dynamics (Kimmel et al. 1990). According to Naselli-Flores and Barone (1997), changes in zooplankton composition occur as an indirect consequence of an increase in water level through the proliferation of efficient grazers that, in turn, control the phytoplankton biomass and thereby produce clear water.

The influence of water inflow depends on its intensity, on the morphometric characteristics of the water body, on the quality of the inflowing water, and on the accompanying load of suspended solids (Godlewska et al. 2003). In reservoirs, increases in water level have been associated with population fluctuations through both hydrological advection and increased concentrations of suspended sediments (Wolfinbarger 1999).

In certain reservoirs, for example, a high water inflow is associated with reductions in the zooplankton density and biomass along with a consequent decrease in chlorophyll-*a* concentration, mainly because of the high input of suspended solids (Godlewska et al. 2003; Hart 2004). In other situations, however, such as the shallow Serra Serrada reservoir (Portugal), high levels of suspended solids and chlorophyll concentrations were recorded in conjunction with minimum water levels (Geraldes and Boavida 2005, 2007).

The few investigations that have focused on the effects of periodic reservoir water-level fluctuations were performed in certain reservoirs in Europe and Australia (Geraldes and Boavida 2005), but until now studies of this nature have not been carried out in Argentina. Management policies implemented at the Embalse Río Tercero reservoir (Argentina) as of the beginning of the operation of the Central Nuclear Embalse (CNE) nuclear-power plant have reduced the range of water-level fluctuations in this water body. The aim of the procedures at the plant was to maintain a relatively constant high-water level in order to insure an invariant supply of water for the plant's cooling system. Accordingly, in times of low precipitation water is introduced from the "Complejo Hidroeléctrico Cerro Pelado—Arroyo Corto" reservoirs 3.6 km upstream so as to maintain a minimum depth of 650 m, only 6.5 m below the height of the spillway. Thus, in times of heavy rainfall, the water inflow from both precipitation and the upstream tributaries causes an overflow from the spillway into the Río Tercero River downstream. Such a circumstance can therefore promote an episode of extended of disturbance to the system and the subsequent possibility of increases in the loss of organisms. During the study period (1999–2001), the annual precipitation was higher than the historical annual mean (758 mm). This increase in rainfall influenced the duration of the spillway-overflow period, as was described by Mac Donagh (2007). The aim of this article was to examine the effects of high- and low-water outflow periods on the plankton community (diversity, density, and biomass) during the conditions of high-water-level maintenance resulting from the management policy implemented in this reservoir.

Study area

Río Tercero Reservoir is located at 32°11′ S, 64°23′ W and 657 m asl. The reservoir area is 4,600 ha with a volume of 7.10^6 m^3 and maximum and mean depths of 46.5 and 12.2 m, respectively. The mean water residence time is 172 days. The watershed area is 3,250 km^2 and rainfall is strongly seasonal, with dry winters and heavy rains during spring and summer.

The reservoir was built in 1936 for hydroelectric production with a small hydroelectric plant (CHFS: 10 MWa), and in 1983 a nuclear power plant (CNE: 600 MWa) was installed. Water for cooling is taken from the middle section of the reservoir and is returned to the riverine zone by means of a 5-km-long open-sky channel. The water level of the reservoir is regulated by the hydroelectric plant (CHFS) outflow and the supply of water stems from an upstream system of reservoirs, the Complejo Hidroeléctrico

Cerro Pelado—Arroyo Corto. The maximum amplitude of the annual water-level change was 14 m before the policies instated by the CNE, whereas after regulation this variation was reduced to a maximum of 6.5 m; this value represents the difference between the minimum required level and the spillway level.

Materials and methods

Three stations along the main axis of the reservoir were considered: St. 1 was located at the site of tributary inflow; St. 2, the central sector, was placed where the nuclear-power plant pumps in water for cooling; and St. 3 was located near the dam (Fig. 1). Integrated samples of the photic layer were obtained at each sampling station. The samples were taken every two months between February 1999 and February 2001. Temperature, pH, dissolved oxygen, and conductivity were measured with a Khalsico Surveyor Hydrolab multimeter. Light extinction was measured with a Li-Cor Ll-185 B and the Secchi depth was also recorded. Soluble reactive phosphorus and total phosphorus were determined by the ascorbic-acid method, the latter after acidic persulfate digestion. Nitrates, nitrites, and ammonium levels were estimated by the cadmium-reduction method and by Kjeldahl analysis; silica was measured by the heteropoly-blue procedure; and total-suspended-solid levels were determined by method 2540 D (APHA 1995).

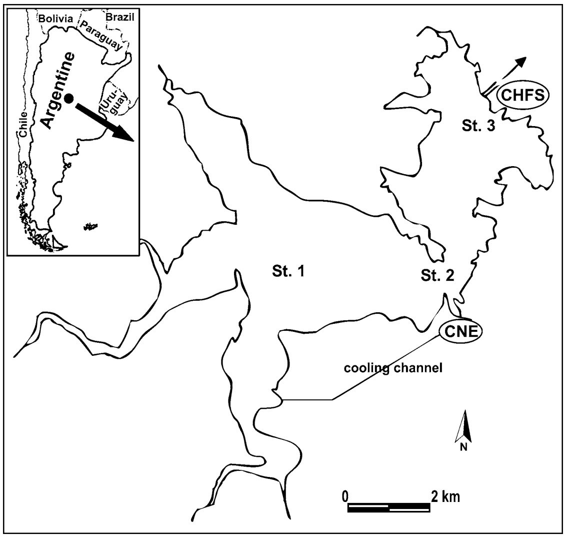

Fig. 1 Location of the sampling stations in the Río Tercero Reservoir: St. 1, site of tributary inflow; St. 2, located where the Nuclear Power Plant pumps water in for cooling and; St. 3, near the dam. CNE: Central Nuclear Embalse

