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Rotifer communities from some Araucanian lakes of southern Chile

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Abstract

During the last decade much information has been produced about the zooplankton communities in southern Chile; however, most of this is related to the crustacean assemblages. The present communication examines the spatial and temporal distribution of rotifer assemblages and their relation to the environmental variables during one-year period in four Araucanian lakes. A total of 19 species was found in these oligotrophic lakes. *Keratella cochlearis, Synchaeta stylata, Trichocerca porcellus, Conochilus unicornis* and *Collotheca pelagica* were widespread, and seven species exhibited a more restricted distribution among the lakes. Species richness varied from 6 to 12; similarly, one or two dominant species usually accounted for more than 80% of the total annual abundance. Similar dominant species occurred in two lakes, but their maximum peaks of abundance differed in time; in the remaining lakes the most important species were different. Calculated rotifer diversity showed a fluctuating pattern, with low values during the year in three lakes, and high ones in Lake Llanquihue. Species diversity was significantly related to species richness in all lakes. Discriminant analysis based on the occurrence and abundances of species throughout the year revealed that the rotifer assemblage in Lake Llanquihue was different from that in the rest of the Araucanian lakes. Furthermore, the same analysis using environmental variables showed that this lake is clearly discriminated from the others on the basis of the ionic composition of the water (*i.e.* Cl^-, Na^+, Mg^{2+}). Rotifer abundances in these lakes were significantly influenced by a number of abiotic variables, including those related to water ionic composition. These relationships may imply that the small differences in chemical characteristics of these lakes influence the structure of the rotifer community.

Introduction

Community structure is generally understood as the definition of species composition, the temporal and spatial distribution of species abundances, and consequently the underlying interactions of the species with their resources and also among themselves. Thus, the identification of structuring factors for one community may lead to high predictability about communities having similar phyletic components and existing in similar environments (Seifert, 1984).

During the last decades considerable information on the effect of abiotic parameters on rotifer species has been derived from both experimental and field studies (Pejler, 1965; Pourriot, 1965; Hoffmann, 1977; Radwan, 1980; Berzins & Pejler, 1989a, b and c). The majority of field studies have involved a wide variety of lake types (Radwan, 1978; Gannon & Stemberger, 1978;

Mäemets, 1983; Berzins & Pejler, 1989b). Zooplankton communities from similar types of lakes should also be considered, because communities from distinct environments or with different species compositions may be structured by different factors.

The Araucanian lakes in southern Chile have been the subject of a continuous general limnological characterization for several years (Campos, 1984; Campos *et al.*, 1983, 1988, 1989, 1990). Further analyses of zooplankton communities in the same geographical area have been mostly related to the crustacean components (Zuñiga & Dominguez, 1978; Dominguez & Zuñiga, 1979; Zuñiga, 1988). Information about rotifers still remains at the level of general distributional aspects (Schmid-Araya, 1991). The present communication examines the structure of rotifer assemblages in relation to environmental variables during a one-year period in four Araucanian lakes.

Material and methods

The studied lakes (Fig. 1) are situated within the major district of Araucanian lakes in south Chile, which ranges between latitudes 39° S and 42° S next to the Andes mountains (Thomasson, 1963). Some basic morphometric characteristics, together with mean annual values of temperature

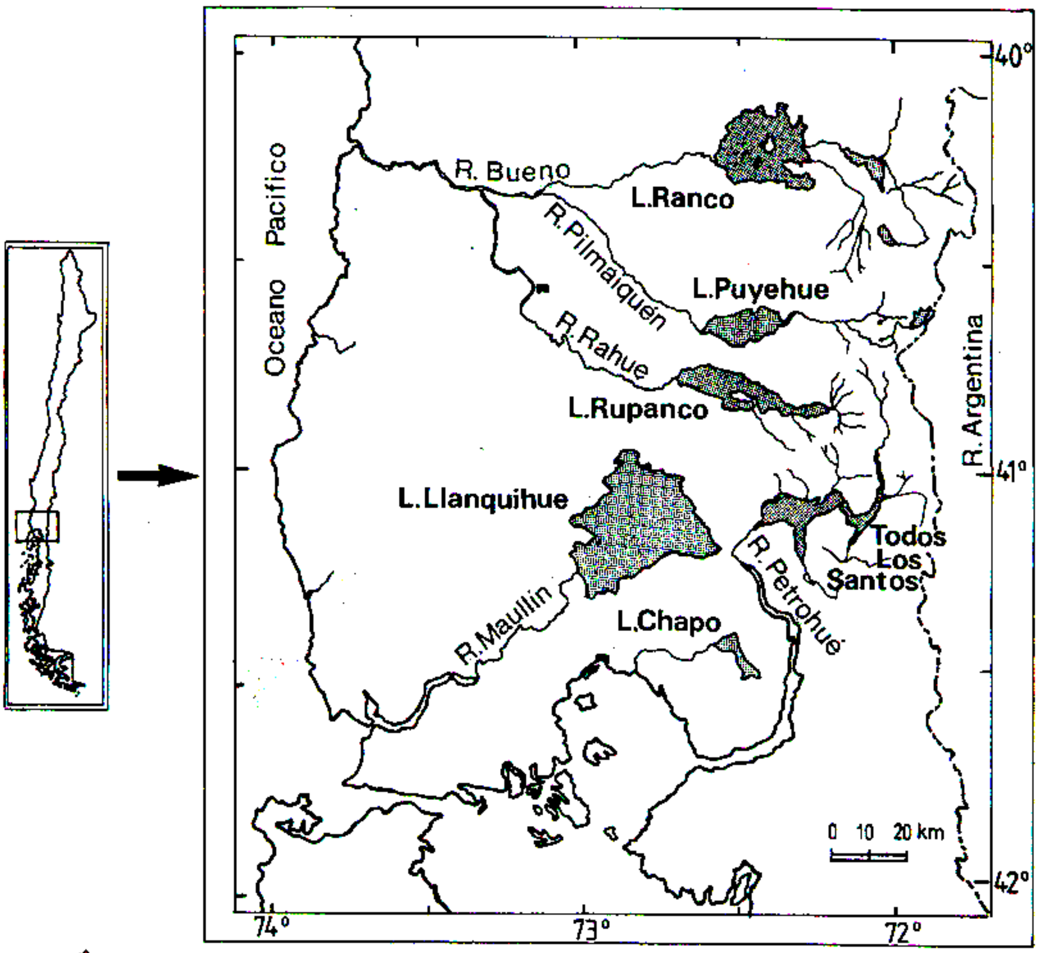


Fig. 1. Map of the study area, showing the location of the investigated lakes within the district of Araucanian lakes. The inset shows the geographical situation in Chile.

and chemical parameters, are summarized in Table 1. Generally, these lakes have a glacial origin, exceed 100 m in depth, and are generally monomictic. The results of Campos (1984) demonstrate a typical pattern of oligotrophy on the basis of low concentrations of nutrients and phytoplankton characteristics.

