

Zooplankton community structure in two Chilean reservoirs

By J. M. SCHMID-ARAYA, LUNZ (Austria) and L. R. ZUÑIGA, Valparaíso (Chile)¹

With 10 figures and 9 tables in the text

Abstract

The zooplankton communities of two Chilean reservoirs were investigated during a year-cycle from September 1983 to November 1984, particularly with regard to the seasonal distribution of species as well as the effect of some environmental factors. Average temperature and oxygen values over the year were similar between the two reservoirs, while high average values of conductivity and chlorophyll-*a*, together with lower water transparency and extreme changes on the water levels were characteristic to Rungue.

A great difference could be seen in the total number of species recorded in both reservoirs, 41 species in Peñuelas (70.7% rotifers, 22.0% cladocerans and 4.9% copepods) compared to 21 species in Rungue (81.0% rotifers, 9.5% cladocerans and 9.5% copepods). Moreover, fluctuating patterns on the average abundance of some zooplanktonic groups, diversity values and species richness, and a massive development of rotifers within a short time were detected in the latter reservoir. This pattern suggest a "disturbance" of the zooplankton community, caused probably by the unstable conditions on the water environment created by the annual water renewal. On the contrary, in Peñuelas average zooplankton abundances and community parameters (species richness and diversity), varied much less and followed the seasonal changes of the year cycle. The predominance of rotifers (few species with high abundances) and low zooplankton diversity values characteristic in Rungue, reflect that this reservoir is either at an early phase on the evolution of its zooplankton community, or reflects a disturbed community when compared to the other reservoir.

Introduction

In reservoirs or man-made lakes, the composition of the plankton communities is the result of a process of colonization and also of species selection (ARMENGOL 1984). Thus, the composition of these communities is influenced by a series of external factors such as the drainage basin, the reservoir orientation and shape, the climatic zone and the degree of human impact. On the

¹ Authors' addresses: Dr. JENNY M. SCHMID-ARAYA, Biologische Station Lunz, Institut für Limnologie der Österreichischen Akademie der Wissenschaften, A-3293 Lunz am See, Austria.

Dr. LUIS R. ZUÑIGA, Instituto de Biología, Sección Ecología, Universidad Católica Valparaíso, Casilla 4059, Valparaíso, Chile.

other hand, man-made lakes tend to be unique in their morphometry, hydrological characteristics and thermal and chemical regimes; as a consequence the character, e.g. of primary production, is highly individualistic (PETERS 1984). Moreover, the horizontal gradient leading to a progressive transition from riverine to lacustrine conditions is an important process in the spatial organization of reservoirs (ARMENGOL *et al.* 1990), which usually is influenced by the rate of water renewal, the seasonal pattern of plankton development (*i.e.* lentic) and the character of the outflows from the reservoir.

Except the high altitude lakes in the Andes mountains, Central Chile (approximately from 32° to 34.5°S) lacks of natural lakes, so that most of the water bodies existing in the area belong to a certain class of artificial nature; they have been built for irrigation, drinking water supply or hydroelectric purposes. Colonization processes, which are important for the understanding of functional mechanisms of reservoirs, have not yet been studied in Chile. Nevertheless, it is possible to investigate some of these water bodies on the basis of comparative limnological data, as for example the zooplankton community in order to observe the influence of environmental parameters on the selection of species, as well as the assemblage itself persisting in each reservoir (MARGALEF *et al.* 1976).

Zooplankton communities in Central Chile reservoirs have been partly evaluated for one group in particular, either Cladocera (DOMINGUEZ & ZUÑIGA 1976) or Rotifera (AVENDAÑO & SAIZ 1977, SOTO *et al.* 1984). The only research dealing with three zooplanktonic groups is that of ZUÑIGA & ARAYA (1982), however orientated mostly to spatial distribution. Therefore, the present paper as a contribution to the understanding of these man-made lakes in the area, has the objective to give results about the structure and distribution of the zooplankton community during a year cycle in two Chilean reservoirs, and to study the possible effect of some abiotic parameters upon the community. At the same time, an attempt is made on comparing both sites, due to their underlying differences with respect to geographical location and water use.

Material and methods

Study area

The research was carried out in two Chilean reservoirs: Peñuelas which is situated approximately 12 km from Valparaíso city (33° 10' S—71° 29' W), and Rungue in a semi-arid area (33° 00' S—70° 53' W) between two mountain ranges 120 km due North of the capital Santiago (Fig. 1). Peñuelas reservoir was built in 1900 in order to supply drinking water, while the construction of Rungue for irrigation purposes ended by 1964. Peñuelas lies at an altitude of 347 m a.s.l., and the area and volume correspond to 19 km² and 0.095 km³, respectively. The maximum length is 15 km and it has a width of 1.85 km; its maximum depth at the dam site is 15 m, while its average depth is 5 m. The shape can be generally described as dendritic, occupying an extense area, nevertheless the water volume is rather low, not exceeding more than a quarter of the theoretical

maximum volume (GARCIA 1984). This reservoir is located in a zone of silt-clay hills and water supply is obtained from precipitation in the drainage basin, so that its water level is highly dependent on the warm temperate climate of the zone. At present, since several years this reservoir is used only as a supplementary source of drinking water, so that its water retention is very irregular, estimated to 2–3 years. However, this period can be shorter when conditions of drought prevail in this geographical zone.

On the other hand, Rungue is situated at 698 m a.s.l., its estimated area is 0.48 km², at maximum level, and its maximum volume is 0.00215 km³. The maximum length of this reservoir is 2.0 km and the width 0.275 km; its maximum depth close to the dam is 15 m and the mean depth is 4 m. As it can be seen in Fig. 1, Rungue resembles an impounded river (Rungue Creek), but water is also pumped into it from the side-way Caleu Creek. Due to the climatic conditions the annual fluctuations of the water level are very extreme. In addition, because of its use for irrigation, the water retention is much shorter than in Peñuelas, and the reservoir is practically emptied every summer.

Sampling

Samples were taken monthly from September 1983 to November 1984 in Peñuelas and from September 1983 to September 1984 in Rungue. At both sites, sampling took place at a fixed station (deepest area, closer to the dam, Fig. 1). Zooplankton samples were collected with a Schindler sampler (30 liters volume capacity, 80 µm mesh net), every two meters up to one meter above the bottom. These samples were fixed in the field with 5% formalin, and identification and counts were carried out under a Wild M5A stereo microscope in different volume aliquots (1, 2 or 5 ml), or in total, depending on the zooplankton densities.

Phytoplankton samples, oxygen, temperature measurements, secchi disc readings and water chemistry were concurrently taken on each sampling date. Water samples were obtained at the same depth intervals with a 5 liter Van Dorn bottle. Oxygen was determined following the modified method of Winkler, and chlorophyll-a with the methodology described in BOYD (1979). Temperature profiles were done using a telethermometer YSI mod. 44, while conductivity was determined with a conductivity-meter YSI 33 SCT. The pH of the water samples was measured with a portable pH-meter ORION 201. Secchi transparency was estimated with a white 20 cm diameter disc.

Data analyses

Before calculations of community parameters, densities of all species were expressed on a per m³ basis for each depth layer throughout the water column. Species diversity was estimated for each depth layer (H'), and also by summing all depths for a particular month (\bar{H}') using the index of SHANNON-WIENER (1963). Equitability was calculated for each depth layer using the index proposed by LLOYD & GHELARDI (1964). Simple linear and multiple regressions, and PCA analyses were carried out using SPSS^x Statistical Package (NIE et al. 1985). Data on species abundances (dependent variable) and physicochemical factors (independent variable) were logarithmically transformed to correct for zero values and normalize the distributions (IBANEZ 1971, ESTRADA 1975, O'BRIEN & ROCK 1978). Stepwise multiple regression was used to investigate the relationship between the density of a given zooplankton species and the physicochemical variables; sequentially multiple linear regression equations were calculated by adding one variable to the regression equation at each step. The significance of the effect of each