Phytoplankton samples were taken with a Van Dorn bottle and counted in 25 ml sedimentation chambers by the Utermöhl method. Chlorophyll *a* was determined by Lorenzen's method (APHA 1995). Zooplankton samples were taken by pumping and sieving 50 l of water through a net of 35 µm pore size and then counted in Sedgwick-Rafter and Bogorov chambers. Phytoplankton biovolume was calculated according to the formula proposed by Hillebrand et al. (1999) and converted according to Reynolds (1984) to pg C by means of a factor of 0.21. Zooplankton biomass was calculated from the formula given by Dumont et al. (1975), Bottrell et al. (1976), and Mc Cauley (1984) and converted to pg according to Gaedke (1992).

In order to describe the temporal variation of the phyto- and zoo-plankton, the terms "dominant" and "codominant" as defined by Reynolds (1997) were used for one or more species that made up at least 50% of the total density. Shannon's diversity index was calculated according to Legendre and Legendre (1983) based on abundances of zoo- and phytoplankton species.

Principal Component Analysis (PCA) was performed on hydrological variables in order to distinguish sampling months with similar hydrological conditions. The variables were monthly water-renewal rate (MRR), monthly precipitation (MP), precipitation over the previous 10 days (PP_{10}), spillway outflow over the previous ten days (SPO_{10}), number of days with continuous outflow (ND), spillway outflow during the continuous outflow (SOCO), and CHFS outflow (CHFSO). A multiple correlation (Spearman Rank Order) was performed to show the relationships between variables. Regression models were used to test the dependence of Secchi depth and seston on chlorophyll-*a* concentrations. Differences between the conditions of low- and high-water outflow were tested for hydrological variables with the Student *t*-test or the Mann–Whitney test. The differences in biological variables related to the two different hydrological conditions were tested with the ANOVA and Kruskal-Wallis tests. Multiple stepwise regressions were performed for biological variables (log-transformed) to determine which variables best explained the results.

Results

During the study period, the maximum water-level decrease was 2.97 m, with this change occurring from April to October 1999. The recovery of the water level was much faster, exceeding the spillway height only one month later, in November 1999 (Fig. 2). During the next year (2000), the drop in water level was lower (1.73 m) and occurred in several steps over 8 months. Heavy rainfall occurred between September 1999 and March 2000 (a total of 1,209 mm), resulting in an extended period of spillway outflow beginning during the first days of that November (Fig. 2). In contrast, the next rainy season was shorter (from October 2000 to February 2001), and the accumulated precipitation was 616 mm.

The monthly renewal rate varied according to the different rainfall intensities, reaching a maximum of 0.5 month^{-1}, in conjunction with extended periods of spillway outflow, and a minimum of 0.08 month^{-1} during a 5-month period without precipitation when the hydroelectric pump was the only outlet (Fig. 3). During this latter dry period, water was supplied from the upstream reservoirs. Samples taken from November 1999 until March 2000 coincided with the highest monthly renewal rates along with higher and longer spillway outflows, whereas the samples obtained from May 2000 and later corresponded to lower monthly renewal rates and lower and shorter spillway outflows (Fig. 3).

The conductivity, pH, dissolved oxygen, and silica showed small variations during the sampling period (Table 1), whereas soluble reactive phosphorus was undetectable on the majority of the sampling occasions.

Secchi-depth measurements ranged from 0.95 m to 3.2 m at St. 1; from 1.3 to 3.3 m at St. 2, and from 2.0 to 4.5 m at St. 3. Temporal variations in Secchi depth followed a similar pattern to the variation in seston and chlorophyll-*a* concentrations (Fig. 4). In this reservoir, the suspended solids are composed mainly of the organic fraction (Eq. 1); then, Secchi depth was correlated with chlorophyll-*a* concentration (Eq. 2).

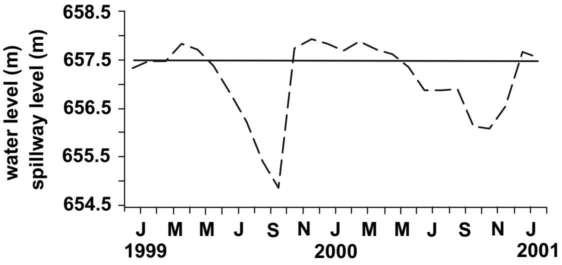

Fig. 2 Water level during the sampling period (dotted line), spillway level (solid line)

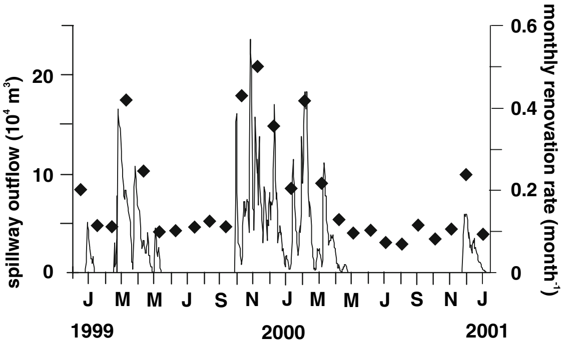

Fig. 3 Monthly renewal rate (black squares) and spillway outflow (solid line) during the sampling period

$$\log(\text{seston})[\text{mg/l}] = 0.40 + 0.47 * \log(\text{chlorophyll } a\ [\mu\text{g/l}]) \quad (1)$$
$$\left(R = 0.72; R^2 = 0.52; F = 37.3; P < 10^{-4}\right),$$

$$\log(\text{Secchi depth})[\text{m}] = 0.68 - 0.2 * \log(\text{chlorophyll } a\ [\mu\text{g/l}])$$
$$\left(R = 0.59; R^2 = 0.35; F = 18.53; P < 10^{-4}\right) \quad (2)$$