The general sampling design was carried out monthly between December 1980 and November 1981 in Puyehue and Rupanco, and from May 1982 to April 1983 in Llanquihue and Todos los Santos. In each lake sampling took place at one station, where water depth was greater than 100 m. Stratified zooplankton samples were collected by vertical hauls from 100 to 50 m, 50 to 25 m, 25 to 10 m, 10 to 5 m, and 5 to 0 m, using an Apstein type net of 80 μm mesh size. These samples were preserved in the field with 5% formalin and later analysed under a dissecting microscope (Wild M5A) at 50 magnifications. Counts were carried out using subsamples (with a variation coefficient less than 10%) or total samples, depending on the zooplankton densities. Phytoplankton samples, oxygen and temperature measurements, Secchi disc readings and water chemistry samples were concurrently taken

Table 1. Limnological characteristics of the Araucanian lakes: (a) Summary of most important morphometric parameters, and (b) mean annual values of physicochemical variables, with their standard deviations in parentheses.

	Puyehue		Rupanco		Llanquihue		T. Santos	
a. Morphometic parameters								
Latitude	40°40'S–72°26'W		40°50'S–72°47'W		41°08'S–72°47'W		41°08'S–72°12'W	
Altitude	184 m		172 m		51 m		189 m	
Maximul length (l_m)	23.5 km		40 km		42.3 km		35.3 km	
Maximum width (b_m)	11.3 km		10.5 km		39.0 km		9.5 km	
Surface area (A_0)	165.4 km^2		236 km^2		870.5 km^2		178.5 km^2	
Maximum depth (z_m)	123 m		140 m		317 m		337 m	
Mean depth (z)	–		94 m		182 m		191 m	
Depth of cryptodepression (z_c)	0 m		0 m		266 m		148 m	
Volume (V)	12.6 km^3		23 km^3		158.6 km^3		34.4 km^3	
Shallow zones (up to 30 m deep)	15%		–		7.5%		7.9%	
b. Water temperature and chemical quality								
	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
Temperature °C	11.82	(3.00)	12.44	(2.75)	12.91	(2.54)	10.61	(2.75)
Oxygen mg l^{-1}	10.50	(0.84)	10.33	(0.91)	10.76	(0.58)	9.93	(1.06)
pH	7.39	(0.16)	7.30	(0.18)	7.29	(0.35)	6.97	(0.36)
CO_2 mg l^{-1}	2.50	(0.76)	2.29	(0.95)	1.36	(0.33)	1.79	(0.54)
Conductivity μS (25 °C)	79.76	(25.88)	62.98	(37.46)	106.44	(23.93)	43.84	(3.94)
Total hardness (Ca + Mg) mval l^{-1}	0.27	(0.04)	0.20	(0.03)	0.32	(0.08)	0.14	(0.03)
Alkalinity mval l^{-1}	0.61	(0.05)	0.44	(0.04)	0.60	(0.04)	0.43	(0.05)
Ca^{2+} mg l^{-1}	1.44	(0.56)	1.38	(0.58)	2.62	(1.19)	1.23	(0.55)
Mg^{2+} mg l^{-1}	2.46	(0.30)	1.62	(0.22)	2.34	(0.33)	1.00	(0.13)
Na^+ mg l^{-1}	4.55	(0.59)	2.86	(0.35)	7.65	(0.81)	1.78	(0.30)
k^+ mg l^{-1}	1.07	(0.25)	0.67	(0.17)	0.83	(0.20)	0.44	(0.18)
Cl^- mg l^{-1}	3.08	(0.47)	2.44	(0.30)	6.56	(0.59)	1.28	(0.23)
SO_2^{2-} mg l^{-1}	3.56	(1.10)	3.46	(1.12)	1.98	(0.45)	2.12	(0.72)
SiO_2 mg l^{-1}	15.36	(3.48)	12.50	(2.69)	2.32	(0.71)	12.38	(0.71)
NO_3^-–N mg l^{-1}	0.24	(0.18)	0.12	(0.10)	0.06	(0.04)	0.06	(0.06)
Total PO_4 μg l^{-1}	4.67	(2.90)	3.72	(3.20)	3.33	(2.16)	2.90	(1.05)
Organic seston mg l^{-1}	1.52	(0.92)	1.50	(0.74)	2.25	(1.74)	2.02	(1.53)

on each sampling date. The results of these analyses are published elsewhere (Campos *et al.*, 1988; 1989, 1990).

Community indices of diversity (Shannon-Wiener) and evenness were calculated accordingly to Pielou (1977) and Lloyd & Ghelardi (1964), respectively. Similarity among months was estimated using the index of overlap of Horn (1966). Data on species abundances and chemical parameters, previously transformed, were treated using the Statistical Package SPSS^x (Nie *et al.*, 1975) for Pearson's correlation, stepwise multiple regression and discriminant analyses. For the separation of lakes, two discriminant analyses (Tabachnick & Fider, 1983; Pielou, 1984) were performed with two groups of data collected during a one-year period. The first was done with 17 transformed physical and chemical parameters, partly summarized in Table 1, and the second, was made with the transformed abundances of all rotifer species occurring in the investigated lakes. Stepwise multiple regression was used to investigate the relationship between the density of a given rotifer species and the physicochemical variables. The program computed sequentially multiple linear regression equations by adding one variable to the regression equation at each step. The significance of the effect of each variable was judged by the significance of the t-value associated with each regression coefficient (Zar, 1984).

