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Subtle relationships: freshwater fishes and water chemistry in southern South America *

Roberto C. Menni[1,2], Sergio E. Gómez[1,3] & Fernanda López Armengol[1,4]
[1] *Consejo Nacional de Investigaciones Científicas*
[2] *Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina*
[3] *Instituto de Limnología de La Plata*
[4] *Facultad de Medicina, Universidad Nacional de La Plata*

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Abstract

We investigated the relationships between water chemistry and the occurrence, distribution, physiology, and morphology of fish faunas. We examined 34 species (ca. 10% of the Argentinean freshwater fish fauna) from 120 localities (5 areas) situated between 26°15′ S (Trancas, Tucumán) and 38°30′ S (Sierra de la Ventana, Buenos Aires). Fourteen chemical features are described by: conductivity, total dissolved solids, temperature, pH, CO_3^{-2}, CO_3H^-, Cl^-, SO_4^{2-}, Ca^{2+}, K^+, Mg^{2+}, Na^+, Mg/Ca, Mg+Ca/Na+K. Three Basic Data Matrices considering the mean, maximum and minimum values of each variable for each fish species were used in a Cluster and Principal Component Analysis. Groups of species clustered in similar ways to particular water chemistries. Similarity was the common occurrence of species in a defined area and preference for a common range of the factors considered. Groups of species so defined showed patterns of distribution related to climate, environment, trophic state and hydrographic complexity. Each cluster included some eurytopic species which appeared together at extreme chemical and geographic characteristics. Twenty four species had ranges of tolerance for the 14 variables and evidence of a grouping according to these ranges. Eighteen species which occurred at maximum or minimum absolute values for more than one factor were ordered along an eurytopy – stenotopy axis. We support the statement that species with a larger tolerance range for most factors have a higher probability of being widely distributed. *Astyanax fasciatus* and *A. bimaculatus* tolerated the highest number of maximum and minimum values, followed by *Jenynsia l. lineata, A. eigenmanniorum* and *Trichomycterus corduvensis*. Groups of species based on chemical factors showed differences in the relative number of basic morphological types.

Introduction

Although many experimental studies have explored the response of fishes to environmental factors (Fry,1971; Braga, 1975; Dunson et al., 1977; Gómez, 1993; Kramer, 1987; Pickering, 1981; Wootton, 1991), fish behavior in relation to complex interactions among diverse variables in nature is difficult to describe. It is difficult to find strong correlations between chemical factors and fish distribution patterns, except under extreme conditions (Stevenson et al., 1974).

Some physical – chemical characteristics are relatively easy to obtain, and have been considered in the evaluation of aquatic environments and their faunas (e.g. Bonetto & Lancelle,1981 for the Paraná River; Geisler et al., 1975 for the Amazon; Ringuelet et al., 1967b for the Pampasic lagoons). As far as the influences on fishes is concerned, the importance of natural water chemical composition on fish occurrence and behavior have, in general terms, either been neglected or considered too difficult to evaluate (Hynes, 1970; Whitton, 1975; Menni et al., 1984). Though the general chemical composition of several basins is known, global values can not be related a priori to the presence

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or absence of fishes, given the habitat variability and the differences in spatial distribution of these organisms.

A synthesis of the predominant view can be seen in the following excerpts from Beadle (1974: 51, 52, 57): 'The apparently insignificant ecological effects of ionic differences within the freshwater range should not surprise us, because, in contrast to the sea, inland waters are chemically unstable and variable by nature, and could have been colonized only by organisms with ionic regulating mechanisms that can function under a wide range of chemical conditions ... It seems, therefore, that within the limits of composition of most inland freshwater, faunal and floral differences are rarely directly explicable in terms of mineral chemical differences ... In conclusion, it may be repeated that in tropical African freshwater (within the salinity range 0.02–5‰) there is so far no evidence of a direct ecological effect of a peculiar mineral composition'.

The opposite opinion has been briefly stated by Roberts (1972: 123). He says, in reference to the water conditions in the Rio Negro of Brazil that 'The characteristics of the basins and the water chemistry play profound roles in determining the distribution and abundance of animals in the Amazon basin'. More exact statements have been given for the association of *Corydoras macropterus* and *Mimagoniates lateralis* with black waters and that of *Corydoras barbatus* with clear waters (Weitzman et al., 1988). The limited distribution of a *Curimata* species in the Rio Negro in Brazil appears to be primarily a consequence of the preference of the species for acidic black waters (Vari, 1988).

We surveyed the relationship between the occurrence of fish species and a set of fourteen physical and chemical variables usually obtained as descriptors of the main features of water.

The combination of Cluster Analysis and Principal Component Analysis used in this paper provides new insights in the study of the shared occurrence of fishes, their geographical peculiarities and environmental characteristics. More importantly, the analysis shows that groups of species react in a similar way to combinations of properties of water, and provides a new framework for the experimental study of physiology and adaptation in freshwater fishes.

Materials and methods

Source of data

The fish composition and the physical and chemical variables from limnetic environments in five zones covering a wide area of the temperate region of Argentina (Figure 1) were used as basic data for the present paper, namely:

(a) Environments in the Sali River basin (Tucumán province). Presence data of 21 fish species and physical – chemical data from 10 localities were available from Miquelarena et al. (1990).
(b) Environments in the Salado River basin (Santiago del Estero province). Presence data of fish species and physical – chemical data from 3 localities were available from Casciotta et al. (1989).
(c) Environments in the Dulce River basin (Santiago del Estero province). Presence data of 3 species and physical – chemical data from 1 locality were available from Casciotta et al. (1989).
(d) Localities in the highland region of northwestern Córdoba. Presence data of 9 fish species and physical – chemical data from 29 localities were available from Menni et al. (1984).
(e) Tributary creeks of the Uruguay River. Presence data of 19 fish species and physical – chemical data from 7 localities were available from López et al. (1984).
(f) Creeks in Sierra de la Ventana highlands (Buenos Aires province). Presence data of 5 fish species and physical – chemical data from 4 localities were available from Menni et al. (1988).

All data were gathered by the senior author during projects under his direction. Complete faunistic lists, environmental descriptions, and physical and chemical synopsis of the studied areas can be obtained from the abovementioned papers. Water samples collected for examination of limnological variables were obtained immediately prior to fishing operations. The water analyses were made at the Chemistry Laboratory of the Instituto de Limnología de La Plata using APHA (1985) techniques. Values of the following variables were obtained (in parenthesis abbreviations, and units used in the text and tabels): Conductivity (COND, μS cm^{-1}), Total dissolved Solids (TDS, mg l^{-1}), temperature (t, °C), pH, CO_3^{-2}, $CO_3^{-}H$, Cl^{-}, SO_4^{+2}, Ca^{+2}, K^{+}, Mg^{+2}, Na^{+} (ions in mg l^{-1}) and the ratios Mg/Ca and Mg+Ca/Na+K.

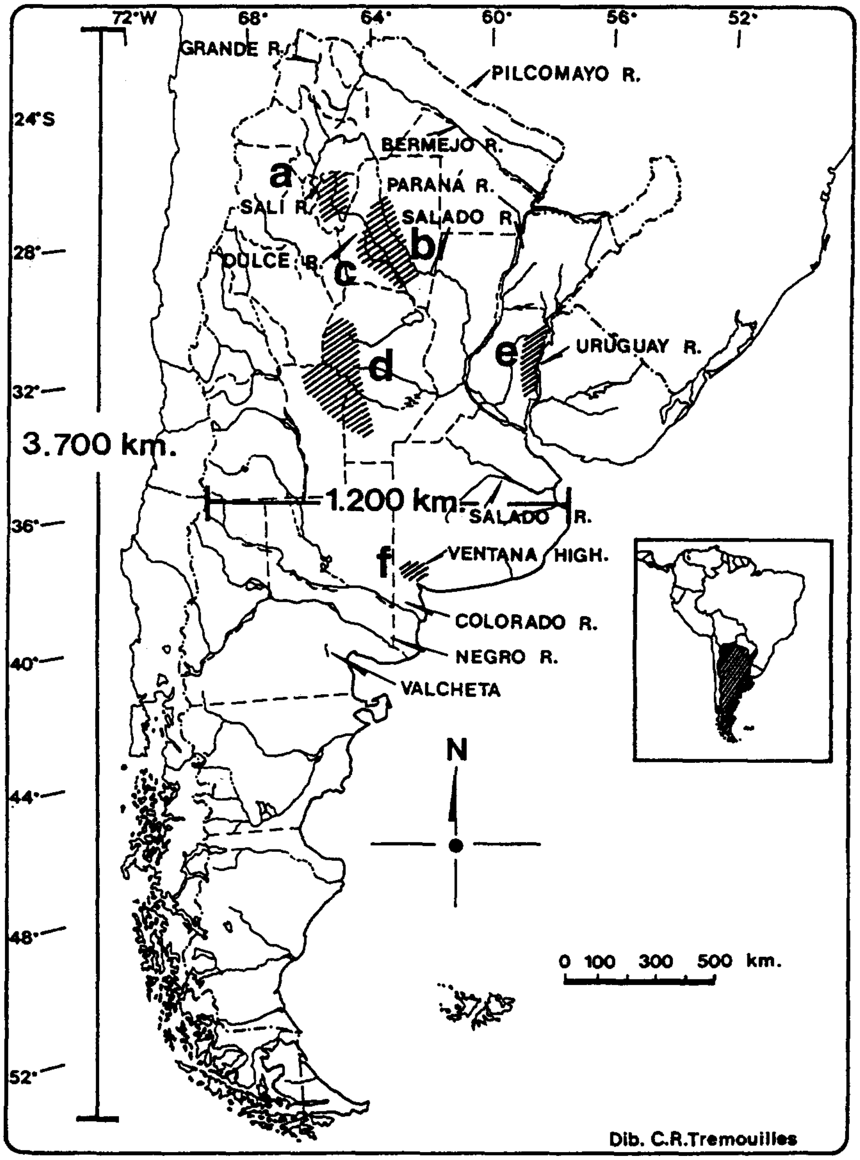

Figure 1. Areas sampled in Argentina. a, environments in the Salí River basin; b, environments in the Salado River basin; c, environments in the Dulce River basin; d, endorrheic basins in highland Córdoba; e, tributary creeks of the Uruguay River; f, streams in Sierra de la Ventana highlands.

The 54 localities that have a full set of physical and chemical data correspond to 44.9% of the total number of localities (N = 120) sampled in the original papers. Thirty four fish species in 12 families were collected. Twenty species (58.8%) are represented in three or more localities (See N values in Table 1). The total number of species considered is about 10% of the total number of the known Argentinean species (López et al., 1987).

For each of the species considered in this study the relationship between body height and body width were calculated based on morphometric data provided by Ringuelet et al. (1967a) and our own.

Numerical analysis

Basic Data Matrices (BDM) were constructed with the following criteria. Values of all variables from the

Table 1. Basic Data Matrix 1 of 34 fish species by 14 physical and chemical variables. The mean value for each variable for each species was used. N = number of samples. See text for groups labels.