PCA performed on hydrological variables showed a clear differentiation between sampling dates that was associated with the spillway outflow, precipitation levels, and renewal rates (Fig. 5, Table 2). The

Table 1 Physical and chemical parameters recorded at Río Tercero Reservoir during the sampling period

	Mean	SD	Min	Max
Temperature (°C)	19.18	5.19	10.58	26.68
Conductivity (µS cm^{-1})	157.20	25.08	124.00	207.20
pH	8.18	0.37	7.34	8.99
Dissolved oxygen (mg l^{-1})	9.01	1.18	7.53	11.72
Silica (mg l^{-1})	5.31	1.93	1.62	10.20
TP (µg l^{-1})	22.33	25.46	7.00	161.00
$NO_2^- + NO_3^{2-}$ (µg l^{-1})	59.88	72.01	1.10	263.26
NH_4^+ (µg l^{-1})	17.85	22.83	n.d.	90.60

SD, standard deviation; Min, minimum value; Max, maximum value, TP, total phosphorus

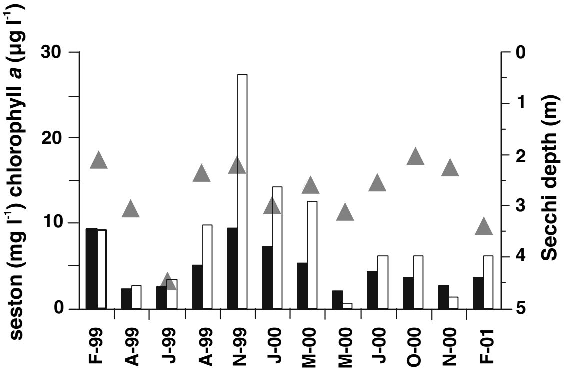

Fig. 4 Seston (black columns) and chlorophyll-*a* (white columns) concentrations and Secchi depth (triangles) measured at each sampling at St. 2

sampling dates located at the extremes of the second axis, represented two opposite situations: November 1999, the beginning of the spillway period and the rainy season, succeeding a long stable period; and May 2000, the last month after a long period of high and uninterrupted spillway outflow. The effluent water from CHFS was mainly constant and did not contribute significantly to the differences recognized between the sampling dates. At this time, it was possible to differentiate two hydrological conditions: high outflow and low outflow. Significant differences were found for MRR ($P = 0.004$), SPO_{10} ($P = 0.048$), ND ($P = 0.048$), SOCO ($P = 0.03$).

No differences in the density or diversity of phyto- and zoo-plankton were found to be related to either high or low outflow. Moreover, the differences in the parameters describing phytoplankton biomass (chlorophyll-*a* concentration and biomass calculated from biovolume measurements) were not significant. Only the zooplankton biomass showed significant differences during these conditions (Table 3).

Zooplankton density and biomass correlated negatively with the hydrological variables. Phytoplankton biomass and chlorophyll-*a* concentration correlated negatively with the euphotic depth and the inorganic nutrients, but positively with seston levels. Phytoplankton density correlated negatively with precipitation levels and temperature (Table 4).

As a result of the multiple stepwise regressions—which at each stage test for those variables to be included or excluded—it could determine that the factors that best explained the phytoplankton density ($R^2 = 0.41$, $P = 0.0002$) were the monthly precipitation (MP) and the euphotic depth (Table 5). The variation in chlorophyll-*a* concentration was accounted for by the euphotic depth, ND, and the dissolved inorganic-nitrogen fractions ($R^2 = 0.59$, $P = 9.6 \times 10^{-6}$). The zooplankton density was a function of the MRR and the ND ($R^2 = 0.30$, $P = 0.003$), whereas its biomass was dependent only on the MRR ($R^2 = 0.15$, $P = 0.002$).

Fig. 5 Result of PCA based on hydrological variables showing the separation between high- and low-outflow sampling dates