Results

Community structure and general species distribution

Nineteen rotifer species were found in these four Araucanian lakes (Table 2). Five species (26%): *Keratella cochlearis cochlearis* (Gosse), *Synchaeta stylata* Wierzejski, *Trichocerca porcellus porcellus* (Gosse), *Conochilus unicornis* (Rousselet) and *Collotheca pelagica* (Rousselet) were widely distributed in the area, whereas the rest (74%) showed a more restricted distribution. During the year there were only one or two dominant species, the most important being *Keratella cochlearis tecta* (Gosse) in Puyehue, *C. pelagica* in Rupanco lake and *S. stylata* and *C. unicornis* in Llanquihue and Todos los Santos.

In these lakes, succession throughout the year among predominating species appears to be distinct (Fig. 2). Thus, *C. unicornis* occurred during autumn in Puyehue but during the early and late summer months in Llanquihue and Todos los Santos, respectively. On the other hand, *C. pelagica* shows a generally constant pattern over the year in Rupanco, Llanquihue and Todos los Santos, with abundance peaks fluctuating from late summer to autumn months among these lakes (Fig. 2).

The depth distributions of total rotifer abundances are shown in Fig. 3. Maximum densities occurred in Puyehue at the end of summer between 10 to 5 m depth, and in Rupanco from summer to autumn from 10 to 0 m. However, in

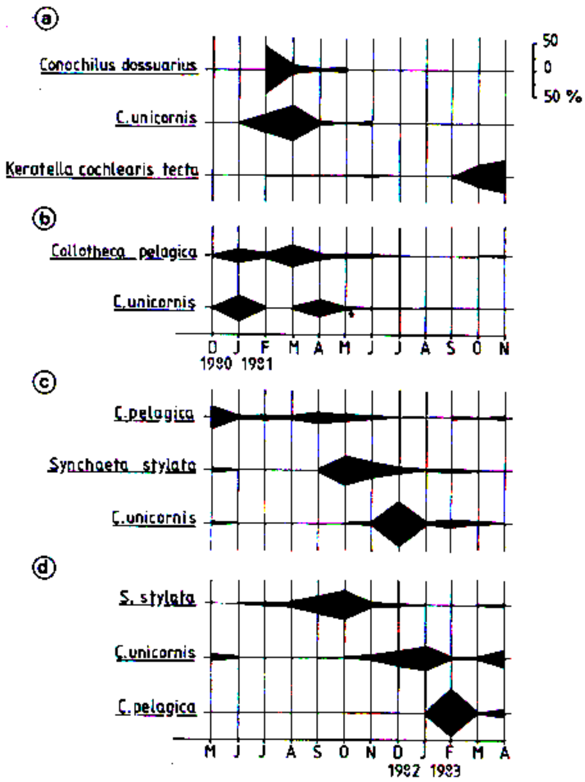


Fig. 2. Temporal changes of dominant rotifer species in each Araucanian lake, expressed as percentage. (a) Lake Puyehue; (b) Lake Rupanco; (c) Lake Todos los Santos, and (d) Lake Llanquihue.

Table 2. The species composition and mean annual abundances (ind m^{-3}), with their standard deviations, of the rotifer communities in four Araucanian lakes.

	Puyehue		Rupanco		Llanhuique		T. Santos	
	x̄	sd	x̄	sd	x̄	sd	x̄	sd
ROTIFERA								
Monogononta								
Fam. Brachionidae								
1. *Keratella chochlearis chochlearis* (Gosse)	–	–	3.03	11.50	21.58	55.62	14.63	60.75
2. *K. cochlearis* var. *tecta* f. *typica* Lauterborn	609.32	3342.8	–	–	–	–	–	–
3. *K. americana* Ahlstrom	–	–	0.03	0.26	–	–	–	–
Fam. Notommatidae								
4. *Cephalodella sp.*	–	–	–	–	10.85	36.32	–	–
Fam. Trichocercidae								
5. *Trichocerca (Diurella) porcellus porcellus* (Gosse)	–	–	0.40	3.10	152.12	465.99	25.60	98.70
6. *Trichocerca similis similis* (Wierzejski)	–	–	0.13	1.03	0.40	3.10	–	–
7. *Trichocerca sp.*	0.40	3.10	–	–	–	–	–	–
Fam. Gastropodidae								
8. *Ascomorpha ovalis* (Bergendal)	–	–	–	–	4.88	22.59	–	–
9. *Ascomorpha sp.*	–	–	–	–	–	–	0.13	1.03
Fam. Synchaetidae								
10. *Synchaeta oblonga* Ehrb.	–	–	–	–	17.58	75.50	–	–
11. *S. stylata* Wierzejski	–		1.33	5.34	803.41	1725.2	731.17	1858.8
12. *Polyarthra dolichoptera dolichoptera* Idelson	4.40	14.60	0.83	3.77	–	–	6.63	20.48
13. *P. vulgaris vulgaris* Carlin	–	–	–	–	11.07	30.07	–	–
Fam. Testudinellidae								
14. *Pompholix sulcata* (Hudson)	–	–	–	–	2.08	8.98	0.17	1.06
Fam. Conochilidae								
15. *Conochilus dossuarius* var. *coenobasis* (Skorikov)	63.70	413.03	–	–	–	–	–	–
16. *C. unicornis* (Rousselet)	813.45	3701.2	108.95	325.16	2131.12	9999.9	672.13	1687.2
Fam. Hexarthridae								
17. *Hexarthra fennica* Levander	–	–	–	–	141.30	415.59	–	–
Fam. Collothecidae								
18. *Collotheca pelagica pelagica* (Rousselet)	0.08	0.65	959.70	2541.6	112.97	177.7	68.62	342.98
Digononta								
19. *Bdelloidea gen. sp.*	–	–	1.25	6.41	–	–	0.17	0.17

the latter lake the rotifers moved deeper down to 25 m in autumn 1981 (April–May). A tendency of much higher rotifer abundances can be seen in the two other lakes, Llanquihue and Todos los Santos; maximum densities occurred from spring to summer and, in contrast to the rest of the lakes, rotifers in Llanquihue were distributed from 50 to 0 m (Fig. 3).

