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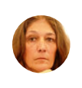

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ECOLOGY OF POTENTIAL HOSTS OF SCHISTOSOMIASIS IN URBAN ENVIRONMENTS OF CHACO, ARGENTINA

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ABSTRACT

Some of the *Biomphalaria* species living in Chaco, such as *B. straminea* and *B. tenagophila,* are natural transmitters of schistosomiasis in Brazil, while those of the genus *Drepanotrema* are not intermediate hosts of the disease. The aim of the present work was to analyze the importance of a selected set of environmental variables in explaining patterns of distributions and relative abundance of planorbid gastropod assemblages. The study sites were located in urban areas of Resistencia City, Chaco Province, and the environmental variables measured were substratum (macrophytes), water quality (pH, O_2, nutrients, among others), as well as other gastropods (Ancylidae, Hydrobiidae and Ampullaridae). Seasonal samplings were carried out in four distinct environments. Thirty-one quantitative samples of gastropods and environmental variables were obtained. In canonical correspondence analysis (CCA), seven environmental variables were retained after a stepwise forward selection, from a total of 26, including [$N\text{-}NH_4^+$], O_2%, and the macrophytes *Eichhornia crassipes, Pistia stratiotes, Panicum elephantipes, Hydrocotyle ranunculoides* and *Canna glauca.* They explained 62% of the variation in planorbid association. *Canna glauca* was the most significant variable, being positively correlated with all of the species of *Drepanotrema.* Axis I separates *B. tenagophila* from *B. straminea,* along a gradient related to increasing O_2% and *P. elephantipes* abundance, as well as decreasing [$N\text{-}NH_4^+$] and *P. stratiotes.* Axis II separates *D. lucidum, D. anatinum* and *D. cimex* from the other planorbid species along a gradient associated with decreasing abundances of *H. ranunculoides* and *C. glauca.* Some common aquatic macrophytes, and to a lesser extent, dissolved oxygen and ammonium in water, may be useful indicators of favorable environmental conditions for potential intermediate hosts of schistosomiasis in Chaco Region.

Key words: Gastropoda, Planorbidae, vector-ecology, schistosomiasis, intermediate-hosts, Chaco Region, Paraná River.

INTRODUCTION

The southern expansion of mansonic schistosomiasis in the Neotropical region (Paraense & Corrêa, 1987) necessitates developing preventive strategies in those areas with major risk of disease penetration. In Argentina, these zones are related to the Guyano-Brazilian subregion, mainly occupied by the Del Plata Basin, that includes geographic areas such as Chaco, Mesopotamia and Pampas (Bonetto, 1994). The most probable colonization path is along the sub-basin of the Paraná River, since the most recent infestation foci of *Schistosoma mansoni* Sambon, 1907 (Trematoda: Digenea), discovered in southern Brazil, were found in localities within that sub-basin in proximity to Argentina. One of these foci was located at San Francisco do Sul, Santa Catarina State, near the headwaters of the Iguazú River (Bernardini & Machado, 1981), with *Biomphalaria tenagophila* (d'Orbigny, 1835) as intermediate host. The other was located in the Piquiri River, a tributary of the Paraná River (Paraense, 1986), with *B. glabrata* (Say, 1818) the intermediate host. Up to now, the latter host has not been detected in Argentina. *Biomphalaria tenagophila* was described with type locality in "Cantón de las Ensenadas", Corrientes Province, Argentina (d'Orbigny, 1835), and *Biomphalaria straminea* from Caracas, Venezuela (Dunker, 1848), was recorded here about 30 years ago. These two

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latter species are very common in freshwater habitats of northeastern Argentina.

A detailed knowledge of the biology of possible hosts of schistosomiasis, as well as the host-parasite relationships established in both natural and urban environments, is necessary for any control strategy (Rumi et al., 1997). Several research studies have been conducted in the Paraná and Uruguay river basins, including species identification, ecology, demography, population dynamics, and spatial distribution of potential intermediate hosts of *S. mansoni* (Bonetto et al., 1982, 1990; Olazarri, 1978, 1984; Rumi, 1991, 1993; Rumi & Hamann, 1990, 1992; Rumi & Tassara, 1985; Tassara & Bechara, 1983). These potential hosts are always species of the genus *Biomphalaria* Preston, 1910 (Mollusca: Gastropoda: Planorbidae), though the studies also treated non-transmitter planorbids of the genus *Drepanotrema* Preston, 1910. Other studies consider the host-parasite relationships with autochthonous trematodes in natural and urban environments (Ostrowski de Núñez et al., 1989, 1991; Rumi & Hamann, 1990, 1992).