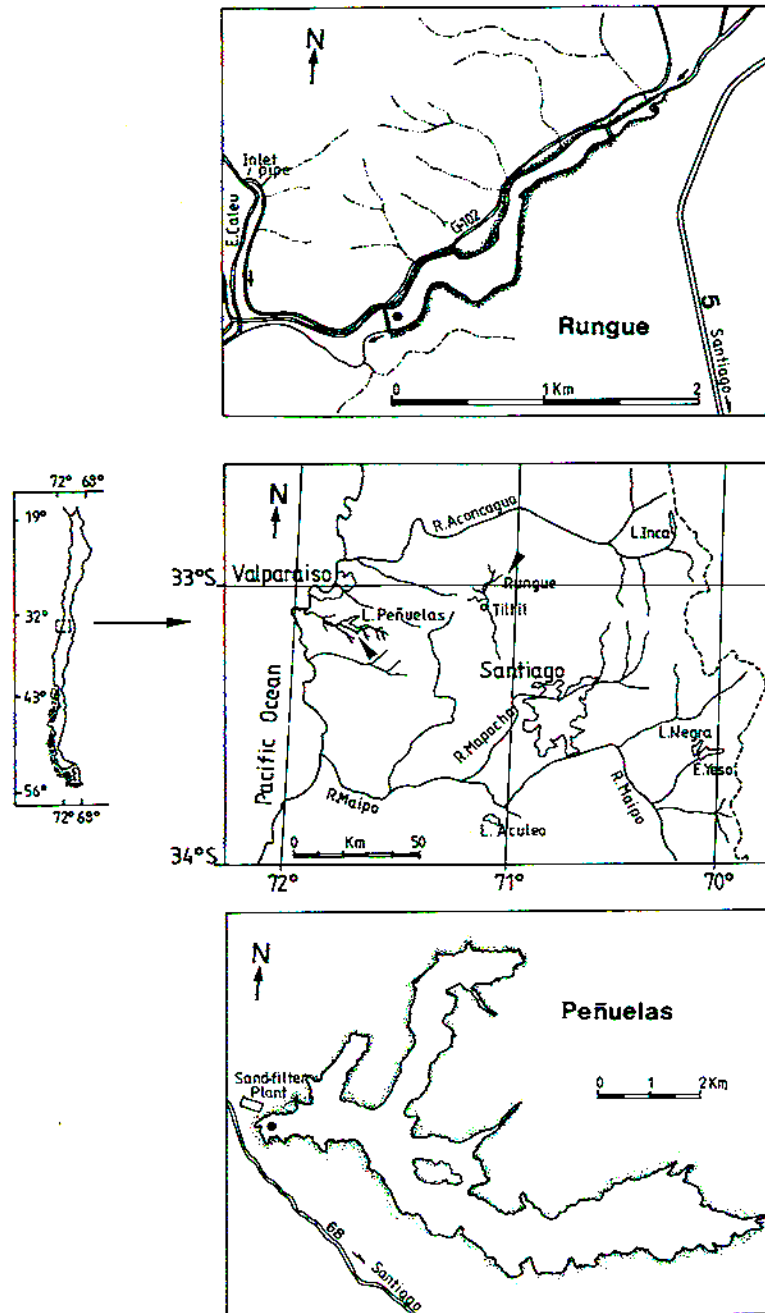


Fig. 1. Map of part of Central Chile showing the location of the two sampling sites: Peñuelas and Rungue reservoirs. The inset shows the geographical location of the sites in Chile.

variable was judged by the significance of the *t*-value associated with each regression coefficient (ZAR 1984).

Results

General characterization of the reservoirs

Temperature profiles of both reservoirs shown in Fig. 2 indicate that there were mostly isothermal conditions during the year cycle in the water column in Peñuelas and Rungue. Weak thermal stratification developed from December 1983 to February 1984 (summer season) in Rungue, but it was interrupted by constant decreases in the water levels. Peñuelas average water temperatures varied from 10° to 23°C during the annual cycle, while a similar range from 6° to 25°C was recorded in Rungue (Table 1).

The oxygen values in the vertical profile along the years 1983–1984 have a more marked pattern in both reservoirs (Fig. 2). The ranges of average values were also very similar from 3.5 to 12.0 mg l⁻¹ in Peñuelas, and from 2.0 to 12.0 mg l⁻¹ in Rungue (Table 1). The lowest value in oxygen content in Peñuelas was 1.8 mg l⁻¹ (19.0% saturation at 17 °C) during March (late summer), and the difference between surface and bottom waters was 2.5 mg l⁻¹. The lowest value in oxygen content observed in Rungue was 1.3 mg l⁻¹ (16.2% saturation at 22 °C) at the beginning of summer (January 84). The decrease of oxygen from surface to bottom was more marked than compared to Peñuelas and corresponded to 7.5 mg l⁻¹. Calculated values of percentage of oxygen saturation (accordingly to MACKERETH 1978), revealed that Peñuelas' waters were oversaturated from August to October 1983 (spring season). The oversaturation also occurred in Rungue, but much later from October to April 1984 and only at the surface layers of the water column.

The pH ranges in both reservoirs were very close to the point of neutrality. Thus, average values given in Table 1 varied from 6.0 to 7.4 in Peñuelas and from 6.9 to 7.3 in Rungue. On the other hand, the average values of conductivity shown in Table 1 evidence a difference between the two lakes. In Rungue, these values were high and ranged from 130 to 1000 $\mu\text{S cm}^{-1}$ (25 °C), while much lower averages (from 75 to 184 $\mu\text{S cm}^{-1}$) were recorded in Peñuelas. The difference in the conductivity values between these reservoirs, could be due to the ionic composition of the drainage basin combined with the fluctuating pattern of water levels, which may influence the concentration of major dissolved elements in the water. It is worthwhile to remark, that a copper mining company was at work in the neighbourhood of Rungue, however without any detectable influence in the reservoir itself.

Secchi depths were generally greater in Peñuelas than in Rungue (Table 1). A distinct phase of water transparency was observed in Peñuelas during the spring season (August–October 1983 and October–November 1984), fol-

Table 1. Monthly average values over the vertical profiles of abiotic parameters measured in Peñuelas and Rungue-reservoirs, Central Chile. - Numbers in parentheses correspond to standard deviation.

Peñuelas *	Aug 83	Sept	Oct	Dec	Jan 84	Feb	Mar	May	June	July	Aug	Sept	Oct	Nov
Temperature (°C)	11.8 (0.45)	13.8 (0.28)	16.9 (0.23)	20.8 (0.87)	22.8 (0.22)	21.5 (0.54)	18.8 (0.96)	15.2 (0.23)	10.4 (0.18)	9.8 (0.43)	11.5 (0.34)	15.1 (1.51)	18.9 (1.62)	18.8 (0.82)
Oxygen (mg l ⁻¹)	11.0 (0.65)	11.5 (1.57)	9.1 (0.43)	7.4 (1.23)	7.1 (0.29)	5.4 (0.88)	3.4 (1.13)	7.8 (0.39)	9.2 (1.41)	8.4 (0.34)	9.1 (0.44)	8.0 (1.00)	6.8 (0.68)	6.5 (0.30)
pH	6.8 (0.07)	7.4 (0.20)	6.8 (0.10)	7.0 (0.20)	7.0 (0.12)	6.8 (0.06)	6.9 (0.08)	7.2 (0.11)	7.2 (0.13)	7.0 (0.12)	6.6 (0.10)	6.0 (0.16)	7.0 (0.12)	6.9 (0.17)
Conductivity (µS cm ⁻¹ 25 °C)	118.0 (4.60)	107.2 (4.22)	183.7 (50.4)	129.2 (5.85)	-	-	127.8 (2.68)	135.0 (4.12)	128.2 (1.30)	129.7 (1.51)	75.6 (2.88)	77.3 (1.97)	87.3 (2.42)	-
Chlorophyll-a (µg l ⁻¹)	-	139.6 (91.2)	55.6 (46.1)	37.6 (37.8)	7.0 (6.61)	106.9 (60.7)	4.1 (2.22)	4.7 (35.5)	39.0 (3.64)	107.1 (89.8)	35.2 (32.0)	152.3 (82.4)	40.3 (54.0)	16.3 (10.1)
Secchi (m)	3.3	3.9	2.7	1.3	1.1	1.6	2.0	1.5	2.0	0.7	1.2	1.9	3.1	2.7
Rungue	Sept 83	Oct	Dec	Jan 84	Feb	Apr	May	June	July	Aug	Sept			
Temperature (°C)	10.9 (1.44)	14.7 (3.37)	20.3 (5.08)	23.0 (1.02)	21.9 (0.62)	19.8 (2.47)	13.0 (0.71)	9.5 (0.00)	8.5 (1.91)	6.7 (1.47)	12.2 (1.99)			
Oxygen (mg l ⁻¹)	6.5 (3.26)	8.9 (1.56)	5.6 (3.11)	5.9 (3.38)	6.2 (3.38)	8.5 (6.34)	6.8 (-)	9.7 (0.09)	7.2 (0.22)	10.1 (2.62)	7.6 (1.67)			
pH	7.0 (0.05)	7.3 (0.18)	7.0 (0.34)	7.2 (0.26)	7.1 (0.14)	7.4 (0.49)	7.2 (0.25)	7.2 (0.04)	6.9 (0.18)	7.0 (0.36)	6.9 (0.38)			
Conductivity (µS cm ⁻¹ 25 °C)	201.5 (6.8)	249.2 (23.4)	440.0 (152.2)	1000.4 (0.89)	-	635.0 (49.5)	605.0 (7.1)	550.0 (494.9)	130.6 (38.4)	208.5 (43.1)	215.3 (64.9)			
Chlorophyll-a (µg l ⁻¹)	8.5 (8.99)	108.4 (96.1)	26.9 (30.0)	11.7 (4.05)	9.8 (4.60)	372.5 (371.9)	33.3 (-)	21.3 (27.1)	51.7 (63.3)	24.5 (17.7)	56.0 (73.8)			
Secchi (m)	0.8	1.7	1.2	0.9	0.3	0.1	0.2	0.7	0.3	0.4	0.7			

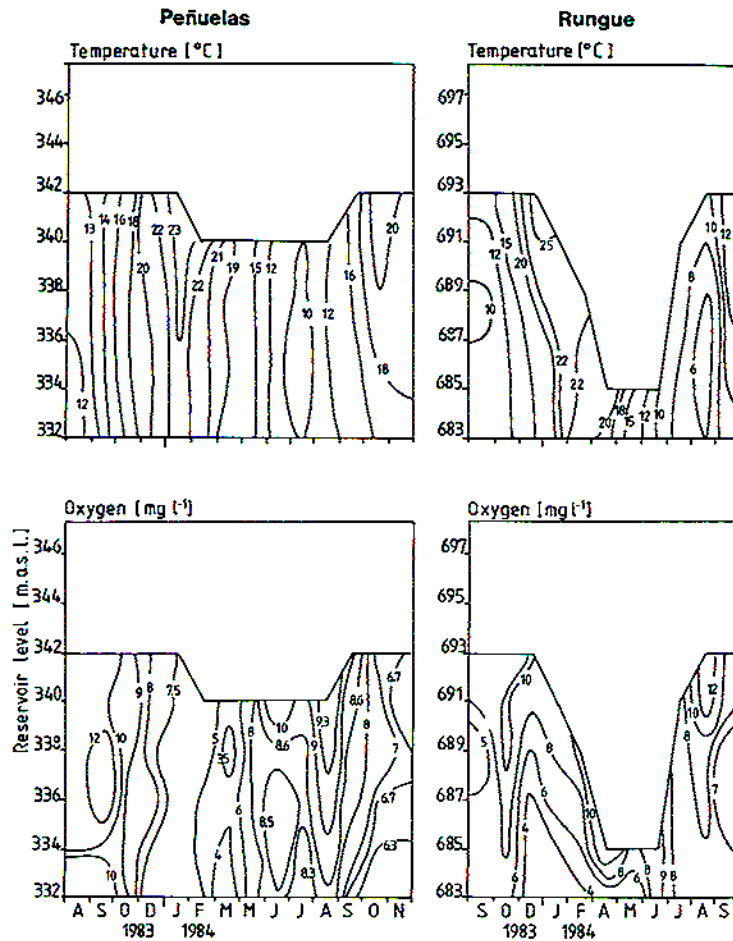


Fig. 2. Depth and temporal distribution of temperature (°C) and oxygen (mg l⁻¹) values in relation to water level fluctuations in two Chilean reservoirs.