	COND	TDS	t	pH	CO_3^{2-}	CO_3H^-	Cl^-	SO_4^{2-}	Na^+	K^+	Ca^{2+}	Mg^{2+}	Mg/Ca	Mg+Ca/ Na+K	N
Ax															
Astyanax eigenmanniorum	627.0	466.9	19.6	7.3	0.0	230.3	52.9	97.4	120.8	8.2	40.7	13.8	0.60	0.90	11
Charax stenopterus	1144.0	812.6	--	7.5	0.0	270.0	145.2	281.0	249.9	11.6	70.8	25.8	0.60	1.10	3
Hoplias m. malabaricus	869.5	621.0	--	7.4	0.0	209.2	109.0	212.1	188.4	9.6	54.8	2.0	0.60	1.30	4
Serrasalmus spilopleura	2944.0	2019.6	--	7.8	0.0	499.7	432.2	835.4	69.3	27.5	164.3	60.5	0.60	0.43	1
Astyanax f. fasciatus	1108.0	788.0	19.8	7.5	0.0	194.8	186.3	228.3	230.4	9.1	74.7	24.3	0.70	1.90	7
Astyanax b. bimaculatus	1084.0	825.1	20.4	7.8	3.9	199.5	171.2	206.0	220.3	10.2	74.0	22.4	0.56	1.56	10
Cheirodon i.interruptus	665.0	500.0	17.0	7.7	1.4	183.0	97.2	106.0	126.0	6.3	45.6	14.5	0.50	1.30	15
Bx															
Bryconamericus iheringi	417.0	361.0	21.6	7.8	6.1	179.6	19.5	34.5	63.6	5.8	35.7	11.1	0.60	1.40	18
Trichomycterus corduvense	502.0	415.0	20.5	7.9	7.4	213.0	25.8	36.0	80.3	7.2	31.5	12.8	0.70	1.30	22
Jenynsia l. lineata	656.3	500.0	20.4	7.8	6.6	189.8	78.4	69.5	117.2	5.9	36.7	12.5	0.52	0.90	17
Cx															
Cnesterodon decemmaculatus	363.2	317.8	24.0	7.3	0.0	181.4	20.8	32.0	57.6	6.6	33.7	11.3	0.60	1.48	4
Cyphocharax voga	187.0	158.0	--	7.2	0.0	110.0	1.1	5.0	20.0	3.9	18.0	6.8	0.62	1.50	3
Pseudocorynopoma doriai	187.0	158.0	--	7.2	0.0	110.0	1.4	5.0	20.0	3.9	18.2	6.8	0.70	1.70	3
Hyphessobrycon anisitsi	166.5	153.5	--	7.3	0.0	93.7	0.3	3.0	19.5	3.7	14.0	5.8	0.66	1.39	2
Diapoma terofali	44.0	47.0	--	7.0	0.0	26.8	0.3	3.0	4.0	3.7	6.6	2.6	0.64	2.08	1
Hyphessobrycon meridionalis	71.0	57.0	--	6.6	0.0	19.5	0.0	5.0	3.3	4.3	6.6	3.2	0.79	2.36	1
Aphyocharax rubropinnis	182.0	164.0	--	7.2	.0.0	116.8	0.3	5.0	22.7	3.4	1.7	5.4	0.52	1.24	2
Pimelodus clarias maculatus	206.0	181.0	--	7.6	0.0	138.7	0.3	5.0	28.7	3.6	17.5	7.0	0.65	1.08	1
Iheringichthys westermanni	206.0	181.0	--	7.6	0.0	138.7	0.3	5.0	28.7	3.6	17.5	7.0	0.65	1.08	1
Corydoras paleatus	233.4	220.7	19.0	7.6	0.0	156.2	5.6	5.3	28.5	3.1	29.6	9.0	0.51	1.70	5
Dx															
Heptapterus mustelinus	425.4	432.0	20.7	8.0	8.2	197.1	10.3	33.8	29.2	3.5	68.5	19.0	0.50	3.60	5
Trichomycterus alterum	529.0	553.0	21.0	8.0	8.8	224.7	13.2	53.7	34.0	3.8	91.0	26.0	0.48	4.05	3
Hypostomus cordovae	472.4	420.8	22.3	7.8	9.2	155.5	22.3	38.5	45.4	3.1	51.3	12.4	0.30	1.70	5
Trichomycterus spegazzinii	555.0	522.0	21.0	8.2	9.6	123.4	60.0	49.0	65.0	4.0	65.0	19.0	0.46	2.50	3
Characidium f. fasciatum	664.0	664.0	21.3	8.4	11.0	207.0	35.0	75.0	53.4	4.3	99.0	22.7	0.34	2.71	2
Jenynsia lineata alternimaculata	1015.0	984.0	23.0	8.2	7.2	207.2	84.4	129.5	108.0	5.7	142.0	37.4	0.44	2.80	2
Ex															
Acrobrycon tarijae	830.0	909.0	20.5	8.8	0.0	291.8	15.3	121.0	56.7	4.7	157.7	38.3	0.40	4.27	1
Pimelodus albicans	830.0	909.0	20.5	7.9	0.0	291.8	15.3	121.0	56.7	4.7	157.7	38.3	0.40	4.27	1
Odontostilbe microcephala	577.0	702.0	19.8	8.2	2.4	205.0	13.4	75.5	83.0	4.5	96.3	24.0	0.43	2.40	2
Oligosarcus jenynsi	850.3	675.1	21.3	7.9	3.6	239.5	88.4	166.9	145.8	9.0	78.6	22.3	0.44	2.00	6
Fx															
Pimelodella laticeps	263.0	247.0	20.0	7.4	0.0	175.7	6.0	6.6	29.5	3.4	36.4	10.3	0.45	2.00	3
Cichlasoma portalegrense	350.0	312.0	--	7.0	0.0	230.5	8.7	11.0	37.3	5.3	50.9	15.9	0.51	2.18	1
Jobertina rachowi	350.0	312.0	--	7.0	0.0	230.5	8.7	11.0	37.3	5.3	50.9	15.9	0.51	2.18	1
Hyphessobrycon luetkeni	158.0	148.0	--	6.8	0.0	94.9	0.3	5.0	16.7	3.2	16.4	3.8	0.38	1.40	1

54 sampled localities where fish occur were recorded. From those values, the mean, maximum and minimum values of each variable for each species of fish were obtained. Therefore the values of each variable for each fish species in each BDM are independent of a given locality, avoiding circularity of reasoning.

Three BDM's of 34 fish species by 14 physical and chemical variables were constructed considering species as OTU's and the variables as characters. The mean (BDM 1), maximum (BDM 2) and minimum (BDM 3) values of each variable for each species was used.

Data processing included the following steps for the three BDM's (Menni & Gosztonyi, 1982): A – Calculate a Pearson's correlation coefficient between each pair of OTU's; B – Link (cluster) together the OTU's in a phenogram using the correlation coefficient calculated in A and applying the unweighted pair-group method using arithmetic averages (UPGMA); and C – Calculate a measure of the distortion between the coefficients obtained in A and the phenogram obtained in B by using the Cophenetic correlation coefficient. This is indicated as CCC in both the text and figures.

The three BDM's were used as input for three Principal Component Analysis. The results of these analyses are represented in bidimensional diagrams displaying the relative position of the OTU's in the space of the principal factors.

For the comparison of the ranges of physical and chemical variables among fish species groups, a non-parametrical test (Wilcoxon) was performed (Rohlf & Sokal, 1969; Sokal & Rohlf, 1979). For comparison of frequencies of biological types the χ^2 test of goodness of fit was used.

Methodological observations

The chosen methodology allows us to obtain a preliminary ordination of all variables in several clusters which provides us with several species groups. We selected for this paper the correlation coefficient, but a check using the Taxonomic distance coefficient (Sokal, 1961) demonstrated that similar ordinations can be obtained with different coefficients. With the species groupings obtained through cluster analysis, we prepared tables displaying the original values of characters used in the BDM, but now ordered according to clustering, based on a tactic already used in a study of marine fish communities (Menni & Gosztonyi, 1982; Menni & López, 1984). This procedure allows to identify which values, or combination of values, support the clustering. As has been extensively discussed, it is not necessary to choose a significance value for the clusters in non-taxonomic analyses, and groups at any level can be studied to find any class of properties (Mello & Buzas, 1968). Cluster analysis allowed us to identify groups of species based on similarity of characters; in this case ranges of values of physical and chemical variables. The Principal Component Analysis identified those characters responsible for each group. It also provided us with a measure of the importance of each factor, and gave us a graphic display of the relative position of species in character space (see Margalef & Estrada, 1980). The representation of the regression lines of the factors, of which we selected a few as examples, show how the values of each character influences the position of the species in that space.

Results

Analysis of the BDM 1 (mean values)

Cluster analysis

The cluster analysis considering mean values of each variable provides six groups of species (Figure 2). We labelled such groups with capital letters followed by an 'x'. The two main clusters including clusters Ax, Bx, and Cx, and clusters Dx, Ex, and Fx respectively, were not labelled.

Table 1 shows the original values of the variables used in the BDM 1, with the species listed according to the phenogram (Figure 2). This disposition allows us to perform a preliminary analysis of the characteristics of the variables in each group of species. Table 1 shows that: the main cluster Ax + Bx + Cx shows maximum values (of means) for 10 variables (exceptions being t, pH, CO_3^{-2} and Mg+Ca/Na+K) and minimum values (of means) for 13 variables (exceptions being pH and Mg/Ca ratio); most maximum values occur in the cluster Ax, while minimum values appear in the cluster Cx; and the main cluster Dx + Ex + Fx includes maximum values (of the means) of t, pH, CO_3^{-2} and Mg+Ca/Na+K ratio, and minimum values of two variables (CO_3^{-2} and Mg/Ca).

In a less quantitative manner it can be seen that: COND and TDS values are higher in the cluster Ax; the cluster Ax shows high values of Cl^-, SO_4^{-2} and Na^+; clusters Dx and Ex show high pH values; clusters Bx and Dx show relatively high values of CO_3^{-2} (while nearly all the waters in which species in other groups occur lack the anion) and higher values of the Mg+Ca/Na+K ratio appear in clusters Dx and Ex.

Although the clusters are based on correlations of the chemical variables, their composition in terms of fish species suggests a relationship with faunistic and

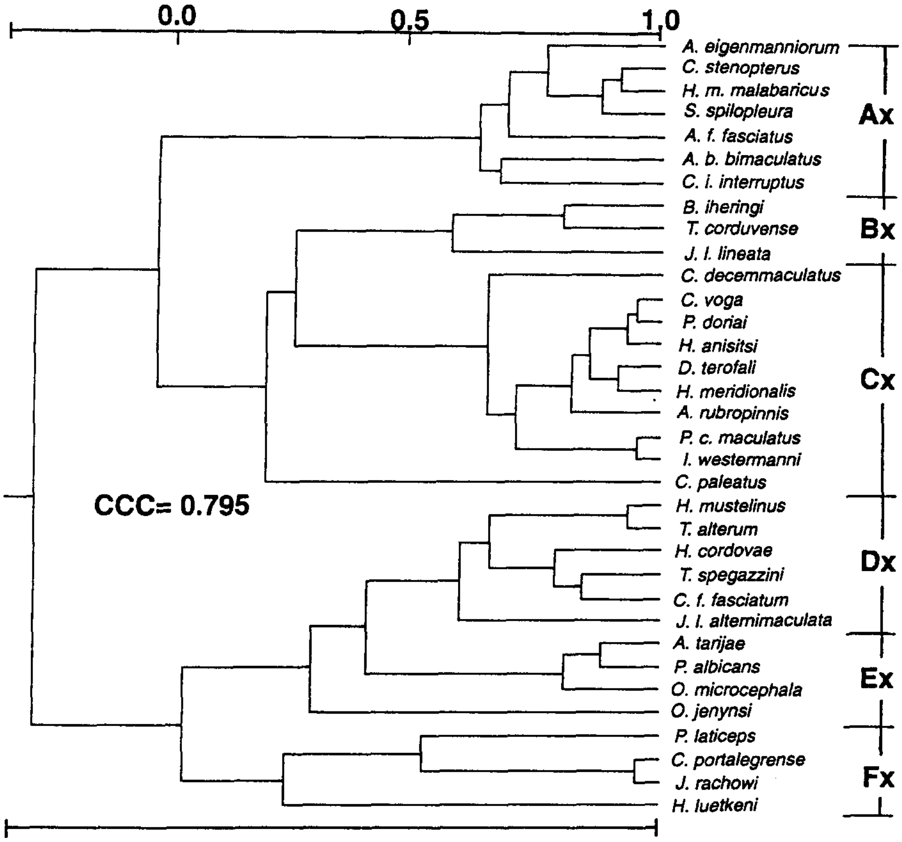

Figure 2. Correlation phenogram (UPGMA) of 34 fish species considering mean values of each limnological physical – chemical variables. See text for group labels.

geographical elements. If the geographical background is considered, it must be noted that the clusters Ax, Bx, and Cx grouped species commonly distributed in the southeastern section of the sampled area, while clusters Dx, Ex and Fx include species which are common in northwestern Argentina.

The small cluster Bx seems to be correlated with particular ecological factors, since it includes species occurring in close association in harsh highland environments of Central Argentina (Menni et al., 1984; Menni & López Armengol, pers. obs.).

The clusters Dx + Ex include 50% of species with rather restricted distributions, suggesting some peculiarities or exclusiveness in the analyzed variables. A confirmation of these interpretations is supported by the following analysis.

Principal component analysis

The PCA based on BDM 1 (mean values), provides the following three components composed by the indicated factors or variables in decreasing order of importance: PC1: COND, TDS, SO_4^{-2}, Mg^{+2} and Na^+; PC2: Mg+Ca/Na+K ratio, Mg/Ca ratio, pH, CO_3^{-2} and Ca^{+2} and PC3: t, CO_3^{-2}, Mg+Ca/Na+K ratio, Ca^{+2} and K^+.

The importance of each component is:

	Eigenvalue	Percent of trace	Accum. percentage
PC1	7.856	56.11	56.11
PC2	3.207	22.91	79.03
PC3	1.061	7.58	86.60

Species are better separated by factors included in the PC2, except *S. spilopleura* (Figure 3). The upper part of the graph includes species composing groups Dx and Ex, while the lower part shows species from the Ax group. Besides the correlation between species and chemical data, the graph suggests a relationship

Table 2. Basic Data Matrix 2 of 34 fish species by 14 physical and chemical variables. The maximum value for each variable for each species was used. M = morphological type, C = compressed, D = depressed, S = subcylindrical. See text for group labels.