With respect to the species richness, these lakes showed a low number of rotifer species throughout the year; the total number in a year ranged from 6 to 12, depending on the lake (Table 2). This fact is reflected in the species diversity calculated per month throughout the water column (Fig. 4). In three lakes, Puyehue, Rupanco and Todos los Santos, the diversity values were low and fluctuated over the year; moreover, in these lakes diversity values lower than 0.150 bits ind^{-1}

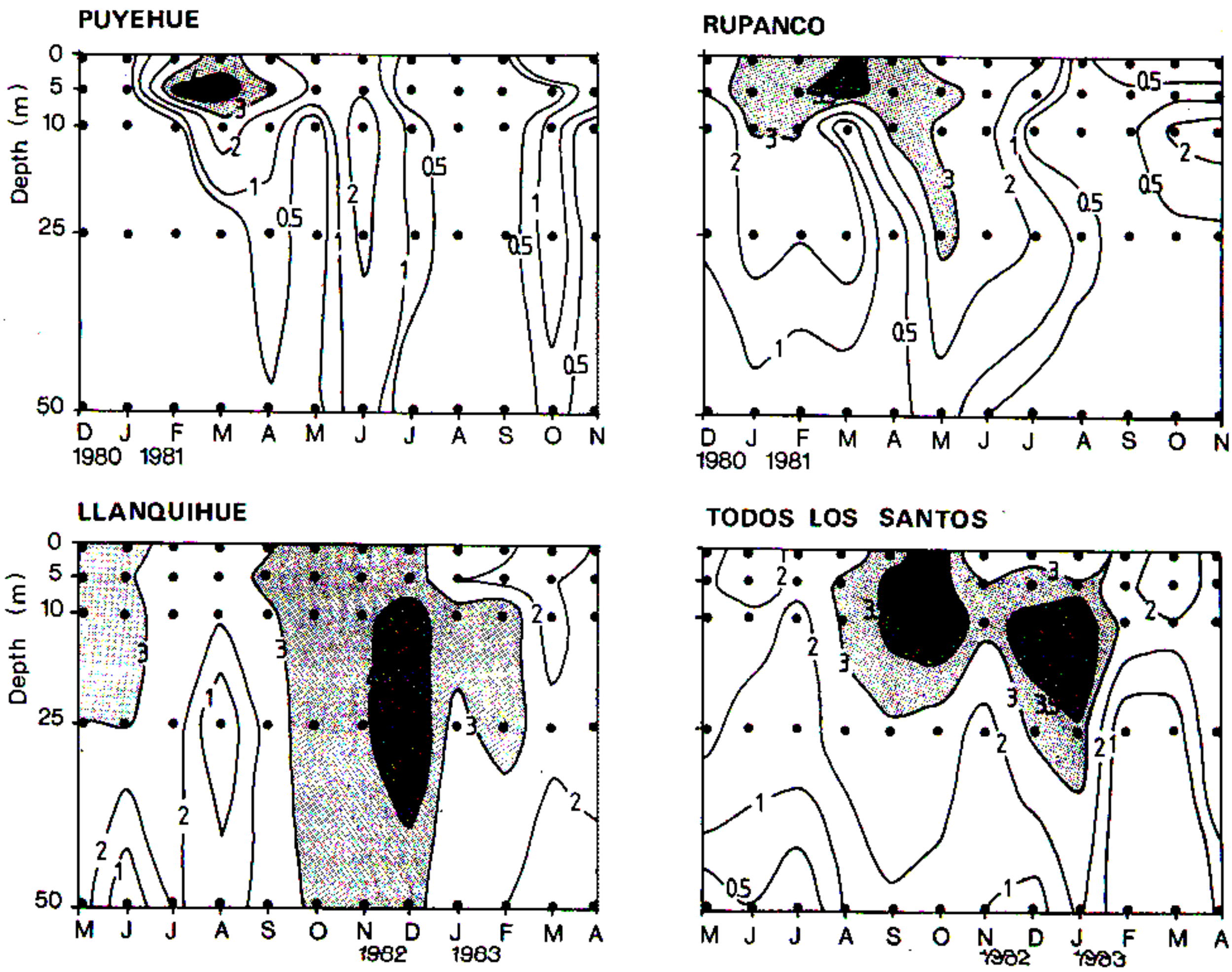


Fig. 3. Monthly depth distribution of total rotifer abundances (ind m^{-3}), expressed as $\log_{10}(x + 1)$, in four lakes.

were a consequence of the dominance of one species. In contrast, lake Llanquihue exhibited much higher diversity values (Fig. 4b). The general trend in all lakes was an increase towards autumn and winter months (April to August), although there were exceptions, with another increase in spring and summer in Rupanco and Todos los Santos. When considering data from all lakes together and from each depth layer, diversity was significantly related to species richness and evenness (Fig. 5a, b). Although there was a low rotifer diversity in these lakes, the few co-occurring species had similar abundances.

Because the above analyses revealed the presence of species groups with a seasonal pattern, it was of interest to determine whether this temporal pattern was random or corresponded to a phenological model. For this purpose the overlap index of Horn R_o (1966) was used for monthly data in each lake.

Generally, the results show two defined periods within a year in most of the lakes (Fig. 6). In the first lake, Puyehue, the rotifer community was very homogeneous between one winter month and the spring, where mainly *K. cochlearis tecta* and *P. dolichoptera* predominated. In the same lake the second period included summer to autumn months, when those species were replaced by *C. unicornis* and *C. dossuarius*. In this lake, during four different months of the year, the rotifer community was completely absent. In comparison, Rupanco lake showed a more homogeneous ro-