lowed by a decrease in water clarity in summer and winter 1984. On the other hand, in Rungue the period of greater water transparency also occurred in spring, decreasing steadily towards the beginning of autumn (April 1984). During this month, the water level was reduced to two meters and there was a bloom of the Euglenophyceae *Trachelomonas* sp. (CARVAJAL, M. A., personal communication). In both lakes, the fluctuations in the chlorophyll-a values were seasonal and also throughout the water column (Table 1, Fig. 3); however, less marked variation in depth was found in Rungue. In this reservoir, low values of chlorophyll-a were recorded in summer 1984 (December–January), followed by an increase in autumn (April 1984). In this month, the highest value of chlorophyll-a occurred, coinciding with the low water level

and the bloom of *Trachelomonas*. In Peñuelas, tendencies to low values could be observed in January, March and June 1984. High values in chlorophyll-a were detected in September 1983 and 1984 (spring season), but the peaks were usually from 4 to 8 m depth (Fig. 3).

Zooplankton composition

A great difference can be seen in the zooplankton composition between the two reservoirs (Tables 2 and 3). Peñuelas had a total of 41 zooplanktonic species, including the Coelenterata *Craspedacusta sowerbyi* which constitutes the first finding in Chile (Table 2). From the total number of species in this lake, 2 correspond to Copepoda, 9 to Cladocera and 29 to Rotifera. However, most important species in abundances and occurrence throughout the year cycle were the copepod *Diaptomus diabolicus*, the cladocerans *Diaphanosoma*

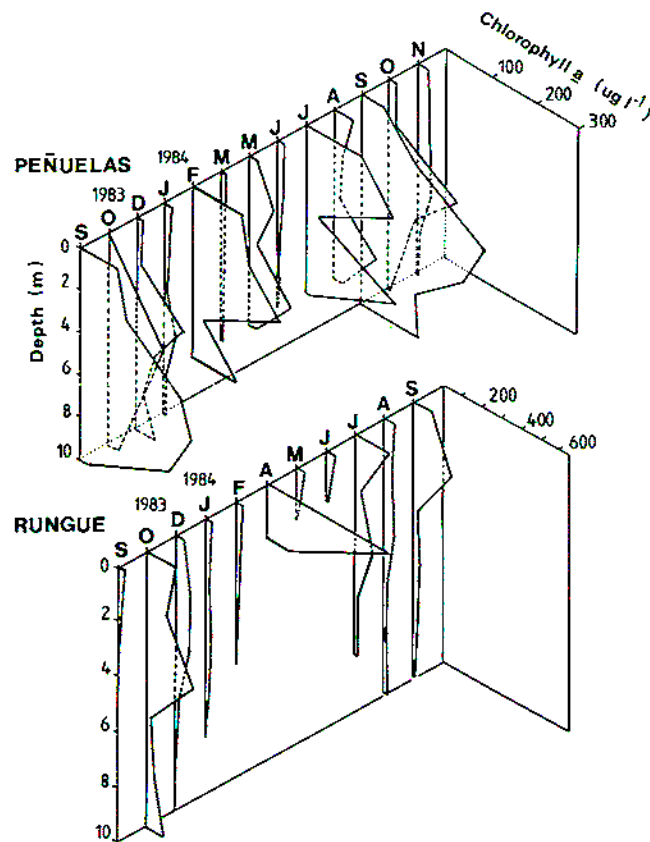


Fig. 3. Depth and temporal distribution of chlorophyll-a ($\mu\text{g l}^{-1}$) in two Chilean reservoirs.

Table 2. Zooplankton species composition of lake Peñuelas, mean annual abundances (No. Ind. l⁻¹), ($\pm 95\%$ CL), and the calculated percentages of abundance and presence over the year.

	\bar{x} ind/m ⁻³	$\pm 95\%$ CL	Dominance %	Presence %
Copepoda				
Calanoida				
Fam. Diaptomidae				
1. <i>Diaptomus diabolicus</i> BREHM	8.96	2.38	6.8	100.0
Cyclopoida				
Fam. Cyclopoidae				
2. <i>Tropocyclops prasinus meridionalis</i> (KIEFER)	0.05	0.03	4×10^{-2}	71.4
Cladocera				
Fam. Sididae				
3. <i>Diaphanosoma chilense</i> DADAY	6.10	2.22	4.6	100.0
Fam. Daphnidae				
4. <i>Daphnia ambigua</i> SCOURFIELD	2.39	1.35	1.8	100.0
5. <i>Ceriodaphnia dubia</i> RICHARD	4.68	2.06	3.6	100.0
6. <i>Moina micrura</i> KURZ	1.27	0.82	1.0	50.0
Fam. Bosminidae				
7. <i>Bosmina longirostris</i> (O.F.M.)	44.79	17.47	33.9	100.0
Fam. Chydoridae				
8. <i>Alona affinis</i> LEYDIG	1×10^{-3}	1.18×10^{-3}	6×10^{-4}	7.1
9. <i>A. guttata</i> SARS	4×10^{-3}	4.35×10^{-3}	3×10^{-3}	14.3
10. <i>A. pulchella</i> var. <i>cambouei</i> (DE GUERNE & RICHARD)	3×10^{-3}	2.65×10^{-3}	2×10^{-3}	21.4
11. <i>Chydorus sphaericus</i> (O.F.M.)	0.05	0.04	4×10^{-2}	71.4
Rotifera				
Monogononta				
Fam. Brachionidae				
12. <i>Platyus quadricornis</i> (EHRB.)	1×10^{-3}	1.18×10^{-3}	6×10^{-4}	14.3
13. <i>Brachionus quadridentatus</i> HERMAN	4×10^{-4}	8.43×10^{-4}	3×10^{-4}	7.1
14. <i>Keratella cochlearis cochlearis</i> (GOSSE)	0.34	0.26	0.3	42.9
15. <i>K. cochlearis</i> var. <i>tecta</i> f. <i>typica</i> LAUTERBORN	28.89	17.97	21.9	78.6
16. <i>K. cochlearis</i> var. <i>hispida</i> (LAUTERBORN)	145.96	5.56	11.3	100.0
17. <i>K. americana</i> AHLSTROM	6.50	2.68	4.9	85.7
18. <i>K. tropica tropica</i> APSTEIN	0.14	0.15	0.1	21.4
19. <i>Anuraeopsis navicula</i> (ROUSSELET)	0.12	0.17	0.1	14.3
Fam. Euchlanidae				
20. <i>Euchlanis dilatata dilatata</i> EHRB.	0.03	0.05	2×10^{-2}	7.1
21. <i>E. triquetra</i> EHRB.	1×10^{-3}	1.18×10^{-3}	6×10^{-4}	7.1
Fam. Trichotriidae				
22. <i>Trichotria pocillum</i> (O.F.M.)	0.02	0.02	2×10^{-2}	35.7
Fam. Lecanidae				
23. <i>Lecane</i> (s.str.) <i>flexilis</i> (GOSSE)	4×10^{-4}	8.43×10^{-3}	3×10^{-4}	7.1
24. <i>Lecane</i> (<i>Monostyla</i>) <i>lunaris lunaris</i> (EHRB.)	4×10^{-4}	8.43×10^{-3}	3×10^{-4}	7.1
Fam. Notommatidae				
25. <i>Monommata longiseta</i> (O.F.M.)	4×10^{-4}	8.43×10^{-3}	3×10^{-4}	7.1
26. <i>Trichocerca</i> (<i>Diurella</i>) <i>porcellus porcellus</i> (GOSSE)	0.09	0.14	7×10^{-2}	21.4
27. <i>Trichocerca</i> (s.str.) <i>elongata elongata</i> (GOSSE)	1×10^{-3}	1.44×10^{-3}	1×10^{-3}	7.1
Fam. Gastropodidae				
28. <i>Ascomorpha ovalis</i> (CARLIN)	1×10^{-3}	1.18×10^{-3}	6×10^{-4}	7.1
Fam. Synchaetidae				
29. <i>Synchaeta oblonga</i> EHRB.	3×10^{-3}	3.67×10^{-3}	2×10^{-3}	21.4
30. <i>S. stylata</i> WIERZEJSKI	4×10^{-4}	8.43×10^{-3}	3×10^{-4}	7.1

Table 2. Continued.