	M	COND	TDS	t	pH	CO_3^{2-}	CO_3H^-	Cl^-	SO_4^{2-}	Na^+	K^+	Ca^{2+}	Mg^{2+}	Mg/Ca	Mg+Ca/Na+K
AM															
A. eigenmanniorum	C	2944	2019.6	25.5	7.8	0.0	499.7	432.2	835.4	693.0	27.5	164.3	60.5	0.90	2.90
C. stenopterus	C	2944	2019.6	--	7.8	0.0	499.7	432.2	835.4	693.0	27.5	164.3	60.5	0.65	1.80
H. m. malabaricus	S	2944	2019.6	--	7.8	0.0	499.7	432.2	835.4	693.0	27.5	164.3	60.5	0.65	2.08
S. spilopleura	C	2944	2019.6	--	7.8	0.0	499.7	432.2	835.4	693.0	27.5	164.3	60.5	0.60	0.43
C.i. interruptus	C	3419	2077.3	22.0	8.9	21.7	499.7	846.2	835.4	800.0	27.5	164.3	60.5	0.65	2.30
O. jenynsi	C.	2944	2019.6	22.0	8.8	21.7	499.7	432.2	835.4	693.0	27.5	164.3	60.5	0.65	4.27
A. b. bimaculatus	C	3419	2077.3	22.0	8.8	21.7	499.7	846.2	835.4	800.0	27.5	164.3	60.5	1.43	4.27
A. f. fasciatus	C	3419	2077.3	20.5	7.9	0.0	499.7	846.2	835.4	800.0	27.5	164.3	60.5	1.43	4.27
BM															
C. decemmaculatus	S	532	486.0	24.0	8.0	0.0	290.9	54.5	87.2	100.0	9.5	50.9	15.9	0.79	2.36
T. corduvense	D	1766	1402.0	31.0	9.6	48.9	542.1	130.5	164.0	291.0	20.6	102.8	34.4	2.12	2.47
C. voga	C	284	237.0	--	7.6	0.0	171.6	3.1	5.0	28.7	4.3	30.7	10.1	0.67	1.80
H. anisitsi	C	206	181.0	--	7.6	0.0	138.7	0.3	5.0	28.7	3.7	17.5	7.0	0.67	1.70
P. doriai	C	284	237.0	--	7.6	0.0	171.6	3.1	5.0	28.7	4.3	30.7	10.1	0.79	2.36
A. rubropinnis	C	206	181.0	--	7.6	0.0	138.7	0.3	5.0	28.7	3.6	17.5	7.0	0.65	1.08
P. clarias maculatus	D	206	181	--	7.6	0.0	138.7	0.3	5.0	28.7	3.6	17.5	7.0	0.65	1.08
I. westermanni	D	206	181.0	--	7.6	0.0	138.7	0.3	5.0	28.7	3.6	17.5	7.0	0.65	1.08
C. paleatus	D	350	312.0	20.0	8.1	0.0	230.5	9.6	11.0	37.3	5.3	50.9	15.9	0.65	2.18
P. laticeps	D	350	312.0	20.0	8.1	0.0	230.5	8.7	11.0	37.3	5.3	50.9	15.9	0.54	2.18
J. l. lineata	S	3419	2077.3	28.5	9.6	48.9	542.1	846.2	622.7	800.0	19.0	142.3	48.0	1.03	2.30
C. portalegrense	C	350	312.0	--	7.0	0.0	230.5	8.7	11.0	37.3	5.3	50.9	15.9	0.51	2.18
J. rachowi	S	350	312.0	--	7.0	0.0	230.5	8.7	11.0	37.3	5.3	50.9	15.9	0.51	2.18
D. terofali	C	44	47.0	--	7.0	0.0	26.8	0.3	3.0	4.0	3.7	6.6	2.6	0.64	2.08
H. meridionalis	C	71	57.0	--	6.6	0.0	19.5	0.0	5.0	3.3	4.3	6.6	3.2	0.79	2.36
H. luetkeni	C	158	148.0	--	6.8	0.0	94.9	0.3	5.0	16.7	3.2	16.4	3.8	0.38	1.40
CM															
B. iheringi	C	1122	909.0	28.5	9.5	39.1	380.7	68.3	131.0	240.0	20.6	157.7	38.3	0.90	4.27
H. mustelinus	D	830	909.0	21.5	8.6	26.5	291.8	19.1	121.0	56.7	4.7	157.7	38.3	0.61	5.59
T. alterum	D	830	909.0	21.5	8.6	26.5	291.8	19.1	121.0	56.7	4.7	157.7	39.3	0.61	5.59
C. f. fasciatum	S	830	909.0	22.0	8.8	21.7	291.8	55.3	121.0	56.7	4.7	157.7	38.3	0.40	4.27
A. tarijae	C	830	909.0	20.5	8.8	0.0	291.8	15.3	121.0	56.7	4.7	157.7	38.3	0.40	4.27
O. microcephala	C	830	909.0	20.5	8.4	4.8	291.8	15.3	121.0	56.7	4.7	157.7	38.3	0.40	4.27
P. albicans	D	830	909.0	20.5	7.9	0.0	291.8	15.3	121.0	56.7	4.7	157.7	38.3	0.40	4.27
H. cordovae	D	830	909.0	25.5	8.9	24.5	291.8	55.3	121.0	98.3	5.6	157.7	38.3	0.50	4.27
J. l. alternimaculata	S	1200	1059.0	25.5	8.6	14.5	291.8	153.6	138.0	160.0	6.8	157.7	38.3	0.48	4.27
T. spegazzinii	D	1200	1059.0	25.5	8.6	14.5	139.8	153.6	138.0	160.0	6.8	125.5	36.5	0.48	4.00

between the species disposition and the geographical distribution of species. This characteristic will appear repeatedly in the rest of the analysis. Species in cluster Ax occur in the southeastern section of the sampled area, and those from cluster Bx in northwestern Argentina. The graph also displays regression lines for selected factors (Mg/Ca and Ca^{+2}; Mg+Ca/Na+K is practically coincident with the PC2). These lines indicate the relative position of a species regarding a given variable. So *A. tarijae*, for example, in the upper border of the diagram, occurs at a Ca^{+2} mean value of 157.7 mg l^{-1}, while *H. meridionalis*, in the opposite position of the line is found at 6.6 mg l^{-1}. Along the PC1 line, *P. laticeps* (mid-left of Figure 3), has TDS values of

247 mg l^{-1}, while *S. spilopleura*, at bottom right, has 2.019 mg l^{-1}. The same kind of analysis can be made for all variables for a particular species. However, we consider that the global responses of species groups to the chemistry is more important in the present analyses, rather than entering in the particular analysis of the behavior of individual species.

Analysis of the BDM 2 (maximum values)

Cluster analysis

In Figure 4 three main groups of species are displayed, labelled AM, BM, and CM, composed of 8, 16, and 10 fish species respectively. The cluster CM, including endemic species, closely agrees with results obtained with the cluster analysis of mean values.

The clear definition of groups in this cluster suggests they have a biological basis. As proposed before, this will be investigated displaying maximum values of each variable for each species in the order provided by the clusters (Figure 4, Table 2). Examination of these elements shows that: in general germs values of variables are the highest in AM, lower in CM and the lowest in BM; values of variables among groups do not overlap in 14 of the 42 possibilities (33%). Groups differ significantly for 11 variables. For two of the remaining three variables, one of the groups significantly differs from the other two (Table 3) and some differences are rather obvious. For example, modal values of COND in the group AM are 3.5 times those of the group CM, and about 10 times as large as in group BM. Similar relationships can be seen in other variables.

The AM group demonstrated the following characteristics: all species in this group are associated with the highest value of SO_4^{-2}, K^+, Ca^{+2} and Mg^{+2}. Three species reach the highest values of COND, TDS, Cl^- and Na^+. Only one other species, *J. l. lineata* in the group BM, reaches the same values. Absence of CO_3^{-2} is frequent; the group shows high and homogeneous values of CO_3H^-, close to the maximum values displayed by two species in the group BM. The Mg+Ca/Na+K ratio is the most variable of all variables and the group shows rather homogeneous values for near all variables. This homogeneity was enhanced by the large number of observations available for the species in this group (see last column in Table 1).

The BM group demonstrated the following characteristics: species in this group show the lowest values for nearly all variables, the exceptions being t and the Mg/Ca ratio. Values are especially lower for SO_4^{-2} and Ca^{+2}. Only two species, *T. corduvense* and *J. l. lineata*, differ from modal values in the group (using the Taxonomic distance coefficient these species are grouped in AM). The presence of *J. l. lineata* gives the group maximum values identical with those in the group AM for COND, TDS, Cl^- and Na^+. Because of the presence of *T. corduvense* the group shows the highest values of t and the Mg/Ca ratio. Because of the presence of *J. l. lineata* and *T. corduvense* the group shows the highest values of pH, CO_3^{-2} and CO_3H^-; Table 2 shows that if the two aformentioned species are omitted, the group is very homogeneous. Their presence gives the group the highest intra-group variation.

Both AM and BM groups show a large proportion of absences of CO_3^{-2}, while the opposite is observed in the group CM.

The CM group demonstrated the following characteristics: the ratio divalent over monovalent ions is the only one absolute maximum in this group (for two species). In addition values are generally very high and there are an homogeneous set of values for many variables. pH values are slightly higher in the CM group and in nearly all cases there are positive values of CO_3^{-2}.

Principal component analysis

The PCA of the BDM 2 (maximum values) provides the following three components: PC1: TDS, COND, CO_3H^-, Mg^{+2}, Na^+; PC2: CO_3^{-2}, pH, t, Ca+Mg/Na+K, SO_4^{-2} and PC3: Ca+Mg/Na+K, Mg/Ca, Ca^{+2}, Mg^{+2}.

	Eigenvalue	Percent of trace	Accum. percent.
PC1	8.71	62.27	62.27
PC2	2.32	16.62	78.89
PC3	1.83	13.12	92.01

Consideration of PC1 and PC2 (Figure 5) provides the following results.

Species in the AM group clearly appear together. Species are also grouped in BM and CM, and are more closely aggregated to each other than with AM. The three groups are well separated along the PC1 component. Along the PC2 the CM group is well separated, but AM and BM overlapped in part of the range. Particular positions are occupied by *T. corduvense* and *J. l. lineata*, which appear isolated from

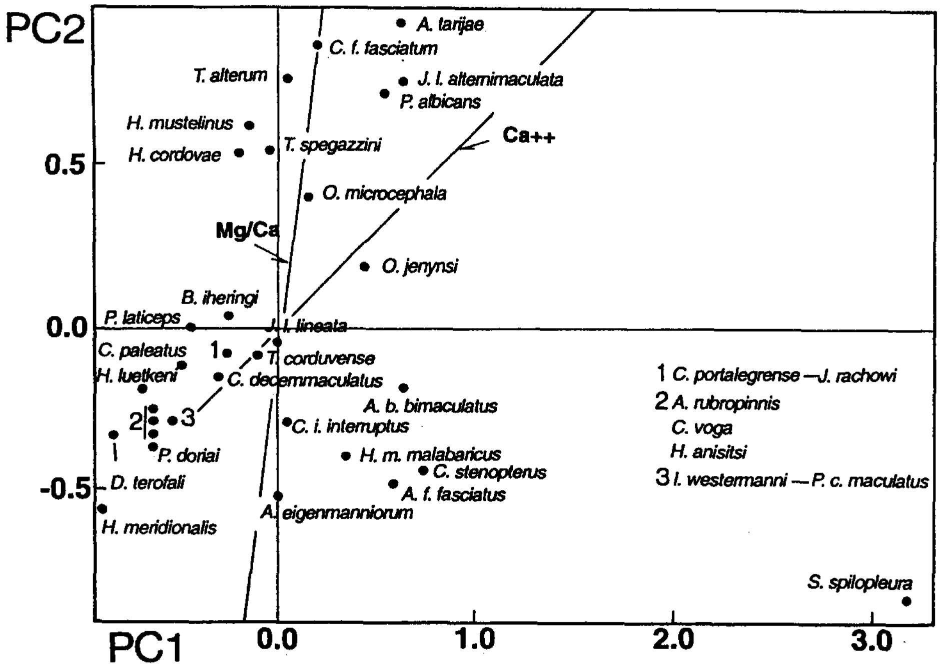

Figure 3. Principal Component Analysis. Bidimensional graph (PC1 vs PC2) displaying the relative position of 34 fish species. The mean value of each variable was used. Regression lines for 2 variables are shown.

Table 3. Comparison between clusters pairs for maximum values of each limnological variable (Wilcoxon two samples test). Figures are probability levels at which the variable distribution show significant differences between cluster pairs. * = two tail test, n.o. = no overlapping variable values between groups, n.s. = no significant differences in the variable distribution between cluster pairs.