Urban environments, like those analyzed in the present paper, are particularly interesting because of the high probability of schistosomiasis transmission to humans, in case this parasitism was found in Argentina. In the humid portion of the Chaco Plains, the Paraná River and its tributaries frequently generate an extensive plain of meanders with hundreds of lakes. Many human settlements are well established at those places, including small towns and medium-sized cities. Therefore, the identification of environmental variables that would allow a rapid evaluation of the potential of a habitat to support planorbids might be a useful strategy to prevent proliferation of the disease.

As a general rule, the environmental alterations produced by human activities modify the adaptive capacities of host species, as well as their abilities to transmit the disease. Consequently, it is necessary to study these hosts in natural and urban environments in order to contrast their dynamics in different conditions. According to ter Braak & Prentice (1988), most species occupy a limited area of the available habitat, tending to be more abundant in their optimal conditions. Consequently, assemblage composition shifts along gradients of environmental variables, and species replacements tend to follow the pattern of spatial and temporal variation of those variables. Gradients are not necessarily physically continuous in space or time, but it is a useful abstraction to explain organism distributions (Austin, 1985). The concept of spatial partition of the life zone also implies the separation of species along "resource gradients" (Tilman, 1982), "regulator gradients" or "complex gradients" (Huston, 1994). This scheme resulted in two classical models: the environmental control, in which environmental variables regulate the presence and abundance of organisms (Whittaker, 1956), and biotic control, in which the relationships among organisms, such as competition and predation (Connell, 1983), are considered as the main factors that structure communities. In an alternative model, Quinn & Dunham (1983) proposed that they are not mutually exclusive, but both contribute.

This paper aims to identify and analyze, in different planorbid assemblages found in urban environments in the city of Resistencia, Chaco Province, Argentina. The most important biotic and abiotic variables that explain their distribution and patterns of relative abundance.

MATERIAL AND METHODS

Study Area

The sampling area was located between Resistencia and Barranqueras (59°15′S, 27°44′W), Department of San Fernando, Chaco Province (Fig. 1). According to Drago (1990), the environments involved in the present study are within in the Paraná River Basin, which encompasses the second most important watercourse in South America after the Amazon. These environments are on the right margin of the alluvial plain of the Middle Paraná River. A large plain of meanders, with very low slope (10 to 12 cm km^{-1}), runs across this sector of the plain. Soils are brown silty-clay, with abundant calcareous material in some places, and elevated alkalinity. An important feature of this alluvial system is the great density of subcircular, shallow waterbodies (< 5 m depth), organized in a drainage arrangement that shows different degrees of connection between lotic and lentic waterbodies. Commonly, they are oxbow lakes and other meander-generated lakes and wetlands, locally named "madrejones". Most of them are rich in floating, submerged or settled