	\bar{x} ind/m ⁻³	±95% CL	Dominance %	Presence %
31. <i>Polyarthra dolichoptera dolichoptera</i> IDELSON	2.61	2.27	2.0	57.1
Fam. Asplanchnidae				
32. <i>Asplanchna (Asplanchnella) girodi</i> (DE GUERNE)	9×10^{-3}	0.01	1×10^{-2}	35.7
Fam. Testudinellidae				
33. <i>Pompholix complanata</i> (GOSSE)	4×10^{-4}	8.43×10^{-3}	3×10^{-4}	7.1
34. <i>P. sulcata</i> (HUDSON)	0.10	0.13	8×10^{-2}	14.3
Fam. Conochilidae				
35. <i>Conochilus dossuarius dossuarius</i> (HUDSON)	2.42	1.12	1.8	42.9
36. <i>C. unicornis</i> (ROUSSELET)	5.08	1.73	3.9	85.7
Fam. Hexarthridae				
37. <i>Hexarthra intermedia intermedia</i> WISZNIEWSKI	4×10^{-4}	8.43×10^{-3}	3×10^{-4}	7.1
Fam. Filiniidae				
38. <i>Filinia terminalis</i> (PLATE)	0.77	0.36	0.6	35.7
Fam. Collotheceidae				
39. <i>Collotheca mutabilis</i> (HUDSON)	0.74	0.38	0.6	42.9
Digononta				
40. <i>Bdelloidea</i> gen.sp.	0.31	0.32	0.2	50.0
Coelenterata				
Trachylina				
Fam. Petasidae				
41. <i>Craspedacusta sowerbyi</i> LANKESTER	0.54	0.32	0.4	35.7

chilense and *Bosmina longirostris*, and the rotifers *Keratella cochlearis* var. *tecta* and *K. cochlearis* var. *hispida*. On the contrary, in Rungue the zooplankton composition was relatively poor, formed by 2 species of Copepoda, 2 of Cladocera and 17 of Rotifera (Table 3). Two new rotifer records for the country were found here, these are *Cephalodella catellina* and *Volga spinifera*. In comparison to the other reservoir, Rungue had a lack of Diaptomidae and the most important species in abundance and presence during the year was the rotifer *Keratella tropica tropica*. Two other species *Brachionus angularis* and *Polyarthra dolichoptera* were dominant in numbers but these were seldom present during the year (Table 3).

The average zooplankton abundances in Peñuelas and Rungue lake during the sampling period is shown in Fig. 4. The highest value at each place was achieved during the autumn or winter season by the rotifers, the average corresponded to 2238 ind l⁻¹ (SD: ± 939, April 1984) in Rungue, and to 421 ind l⁻¹ (SD: ± 156, July 1984) in Peñuelas. In the latter lake, cladocerans follow in mean abundance with 23 ind l⁻¹ (SD: ± 100, August 1984), while Copepoda with an average of 36 ind l⁻¹ (SD: ± 17.0) and Coelenterata with 5 ind l⁻¹ (SD: ± 2) had lower densities compared to the other groups during the same summer month (December 1983).

In Rungue, the average abundances of cladocerans and copepods were also lower, the highest values occurred in summer and were 11 ind l⁻¹ (SD: ± 9, in

Table 3. Zooplankton species composition of lake Rungue, mean annual abundances (No. Ind. l⁻¹), ($\pm 95\%$ CL), and the calculated percentages of abundance and presence over the year.

	\bar{x} ind l ⁻¹	$\pm 95\%$ CL	Dominance %	Presence %
Copepoda				
Cyclopoida				
Fam. Cyclopidae				
1. <i>Metacyclops mendocinus</i> (WIERZERSKI)	5.42	2.91	2.7	63.6
2. <i>Tropocyclops prasinus meridionalis</i> (KIEFER)	3×10^{-3}	3×10^{-3}	2×10^{-3}	18.2
Cladocera				
Fam. Moinidae				
3. <i>Moina micrura</i> (KURZ)	0.83	0.99	0.4	36.4
Fam. Bosminidae				
4. <i>Bosmina longirostris</i> (O.F.M.)	0.07	0.05	3×10^{-2}	63.6
Rotifera				
Monogononta				
Fam. Brachionidae				
5. <i>Brachionus angularis</i> (GOSSE)	65.76	94.14	31.9	36.4
6. <i>B. calyciflorus</i> (PALLAS)	1.83	2.50	0.9	27.3
7. <i>B. quadridentatus</i> HERMAN	0.21	0.42	0.1	18.2
8. <i>Keratella tropica tropica</i> (EHRB.)	32.22	23.99	15.9	63.6
9. <i>Anuraeopsis navicula</i> (ROUSSELET)	23.38	33.22	11.5	9.1
Fam. Euchlanidae				
10. <i>Euchlanis dilatata dilatata</i> (EHRB.)	2×10^{-3}	3×10^{-3}	1×10^{-3}	9.1
Fam. Trichotriidae				
11. <i>Volga spinifera</i> (WESTERN)	3×10^{-3}	3×10^{-3}	2×10^{-3}	18.2
Fam. Colurellidae				
12. <i>Lepadella triptera</i> (EHRB.)	0.30	0.43	0.2	18.2
Fam. Lecanidae				
13. <i>Lecane</i> (s.str.) <i>luna luna</i> (O.F.M.)	0.20	0.16	0.1	18.2
14. <i>Lecane</i> (<i>Monostyla</i>) <i>lunaris</i> EHRB.	4×10^{-3}	4×10^{-3}	2×10^{-3}	18.2
15. <i>Lecane</i> (<i>M.</i>) sp.	2×10^{-3}	1×10^{-3}	8×10^{-4}	9.1
Fam. Notommatidae				
16. <i>Cephalodella catellina</i> (O.F.M.)	2×10^{-3}	1×10^{-3}	8×10^{-4}	9.1
17. <i>Cephalodella</i> sp.	0.02	0.03	1×10^{-2}	27.3
Fam. Synchaetidae				
18. <i>Polyarthra dolichoptera</i>	68.81	101.36	33.9	36.4
Fam. Testudinellidae				
19. <i>Pompholix complanata</i> (GOSSE)	5.01	5.99	2.5	18.2
Fam. Hexarthridae				
20. <i>Hexarthra</i> sp.	0.20	0.21	0.1	18.2
Digononta				
21. <i>Bdelloidea</i> gen.sp.	0.15	0.02	6×10^{-2}	45.5

February 1984) and 25 ind l⁻¹ (SD: ± 10 , in January 1984) for each group separately (Fig. 4).

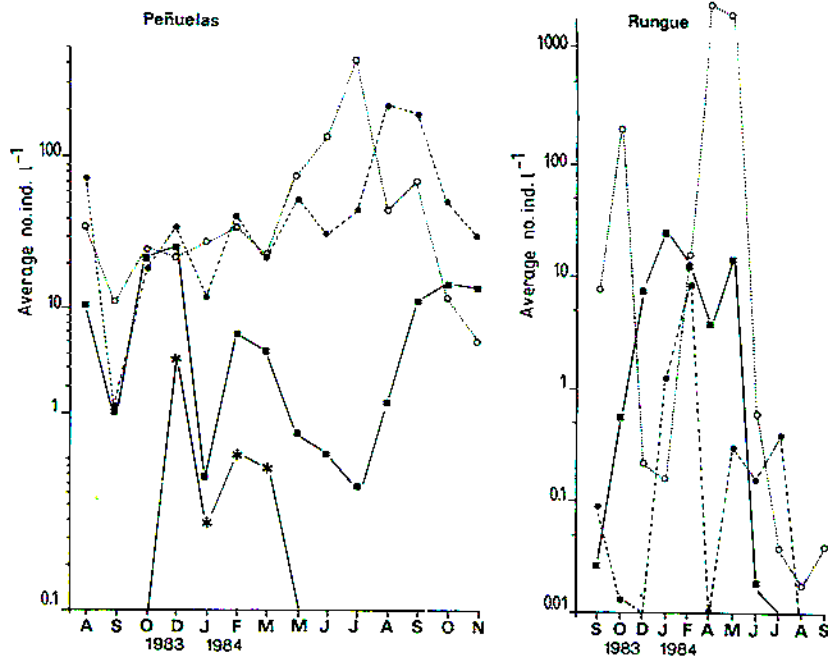


Fig. 4. Monthly mean abundance values over the vertical profile in Peñuelas and Rungue reservoirs of three zooplanktonic groups: Copepoda (black squares), Cladocera (black circles) and Rotifera (empty circles) in Peñuelas and Rungue reservoirs. Solid lines and asterisks represent *C. sowerbyi* in Peñuelas reservoir.

The succession of those numerically important zooplankton species in lake Peñuelas is illustrated in Fig. 5. The species replacement throughout time is clear, thus spring species are: *Diaptomus diabolicus*, *Craspedacusta sowerbyi*, *Moina micrura*, *Diaphanosoma chilense* and *Conochilus unicornis*. In summer, the average densities of those numerically most important species decreased, however *Conochiloides dossuarius* achieved its maximum abundance peak (Fig. 5 e). Lower density peaks during summer can be seen in *D. diabolicus*, *Daphnia ambigua* and *Keratella americana* (Fig. 5 a, b and e). Nevertheless, in this reservoir the latter species had its maximum density peak during the autumn. Winter species are: *B. longirostris*, *K. cochlearis* var. *tecta*, *K. cochlearis* var. *hispidata* and *P. dolichoptera*. The cladoceran *Ceriodaphnia dubia* occurred with a maximum peak during spring, however not at the same level in both years (Fig. 5 c).