	COND	TDS	t	pH	CO_3^{2-}	CO_3H^-	Cl^-	SO_4^{2-}	Na^+	K^+	Ca^{2+}	Mg^{2+}	Mg/Ca	Mg+Ca/ Na+K
AM–BM	0.001	0.001	n.s.	0.10*	0.20*	0.01*	0.001	n.o.	0.001	n.o.	n.o.	n.o.	n.s.	0.200*
BM–CM	0.001	0.001	n.s.	0.01*	0.02*	0.01*	0.010*	0.002*	0.010*	0.2*	0.001	0.002*	0.010*	n.o.
CM–AM	n.o.	n.o.	n.s.	n.s.	0.20*	n.o.	n.o.	n.o.	n.o.	n.o.	n.o.	n.o.	0.005	0.025

their BM group, a difference clearly explained by values in Table 2. *Bryconamericus iheringi* is somewhat isolated from its group (CM) along both components. Along PC1, species in opposite sections of the diagram (Figure 5) show different values for several variables. *Astyanax bimaculatus* shows a TDS value of 2.077.3 and a CO_3H^- value of 499.7 mg l^{-1}, while *H. meridionalis* has 57 and 19.5 mg l^{-1}, respectively. Intermediate values are shown by *P. albicans* with 909 and 291.8 mg l^{-1}, respectively. Along PC2, *H. cordovae* shows CO_3^{-2} and pH values of 24.5 mg l^{-1} and 8.9, while *J. rachowi* shows 0.0 and 7.0, respectively.

Factors which contribute the least to each component can provide interesting information. For example, along PC2, *H. luetkeni* shows the same lack of CO_3^{-2} that does *S. spilopleura*, but pH values are 6.8 and 7.8, and SO_4^{-2} values 5.0 and 835 mg l^{-1}, respectively.

The combination of components PC1 and PC3 (Figure 6), provides a separation of groups as good or indeed better than components PC1 and PC2. All species in AM appear tightly clustered. *Trichomycterus corduvense, J. l. lineata* and *B. iheringi* show the same positions already observed. This diagram shows the importance PC1 has in the basic separation of the groups and the importance of PC3 factors in the segregation of the CM group. All these factors depend upon Ca^{+2} and Mg^{+2}.

Consideration of components PC2 and PC3 (Figure 7) shows that the absence of PC1 with its strong emphasis in COND and TDS, which segregates the AM group, allows a good definition of the CM group.

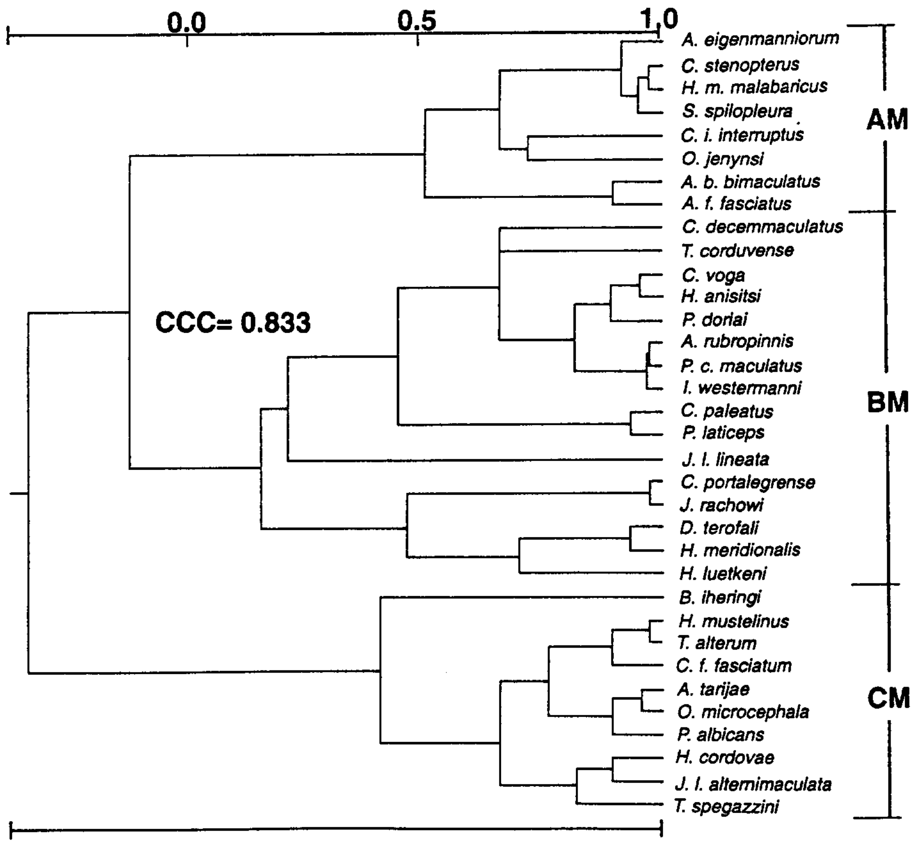

Figure 4. Correlation phenogram (UPGMA) of 34 fish species considering maximum values of each limnological physical – chemical variables. See text for cluster labels.

Analysis of the BDM 3 (minimum values)

Cluster analysis

Clusters obtained using the minimum values (Figure 8) of each variable, clearly defines groups of species that are consistent with those obtained through cluster analysis based on maximum values. Letters to the right of species names in Table 4 indicate the cluster in which the species is placed according to maximum values (Table 2). There is agreement among groups in both analyses. The percentage of agreement (number of coincidences over total number of species) is 67.6%, i.e., 23 of 34 species were in the same group in both BDM analyses.

General results of this analysis show that five variables include zero values. The Am group has the higher number of cases with zero values (4 cases); all species tolerate absence of CO_3^{-2}; five species tolerate absence of Cl^-; three species tolerate absence of Mg^{+2} and one specie tolerates absence of SO_4^{-2}.

Values of variables among groups do not show overlap in 6 out of 42 possible cases (14.3%). Testing differences among groups shows they differ significantly for 7 variables. Differences in CO_3^{-2} are not significant (all values zero). For the remaining 6 variables one group differs significantly from the other two (Table 5).

The Am group has the following characteristics: in general terms, species in this group have the lowest values for all variables (Table 4); the minimum absolute values for 12 variables, exceptions being SO_4^{-2} and CO_3H^-; it tolerates very low values or absence (three species) of Mg^{+2}; one species, *T. corduvense*, tolerates zero values of Cl^-; species in the group tolerate very low values of COND and TDS; low values of Mg^{+2} and Ca^{+2} agree with low values (including the lowest) of the Mg+Ca/Na+K ratio; species in this group tolerate the minimum registered temperature values (10.2 °C), a half of the values tolerated by species in the other groups, and they tolerate low pH values (range 6.6–

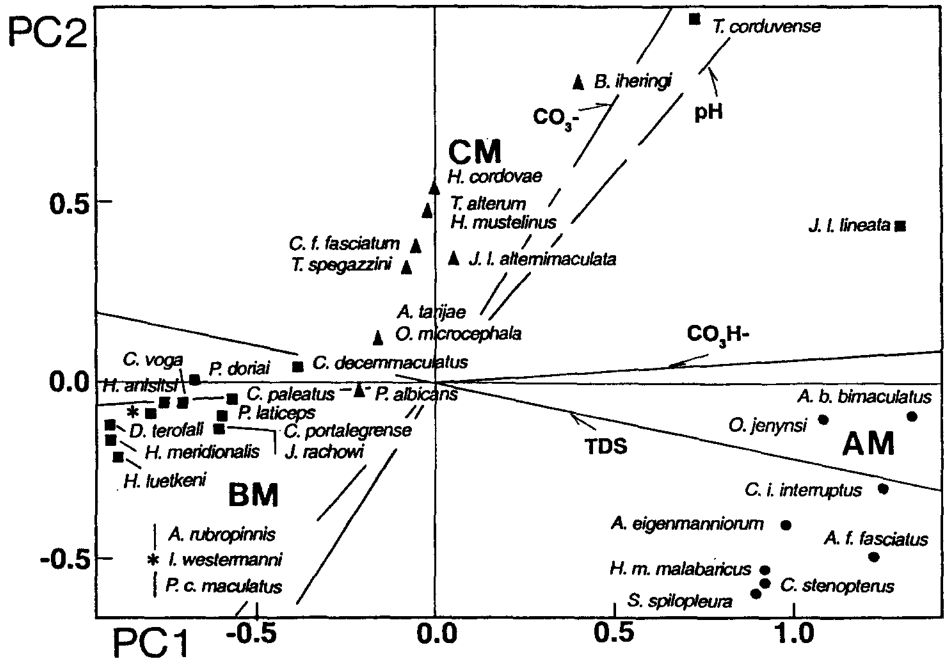

Figure 5. Principal Component Analysis. Bidimensional graph (PC1 vs PC2) displaying the relative position of 34 fish species. The maximum value of each variable was used. Regression lines for 4 variables are shown. See text for group labels.

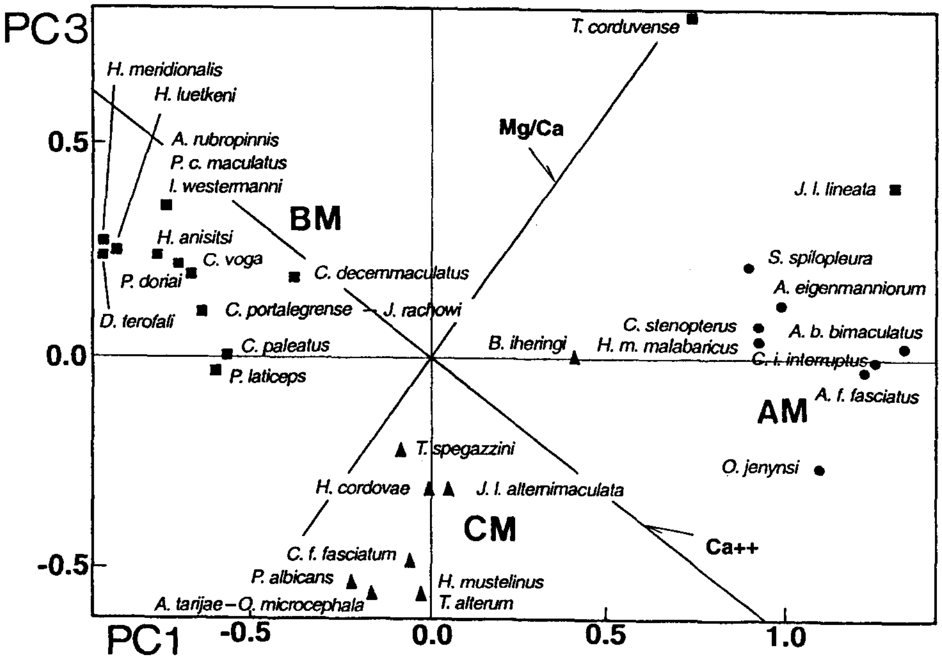

Figure 6. Principal Component Analysis. Bidimensional graph (PC1 vs PC3) displaying the relative position of 34 fish species. The maximum value of each variable was used. Regression lines for 2 variables are shown. See text for group labels.

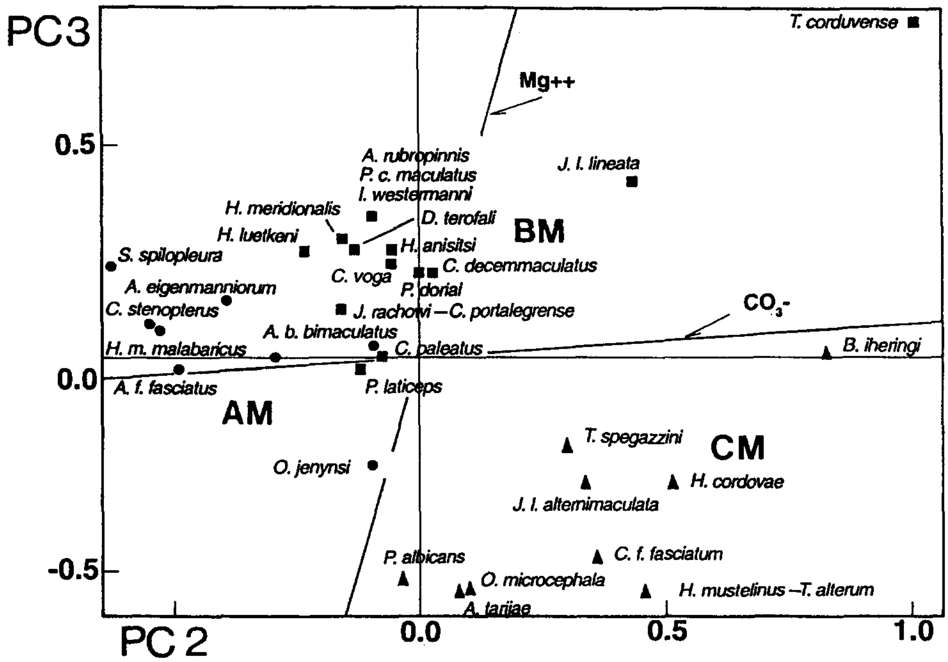

Figure 7. Principal Component Analysis. Bidimensional graph (PC2 vs PC3) displaying the relative position of 34 fish species. The maximum value of each variable was used. Regression lines for 2 variables are shown. See text for group labels.