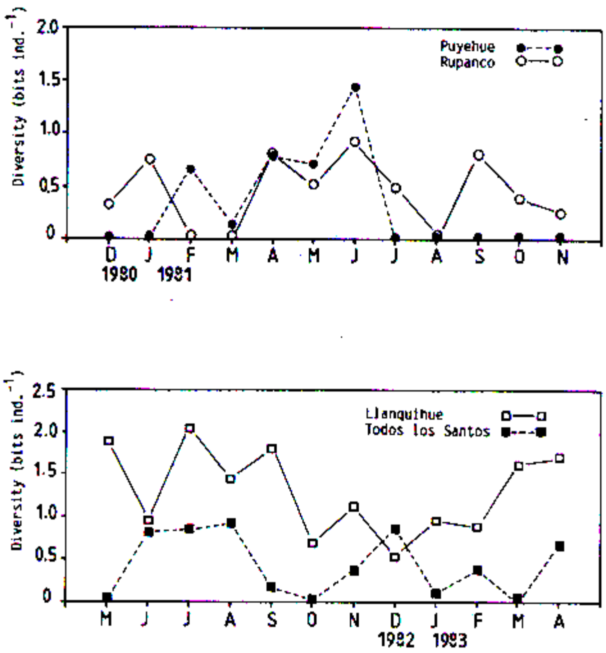


Fig. 4. Rotifer species diversity (H′) per month, estimated from the water column in four Araucanian lakes. Full circles: Puyehue; open circles: Rupanco; full squares: T. Santos; open squares: Llanquihue

tifer assemblage throughout the year; a separate group constituted by August–September 1981 was due to a low rotifer density and the exclusive presence of *K. cochlearis cochlearis* and *T. porcellus*. In Llanquihue as well as in Todos los Santos, the rotifer community showed a more heterogeneous pattern throughout the year, but it is possible to visualize two main periods, which differ between the lakes – spring-summer and autumn-winter in Llanquihue, and winter-spring and summer-autumn in Todos los Santos.

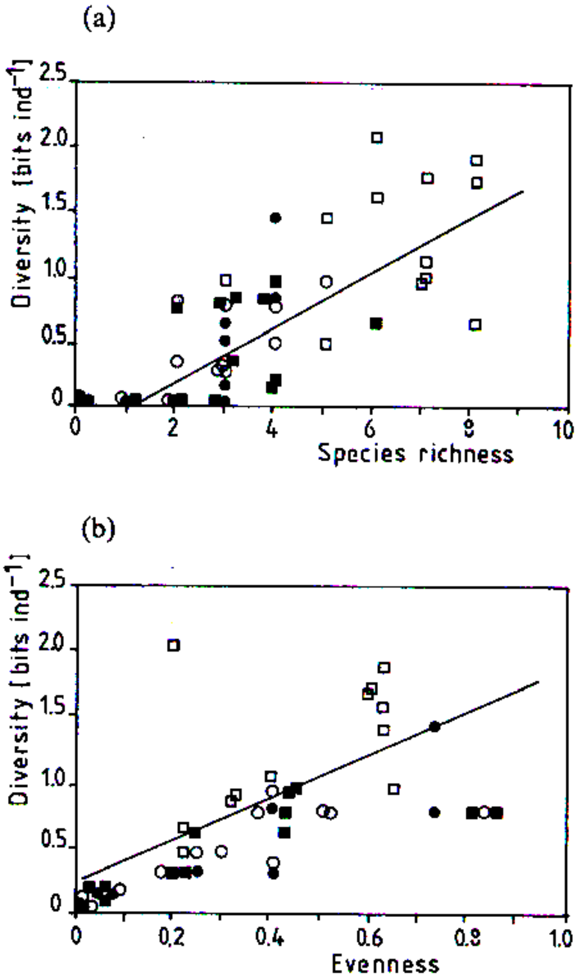


Fig. 5. The relationship between rotifer species diversity and its components: a) species richness and b) evenness. (Symbols represent data from each lake, as in Fig. 4).
Regression equation for a: $Y = -0.089 + 0.199\,X$; $r^2 = 0.582$, $df = 1{,}46$, $F = 64.114$, $P < 0.0001$).
Regression equation for b: $Y = 0.105 + 1.724\,X$; $r^2 = 0.590$, $df = 1{,}46$, $F = 65.796$, $P < 0.0001$).

Discriminant analyses and the effect of environmental variables

The results obtained with the first discriminant analysis using the 17 environmental variables in all lakes are shown in Table 3 and illustrated in Fig. 7a. Two discriminant functions for this set of data accounted for more than 85% of the between-group variability. The first discriminant function maximally separates Llanquihue from Todos los Santos, with Puyehue and Rupanco falling between these two groups (Fig. 7a). The matrix of correlations between variables and the discriminant function suggest that the main variables distinguishing these separated groups are chloride (Cl^-) and sodium (Na^+) concentrations (Table 3). Generally, lake Llanquihue exhibits higher annual mean values with respect to these two environmental parameters (Table 1). Thus, because the analysis included a complete year, it also indicates the tendency of more saline water throughout the year. Although discriminant function II accounted for only 9.19% of the total vari-