The annual succession of the numerically most abundant species in Rungue, illustrated in Fig. 6, shows that the copepod *Metacyclops mendocinus* has its maximum density in summer. The cladoceran *M. micrura* has its abundance peak during late summer, which indicates a difference compared to its temporal occurrence in Peñuelas. In Rungue, the most abundant species ap-

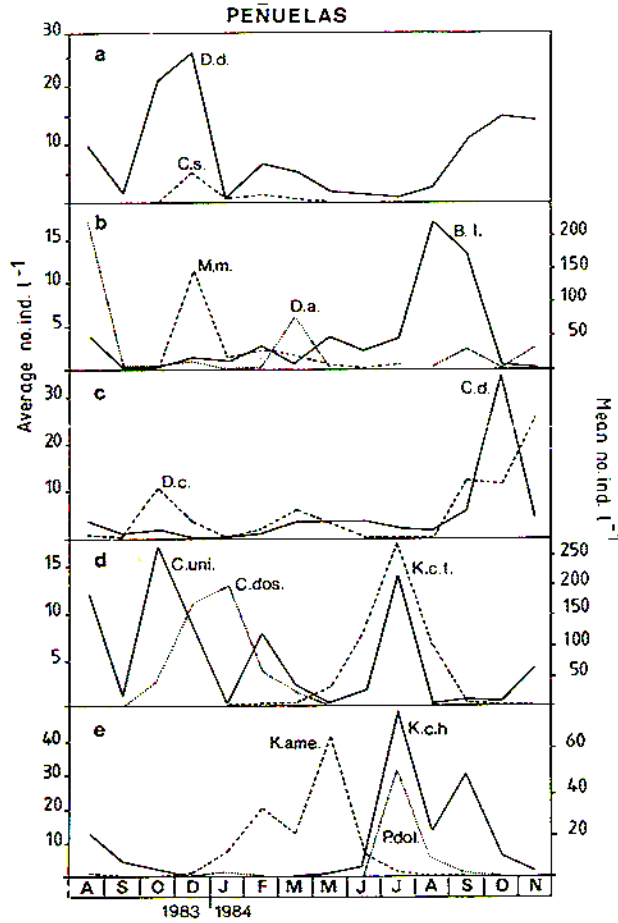


Fig. 5. Zooplankton species succession in Peñuelas reservoir. a) *D. diabolicus* (D.d.) and *C. sowerbyi* (C.s.). b) *M. micrura* (M.m.), *D. ambigua* (D.a.) and *B. longirostris* (B.l.); refer to the scale at the right hand side. c) *D. chilense* (D.c.) and *C. dubia* (C.d.). d) *K. cochlearis* var. *tecta* (K.c.t.; refer to the scale at the right hand side), *C. dossuarius* (C.dos.) and *C. unicornis* (C.uni.). e) *K. cochlearis* var. *hispida* (K.c.h.; refer to the numbers at the right hand side), *K. americana* (K.ame.) and *P. dolichoptera* (P.dol.).

peared in autumn when the water level was extremely low, nonetheless with great differences in the number of individuals. High abundances during the same month (April 1984) can be observed in *P. dolichoptera*, *Brachionus calyciflorus* and *Anuraeopsis navicula*. *B. angularis*, *Pompholix complanata* and *K. tropica* predominate a month later (Fig. 6 b, c and d). During the winter season there were no abundant species, probably as a consequence of the water release occurring at the end of summer.

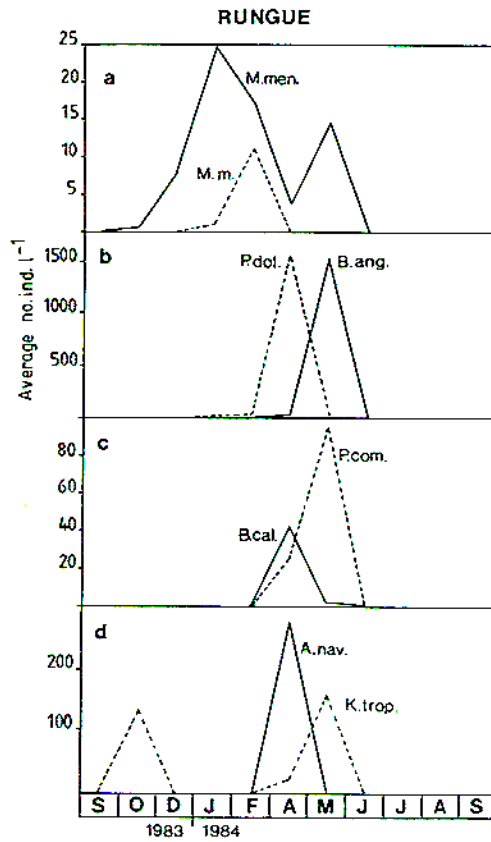


Fig. 6. Zooplankton species succession in Rungue reservoir. a) *M. mendocinus* (M.men.) and *M. micrura* (M.m.). b) *B. angularis* (B.ang.) and *P. dolichoptera* (P.dol.). c) *B. calyciflorus* (B.cal.) and *P. complanata* (P.com.). d) *K. tropica tropica* (K.trop.) and *A. navicula* (A.nav.).

Having in mind, that the community structure is the result of the expression of each species component, the general dynamics of these taxa can be reflected in changing schemes on the community during a year cycle. In order to detect seasonal fluctuations at a community level, the diversity index was calculated as the sum of all depths sampled in each month and for each lake. The results shown in Fig. 7 a, clearly indicate two phases of the zooplankton community in Peñuelas. The first period is characterized by an increasing accumulated diversity from spring until the end of summer (2.09 to 3.27 bits ind⁻¹), while the second phase corresponds to a decreasing diversity from autumn towards winter (2.04 to 1.09 bits ind⁻¹). The species richness in this lake range from 11 to 26 species and shows three maximum peaks: in August 1983, in summer and winter 1984 (Fig. 7 a).

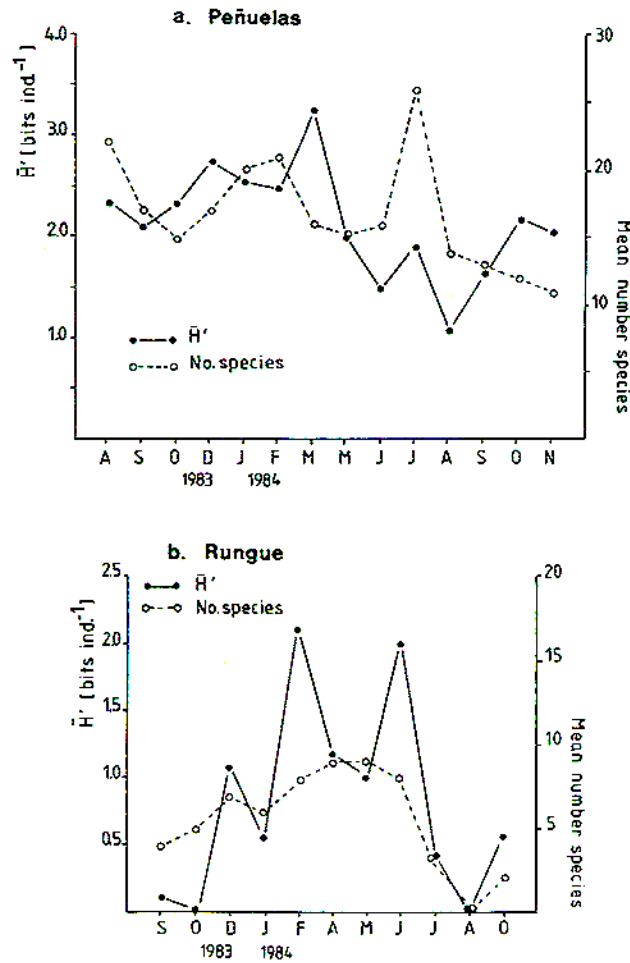


Fig. 7. Monthly accumulated zooplankton diversity (solid lines) and species richness (dashed lines) in Peñuelas and Rungue reservoirs.

In Rungue, the values of this calculated diversity were markedly fluctuating during the year (Fig. 7 b). Thus, there was a tendency to increase from spring to summer (0.03 to 2.13 bits ind⁻¹), followed by a decrease in autumn. At the beginning of winter (June 84), this summed diversity increased to a similar value of that in summer, but the next months were characterized by a marked decrease. Compared to the other lake, species richness is very low, from 0 to 9 species and it is possible to visualize only shallow peaks in December 1983 and in autumn 1984 (Fig. 7 b).

To detect any divergences from the summed diversity per month, the zooplankton diversity was calculated at each depth over the year in both reservoirs

(Fig. 8). In Peñuelas these values of diversity were different from the accumulated one in September 1983, February, June and September 1984; however, the differences throughout the water column were not so marked as to show any stratified pattern (Fig. 8 a). On the other hand, in Rungue the values of diversity in the depth profile were different from the accumulated one in December 1983, May and July 1984. Only in December, the diversity values show a slight tendency to stratification in the water column (Fig. 8 b).

The fluctuation of diversity values in Peñuelas was not significantly related to species richness, but to the equitability or evenness with which the number of individuals are distributed among the species in the community (Table 4 a). On the contrary, in Rungue there is a significant relationship to both parameters: species number and equitability (Table 4 b). In Peñuelas a significant com-

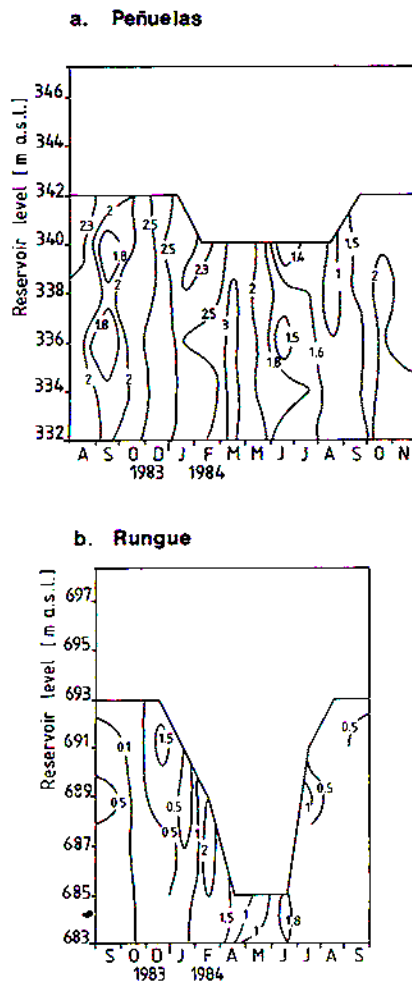


Fig. 8. Depth and temporal distribution of zooplankton diversity values (bits ind^{-1}) in relation to water level fluctuation in two Chilean reservoirs.

bined effect was found between the zooplankton species diversity and water temperature and oxygen (Table 5). The effect is clear, at high values of temperatures, water oxygen content is low and the species diversity is high. Nevertheless, these two abiotic parameters influenced significantly the diversity component of equitability rather than species richness (Table 5). In Rungue it was not possible to detect any kind of relation between abiotic variables and these community parameters.