6.9), though some species in other groups also occur at these values.

The Bm group shows 12 variables with intermediate values relative to other groups (exceptions being the Mg/Ca ratio, and t because of lack of data); four species in this group (*C. decemmaculatus, C. voga, P. doriai* and *H. meridionalis*) occur in areas which have the minimum absolute values of pH, CO_3H^- and Cl^- (minimum of Cl^- is zero).

The Cm group has the following characteristics: in general terms the group shows the highest values for 11 variables (exceptions being t and the Mg/Ca ratio; $CO_3^{-2} = 0$ in all cases). In descriptive terms, they do not tolerate minimum values as other species do; one species in the group, *H. cordovae*, has the minimum absolute values for SO_4^{-2} (only case) and K^+; mean COND and TDS values in this group are approximately tenfold in the Am group; the first three species in the group tolerate values of COND, TDS, Na^+, K^+ and Ca^{+2} as low as in the Am group and temperature in this group double that in Am.

Principal component analysis

The PCA of BDM 3 (minimum values) provides the following three components composed by the indicated variables: PC1: COND, TDS, Mg^{+2}, K^+ and SO_4^{-2}; PC2: Mg+Ca/Na+K ratio, pH, t, Cl^- and Mg/Ca ratio; PC3: Mg/Ca ratio, t, Ca^{+2}, K^+ and pH.

	Eigenvalue	Percent of trace	Accum. percent.
PC1	8.59	66.10	66.10
PC2	2.05	15.83	81.94
PC3	1.51	11.66	93.59

If we consider the bidimensional space defined by components PC2 and PC3 (Figure 9) it can be seen that: the Am group, which includes the species with the lowest values for the considered variables, is clearly depicted in the diagram (upper left). Considering the position of these species in the diagram, and those opposed to them along the regression line of the Mg/Ca ratio, we have *J. l. lineata, A. eigenmanniorum* and *B. iheringi* with 0.0 values, or *C. interruptus* with 0.22, against *H. meridionalis* with 0.79. An intermediate place and value is shown by *D. terofali* with 0.64. Three other species are displayed as separate in the diagram; they are *A. tarijae, P. albicans* and *J. l. alternimaculata* which are inside Cm (Figure 8) of the cluster analysis. Values in Table 4 show that the former two species

Table 4. Basic Data Matrix 3 of 34 fish species by 14 physical and chemical variables. The minimum value for each variable for each species was used. Letters in the second column show the place of the species in the maximum – based cluster. See text for group labels.

		COND	TDS	t	pH	CO_3^{2-}	CO_3H^-	Cl^-	SO_4^{2-}	Na^+	K^+	Ca^{2+}	Mg^{2+}	Mg/Ca	Mg+Ca/ Na+K
Am															
A. eigenmanniorum	A	58	53.0	10.2	6.6	0	30.7	0.6	2.0	11.0	0.4	4.9	0.0	0.0	0.26
B. iheringi	C	30	46.0	10.2	6.7	0	20.0	0.3	2.0	2.6	0.4	4.2	0.0	0.0	0.26
J. l. lineata	B	65	53.0	10.2	6.7	0	30.7	1.2	1.4	5.2	0.6	4.9	0.0	0.0	0.30
C. i. interruptus	A	44	47.0	10.2	6.9	0	26.8	0.3	1.4	4.0	0.6	6.6	2.6	0.22	0.31
T. corduvense	B	56	53.0	10.2	6.7	0	29.8	0.0	1.0	8.8	0.9	4.9	0.8	0.22	0.26
Cm															
A. b. bimaculatus	A	30	46.0	19.0	7.0	0	20.0	7.3	6.4	2.6	1.8	4.2	3.6	0.29	0.31
A. f. fasciatus	A	30	46.0	19.2	7.0	0	20.0	0.3	3.0	2.6	1.8	4.2	2.6	0.40	0.31
H. cordovae	C	58	93.0	20.0	6.7	0	39.8	0.6	0.0	5.2	0.4	4.9	0.4	0.12	0.36
S. spilopleura	A	2944	2019.6	--	7.8	0	499.7	432.2	835.4	69.3	27.5	164.3	60.5	0.60	0.43
O. jenynsi	A	206	181.0	20.5	7.5	0	107.9	0.3	5.0	20.0	3.2	17.5	7.0	0.29	0.43
C. f. fasciatum	C	497	420.0	20.5	7.9	0	122.6	15.3	2.8	50.0	3.8	40.7	7.2	0.29	1.15
O. microcephala	C	324	494.0	19.0	7.9	0	117.7	11.5	30.0	56.7	4.2	34.8	9.7	0.40	0.52
C. paleatus	B	156	181.0	18.0	7.0	0	115.4	0.3	1.4	23.3	1.2	17.5	4.9	0.29	1.08
P. laticeps	B	156	192.4	20.0	7.0	0	125.0	3.1	3.9	23.3	1.2	27.7	4.9	0.29	1.80
H. mustelinus	C	208	237.0	19.5	7.3	0	107.9	3.1	3.0	15.3	2.2	30.5	8.1	0.40	1.80
T. alterum	C	208	243.0	20.5	7.5	0	107.9	5.2	7.0	20.0	3.2	30.5	8.1	0.40	2.30
T. spegazzinii	C	208	243.0	19.5	7.5	0	107.9	8.7	3.0	15.3	2.2	30.5	8.1	0.43	1.30
A. tarijae	C	830	909.0	20.5	8.8	0	291.8	15.3	121.0	56.7	4.7	157.7	38.3	0.40	4.27
P. albicans	C	830	909.0	20.5	7.9	0	291.8	15.3	121.0	56.7	4.7	157.7	38.3	0.40	4.27
J. l. alternimaculata	C	830	909.0	20.5	7.9	0	122.6	15.3	121.0	56.7	4.7	125.5	36.5	0.40	1.30
Bm															
C. stenopterus	A	206	181.0	--	7.3	0	138.7	0.3	5.0	28.0	3.6	17.5	7.0	0.60	0.43
P. clarias maculatus	B	206	181.0	--	7.6	0	138.7	0.3	5.0	28.7	3.6	17.5	7.0	0.65	1.08
I. westermanni	B	206	181.0	--	7.6	0	138.7	0.3	5.0	28.7	3.6	17.5	7.0	0.65	1.08
C. decemmaculatus	B	71	57.0	24.0	6.6	0	19.5	0.0	5.0	3.3	4.3	6.6	3.2	0.51	0.62
C. voga	B	71	57.0	--	6.6	0	19.5	0.0	5.0	3.3	3.6	6.6	3.2	0.54	1.08
P. doriai	B	71	57.0	--	6.6	0	19.5	0.0	5.0	3.3	3.6	6.6	3.2	0.54	1.08
H. m. malabaricus	A	44	47.0	--	7.0	0	26.8	0.3	3.0	4.0	3.7	6.6	2.6	0.54	0.43
H. anisitsi	B	127	126.0	--	7.0	0	48.7	0.3	1.0	10.3	3.6	11.0	4.5	0.65	1.08
D. terofali	B	44	47.0	--	7.0	0	26.8	0.3	3.0	4.0	3.7	6.6	2.6	0.64	2.08
H. meridionalis	B	71	57.0	--	6.6	0	19.5	0.0	5.0	3.3	4.3	6.6	3.2	0.79	2.36
A. rubropinnis	B	158	148.0	--	6.8	0	94.9	0.3	5.0	16.7	3.2	16.4	3.8	0.38	1.08
H. luetkeni	B	158	148.0	--	6.8	0	94.9	0.3	5.0	16.7	3.2	16.4	3.8	0.38	1.40
C. portalegrense	B	350	312.0	--	7.0	0	230.5	8.7	11.0	37.3	5.3	50.9	15.9	0.51	2.18
J. rachowi	B	350	312.0	--	7.0	0	230.5	8.7	11.0	37.3	5.3	50.9	15.9	0.51	2.18

show high values for the Mg+Ca/Na+K ratio, and that all three share very high values of CO_3H^-, Cl^-, SO_4^{-2} and Ca^{+2}.

Though other groups are not clear, general positions of species are in good agreement with the cluster analysis, and make possible a detailed analysis for each species in particular. The above-mentioned groups are objectively shown, but the separation of the main groups in Figure 9 requires the cluster analysis to be traced.

Considering the PC1 and PC3 (Figure 10) it can be seen that *S. spilopleura*, with a maximum value (only one data in all), is extremely segregated. Aside from this species, *A. tarijae, P. albicans* and *J. l. alternimac-*

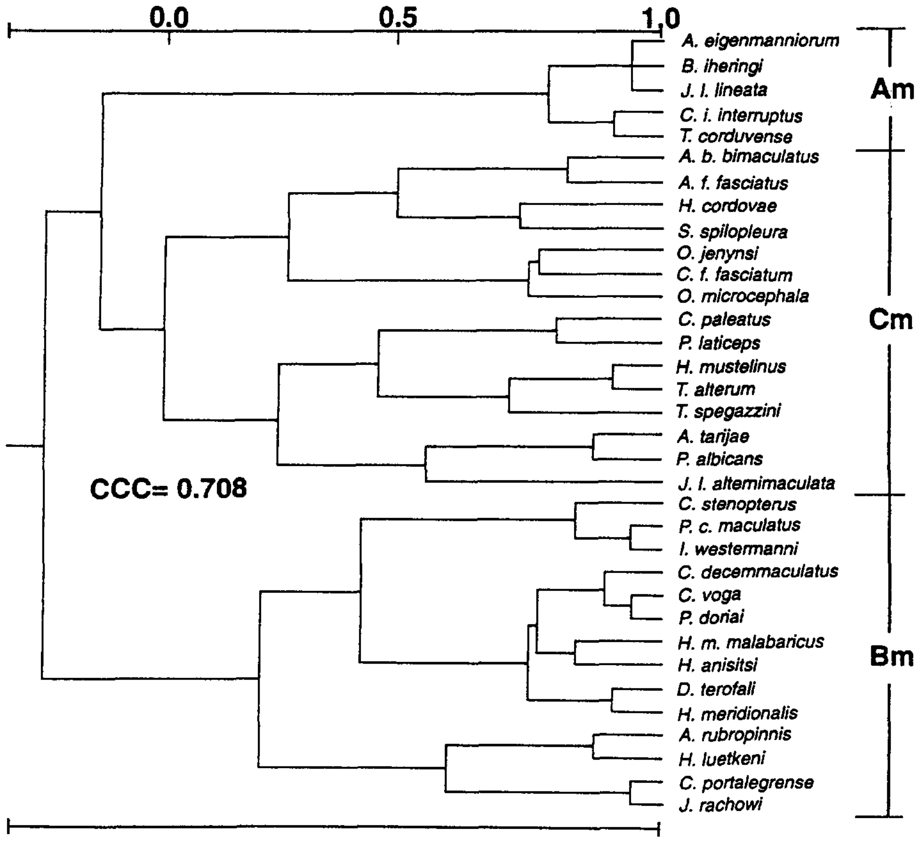

Figure 8. Correlation phenogram (UPGMA) of 34 fish species considering minimum values of each limnological physical – chemical variables. See text for cluster labels.

Table 5. Comparison between cluster pairs for minimum values of each limnological variable (Wilcoxon two samples test). Numbers are probability levels at which the variable distribution show significant differences between cluster pairs. * = two tail test, n.o. = no overlapping variable values between groups, n.s. = no significant differences in the variable distribution between cluster pairs.

	COND	TDS	t	pH	CO_3^{2-}	CO_3H^-	Cl^-	SO_4^{2-}	Na^+	K^+	Ca^{2+}	Mg^{2+}	Mg/Ca	Mg+Ca/ Na+K
Am–Cm	0.02*	0.010	n.o.	0.001	n.s.	0.02*	0.010	0.02*	0.05*	0.01*	0.05*	0.001	0.001	0.001
Am–Bm	0.01	0.010	n.o.	n.s.	n.s.	n.s.	n.s.	0.01*	n.s.	n.o.	0.005	0.001	n.o.	n.o.
Cm–Bm	0.05	0.025	n.o.	0.005	n.s.	0.10	0.001	n.s.	0.20*	0.20*	0.050	0.025	0.001	n.s.

ulata, again appear clearly separated from the other species of Cm and they have the maximum values for all variables in the PC1 (Table 4). Along the PC3, the Am group is clearly segregated at the upper left of the diagram.