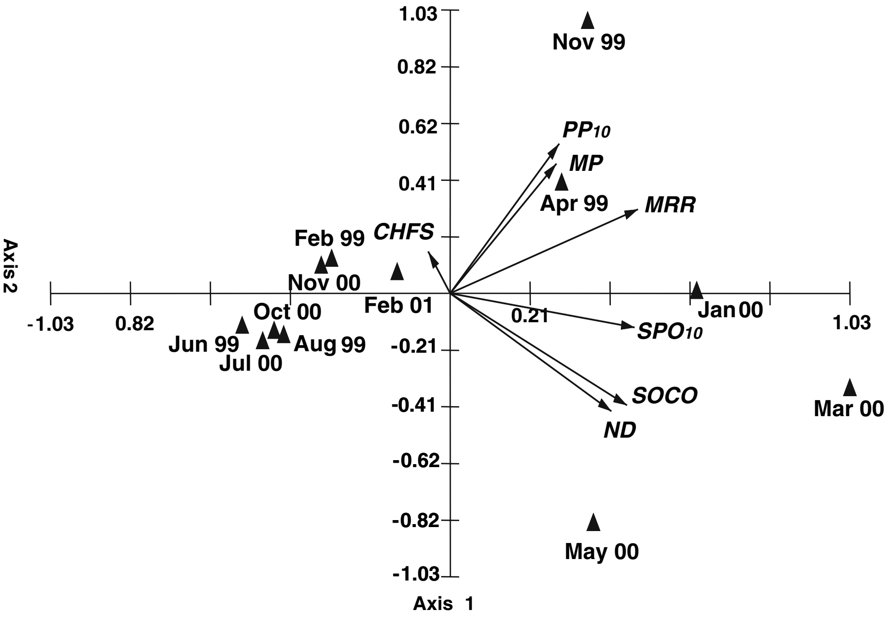

Table 2 Loading of variables on PCA

	MRR	SPO_{10}	ND	SOCO	CHFSO	MP	PP_{10}
PC1	0.485	0.476	0.416	0.456	−0.056	0.274	0.281
PC2	0.305	−0.123	−0.428	−0.407	0.153	0.472	0.545
PC3	0.134	0.092	0.028	0.036	0.963	−0.158	−0.138

MRR, monthly renewal rate; SPO_{10}, spillway outflow occurring during the previous 10 days; ND, number of days with continuous outflow; SOCO, spillway outflow occurring during the continuous outflow; CHFSO, hydroelectric-power-plant outflow; MP, monthly precipitation; PP_{10}, precipitation occurring during the previous 10 days

Table 3 Results of ANOVA and Kruscal-Wallis test performed on biological variables (log transformation) for test differences between high- and low-outflow conditions

Phytoplankton		
Density	$X^2 = 1.36$	$P = 0.24$
Biomass	$X^2 = 3.04$	$P = 0.08$
Diversity	$X^2 = 0.78$	$P = 0.38$
Chlorophyll *a*	$X^2 = 0.06$	$P = 0.81$
Zooplankton		
Density	$F = 2.72$	$P = 0.11$
Biomass	$F = 4.20$	$\mathbf{P = 0.05}$
Diversity	$F = 3.78$	$P = 0.06$

Bold value represent significance of the test was 0.05

Phyto- and zoo-plankton diversity peaked during the conditions of high renewal rate, reaching their maxima at St. 2 (3.63 and 2.38, respectively). The highest phytoplankton diversity was coincident with the intermittent spillway-outflow period (April 1999) and later diminished during conditions of continued outflow (summer 1999–2000). The minimum phytoplankton-diversity value was recorded in July 2000 (0.99) at St. 1 and was related to the high abundance of *Actinocyclus normanii*. By contrast, the minimum zooplankton-diversity value was recorded in October 2000 (1.02), also at St. 1, resulting from the presence of few species of cladocerans. Both minima were recorded in coincidence with low renewal rates.

The maximum phytoplankton density was recorded at St. 1 in July 2000 (6.6×10^6 ind. l^{-1}; Fig. 6), while the zooplankton peak (1.5×10^3 ind. l^{-1}) occurred at St. 2 at the end of the study period. The minimum densities were recorded at St. 3 (phytoplankton: 1.5×10^5 ind. l^{-1} in November 2000, and zooplankton: 48 ind. l^{-1} in November 1999). Considering the spatial variation of density on each sampling occasion, a decrease in phytoplankton concentration occurred that proceeded from the riverine zone toward the dam, whereas the zooplankton generally reached higher densities within the central area of the reservoir (St. 2; Fig. 6).

The dinoflagellate *Ceratium hirundinella* was an either dominant or codominant species from November 1999 to March 2000, when it reached its maximum density (1.2×10^6 ind. l^{-1}) at St. 1 (Fig. 6). Later,

Table 4 Spearman rank order correlations

	Hydrological variables						Physical variables				Inorganic nutrients		
	MRR	SPO_{10}	ND	SOCO	MP	PP_{10}	T	ZM	ZE	SS	PO_4^{-2}	$NO_2^- + NO_3^{-2}$	NH_4^+
Phytoplankton													
Density					(−)**	(−)*	(−)**						
Biomass	(+)**					(+)*		(−)*	(−)**	(+)**	(−)**	(−)**	
Chlorophyll *a*									(−)**	(+)**	(−)*	(−)**	
Zooplankton													
Density	(−)*												
Biomass	(−)*	(−)**	(−)**	(−)**			(−)*						(+)*

MRR; SPO_{10}; ND; SOCO; MP and PP_{10}, as in Table 2. Zm, mixing zone depth; ZE, euphotic zone depth; SS, suspended solids. Only significant correlations were shown; the sign of the correlation is indicated between parenthesis (−/+), * $P < 0.05$, ** $P < 0.01$

Table 5 Results of the multiple step-wise regressions

Dependent variables	Independent Variables	Standard partial regression coefficients	*t*	*P*
Log phytoplankton	MP	−0.606	−4.386	0.000
Density	ZE	−0.387	−2.804	0.008
Log chlorophyll *a*	ZE	−0.389	−3.092	0.004
	ND	−0.432	−3.539	0.001
	$NO_2^- + NO_3^{-2}$	−0.395	−3.054	0.005
	NH_4^+	−0.357	−2.980	0.006
Log zooplankton	RR	−0.540	−3.572	0.001
Density	ND	0.310	2.055	0.047
Log zooplankton biomass	RR	−0.390	−2.477	0.018

MP, monthly precipitation; RR, monthly renewal rate; ND, number of days with continuous outflow; ZE, euphotic zone depth

Actinocyclus normanii became dominant during July and October (5.3×10^6 and 2.9×10^6 ind. l^{-1}, respectively). Notably, during the same months, the highest density of *A. normanii* (7.0×10^6 and 7.8×10^6 ind. l^{-1} representing 97% and 92% of the total density for those months, respectively) was observed in the aphotic zone of St. 1. On other sampling occasions several species such as *Anabaena spiroides*, *Aulacoseira alpigena*, *Monoraphidium minutum*, and *Cryptomonas* spp. were numerically important (Fig. 6).