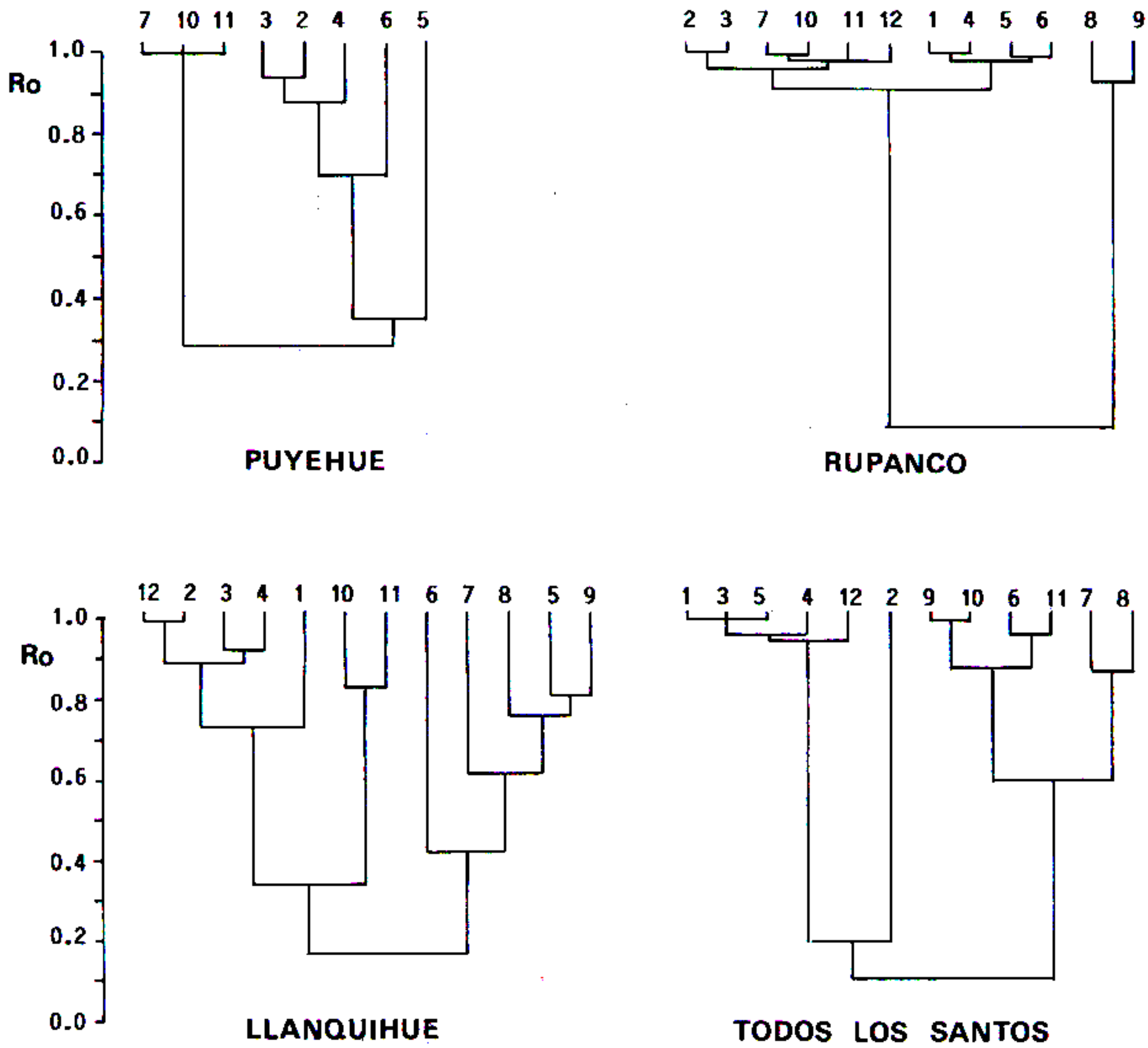


Fig. 6. Temporal similarity of the rotifer communities in each of four lakes, based on the overlap index of Horn (R_o). The numbers represent months of the year.

ability, it was well correlated with magnesium (Mg^+) and silica (SiO_2^-) concentrations. Annual mean values of the first variable were more similar in Todos los Santos and Rupanco than in Puyehue, but these three lakes showed higher annual means of silica than Llanquihue (Table 1).

The second analysis, based on the abundances of the total number of rotifers, produced three discriminant functions which accounted for more than 95% of the data variability (Table 4). Two functions were used to illustrate the lake separation (Fig. 7b). The first function clearly distinguished lake Llanquihue from the rest of the lakes, and correlations higher than 0.45 were shown by the species *Polyarthra vulgaris* and *Hexarthra fennica* (Table 4). These two species occurred exclusively in Llanquihue; their distribution may reflect a preference for more saline waters. Only one species, *S. stylata*, had a high correlation value in the second discriminant function, which slightly separated Puyehue from Rupanco and Todos los Santos. In the first lake, this species did not ap-

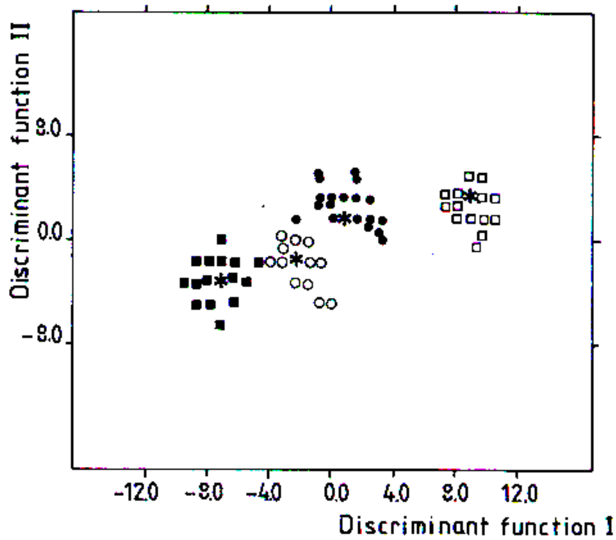
Table 3. The results of the first discriminant analysis showing the correlations between 17 physicochemical variables and two discriminant functions, as their relative contribution to the separation of Araucanian lakes. Underlined coefficients are those greater than 0.45.

Percentage of variance	Discriminant functions	
	I	II
	78.01	9.19
Parameters:		
Temperature	−0.016	−0.131
Oxygen	−0.072	0.024
pH	−0.037	0.038
CO_2	0.009	0.037
Conductivity	−0.045	0.112
Total hardness	0.193	0.373
Alkalinity	0.262	0.431
Ca^{2+}	0.066	0.095
Mg^{2+}	0.320	<u>0.588</u>
Na^{+}	<u>0.634</u>	0.052
k^{+}	0.181	−0.062
Cl^{-}	<u>0.720</u>	−0.262
SO_4^{2-}	−0.313	0.351
SiO_2^{-}	−0.264	<u>0.679</u>
NO_{3-}–N	0.024	−0.091
Total PO_4	−0.318	0.058
Organic Seston	0.229	−0.021

pear; in the other lakes (including Llanquihue) its mean abundances fluctuated from lake to lake (Table 2). On the third discriminant function (15.78% of the variance), the species *K. cochlearis tecta* and *C. pelagica* had higher correlations (Table 4); the first species only inhabited lake Puyehue, whereas the second species fluctuated in mean abundance from one lake to another (Table 2).