Discussion

Results obtained through the analysis of correlations between presence of fish species, and physical and chemical characteristics of the water indicated good relationships between these elements. These relationships have not been clearly viewed in the past. Groups of species demonstrated by cluster and principal component analysis can be considered as real associations

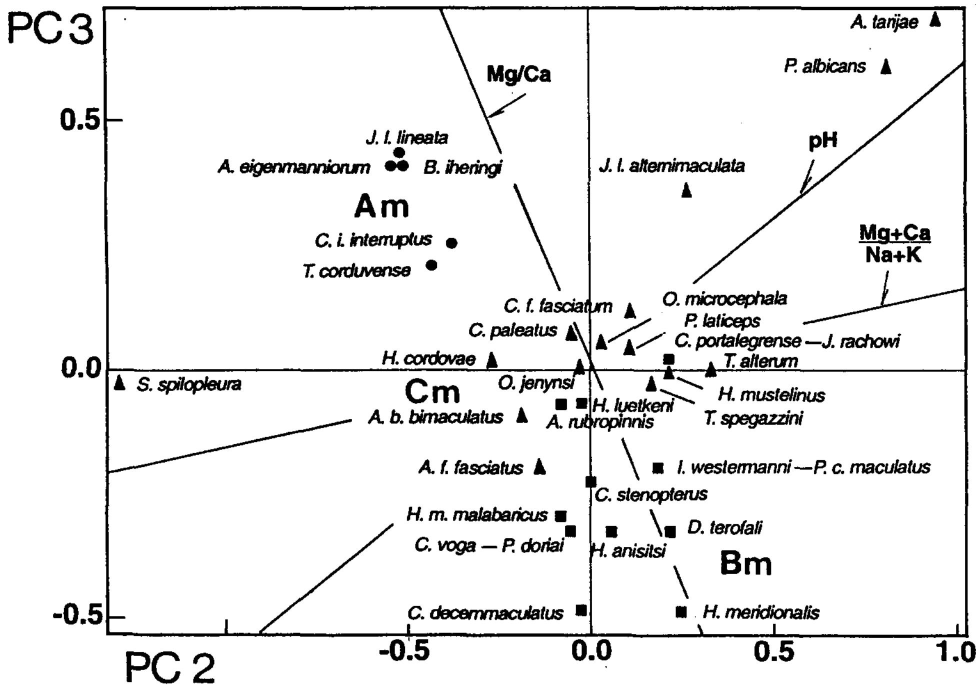

Figure 9. Principal Component Analysis. Bidimensional graph (PC2 vs PC3) displaying the relative position of 34 fish species. The minimum value of each variable was used. Regression lines for 3 variables are shown. See text for group labels.

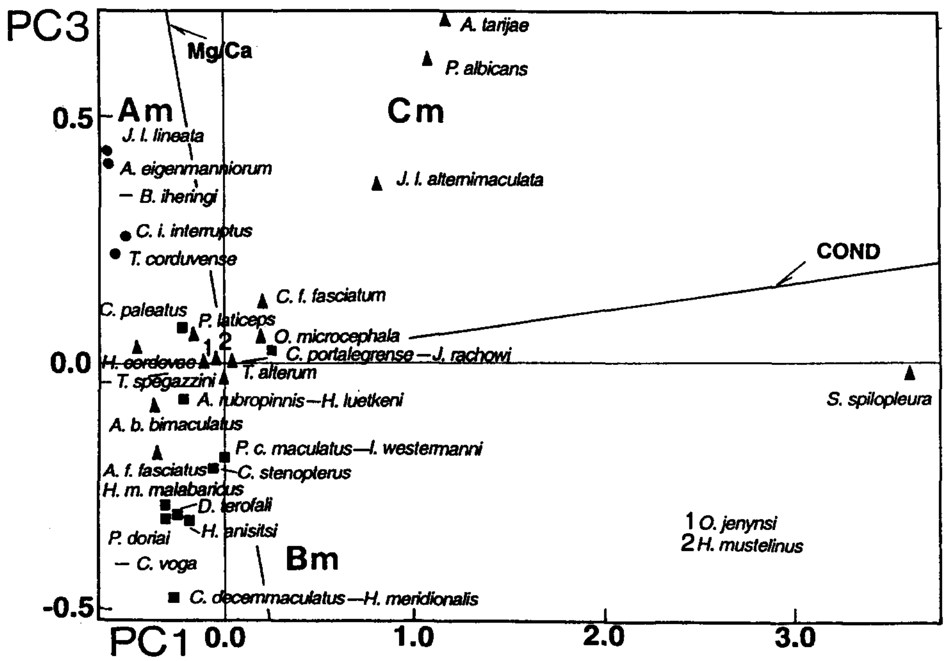

Figure 10. Principal Component Analysis. Bidimensional graph (PC1 vs PC3) displaying the relative position of 34 fish species. The minimum value of each variable was used. Regression lines for 2 variables are shown. See text for group labels.

in the sense of Margalef (1974). The reality of these associations provides a better understanding of how and why fishes are organized in the subtropical and temperate zone (the area being sampled in Argentina for this study roughly corresponding to the Paranensean Dominion of Ringuelet, 1975). In this large region, the general patterns of organization seen before were the impoverishment of the Paranensean fauna in an East-West direction (Ringuelet, 1975; Menni & Gómez, 1995), the latitudinal variation of richness in western Argentina (Arratia et al., 1983) and the differences in the specific composition of basins. The results within geographical, physiological, and morphological frameworks are outlined below.

The geographical counterpart

The patterns of water-chemical characteristics, as noted above, suggest some agreement between these factors and fish distribution. These relationships can be followed from Table 6. Species are clustered based on maximum values of chemical variables (Table 2, Figure 4). Columns show the sampled basins listed according to their positions in a northwest-southeast axis. Table 6 shows the distribution in species clusters defined on the basis of the chemical composition of the water where they were collected.

The AM group is represented by several species in the basins under consideration, with the exception of Sierra de la Ventana. Here all the clusters are under represented (see below). All the species of AM occur in the Salado River. In all basins there are at least 50% of the species from the cluster (except Sierra de la Ventana).

The BM cluster is well represented in the Uruguay River (75% of the species present), and the Salí River (50% of species present). Most species in this cluster do not occur in the Salado River.

All the species in the CM cluster occur in the Salí River, 50% of them in this river alone. This cluster is not represented in the Salado River.

In summary, species tend to cluster by basin (Figure 11). Cluster AM has 100% presence in the Salado River, BM has 75% presence in the Uruguay River tributaries, and CM has 100% presence in the Salí River. Note the presence in the Salí River of a set of species, such as *H. cordovae*, occurring exclusively in this basin or in other basins of northewestern Argentina, but in general not southward or eastward. These species are totally absent from the Salado River. *Trichomycterus alterum* occupies the Salí River basin in the eastern, lower above sea level localities, and is found in other localities to the West and Northwest of this basin (see summary in Miquelarena et al., 1990). *Jenynsia lineata alternimaculata* is also restricted to northwest-

Table 6. Geographic distribution of 34 fish species in 6 basins. Species listed according to maximum – value clusters; basins roughly in a NW–SE direction. + = reported in literature, * = presence with chemical data available, ** = presence only in that basin with chemical data available. Basins: a, Salí River; b, Salado River; c, Dulce River; d, endorrheic basins in Córdoba; e, Uruguay River; f, streams in Sierra de la Ventana.

	a	b	c	d	e	f
Cluster AM						
A. eigenmanniorum		*	+	*		
C. stenopterus		*			*	
H. m. malabaricus		*	+	+	*	
S. spilopleura		*			+	
C. i. interruptus	*	*		*	*	*
O. jenynsi	*	*		*	*	
A. b. bimaculatus	*	*	*			
A. f. fasciatus	*	*	*	+	*	
Cluster BM						
C. decemmaculatus	*	*	*	*	*	+
T. corduvense	*			*		
C. voga				+	*	
H. anisitsi					*	
P. doriai					*	
A. rubropinnis			+		*	
P. c. maculatus	+		+		*	
I. westermani					*	
C. paleatus	*			+	*	*
P. laticeps	*			+	*	*
J. l. lineata	*	*	+	*		*
C. portalegrense	*	+	+			
J. rachowi	*					
D. terofali					*	
H. meridionalis					*	
H. leutkeni					*	
Cluster CM						
B. iheringi	*			*	*	*
H. mustelinus	*		+		*	
T. alterum	**					
C. f. fasciatum	*				+	
A. tarijae	**					
O. microcephala	**					
P. albicans	*		+		+	
H. cordovae	*			*		
J. l. alternimaculata	**					
T. spegazzinii	**					

ern Argentina and Boliva (Miquelarena et al., 1990). *Trichomycterus spegazzini* also has a restricted distribution in northern Argentina (Ringuelet et al., 1967a; Ringuelet, 1975; Arratia et al., 1983; Menni et al., 1992).

Miquelarena et al. (1990) stated that *O. microcephala* is more abundant and widely distributed than known before. It occurs in both the Paraná and the Paraguay rivers, but was not captured in any of the other localities sampled by us. The cases of *H. cordovae* and *A. tarijae* are similar.

The fish fauna in Córdoba, particularly in the western section of the province, is composed of species shared with several basins, most of the species clustered in groups AM and BM. It is similar to the faunas in the Salado and Uruguay basins sharing 7 and 9 species respectively. With respect to the Uruguay and Paraná rivers, the Córdoba fauna is an impoverished one, lacking endemics, but with a couple of species, *T. corduvense* and *H. cordovae* with restricted distributions. The combination of species in Sierra de la Ventana (Menni et al., 1988), where no endemics occur, suggests a mixed origin in terms of the groups considered. In this area, species placed in different clusters according to water composition, are living together. This suggests that in each cluster there are species which, although preferring the variable range of that cluster, have a higher tolerance than the rest of the species and reach a wider distribution (Figure 12). So, each cluster includes some eurytopic species, which appear in marginal areas with some extreme characteristics. According to several authors (MacDonagh, 1934; Ringuelet, 1975, 1978, 1981; Menni et al., 1988), Sierra de la Ventana is the southern border of the Paranensean fauna in southeastern Argentina, that is with the exception of the endemic *Gymnocharacinus bergi* in Valcheta Creek of the Somuncurá plateau (Menni & Gómez, 1995) and the Chilean species of *Cheirodon*. To the West, this limit is placed further north in the San Luis province.

The hypothesis can be advanced that the species which resist the harsh conditions (Wootton, 1991) in Ventana, especially the lower temperatures (Gómez, 1993), are Paranensean species with a high resistance to particular ecological factors in the area, such as a colder climate, lower TDS, and a lower productivity. The presence of *G. bergi* in the Somuncurá plateau, that of *Cheirodon* in Chile, and that of fossil *Pimelodus* and *Callichthys* in Bahia Blanca (southeast of Sierra de la Ventana, Cione, 1986), together with a bulk of information on other organisms (Ringuelet, 1978), support the wider meridional distribution of the Paranensean (or Brazilian) fauna in the past. If this is so, several processes have influenced the present distribution. Isolation of species is explained by geological or climatic events, desertification in particular (Ringuelet, 1978, 1981). The small ichthyofauna from Ventana has a physiological resistance to relatively harsh climactic and chemical factors. Gómez (1993, in press) noted that Paranensean species inhabiting the Buenos Aires province can be ordered along an eurytopic–stenotopic axis based on their increasing resistance to cold and salinity. Fishes from Sierra de la Ventana are a subset of Paranensean fauna, impoverished by ecological factors, or, at least, maintained by them in its present composition. These species also inhabit the Paraná River and related localities.

The northwestern fauna from the Salí River and northwestern Córdoba seem to require a different explanation. The corresponding cluster of species (CM, and also Cm) show certain endemic species (double asterisks in Table 6). General conditions in this area are more complex than to the South, which has provided more opportunities for the appearance of endemics (the Salí and many Córdoba basins are endorrheic at present: Menni et al., 1984).

A similar analysis performed with the minimum values (Table 4) based on clustering (Figures 8, 13, Table 7) is consistent with the preceding one.

Differences among several basins regarding water composition, and the consistent differences among their fish faunas, together with the consideration of climate, trophic state and hydrographic complexity (Casciotta et al., 1989; Menni et al., 1988; Miquelarena et al., 1990) provide an insight into causal explanations of distributional patterns related to those noted by Mac Donagh (1934), Ringuelet (1975), Arratia et al. (1983), and Menni et al. (1984, 1988).