Rotifers predominated, especially *Polyarthra vulgaris* and *Conochilus unicornis* (Fig. 6). Cladocerans reached their maximum densities between July and October 2000 (mean: 47 ind. l^{-1}, range: 16–115 ind. l^{-1}) and were mainly represented by *Bosmina huaronensis*, though secondarily so by *Daphnia laevis*. In November 2000, the largest cladocerans reached high density, and *D. laevis* predominated in terms of biomass at all sampling stations (51%, 46%, and 44% at St. 1, St. 2, and St. 3, respectively; Fig. 7).

The peaks and troughs of phytoplankton biomass were detected during conditions of spillway outflow. The maximum biomass was recorded in March 2000 (202×10^2 μg C l^{-1} at St. 1) and coincided with high renewal rates and heavy rainfall. Subsequently, the minimum in biomass was recorded in May 2000 (1.14×10^2 μg C l^{-1} at St 3) related to a notable change of the specific composition (Fig. 7). The size of *Ceratium hirundinella* was responsible for its major contribution to the total phytoplankton biomass during those sampling occasions when this alga became dominant (Fig. 7). Intermediate values of biomass were found during times of minor renewal rates, although *Actinocyclus normanii* underwent a biomass maximum under such conditions and dominated in July and October 2000 at the times of its density peaks (Figs. 6 and 7). The maximum of zooplankton biomass was observed at St. 2 in May 2000, as a result of the contribution of *Asplanchna girodi* (Fig. 7), whereas the minimum value was recorded at St. 3 in April 1999 (4.68 μg C l^{-1}). Under different hydrological conditions the calanoid *Notodiaptomus incompositus* contributed the most to the total biomass because of its large size (Fig. 7). The larger cladocerans dominated in terms of biomass in November 2000, after an extended period with the lowest renewal rates and thus in the absence of spillway outflow.

Discussion

Reservoirs with high water-level fluctuations—such as Albert Falls in Southern Africa, which experiences water-level changes of up to 13 m—exhibit the most pronounced variation in water transparency (from >3 m to <0.3 m) as a result of flooding following drought conditions. Furthermore, the peaks in chlorophyll abundance coincide with the highest levels of transparency, indicating that suspended solids have negative effects on algal production (Hart 2004). In contrast, at the Río Tercero Reservoir, the suspended solids were explained mostly by chlorophyll *a,* so that here turbidity was not a limiting factor for algal growth. In other examples, such as the shallower Serra Serrada reservoir, the highest levels of suspended solids and concentrations of chlorophyll *a* coincided with the minimum water levels, probably because of the water turbulence generated during the