The relationship between the abundances of rotifer species occurring in all lakes and the physicochemical variables was investigated using a stepwise multiple regression analysis. The results show that for most of the rotifer species there is a combined effect of several environmental parameters on the densities of a given species (Table 5). Only one species, *Polyarthra dolichoptera*, was significantly related to one single variable such as the silica concentration; this kind of relationship probably was an indirect one, because

(a)



(b)

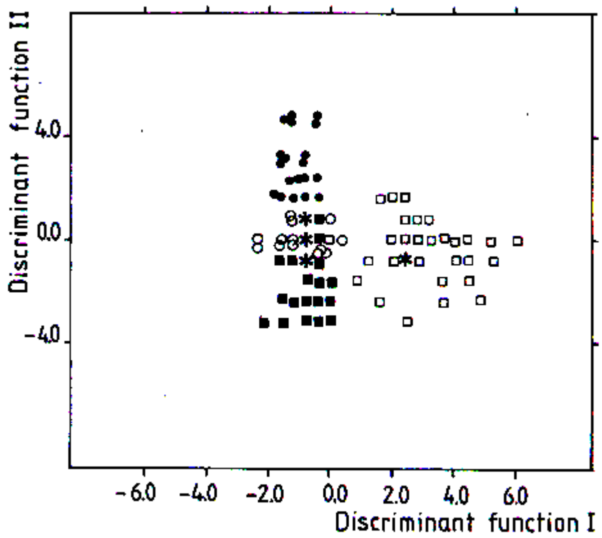


Fig. 7. Lake ordination based on the discriminant analyses derived from: (a) 17 physicochemical variables, and (b) the abundances of all rotifer species. The symbols are as in Fig. 4.

in some of the Araucanian lakes, silica follows the maxima and minima of phytoplankton abundances mainly constituted by diatoms (Campos *et al.*, 1988). On the other hand, species inhabiting four lakes, like *C. unicornis* and *C. pelagica*, were found significantly related to two physico-

Table 4. The results of the second discriminant analysis showing the correlations between the abundances of rotifer species with three discriminant functions, as their relative contribution to the separation of Araucanian lakes. Underlined coefficients are those greater than 0.45.

	Discriminant functions		
	I	II	III
Percentage of variance	62.16	22.06	15.78
Species:			
Keratella cohclearis cochlearis	0.351	−0.047	−0.100
K. cochlearis tecta	−0.163	0.167	<u>0.556</u>
K. americana	−0.027	0.077	−0.131
Cephalodella sp.	0.236	0.055	0.057
Trichocerca porcellus	0.331	−0.152	0.020
T. similis	0.054	0.059	−0.057
Trichocerca sp.	−0.041	0.042	0.139
Ascomorpha ovalis	0.200	0.046	0.048
Ascomorpha sp.	0.008	−0.127	0.009
Synchaeta oblonga	0.231	0.054	0.056
S. stylata	0.350	−<u>0.650</u>	−0.094
Polyarthra dolichoptera	−0.135	−0.210	0.010
P. vulgaris	<u>0.468</u>	0.108	0.113
Pompholix sulcata	0.142	−0.019	0.016
Conochilus dossuarius	−0.087	0.090	0.298
C. unicornis	0.173	−0.169	−0.003
Hexarthra fennica	<u>0.490</u>	0.114	0.120
Collotheca pelagica	0.231	0.343	−<u>0.560</u>
Bdelloidea gen. sp.	0.012	0.083	−0.089

chemical parameters. For *C. unicornis*, calcium and pH seemed to have a positive effect on abundances, whereas for *C. pelagica*, temperature had a positive effect but silica concentration a negative one (Table 5).

A more complex interaction with the environmental variables was found between those species appearing in three lakes. Silica was the most common parameter included in the relationships, and in all species (*K. c. cochlearis*, *T. p. porcellus* and *S. stylata*) the effect was negative. This may indicate independence from algal development. Organic seston was also included in the analysis as a variable which could affect detritivorous rotifers, but this variable was not significant. Parameters related to ionic composition (*i.e.* Ca^{2+}, Mg^{2+}, Cl^{-}) were also found to have an effect on the rotifer densities, but the relationship was difficult to generalize due to the variability of the effect from one species to another.

On the other hand, partial correlations between total abundances and number of rotifer species with the environmental variables showed a high amount of interrelatedness for parameters associated with ionic composition (Table 6). At the same time, the effect of the crustaceans, represented by total abundances and species numbers of Copepoda and Cladocera, was observed only for the latter group (Table 6). An increase in cladoceran abundance and also of species seemed to coincide with a decline in rotifer densities and species.

Discussion

Some of the Araucanian lakes can be separated using both physicochemical factors and the rotifer community. Although the lakes are oligotrophic and occur in the same geographic area, it is clear that Llanquihue shows a higher content

Table 5. The results of the stepwise multiple regression for the prediction of abundances of 6 rotifer species occurring in most Araucanian lakes. Only variables that accounted for significant variability were retained. Coeff. is the regression coefficient associated with each independent variable; the *t*-value and associated probability (*P*) indicate of each variable in the prediction.

Variable	Coeff.	*t*-value	*P*
1. *K. c. cochlearis* (*F*: 19.780; *df*: 4,235; $P<0.0001$)			
Calcium	0.654	4.083	0.0001
pH	3.084	5.113	<0.0001
Silica	−0.169	−4.645	<0.0001
Total hardness	−2.352	−3.162	0.0018
Intercept	−7.124	−4.671	<0.0001
2. *T. p. porcellus* (*F*: 15.550; *df*: 4,235; $P<0.0001$)			
Chloride	−0.730	−3.960	0.0001
Conductivity	0.088	2.634	0.0090
Silica	−0.415	−6.417	<0.0001
Total hardness	1.944	2.186	0.0298
Intercept	1.075	2.611	0.0096
3. *S. stylata* (*F*: 23.527; *df*: 4,236; $P<0.0001$)			
Silica	−0.399	−5.181	0.0028
Magnesium	−1.380	−4.328	0.0001
NO_3–N	−1.439	−2.461	0.0146
Intercept	4.418	8.696	<0.0001
4. *P. dolichoptera* (*F*: 13.788; *df*: 1,238; *P*0.0003)			
Silica	0.094	3.713	0.0003
Intercept	−0.167	−1.993	0.0474
5. *C. unicornis* (*F*: 12.161; *df*: 2,237; $P<0.0001$)			
pH	4.250	3.089	0.0022
Calcium	0.777	3.229	0.0014
Intercept	−11.637	−3.169	0.0017
6. *C. pelagica* (*F*: 21.926; *df*: 2,237; $P<0.0001$)			
Temperature	0.672	4.444	<0.0001
Silica	−0.272	−4.043	0.0001
Intercept	−0.771	−1.295	0.1966

of chloride and sodium (annual mean: 6.56 ± 0.59 mg l^{-1} and 7.65 ± 0.81 mg l^{-1}, respectively, Table 1). Lakes segregated by differences in ionic content also have dissimilar rotifer faunas. The presence of *H. fennica* and *P. vulgaris* in Llanquihue confirms the different chloride and sodium concentrations; these two species have been reported to occur in weakly saline waters (Ruttner-Kolisko, 1971).