The ecophysiological counterpart

Classical studies mainly conducted under laboratory conditions referred to lethal and limiting factors (Fry, 1971; Ward & Parrish,1982). Only a few of the species treated in the present paper have studied with regard to those factors. Information is available on the cold resistence of *Pimelodus clarias, P. albicans*, and *Hoplias m. malabaricus* (Dioni & Reartes, 1975). Responses of *Jenynsia lineata* to increasing salinities are provided by Thormalen de Gil (1949), Soriano – Señorans & Orsi (1960), and Gluzman de Pascar (1968). An evaluation of the resistance to salinity and

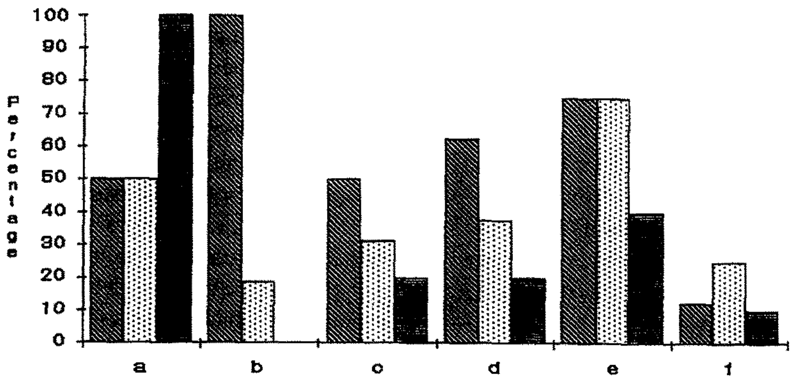

Figure 11. Percentages of species from maximum value – based clusters (AM: diagonal lines, BM: stippled, CM: horizontal lines) occurring in the considered basins: a, Salí River; b, Salado River; c, Dulce River; d, endorrheic basins in Córdoba; e, Uruguay River; f, streams in Sierra de la Ventana.

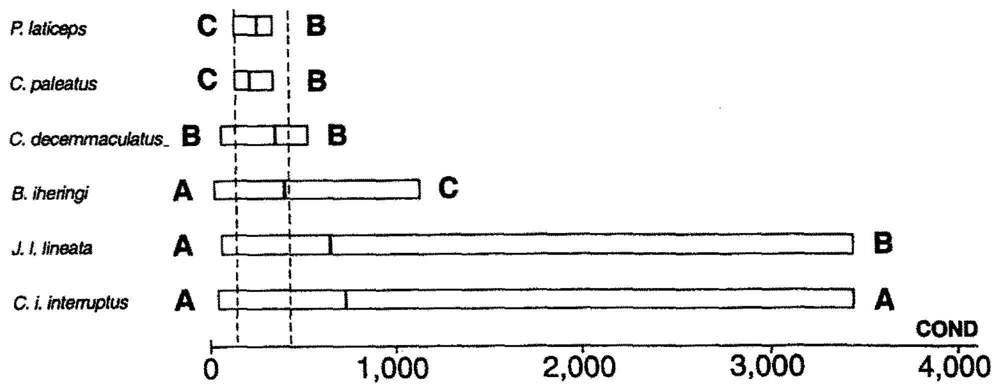

Figure 12. Total conductivity range for fishes from Sierra de la Ventana highlands. For each species, mean value (vertical bar) and the cluster to which they belong (A, B, or C; minimum left, maximum right) are shown. Dotted lines indicate conductivity range in Sierra de la Ventana environments.

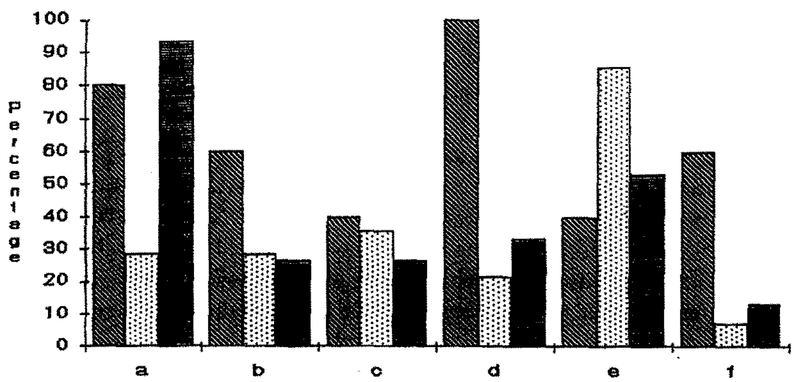

Figure 13. Percentages of species from minimum value – based clusters (Am: diagonal lines, Bm: stippled, Cm: horizontal lines) occurring in the considered basins: a, Salí River; b, Salado River; c, Dulce River; d, endorrheic basins in Córdoba; e, Uruguay River; f, streams in Sierra de la Ventana.

Table 7. Geographic distribution of 34 fish species in 6 basins. Species listed according to minimum – value clusters; basins roughly in a NW – SE direction. + = reported in literature, * = presence with chemical data available, ** = presence only in that basin with chemical data available. Basins: a, Salí River; b, Salado River; c, Dulce River; d, endorrheic basins in Córdoba; e, Uruguay River; f, streams in Sierra de la Ventana.

	a	b	c	d	e	f
Cluster Am						
A. eigenmanniorum		*	+	*		
B. iheringi	*			*	*	*
J. l. lineata	*	*	+	*		*
C. i. interruptus	*	*		*	*	*
T. corduvense	*			*		
Cluster Cm						
A. b. bimaculatus	*	*	*			
A. f. fasciatus	*	*	*	+	*	
H. cordovae	*			*		
S. spilopleura		*			+	
O. jenynsi	*	*		*	*	
C. f. fasciatum	*				+	
O. microcephala	**					
C. paleatus	*			+	*	*
P. laticeps	*			+	*	*
H. mustelinus	*		+		*	
T. alterum	**					
T. spegazzinii	**					
A. tarijae	**					
P. albicans	*		+		+	
J. l. alternimaculata	**					
Cluster Bm						
C. stenopterus		*			*	
P. c. maculatus	+		+		*	
I. westermanni					*	
C. decemmaculatus	*	*	*	*	*	+
C. voga				+	*	
P. doriai					*	
H. m. malabaricus		*	+	+	*	
H. anisitsi					*	
D. terofali					*	
H. meridionalis					*	
A. rubropinnis			+		*	
H. luetkeni					*	
C. portalegrense	*	+	+			
J. rachowi	*					

cold along a geographical gradient is given by Gómez (1993, in press) for eight species.

Data obtained from the present work for 24 species provides the tolerance range to 12 factors and two ratios. For another 10 species a single value from one locality was obtained (Tables 2 and 4).

The analysis shows that species are grouped according to their tolerance ranges. As an example Figure 14 shows conductivity ranges for all species (see also Figure 12), with the widest tolerance ranges occurring in species of group AM.

Here we analyze the absolute maximum and minimum values of each factor for each species, considering these values as indicators of species responses to each factor.

The species discussed below tolerate, for at least one variable, one absolute maximum or minimum value (all species tolerate an absolute minimum of 0.0 for CO_3^{-2}). Table 8 was constructed with the maximum absolute values from the BDM 2 (maximum values) and with minimum absolute values from BDM 3 (minimum values). Eighteen of 24 species, for which a range is known, tolerate absolute maximum or minimum values of two or more parameters. In this context it can be seen that *A. bimaculatus* and *A. fasciatus* are the species which tolerate the largest number of maximum (8) and minimum (5) values, which are the same for both. The magnitude of the range for COND, TDS, Na^+ and Ca^{+2}, correspond to the absolute maximum and minimum values in all cases (Tables 2 and 4). For these factors both species show the widest ranges observed (Table 8). They appear associated together in both the clusters of maximum and minimum values and also in a consensus analysis.

Jenynsia l. lineata tolerates 7 maximum and 4 minimum values, only in one case the same factor (CO_3^{-2}). While all species reach a minimum of 0.0 for this ion, *J. l. lineata* and *T. corduvense* reach the absolute maximum. *Astyanax eigenmanniorum* tolerates 4 maximum and 7 minimum values, being the same in two cases (K^+ and Mg^{+2}). *Trichomycterus corduvense* tolerates 5 maximum and 4 minimum values, being the same in two cases (t and CO_3^{-2}). The maximum – temperature values observed for this species are higher than those observed as lethal in the laboratory (23 °C) for the Chilean species of the same genus (Arratia, 1983). These five species are the most eurytopic among those studied here. Several independent sources support the consistency of this analysis. *Jenynsia l. lineata* has a very wide geographical and ecological distribution (See Ringuelet, 1975 and Menni et al., 1984), and its euryhalinity has been demonstrated experimentally (Thormalen de Gil, 1949; Gómez, 1993). Species of *Trichomycterus* have rather restricted distributions and there are several endemic species. In this case we

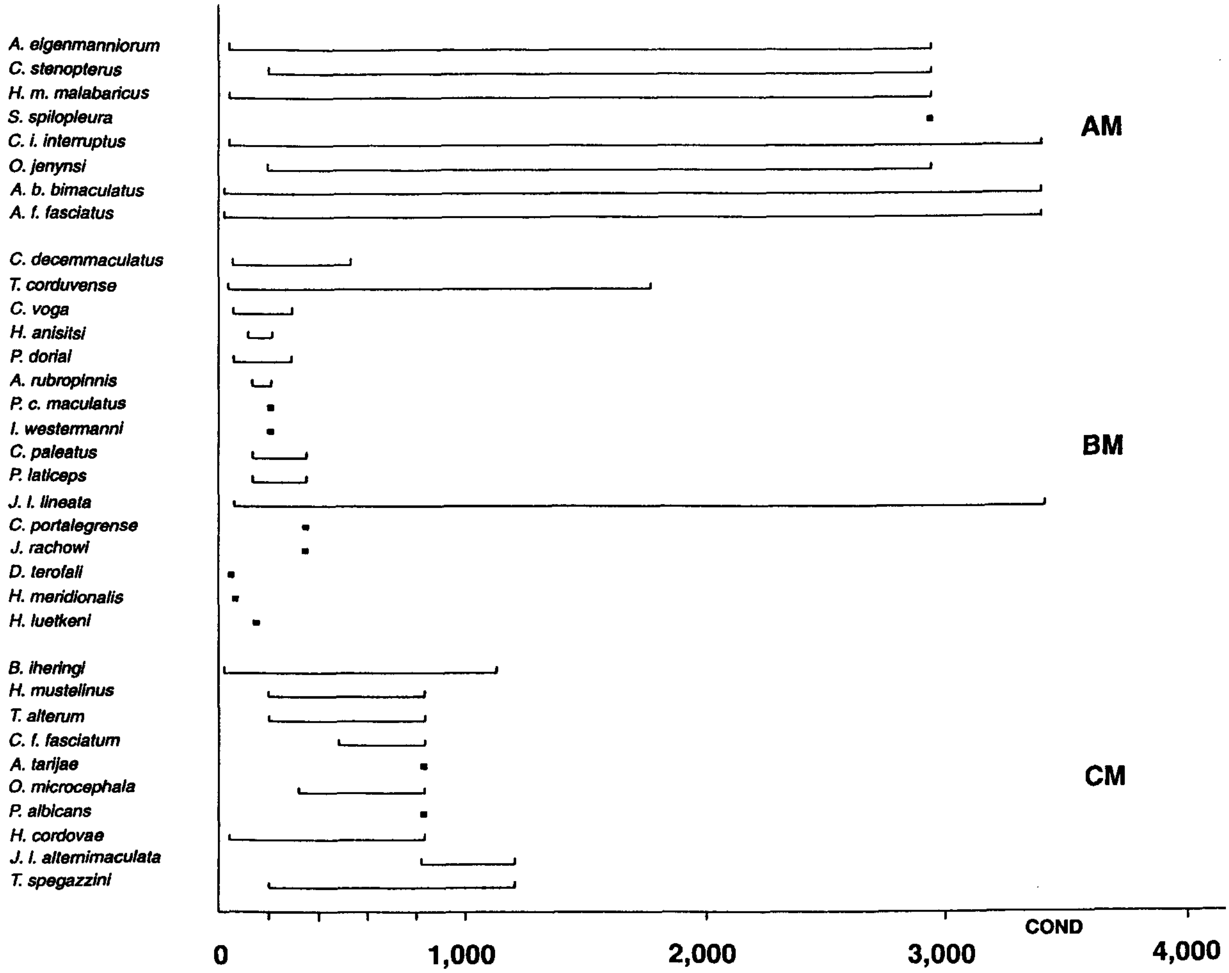

Figure 14. Conductivity range for all 34 species. Order of species according to the phenogram based on maximum values.

think that historical causes are more important that ecological ones, but *T. corduvense* is the species with the widest geographical range within the genus (Ringuelet, 1975; Menni et al., 1984). The genus *Astyanax* is rich in species with considerable taxonomic complexity. For example *A. fasciatus* is strongly eurytopic (Table 8) and has a distribution from the USA to Argentina. This raises the question of whether or not it actually is a single species. This support Pianka's (1982) statement that species with larger tolerance ranges for all factors have a larger probability of being widely distributed.

Other species tolerate maximum and minimum absolute values of different factors. *Cheirodon interruptus* tolerates 8 maximum and 2 minimum values and *B. iheringi* tolerates 10 minimum but no maximum values.

Other species tolerate maximum or minimum absolute values of a few factors. *Charax stenopterus, H. m. malabaricus, S. spilopleura* and *O. jenynsi* tolerate the same maximum values (SO_4^{-2}, K^+, Ca^{+2} and Mg^{+2}) and the minimum for CO_3^{-2}. These four species appear associated in the cluster based on minimum values (Figure 8). *Cnesterodon decemmaculatus, C. voga, P. doriai* and *H. meridionalis* tolerate 4 minimum values (pH, CO_3^{-2}, Co_3H^- and Cl^-). *Hypostomus cordovae* tolerates 3 minimum values (K^+, SO_4^{-2} and CO_3^{-2}), being the single species for that minimum of SO_4^{-2}. These conditions are related with its absence from the Paraná and La Plata rivers. *Heptapterus mustelinus* and *T. alterum* show maximum values for the Mg+Ca/Na+K ratio, which agrees with a characteristic of the Salí River basin (Miquelarena et al., 1990).