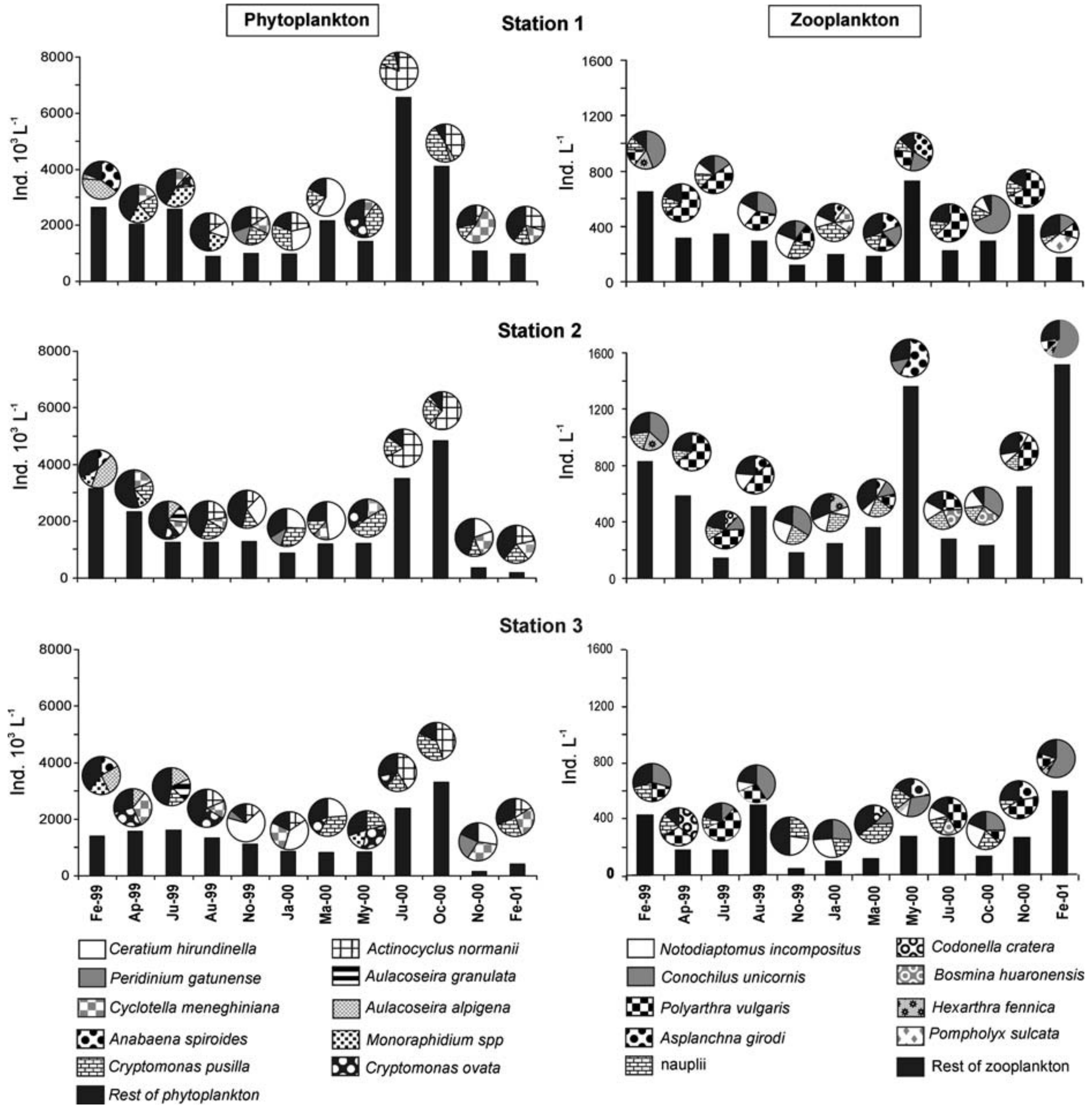

Fig. 6 Total phyto- and zoo-plankton density (black bars) and dominant species contributions (pie graphs) at the three sampling stations during the study period

emptying phase along with the disruption of stratification at the end of that phase (Geraldes and Boavida 2005, 2007). In the case of the Río Tercero Reservoir, the highest suspended-solid levels and chlorophyll-*a* concentrations coincided with phases of maximum water levels and with high outflow. For this reason, the origin of these latter peaks could be not associated with sediment resuspension: rather, the bioseston must originate from in-situ generation within the euphotic zone, or alternatively, from upstream sources.

Water-renewal rates at the Río Tercero Reservoir were always low enough to support in-situ phytoplankton development, in agreement with Kimmel et al. (1990). Furthermore, the negative correlations found between the amounts of chlorophyll *a* and total