Table 6. Partial correlations between the total abundance of rotifers and the number of species with each of 17 physico-chemical variables and two other biotic groups of the zooplankton in the Araucanian lakes; (n: 240; * $P<0.01$, ** $P<0.01$.)

	Rotifer abundance	Rotifer number species
Temperature	−0.009	0.094
Oxygen	−0.061	0.060
pH	0.127	0.148
CO_2	0.174*	−0.402**
Conductivity	0.024	0.296**
Total hardness (Ca + Mg)	−0.522**	0.287**
Alkalinity	−0.038	0.177*
Ca^{2+}	0.120	−0.384**
Mg^{2+}	−0.177**	0.110
Na^+	0.075	0.043
K^+	−0.267**	0.020
Cl^-	0.166*	0.494**
SO^{2-}	−0.333**	−0.398**
SiO_2	−0.343**	−0.315**
NO_3–N	−0.313**	−0.315**
Total PO_4	0.039	−0.068
Organic Seston	−0.027	0.043
Copepoda abundance	−0.146	−0.089
Cladocera abundance	−0.015	−0.235**
Copepoda number of species	−0.114	−0.047
Cladocera number of species	−0.228**	−0.168*

The complex interaction of the effect of environmental variables upon a number of rotifer species indicates that more than one factor affects of rotifer distribution in these lakes. Several studies have shown the influence of abiotic factors on rotifer occurrence and density fluctuations; the most common parameters have been temperature and oxygen (Hoffman, 1977; Herzig, 1987). Because temperature within this geographical area is not a factor which varies much from lake to lake throughout the year, its influence on *C. pelagica* emphasizes the seasonality of the species in these lakes. Berzins & Pejler (1989a) have shown that this species has a very wide range of temperature tolerance. In the Araucanian lakes, the species shows a clear summer peak in lakes characterized by lower mean annual temperatures (*i.e.* Todos los Santos) and a perennial pattern in lakes with higher annual mean temperatures (*i.e.* Rupanco, Llanquihue, Table 1).

Another main abiotic parameter having an effect on rotifer communities is the pH. In this study pH significantly influenced the abundances of *K. c. cochlearis* and *C. unicornis* in combination with other parameters. Despite the relatively low variability of pH observed in these lakes (lowest annual mean: 6.97, highest annual mean: 7.39, Table 1), the effect was positive and significant. *K. c. cochlearis* has been reported as occurring in non-acid lakes (Siegfried *et al.*, 1984; Mac Isaac *et al.*, 1987).

The abundance and number of species of rotifers were negatively correlated with silica concentrations. The inverse relationship with this parameter also occurs with rotifer species which seem to be independent of algal development and feed on detritus with its associated bacteria (*i.e.* *K. c. cochlearis*, *C. pelagica*, Pourriot, 1977). The same relationship has been observed for total rotifer abundance by Méthot & Pinel-Alloul (1987), who suggested the existence of two simultaneous events – first the reduction of silica due to increasing phytoplankton production and then the increase of rotifers because of the rise of bacterioplankton during the decomposition of organic matter.

The interactions between crustaceans and the rotifer communities suggest an influence from the cladocerans, if data from the four lakes are pooled (Table 6). In these lakes the crustacean communities have a low species richness, and the dominant species vary among lakes (Zuñiga, 1988). The most important copepod species are *Boeckella gracilipes* Daday, *Diaptomus diabolicus* Brehm and *Mesocyclops longisetus* (Thiebaud); most common cladocerans are *Eubosmina hagmanni* Stingelin, *Diaphanosoma chilense* Daday, *Ceriodaphnia dubia* (Richard), *Daphnia ambigua* Scourfield and *D. pulex* (De Geer). Invertebrate predator species as known in the Northern Hemisphere do not occur in the area, and fish predation is practically unknown. Three specific mechanisms explaining an inverse relationship between rotifers and cladocerans have been proposed (see Threlkeld & Choinski, 1987, and references therein). MacIsacc & Gilbert (1989) have further investigated the role of body size in the interactions between these two groups. In the studied Araucanian lakes, it seems that body size and abundance of cladocerans may affect the rotifer community, because a higher number of rotifer species and densities were found in Llanquihue and Todos los Santos. In Llanquihue, only the relatively small-sized cladoceran *E. hagmanni* occurs, while in Todos los Santos the same species co-occurs with low numbers of *D. pulex*. In the two other lakes, Puyehue and Rupanco, higher cladoceran abundances and large-sized daphnids coincide with low numbers of rotifer species. Interactions of crustaceans and rotifers, and those of rotifers and phytoplankton, deserve further examination in these lakes.

The rotifer fauna of these lakes is composed of species which have been classified as typically oligotrophic, like *Ascomorpha ovalis* and *C. unicornis* (Mäemets, 1983; Berzins & Pejler, 1989b). However, these species are intermingled with others which have been associated with meso-eutrophic waters, as for example *K. c. tecta*, *Pompholix sulcata* and *T. p. porcellus* (Mäemets, *op. cit*). These four Araucanian lakes represent only a part on the whole district for the distribution of rotifers, and the examination of the effect of physicochemical variables in this study is not exhaustive. Similar observations using other lakes in the area have also demonstrated a segregation of lakes on the basis of the crustacean community (Araya, 1983), even when the differences of physicochemical factors were less extreme than in the present study.

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