The species are associated in a different manner according to the factors they tolerate as a maximum or a minimum. Note that *B. iheringi* (10 minimum values, no maximum) appears clearly associated with eurytopic species (Cluster Am) in the minimum based cluster, but not in the maximum based. *C. interruptus*, with 8 maximum and 2 minimum values, appears in the same eurytopic species group both in maximum and minimum based clustering. According to its behavior with respect to COND and TDS (it tolerates the maximum registered values), the species occurs in the Salado River basin, where *B. iheringi* was not obtained. *Bryconamericus iheringi* is common in Bonaerensean lentic environments (lagunas), and in mountain creeks with low TDS values (Ringuelet et al., 1976b; Ringuelet, 1975; Menni et al., 1988).

In the case of having a unique sample for one species, the analysis indeed allows us to evaluate whether or not the value of a given parameter is near a mean, a maximum or a minimum. This is so because species with only one value for each variable are drastically segregated in the PCA based on values of a different type of that to which the sample belongs. If one species with a single sample is clearly grouped in the PCA based on maximum values as known from species with a range, it is probable that the single value is a maximum. With this value the species is clearly separated from its own group in PCA based on minimum or mean values. A clear sample is *S. spilopleura* (Table 4, Figure 10). The same reasoning can be applied to the already discussed group formed by *A. tarijae*, *P. albicans* and *J. l. alternimaculata*, with only one set of values (Table 4, Figure 10). The group is isolated in the PCA based on minimum values, but grouped in the maximum based one.

Each species responds in an 'eurytopic' manner to its own combination of factors; for example *A. bimaculatus* and *A. fasciatus* to COND and TDS, and *A. eigenmanniorum* to K^+ and Mg^{+2}. The analysis shows some segregation between congeners *H. meridionalis* and *H. luetkeni*, because the latter do not support any minimum.

The different tolerances to the factors studied in this work can be considered a measure of species position along an eurytopic-stenotopic axis. Table 8 shows the 18 species which support maximum or minimum absolute values for more than one factor ordered according to decreasing numbers of factors. Gómez (1988, in press) proposed two sequences of species from the Buenos Aires province, based on their resistance to salinity and cold. Four of these species *(J. lineata, S. spilopleura, C. decemmaculatus*, and *C. voga)* appear in our samples. For these species, positions in the sequences are coincident with our proposal in Table 8. Data from Dioni & Reartes (1975) on resistance to cold support that *H. m. malabaricus*, included in our list, is more resistent than *P. clarias maculatus* and *P. albicans*, which, according to our data do not appear at extreme values.

Cluster composition and morphology

Groups identified on the basis of water chemistry show differences in the relative abundance of morphological types. These relationships between morphology and environmental characteristics, as already discussed by Gatz (1979a, 1979b), Watson & Balon (1984) and Winemiller (1991, 1992), are also evident when chemical variables are used to group species.

Ringuelet et al. (1967a) and Ringuelet (1975) proposed a descriptive classification of biological types of Argentinean fishes based on several morphological, adaptive, and behavioral characteristics as well as classes of habitat. Their system is consistent enough to allow for an understanding of the main relationships between morphology and ecology of Neotropical fishes. In the present context, only three basic morphological types of fishes are considered according to relative measurements of body height and body width: depressed, when body height is less than body width; compressed, when body height is larger than body width and subcylindrical when the two measurements are alike (Table 2).

In general, depressed body forms are related to increasing current velocity whereas deep bodied forms are mainly found in middle or surface water swimmers. Also many other morphological features can be related to general ecology and types of habitat (Alexander, 1967; Gosline, 1973; Gatz, 1979a; Winemiller,1991). A model has been proposed where the ratio between the exponent of the metabolic equation and the exponent of the length–weight relationship have different values for different ecological groups. *A. eigenmanniorum, B. iheringi* and *O. jenynsi* show values around 2.458 while *P. maculatus* and *H. m. malabaricus* show values around 1.841 (Freyre & Protogino, 1993). These two groups, based on an independent biological trait are consistent with the following analysis.

Gatz (1979a) discussed the variation and interrelationships among 56 morphological characters and the

Table 8. Tolerance ranges for species tolerating at least one absolute maximum or one absolute minimum value. Number under the species name is the total of absolute values tolerated. Last column shows the number of tolerated maximum or minimum values, or both.

		COND	TDS	t	pH	CO_3^{2-}	CO_3H^-	Cl^-	SO_4^{2-}	Na^+	K^+	Ca^{2+}	Mg^{2+}	Mg/Ca	Mg+Ca /Na+K	
A. b. bimaculatus	M	3419	2077.3	--	--	—	--	846.2	835.4	800.0	27.5	164.3	60.5	--	--	8
(13)	m	30	46.0	--	--	0.0	--	--	--	2.6	--	4.2	--	--	--	5
A. f. fasciatus	M	3419	2077.3	--	--	--	--	846.2	835.4	800.0	27.5	164.3	60.5	--	--	8
(13)	m	30	46.0	--	--	0.0	--	--	--	2.6	--	4.2	--	--	--	5
A. eigenmanniorum	M	--	--	--	--	--	--	--	835.4	--	27.5	164.3	60.5	--	--	4
(11)	m	--	--	10.2	6.6	0.0	--	--	--	--	0.4	--	0.0	0.00	0.26	7
J. l. lineata	M	3419	2077.3	--	9.6	48.9	542.1	846.2	--	800.0	--	--	--	--	--	7
(11)	m	--	--	10.2	--	0.0	--	--	--	--	--	--	0.0	0.00	--	4
C. i. interruptus	M	3419	2077.3	--	--	--	--	846.2	835.4	800.0	27.5	164.3	60.5	--	—	8
(10)	m	--	--	10.2	--	0.0	--	--	--	--	--	--	--	--	--	2
B. iheringi	M	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0
(10)	m	30	46.0	10.2	--	0.0	--	--	--	2.6	0.4	4.2	0.0	0.00	0.26	10
T. corduvense	M	--	--	31.0	9.6	48.9	542.1	--	--	--	--	--	--	2.12	--	5
(9)	m	--	--	10.2	--	0.0	--	0.0	--	--	--	--	--	--	0.26	4
C. stenopterus	M	--	--	--	--	--	--	--	835.4	--	27.5	164.3	60.5	--	--	4
(5)	m	--	--	--	--	0.0	--	--	--	--	--	--	--	--	--	1
H. m. malabaricus	M	--	--	--	--	--	--	--	835.4	--	27.5	164.3	60.5	--	--	4
(5)	m	--	--	--	--	0.0	--	--	--	--	--	--	--	--	--	1
S. spilopleura	M	--	--	--	--	--	--	--	835.4	--	27.5	164.3	60.5	--	--	4
(5)	m	--	--	--	--	0.0	--	--	--	--	--	--	--	--	--	1
O. jenynsi	M	--	--	--	--	--	--	--	835.4	--	27.5	164.3	60.5	--	--	4
(5)	m	--	--	--	--	0.0	--	--	--	--	--	--	--	--	--	1
C. decemmaculatus	M	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0
(4)	m	--	--	--	6.6	0.0	19.5	0.0	--	--	--	--	--	--	--	4
C. voga	M	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0
(4)	m	--	--	--	6.6	0.0	19.5	0.0	--	--	--	--	--	--	--	4
P. doriai	M	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0
(4)	m	--	--	--	6.6	0.0	19.5	0.0	--	--	--	--	--	--	--	4
H. meridionalis	M	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0
(4)	m	--	--	--	6.6	0.0	19.5	0.0	--	--	--	--	--	--	--	4
H. cordovae	M	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0
(3)	m	--	--	--	--	0.0	--	--	0.0	--	0.4	--	--	--	--	3
H. mustelinus	M	--	--	--	--	--	--	--	--	--	--	--	--	--	5.59	1
(2)	m	--	--	--	--	0.0	--	--	--	--	--	--	--	--	--	1
T. alterum	M	--	--	--	--	--	--	--	--	--	--	--	--	--	5.59	1
(2)	m	--	--	--	--	0.0	--	--	--	--	--	--	--	--	--	1

general ecology of 44 species of stream fishes. Gatz (1979a) stated that there should be strong correlation between such a feature (a morphological one) and some manifestations of its biological role. Also there should be a correlation between this feature and others associated with the same role, so that some significance portion of the biology of a freshwater stream fish is determined by its morphology.

From 34 species considered, 18 were compressed (52.95%), 10 depressed (29.41%), and 6 subcylindrical (17.64%). These frequencies can be expected for each category in any subset of those species sampled at random. Instead, percentages of morphological types differ from those quoted above (Figures 15 and 16). Within clusters CM and Cm, which group a majority of endemic species or species with restricted distributions, the number of depressed species is 50% and

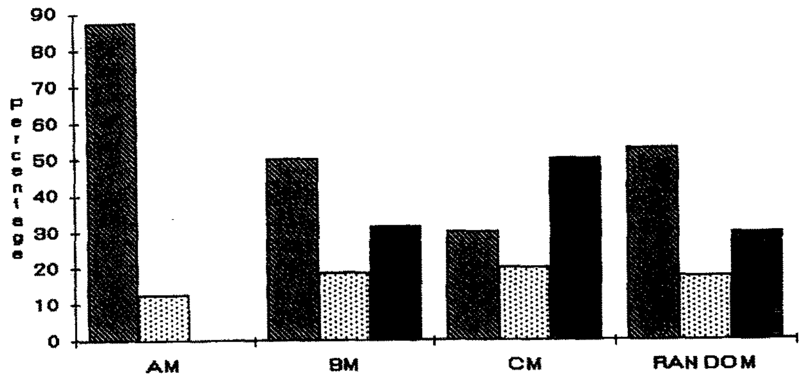

Figure 15. Percentage of species from each morphological type (Compressed: diagonal lines, Subcylindrical: stippled, Depressed: horizontal lines) occurring in clusters based on maximum values (AM, BM, CM).

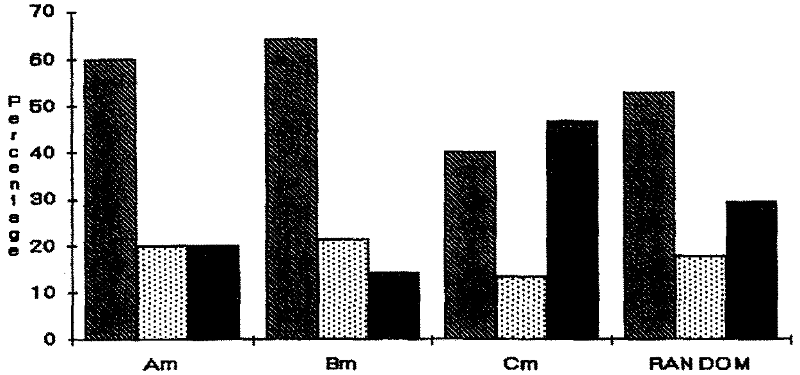

Figure 16. Percentage of species from each morphological type (Compressed: diagonal lines, Subcylindrical: stippled, Depressed: horizontal lines) occurring in clusters based on minimum values (Am, Bm, Cm).

46.7% respectively. This is larger than expected at random (29.4%). Within the same clusters, the number of compressed forms is 30% and 40% respectively. The value expected at random for this type, is 52.9% (Figures 15 and 16).

Clusters AM and Am, containing many eurytopic species, show a predominance of compressed forms, and a single depressed form in Am and none in AM.

The BM cluster, where typical Paranoplatensean species are grouped, show frequencies of the three types similar to those randomly expected (BM $p < 0.95$; Bm $p < 0.95$). This suggests that the area closely related with the Paraná and Uruguay rivers is, at present, the 'normal' or common habitat for subtropical species in Argentina. This area provides the optimal conditions for diversity and abundance, because of its size, variety of habitats, food richness, and complex ecology.

Frequencies of the subcylindrical forms are similar among clusters (12.5–21.4%), with values close to those expected at random (Figures 15 and 16).

The preceding analysis shows that there is a correlation between water chemistry, types of environment, distribution, and the history of particular faunas which has been largely underestimated in past work. We do not imply that water chemical characteristics are the cause of these differences, though we do assume that differential clustering of species according to chemical water traits indicates the presence of different fish communities. One attribute of these communities is, of course, their specific composition. Ecological relationships can be inferred from an analysis of morphological features (Winemiller, 1991). In the present study the converse approach was used to show that species clusters derived from ecological traits show different composition in term of species, distribution patterns, physiological features, and relative incidence of biological types.

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