The changes in the species abundances and their relationship to environmental factors (temperature, oxygen, pH, conductivity, chlorophyll-a and water transparency) were further investigated using simple or multiple stepwise regression analysis (Tables 6 and 7). In Peñuelas, temperature was found to be significantly related to the abundances of six species. Increasing values of this parameter, promote the increase of abundances of *D. diabolicus* and *D. chilense*, while for one cladocera and three rotifer species the effect is negative (Table 6 a). Only three species are significantly related to conductivity values in the same lake, in all cases the increase is associated to higher

Table 4. Regression equations relating the zooplankton species diversity values (H') to species richness and equitability in two Chilean reservoirs.

Variable	a	±SE	b	±SE	df	F	P
a) Peñuelas Reservoir							
Species richness	1.487	0.236	0.050	0.021	1,76	5.906	0.0174
Equitability	0.185	0.119	2.158	0.135	1,76	256.520	<0.0001
a) Rungue Reservoir							
Species richness	-0.031	0.093	0.197	0.025	1,46	64.606	<0.0001
Equitability	0.0136	0.057	1.359	0.099	1,46	189.569	<0.0001

df = Degrees of freedom; F = variance ratio; P = probability level.

Table 5. Multiple regression analysis for the prediction of two community parameters in Peñuelas reservoir: zooplankton species diversity and equitability. Only variables that accounted for significant variations were retained.

Variable	Coeff.	t-value	P
a) Zooplankton species diversity (n: 78; F: 21.273; P<0.0001)			
Temperature	0.054	3.939	0.0002
Oxygen	-0.054	-2.080	0.0410
Intercept	1.596		
b) Equitability (n: 78; F: 37.231; P<0.0001)			
Temperature	0.028	5.749	<0.0001
Oxygen	-0.019	-2.061	0.0428
Intercept	0.552		

Coeff. is the regression coefficient associated with each independent variable; the t-value and associated probability (P) indicate the significance of each variable in the prediction of species diversity or equitability.

abundances of *T. prasinus*, *K. americana* and *C. unicornis* (Table 6 b). In the same lake, combined effect of temperature and oxygen, and also of these two variables plus water conductivity on the densities of some zooplankton species can be seen in Table 7 a, b. Four species seem to be significantly affected by both temperature and oxygen. *M. micrura* and *K. c. var. hispida* increase in abundances when water temperature is low and there is a higher oxygen content (winter season). On the contrary, *F. terminalis* and *C. sowerbyi* are related to higher values of temperature with consequently lower oxygen content.

Combined significant effect of three parameters, water temperature, conductivity and oxygen, on the abundance of *C. dossuarius dossuarius* is shown in Table 7 b; however, the *t*-value of the oxygen variable was not significant at the same level as the other two abiotic parameters.

In Rungue, in contrast to Peñuelas only one species was found significantly related to abiotic parameters. Table 8, shows the results obtained on the effect of environmental variables on the densities of *M. mendocinus*. Combined significant effect of temperature and oxygen seem to influence the occurrence of this copepod; the species is present at high values of water temperature with low oxygen concentration.

Because of the obvious relationships found between the abundances of some zooplanktonic species and the abiotic parameters, and the closely related species replacing each other in time, it was necessary to summarize these existing relationships with an ordination procedure. From several methods widely spread in the literature, the zooplankton data (previously $\log_{10}(x + 1)$ transformed) were treated by a principal component analysis (PCA).

Table 6. Regression equations relating the transformed abundances ($\log x + 1$) of some zooplanktonic species to temperature ($^{\circ}\text{C}$) and conductivity ($\mu\text{S cm}^{-1}$, 25°C) in Peñuelas reservoir.

Species	ln a \pm SE	b \pm SE	df	F	P
a) Temperature					
<i>D. diabolicus</i>	0.217 \pm 1.175	1.151 \pm 0.416	1,75	7.674	0.0071
<i>D. chilense</i>	-4.152 \pm 1.582	2.460 \pm 0.560	1,75	19.331	<0.0001
<i>C. sphaericus</i>	5.026 \pm 1.081	-1.547 \pm 0.383	1,76	16.378	0.0001
<i>K.c.var. tecta</i>	17.012 \pm 1.936	-5.326 \pm 0.684	1,76	60.602	<0.0001
<i>P. dolichoptera</i>	6.767 \pm 1.893	-2.081 \pm 0.669	1,76	9.679	0.0026
<i>Bdelloidea</i> gen.sp.	5.713 \pm 1.200	-1.866 \pm 0.424	1,76	19.356	<0.0001
b) Conductivity					
<i>T. prasinus</i>	-5.538 \pm 1.778	1.288 \pm 0.374	1,59	11.848	0.0011
<i>K. americana</i>	-14.852 \pm 2.883	3.637 \pm 0.607	1,59	35.910	<0.0001
<i>C. unicornis</i>	-16.361 \pm 3.399	3.953 \pm 0.715	1,59	30.529	<0.0001

\pm SE = Standard error; df = degrees of freedom; F = variance ratio; P = significance level.

Table 7. Multiple regression analysis for the prediction of transformed density data of some zooplanktonic species in lake Peñuelas. Only variables that accounted for significant variation were retained.

Variable	Coeff.	t-value	P
a) Temperature and Oxygen			
1. <i>M. micrura</i> (n: 76; F: 19.783; P < 0.0001)			
log Temperature	-2.092	-3.449	0.0009
log Oxygen	1.842	2.758	0.0073
Intercept	0.468		
2. <i>K. cochlearis</i> var. <i>hispida</i> (n: 77; F: 44.019; P < 0.0001)			
log Temperature	-3.707	-6.082	< 0.0001
log Oxygen	1.670	3.014	0.0035
Intercept	9.848		
3. <i>F. terminalis</i> (n: 77; F: 28.230; P < 0.0001)			
log Temperature	2.747	4.563	< 0.0001
log Oxygen	-1.524	-2.784	0.0068
Intercept	-3.533		
4. <i>C. sowerbyi</i> (n: 77; F: 31.730; P < 0.0001)			
log Temperature	2.468	4.624	< 0.0001
log Oxygen	-1.552	-3.197	0.0020
Intercept	-2.809		
b) Temperature, Conductivity and Oxygen			
5. <i>C. dossuarius dossuarius</i> (n: 60; F: 42.697; P < 0.0001)			
log Temperature	3.581	6.303	< 0.0001
log Conductivity	3.034	6.843	< 0.0001
log Oxygen	-0.975	-2.153	0.0355
Intercept	-21.057		

Coeff. is the regression coefficient associated with each independent variable; the *t*-value and associated probability (P) indicate the significance of each variable in the prediction.

Table 8. Multiple regression analysis for the prediction of transformed abundances of *M. mendocinus* in lake Rungue. Only variables that accounted for significant variability were retained.

Variable	Coeff.	t-value	P
<i>M. mendocinus</i> (n: 41; F: 29.460; P < 0.0001)			
log Temperature	2.029	3.297	0.0021
log Oxygen	-1.137	-2.718	0.0098
log Conductivity	0.909	2.374	0.0227
Intercept	-6.492		

Coeff. is the regression coefficient associated with each independent variable; the *t*-value and associated probability (P) indicate the significance of each variable in the prediction.

Fig. 9, shows the distribution of 22 species from lake Peñuelas (percentage of annual abundance > 0.04 %) in the space formed by the first three principal

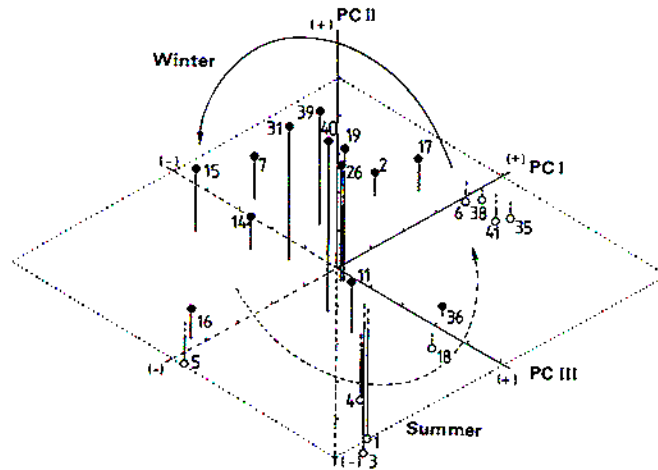


Fig. 9. Principal component ordination of 22 zooplanktonic species from Peñuelas reservoir. Numbers represent the species listed in Table 2.

components. They account for 57% of the total variation on the data, the first accounting for 26%, the second for 22% and the third for 9%. The first component summarizes the variation in the community of two groups, from high abundances of *T. prasinus*, *M. micrura*, *K. americana*, *F. terminalis*, *C. dossuarius* and *C. sowerbyi* to that of high densities of *K. cochlearis* var. *hispida* and *C. dubia*. The second component represents the variation from high numbers of *K. cochlearis* f. *tecta*, *T. porcellus*, *A. navicula*, *P. dolichoptera*, *C. mutabilis* and *Bdelloidea* Gen. sp. to that of high densities of *D. diabolicus*, *D. ambigua* and *D. chilense*. The third component summarizes variation for two other groups, among them two cladocerans and three rotifer species (Fig. 9).