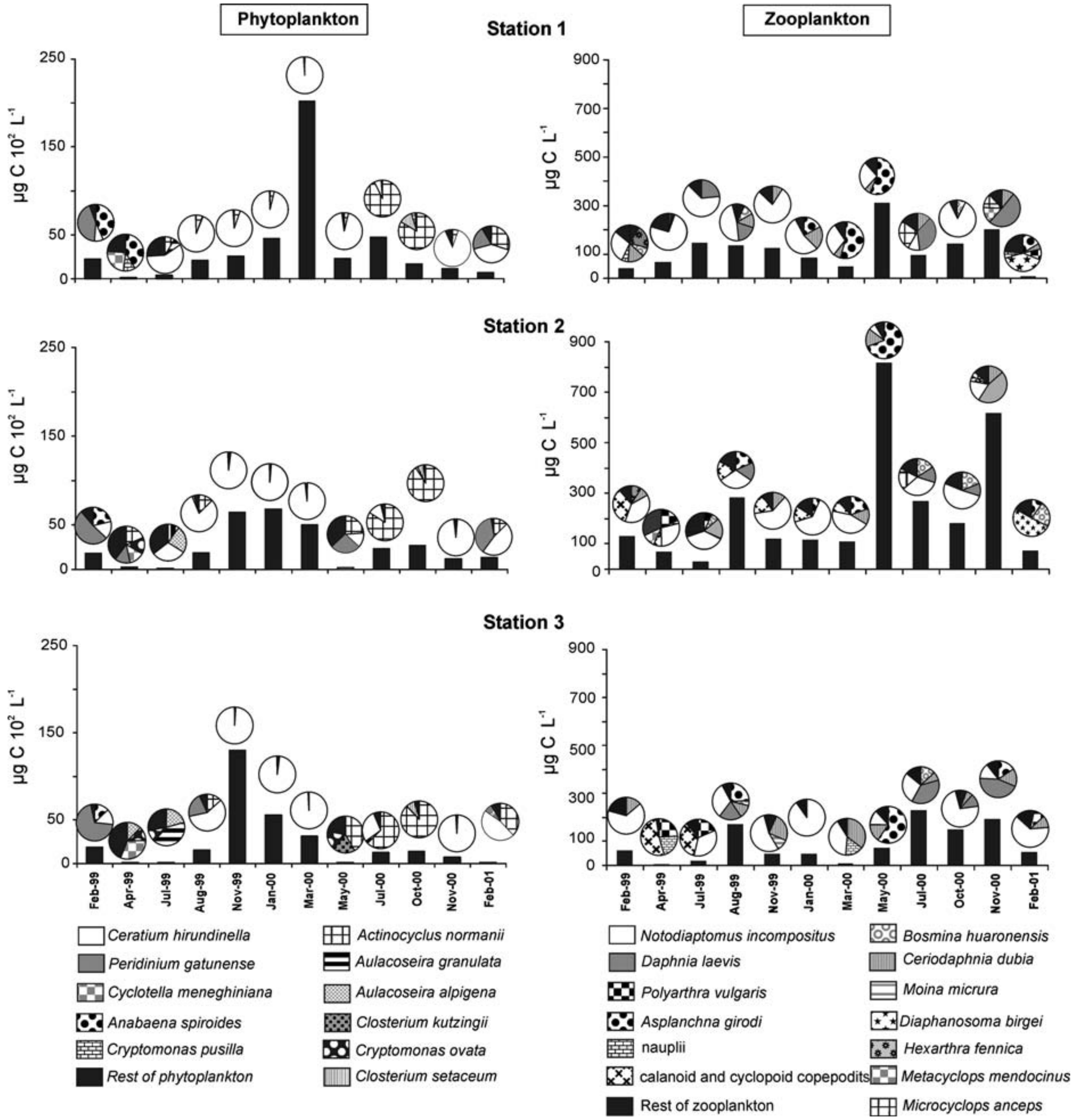

Fig. 7 Total phyto- and zoo-plankton biomass (black bars) and dominant species contributions (pie graphs) at the three sampling stations during the study period

dissolved nutrients indicated that the latter can be depleted by in-situ phytoplankton growth, as indicated by Zeng et al. (2006) in another reservoir having adequate residence time for the growth of alga in situ during the rainy and dry seasons alike. In the Río Tercero Reservoir, the temperatures in winter and the mixing depth did not restrict algal development; but because of the characteristically low nutrient concentrations (Mac Donagh et al. 2005), high phytoplankton densities and high zooplankton biomass were reached only when the reservoir was supplied with water and accompanying inocula from the upstream reservoirs. This input was detected by the extraordinary density of *A. normanii* recorded at

St. 1 (mainly at the aphotic zone) and its diminution toward the dam zone in July and October 2000.

The lack of significant negative correlations between the zooplankton density and either the phytoplankton density or the chlorophyll-*a* concentrations suggests either that the zooplankton did not control algal growth or that the effects of their clearance became notable after a time lag. Rotifers with low clearance rates, such as *P. vulgaris* (Stemberger and Gilbert 1985) and *C. unicornis* (Armengol et al. 2001), were predominant zooplankton species in the reservoir. The latter rotifer can ingest only the smaller algae (<10 µm), and even bacteria or detritus (Armengol et al. 2001; Cruz Pizarro 1993; Gilbert and Bogdan 1984), so that the lack of correlation here could be explained by the low affinity of these rotifers for algal consumption. Moreover, the small palatable phytoplankton taxa (*Cyclotella meneghiniana*, *Cryptomonas* spp., *Monoraphidium minutum*) prevailed during a great part of this study period when inefficient grazers predominated.

During low-outflow conditions, phytoplankton might have in fact been consumed efficiently by zooplankton. In this instance, populations of small cladocerans were replaced by larger and more efficient ones. For this reason, the peak populations of *A. normanii* disappeared. *Actinocyclus normanii* cells are smaller than 30 µm and may be an important palatable fraction of the phytoplankton in this reservoir. Matveev (1991), in another Argentinean subtropical lake, demonstrated a negative correlation between *D. laevis* maxima and minor than 30-µm phytoplankton biovolume, but after a 12-day lag. Moreover, the maximum density of *D. laevis* in November 2000 here (33 ind. l^{-1}) was nearly equal to values reported by other authors (30 ind. l^{-1}) for the threshold for development of clear-water phases in lakes and reservoirs (Talling 2003; Lehman et al. 2007).

Geraldes and Boavida (2007) compared two reservoirs and found that in the one with the higher water-level fluctuations, rotifers such as *Keratella cochlearis*, *Conochilus* sp., and *Asplanchna priodonta* predominated; whereas in the other, cladocerans and copepods did so. Likewise, Godlewska et al. (2003) found that high water-outflow conditions eliminated the large species of cladocerans and copepods and favored the development of rotifers. Consistent with the findings of these authors, copepods usually predominated in this reservoir, it being characterized by small water-level fluctuations. After an extended high-outflow period a replacement of copepods by rotifers occurred, whereas cladocerans only dominated at the ending of a period without outflow.

In the Río Tercero Reservoir, the policy management of the nuclear power plant requires high minimum-water level throughout the year, thus overflows takes place earlier on years of excessive precipitation, producing system disturbances and the possibility of organism loss. Once the spillway outflow ceased, more stable conditions obtained, allowing the appearance of significant biological interactions. Then, when precipitations diminished; internal variables became regulatory, with a consequent prevalence of organisms characterized by long life cycles and a greater capacity to generate clear-water conditions (e.g., the species of larger cladocerans).

In the majority of reservoirs, low water-level fluctuations indicate a greater stability of the system (Geraldes and Boavida 2005), but in certain situations this conclusion does not apply. In the study here, we emphasize that disturbances of the plankton community occurred even despite water-level stability that was associated with maximum high-water levels throughout the year and spillway outflow during exceptionally rainy periods. With this regulatory system, the spillway outflow—when it occurs—produces a clear disturbance to the plankton community, as revealed by structural changes.

On the basis of these results, we conclude that even under apparently stable conditions (minimum water-level fluctuations), the regulation of the inflow and outflow of this reservoir influences the relative importance of the different variables shaping the community structure. This new information is thus applicable to the formulation of management decisions that, in the development of future policies, would take into account the importance of the issue of regulating the inflow and outflow in terms of the consequences with respect to the plankton community inhabiting the reservoir.