A similar procedure of PCA was carried out separately for some of the abiotic parameters, previously logarithmically transformed. The correlations of factor scores of these environmental variables (Table 9 a), provide a measure of the importance of individual parameters in controlling the zooplankton groups in lake Peñuelas. These correlations indicate that variation along the first component (accounting 30.6% of variation) is from variables such as conductivity and pH. The relative position of oxygen values in relation to temperature is the most important characteristic of the second component (29.4% of variation). These results emphasize that the zooplankton species succession in Peñuelas reservoir is markedly influenced by a series of abiotic factors. In some cases, the ionic content of the water is the main factor determining the distribution of some species (*T. prasinus*, *K. americana*, or *C. dossuarius*), others species are related to the mixing of waters, indicated by the gradient between

oxygen (*M. micrura*, *F. terminalis*, *C. sowerbyi*) and temperature (*D. diabolicus*, *D. ambigua*, *D. chilense*).

Table 9. Rank correlations between environmental variables and three first principal components for: a. Lake Peñuelas and b. Rungue reservoir.

	Principal Component	
	1	2
a) Peñuelas		
Temperature	-0.010	0.846
Oxygen	-0.014	-0.851
Conductivity	0.802	0.126
pH	0.804	-0.119
Chlorophyll-a	-0.491	0.000
Percentage of explained variances by each axis	30.60	29.40
b) Rungue		
Temperature	0.937	0.080
Oxygen	-0.299	0.850
Conductivity	0.922	0.044
pH	0.459	0.789
Chlorophyll-a	0.158	0.777
Percentage of explained variances by each axis	47.10	33.10

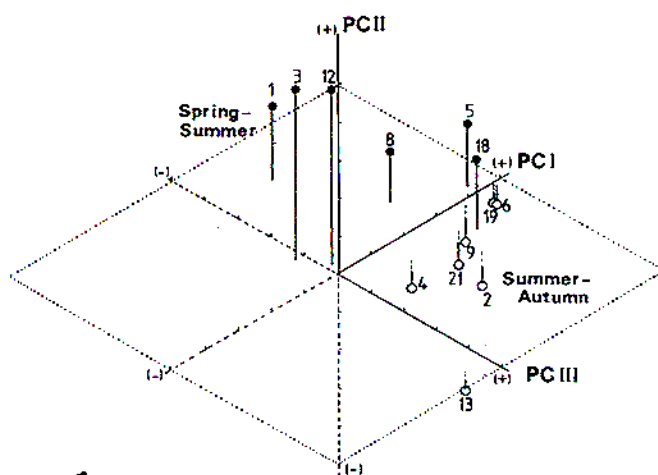


Fig. 10. Principal component ordination of 13 zooplanktonic species from Rungue reservoir. Numbers represent the species listed in Table 3.

The results obtained for the PCA analysis on 13 zooplankton species from Rungue are shown in Fig. 10. Three components accounted for 80.2% of the variance of the data, the first accounting 38%, the second for 17.4% and the third for 12.5%. The first component summarizes the variation of the high abundances of six species all rotifers, while the second component represents the variation of *M. micrura* and *L. triptera*. The third component shows the variability of high abundances of *L. luna*. When applying the PCA analysis to the environmental variables in this reservoir, two principal components were obtained (80.2% of total variance; Table 9 b). The results of the factor scores of the abiotic variables in Rungue, shows that temperature and conductivity are the most important parameters on the first component (47.10% of variation). The second component (33.10%) summarizes the variation of oxygen, pH and chlorophyll-a.

Discussion

Despite the great water level fluctuation in Rungue reservoir, the range of temperature and oxygen values were not extremely different between the two studied reservoirs (Table 1). However, variability throughout the water column, reflected in the standard deviation, was more marked in Rungue than in Peñuelas. The changes in oxygen and temperature in Peñuelas, were mostly seasonal than vertically through the water column (Fig. 2). Furthermore, taking into account its morphometric parameters (lake surface-area and depth), its degree of wind exposure and the orientation to the predominating winds, it is possible to conclude that these factors control the elimination of vertical temperature differences. This contrasts with other reservoirs in Central Chile, such as Rapel (34° 10' S, 79° 29' W) and El Plateado (33° 04' S, 71° 39' W), both defined as temperate monomictic lakes, respectively by CABRERA et al. (1977) and DOMINGUEZ et al. (1976).

Rungue reservoir showed a tendency to temperature stratification with consequent oxygen depletion during the summer of 1984 (Fig. 2), but the extreme water level reduction between February to April 1984 (from 6 to 2 m), disrupted probably any further development, a fact which unables to categorize its water temperature regime.

On the other hand, variables such as conductivity, chlorophyll-a and water transparency were clearly different from one lake to another. High values of conductivity characterized Rungue and contrasted to much lower values in Peñuelas (Table 1). This may be a consequence of either water level fluctuation, soil composition or the evaporation process within the drainage basin; this reservoir is situated in an extreme semi-arid area with low precipitation. Waters of Peñuelas are much clearer (Table 1) than in Rungue where turbidity is mainly due to suspended clay particles, except in April 1984 when the lowest

secchi measurement (0.1 m) was the result of a phytoplankton bloom. This seems to be characteristic of easily-erodible soils and semi-arid climates, where the slopes lack of protective vegetation cover (PETTS 1984).

Chlorophyll-a values, varied in both reservoirs seasonally and throughout the depth layers. The range detected in Peñuelas is very similar to that reported in the same lake by MONTECINO & CABRERA (1984). In addition, these authors gave ranges of trophic status for other water bodies in Central Chile. Considering their diagnosis, Peñuelas and Rungue would fall into the category of eutrophic lakes.

With respect to the zooplankton species composition, the majority of them are widely distributed in the country (ARAYA & ZUÑIGA 1985, RUIZ & BAHAMONDE 1989, SCHMID-ARAYA 1990). But, some general remarks need to be pointed out: firstly, the rotifer species *Wolga spinifera*, defined as benthic-littoral in Europe (MARGALEF et al. 1976, KOSTE 1978), has been recorded here for the first time. It is a rare species, occurring in Rungue during the summer season (January, February 1984) between 0 to 2 m; the species was also found in Argentina in habitats with similar pH, but slightly lower values of conductivity (JOSÉ DE PAGGI 1982). Secondly, the jellyfish, *Craspedacusta sowerbyi* found in Peñuelas also constitutes the first finding in the plankton of Chilean waters, and it was numerous during the spring and summer months (Fig. 5 a). Although it was not possible to observe clearly prey items, possibly due to the fixing technique, it was found a significant negative correlation with abundances of *Ceriodaphnia* ($r = -0.670$, $n = 77$, $P < 0.001$) and *Keratella cochlearis* var. *hispida* ($r = -0.82$, $n = 77$, $P < 0.001$). These indirect estimations coincide remarkably with those stated by CHAPMAN & GREEN (1987) for populations of the jellyfish in lake Kainui, New Zealand. It seems possible that the species may have a predatory effect on some zooplanktonic species in this Chilean lake; predators such as *Leptodora* and *Heterocope*, common in the Northern Hemisphere, are not present in Chile (ZUÑIGA 1988). Therefore, if *C. sowerbyi* successfully persists in Peñuelas, then it would constitute an ecological equivalent of those invertebrate predators.

The total number of zooplanktonic species over the year is remarkably different between Peñuelas and Rungue (41 to 21, respectively, Tables 2, 3). A striking characteristic of the latter is the absence of Diaptomidae (the most common freshwater calanoid in Central Chile), and the clear predominance of Rotifera in total presence (76.2%) and total abundance (96.9%). In general the absence of some crustaceans in Rungue, particularly of diaptomids and daphnids, may be the consequence of a series of related factors such as changes on water levels, the flushing rate, high trophy and also the turbidity of the water. The first two factors, seem to be important for copepods, a *k*-strategist group (sensu ALLAN 1976), which is adapted to more stable environments due to its reproduction mode and longer generation times. Poor crustacean fauna

has been evidenced in tropical lakes under extreme floods by HARDY et al. (1984), while natural lakes with high flushing rates favour the growth of smaller bosminids and rotifers (SPRULES & JIN 1990). Similarly, DUNCAN (1983) also recorded a poor crustacean fauna in Parakrama Samudra (Sri Lanka), and attributed the phenomenon to young-fish predation and rare macrophytes refuges. In Rungue reservoir, both factors are absent, so that it seems more likely that the limited crustacean development is due to the other parameters stated here. At the same time, turbidity of the water (indicated by the low transparency), may also influence the presence of these crustaceans, as the inorganic particles interfere with the filter-feeding mode (HANEY & BUCHANAN 1987). Daphnids have also been reported to be absent when high levels of turbidity prevail in subtropical reservoirs (HART 1986).

On the other hand, the dominance of rotifers is a typical character of an early stage of colonization process within the history of a reservoir (RZOSKA 1966, KASYMOV et al., 1972, POPOVA et al., 1972, ARMENGOL 1980, PINEL-ALLOUL et al. 1989, amongst others). Rotifers are generally viewed as opportunistic (r -strategists) with a rapid response to resource explosion, hence they have been suggested to inhabit more unpredictable environment (ALLAN, 1976). Thus, protozoans and rotifers dominate the composition and abundance of the zooplankton community in situations of high water velocity, within a series of reservoirs (ARMENGOL, 1984, ARMENGOL et al., 1988). Similarly, high mean flushing rates probably favoured r -strategists in lake Bieler See, Switzerland (BERNER-FRANKHAUSER, 1986), and more evidence of the predominance of small organisms (rotifers and small bosminids) in a rapidly flushing system has been given by SPRULES & JIN (1990).

The examination of Fig. 6 clearly indicates that only some species, multiply rapidly and disappear within a short time in this lake, particularly at the period of time when the water level is reduced (end of summer). Rungue, which resembles an impounded river with a drastic change on water level, shows that few species can adapt to these conditions, and those successful colonizers could achieve great abundances as 2240 ind l⁻¹ in *P. dolichoptera* and 1929 ind l⁻¹ in *B. angularis*.

In Rungue three species of the genus *Brachionus* coexist, nonetheless their maximum abundances differ either in numbers or temporally; in this way, *B. quadridentatus* showed lower abundances compared to the other two brachionids (10 ind l⁻¹ at 2 m depth in May 1984). *B. angularis* and *B. calyciflorus* overlapped markedly between April–May 1984 (autumn season, Fig. 6 b, c), but their maximal peaks were in different months. MIRACLE et al. (1987) studying the distribution of *Brachionus* assemblages, have demonstrated that the oligohaline species (*B. angularis*, *B. calyciflorus*) are well correlated to major constituents of water salinity, whereas the preference of *B. quadridentatus* appears to be those lagoons which are sulphaterich, with high ratios of Cl⁻/SO₄²⁻ and low ratios of Alk/Ca²⁺ + Mg²⁺.

In Peñuelas reservoir, the percentage of species present corresponded to 68.3% rotifers, 19.5% cladocerans and 4.9% copepods, whose respective total abundance during the year were: 47.8%, 44.9% and 6.8%. The species richness in this lake is due to the mixture between truly planktonic and benthic species, among the latter the genus *Alona*, *Chydorus* for cladocerans, and the genus *Platyas*, *Trichotria* and *Lecane* for rotifers. In contrast to Rungue, this lake which is surrounded by a dense terrestrial vegetation, has representative populations of aquatic macrophytes like: *Ludwigia peploides montevidensis* (SPRENGEL), *Hydrocotyle modesta* CHAM & SCHLETDL, *H. ranunculoides* L., *Paspalum distichum* L. and *Potamogeton berteroi* (GARCIA 1984).

Among the rotifers five species of *Keratella* coexist in this lake, including three morphotypes such as *K. cochlearis* var. *hispida*, *K. cochlearis* var. *tecta* and *Keratella cochlearis cochlearis*. RUTTNER-KOLISKO (1974), summarized the way ecological factors determine the morphological variation in the species in a diagram. Accordingly the form *tecta* is typical of warm eutrophic sites and *hispida* of turbulent waters. The presence of the latter might be related to the water mixing, since this lake showed no thermal stratification during the year. Lately, GALKOVSKAYA & MITYANINA (1989) evidenced that the three forms inhabit different layers in the water column, a fact that these authors explain by the trophic conditions. In Peñuelas, *K. cochlearis cochlearis* is poorly represented in numbers and more abundant are *tecta* and *hispida*, especially in winter 1984 (July, Fig. 5 d, e). Their abundances throughout the year cycle were significantly related to temperature (form *tecta*, Table 6) and to the combined effect of this parameter and oxygen (form *hispida*, Table 7). Cases of simultaneous occurrence of several forms of *K. cochlearis* in lakes are known (i.e. PEJLER 1962, HILLBRICHT-ILKOWSKA 1972, 1983, HOFMANN 1983), but among these authors there is a divergence on the interpretation why the development of the different forms occurs. The data of Peñuelas contributes as a further example of the presence of separate "sub-populations", since some differences in size [lorica length and caudal spine accordingly to HOFMANN (1983)] were detected. But, in order to confirm this hypothesis here, morphological characteristics in these forms need to be examined deeper.

As it was described above, the greater species richness existing in Peñuelas compared to Rungue is due to the presence of benthic-littoral and pelagic species. Consequently, the calculated summed diversity throughout the water column was also found higher in Peñuelas than in Rungue, from 1.09 to 3.27 bits ind⁻¹ and from 0 to 2.02 bits ind⁻¹, respectively for each water body (Fig. 7 a, b). At the same time, the index shows two phases of the zooplankton community of Peñuelas, which contrasted to a more fluctuating pattern in the other reservoir. In the first lake, the increasing diversity values from spring to summer reveals an augmentation of the community structure followed by a decrease on the organization towards winter. In this lake, species diversity was

related to equitability rather than species richness (Table 4 a). This seasonal change on the zooplankton diversity and accordingly with the zooplankton equitability, was significantly related to the combined effect of temperature and oxygen during the year cycle (Table 5 a, b). On the contrary a varying response of the zooplankton community structure was observed in Rungue. Here the species diversity was related to species richness and to equitability (Table 4 b).

The decrease on the number of species, and also lower diversity values have been suggested to be related to shorter periods of water retention in Spanish reservoirs (MARGALEF et al. 1976). Hence, despite the fact that this variable was not measured in this study, it is possible to infer it from the extreme water level reduction, particularly occurring in Rungue. Fig. 7 b, shows that after April 1984 in this reservoir (lowest water level), the number of species and their abundances decreased drastically even to the point to disappear completely (August 1984). Between these two months due to precipitations in the area, water levels increased slowly again, so that water drained into it from the tributary and from the pumping station of the side creek. This process demonstrates the underlying instability of the environment which as a result, shows the disappearance of the species and the disruption of any kind of organization within the zooplankton community. This situation is likely to be repeated every year, since the water of the reservoir is annually renewed. Therefore it is clear, that the observed community is an early successional stage, where only r -strategists are expected to colonize rapidly after a period of time. In contrast, Peñuelas reservoir which is also under water level changes, because of its use as drinking water supply, shows that the zooplankton community is not exposed to such a fluctuating environment and the organization of it, markedly follows the seasonal changes during the year.

Generally, the regression analyses and the PCA ordination carried out with data from both reservoirs, show that seasonal variability on the zooplankton species composition and their abundances is markedly associated to the variability on the water mineralization (estimated from the conductivity values), and the monthly differences of temperature and oxygen (Tables 6, 7 and 8). With respect to the environmental variables, these were found different between the two studied reservoirs, especially those related to water mineralization. So, the underlying regional differences of the two lakes might be plausible, when taking into account that the degree of water mineralization depends on rock and soil composition, and on rainfall (MARGALEF 1975, ESTRADA 1975).

Despite these differences, the results of the principal component analyses, based on environmental variables (Table 9), coincide remarkably with published results from reservoirs within a Mediterranean type of climate (ARMENGOL 1984, ARMENGOL et al. 1990). Although in this study with Chilean re-

servoirs, less variables were measured, those more correlated with the first and second principal components were the same as those of studied Spanish Mediterranean reservoirs: water conductivity and the combination of temperature and oxygen. This finding may reflect that a degree of similarity exists with respect to the environmental factors in reservoirs situated in similar climatic areas as for example in the semi-arid zone.

During the period of study in Peñuelas, the seasonal segregation of zooplankton species was clear, and the arrangement of species in the principal component space (Fig. 10), is similar to the species replacement pattern found with numerically important taxa throughout the year (Fig. 5). However, in the PC space, it is also possible to observe some species occupying an intermediate position among seasonal groups. The temporal segregation in this lake, may be due to the fact that most physico-chemical variables varied seasonally (especially temperature and oxygen), rather than throughout the water column.

In Rungue the majority of zooplankton species are also arranged in groups within the PC space, mainly in two assemblages, one of the species occurring in spring—summer (before the reduction of water levels), and the other in summer—autumn during the low water level (Fig. 10). The lack of taxa groups during the winter season is clear, and as it was explained before, during that time the refilling of the reservoir took place.

Seasonal segregation patterns for zooplankton using an ordination procedure in reservoirs have been evidenced by TOJA (1980), ARMENGOL (1984), and lately by LEPS et al. (1990). However, the latter authors stressed the fact that with multivariate analyses the dynamics between zooplankton and phytoplankton cannot be discovered. Here, in these analyses the complex interaction of zooplankton species to food resources has not been included, so that some results may be interpreted cautiously due to the possibility that the real biological effector is an unmeasured variable involving for example qualitative or quantitative nutritional conditions. On the other hand, another possible interpretation of PC analyses, is to take into account that distances between zooplankton filter-feeding species in the space might be a measure of the difference between their available niche in the system (MIRACLE 1974). In this way, it would seem possible to explain the distances further apart of some congeneric rotifer species (*Keratella*, *Conochilus*) in Peñuelas reservoir (Fig. 10), or those various overlapping rotifers species particularly during two months of the year in Rungue (Fig. 11). Certainly the assumption needs further investigation in the future in these lakes, as well as to observe whether the temporal patterns of zooplanktonic species persist or differ within successive years, as it has been already studied in other reservoirs (LEPS et al. 1990).

In conclusion, the zooplankton community in lake Peñuelas reveals a greater degree of complexity when compared to that of Rungue reservoir. Similarly, in Rungue the species composition reveals that most of the successful

species are rotifers with sizes ranging from 80 μm to 150 μm , whose reported food preferences is mostly detritus-bacteria. In Peñuelas, successful species are a combination of cladocerans, copepods and rotifers, which includes a variety of feeding habits (large and small herbivores among the crustaceans and detritus feeders among other types within the rotifers). This demonstrates that in Rungue there is a limited number of trophic levels and there are loosely interactions among species in the food web.

Because of the repeated pattern of emptying the reservoir every summer, the community observed is either a reflection of an early successional stage of the development of zooplankton or represents a disturbed system, which contrasts to a more mature community in Peñuelas. Obviously, the zooplankton composition in both man-made lakes depends on the historical factors, the climatology, geological characteristics of the basin, as well as the fluctuation of water levels and the inflow of allochthonous organic matter. Easily-erodible soil without vegetation cover is a general characteristic of Rungue together with drastic fluctuations of water levels. Thus, it contrasts to a reservoir like Peñuelas where the drainage basin presents a more dense vegetation cover (although pine monoculture in some areas), and where the water levels fluctuate much less.

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