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References

APHA (1995) Standard methods for the examination of water and wastewater. Washington

Armengol X, Boronat L, Camacho A, Wurtsbaugh WA (2001) Grazing by a dominant rotifer *Conochilus unicornis* Rousselet in a mountain lake: in situ measurements with synthetic microspheres. Hydrobiologia 446–447:107–114. doi:10.1023/A:1017591004514

Bottrell HD, Duncan A, Gliwicz Z, Grygierek E, Herzig A, Hillbritcht-Ilkowska A et al (1976) A review of some problems in zooplankton productions studies. Norw J Zool 24:419–459

Cruz Pizarro L (1993) Function of zooplankton in lake ecosystems. In: Salánki J, Bíró P (eds) Limnological bases of lake management. Proceedings of ILEC/UNEP International Training Course, Hungary

Dumont H, Van De Velde I, Dumont S (1975) The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19:75–97. doi:10.1007/BF00377592

Gaedke U (1992) The size distribution of plankton biomass in a large lake and its seasonal variability. Limnol Oceanogr 37:1202–1220

Geraldes AM, Boavida MJ (2005) Seasonal water level fluctuations: implications for reservoir limnology and management. Lakes Reserv Res Manage 10:59–69. doi:10.1111/j.1440-1770.2005.00257.x

Geraldes AM, Boavida MJ (2007) Zooplankton assemblages in two reservoirs: one subjected to accentuated water level fluctuations, the other with more stable water levels. Aquat Ecol 41:273–284. doi:10.1007/s10452-006-9057-z

Gilbert JJ, Bogdan KG (1984) Rotifer grazing: in situ studies on selectivity and rates. In: Meyers DG, Strickler JR (eds) Trophic interactions within aquatic ecosystems. American Association for the Advancement of Science, Boulder, USA

Godlewska M, Mazurkiewicz-Borón G, Pociecha A, Wilk-Wožniak E, Jelonek M (2003) Effects of flood on the functioning of the Dobczyce reservoir ecosystem. Hydrobiologia 504:305–313. doi:10.1023/B:HYDR.0000008530.31142.81

Hart RC (2004) Cladoceran periodicity patterns in relation to selected environmental factors in two cascading warm-water reservoirs over a decade. Hydrobiologia 526:99–117. doi:10.1023/B:HYDR.0000041610.56021.63

Hillebrand H, Dürslen C-DKD, Pollingher U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. J Phycol 35:403–424. doi:10.1046/j.1529-8817.1999.3520403.x

Kimmel BL, Lind OT, Paulson LJ (1990) Reservoir primary production. Willey, New York, pp 133–194

Legendre L, Legendre P (1983) Numerical ecology. Elsevier, Amsterdam

Lehman JT, Platte R, Ferris J (2007) Role of hydrology in development of a vernal clear water phase in an urban impoundment. Freshw Biol 52:1773–1781. doi:10.1111/j.1365-2427.2007.01808.x

Mac Donagh ME (2007) Variables estructurantes del plancton de un embalse regulado por el funcionamiento de una central nuclear. Tesis Doctoral UNLP

Mac Donagh ME, Casco MA, Claps MC (2005) Colonization of a neotropical reservoir (Córdoba, Argentina) by *Ceratium hirundinella* (O. F. Muller) Berg. Ann Limnol 41:291–299

Marzolf RG (1990) Reservoir as environments for zooplankton. In: Thronton KW, Kimmel BL, Payne FE (eds) Reservoir limnology: ecological perspectives. Wiley-Interscience, pp 195–208

Matveev V (1991) Exploitative and interference competition among planktonic crustaceans in a subtropical lake. Arch Hydrobiol 123(1):53–68

Mc Cauley E (1984) The estimation of the abundance and biomass of zooplankton in samples. In: Downing J, Rigler F (eds) A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific Publications

Naselli-Flores L, Barone L (1997) Importance of water-level fluctuation on population dynamics of cladocerans in a hypertrophic reservoir (Lake Arancio, south-west Sicily, Italy). Hydrobiologia 360:223–232

Reynolds CS (1984) The ecology of freshwater phytoplankton. Cambridge University Press

Reynolds CS (1997) Assembly of pelagic plant communities. In: Reynolds CS (ed) Vegetation processes in the pelagic: a model for ecosystem theory. Ecology Institute, Germany, pp 205–289

Stemberger RS, Gilbert JJ (1985) Body size, food concentration, and population growth in planktonic rotifers. Ecology 66:1151–1159. doi:10.2307/1939167

Talling JF (2003) Phytoplankton-zooplankton seasonal timing and the 'clear-water phase' in some English lakes. Freshw Biol 48:39–52. doi:10.1046/j.1365-2427.2003.00968.x

Wilk-Wožniak E, Pociecha A (2007) Dynamics of chosen species of phyto- and zooplankton in a deep submontane dam reservoir in light of differing life strategies. Oceanol Hydrobiol Stud 36:35–48

Wolfinbarger WC (1999) Influence of biotic and abiotic factors on seasonal succession of zooplankton in Hugo Reservoir, Oklahoma, U.S.A. Hydrobiologia 400:13–31. doi:10.1023/A:1003738608697

Zeng H, Song L, Yu Z, Chen H (2006) Distribution of phytoplankton in the Three-Gorge reservoir during rainy and dry seasons. Sci Total Environ 367:999–1009. doi:10.1016/j.scitotenv.2006.03.001