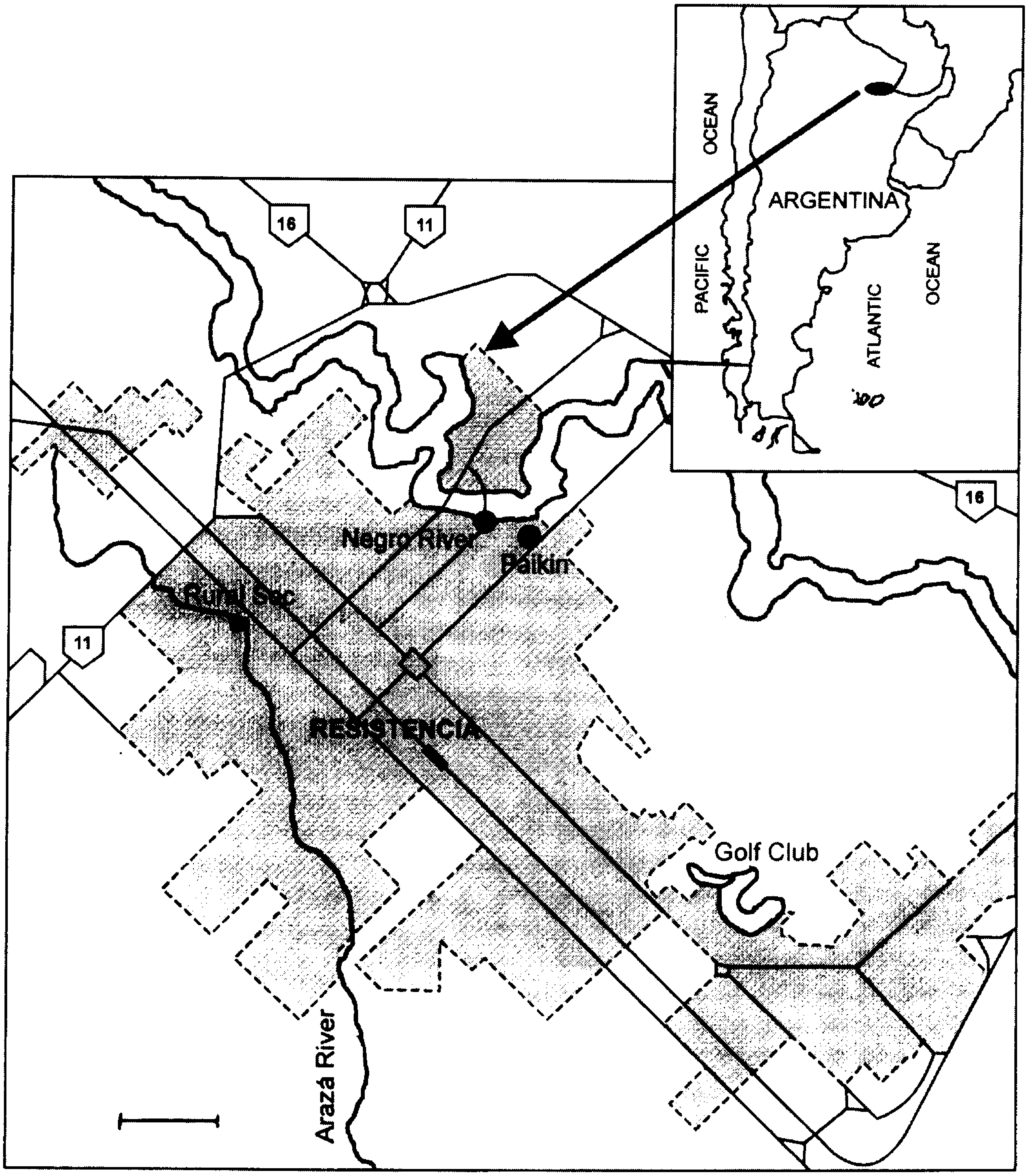

FIG. 1. Geographic location of the study area and sampled biotopes. Scale bar = 1km.

aquatic vegetation, surrounded by hydrophilic gallery forests. In the plain of meanders, lakes are found in different states of succession, beginning with the active meandering river channel, followed by recently generated lakes, ending in the almost complete coverage of the pond basin with palustrine vegetation and sediments. Usually these ponds are shallow (up to 2 m deep).

The climate of eastern Chaco is subtropical, subhumid mesothermal, with a mean annual temperature of 23°C, and monthly averages between 17°C in July and 28°C in January. The mean annual rainfall ranges between 950 and 1,100 mm, distributed almost uniformly around the year, with peaks in spring (September–October) and fall (March–April).

Sampling Scheme

Selection of variables, identified a priori as presumably important for colonization and development of planorbid populations, was based on three criteria:

(1) Relationships with the substratum—mainly composed of aquatic vegetation, and described at the scale of their relative abundances. The pulmonate snail uses macrophytes as sites for reproduction, feeding, and shelter. Consequently, a decrease in abundance of macrophytes generally results in a decrease of gastropod populations (Thomas & Daldorph, 1994).

(2) Relationships with water quality variables—including indicators of the trophic state of the selected habitats (nutrient concentrations), as well as other variables related to the snail abundance along regulator gradients (pH, oxygen, and calcium concentrations).

(3) Relationships with other members of the mollusk assemblages—also referred to a scale of relative abundance, representing potential competitors or making up a part of multispecific associations.

To include the four climatic seasons, samplings were carried out quarterly, between February 2, 1988, and October 23, 1989. This area was first widely surveyed to inventory habitats. Four sampling sites were selected based on their planorbid richness: Negro River, at the Municipal Beach of Resistencia City; Paikín, a oxbow-lake related to a suburb of the same name, used as garbage deposit by people living in a group of huts without a sewer system; Rural Society, a pond within the "Rural Society" of Chaco Province, belonging to the Arazá River corridor, which was partially channeled underground; and Golf Club, a pond near the Resistencia "Golf Club", being probably an old oxbow-lake of the Negro River. The Negro and the Arazá rivers cross the city of Resistencia NE-SW toward the city of Barranqueras, draining into the Paraná River (Fig. 1). The present human population inhabiting both cities is around 300,000 people.

Gastropod sampling was carried out with a mean collection time of 41 min (standard deviation, 18 min) within a range of about 6.5 h (from 9:30 to 16:00); snail abundance was determined as capture per unit effort (CPUE) in terms of specimens hour^{-1}. Collections were made with simple meshed, standard samplers (Thiengo, 1995), locally named "copos" (1 mm mesh size, and 13.5 cm frame diameter). Thirty-one samples were obtained from the littoral zone of the habitats (0.5–1.0 m deep).

Collected material was carried alive to the laboratory and prepared for identification, dissection of soft parts, counting and measuring. The planorbid specimens were relaxed in a Nembutal solution 0.01% for approximately 24 h, according to the method described by Paraense (1986). Afterwards, they were sacrificed by immersion in water at 65–70°C for 45–55 sec, and submerged in fresh water equilibrated with air temperature. Finally, the prepared material was fixed in a Raillet-Henry solution (Paraense, 1976), to facilitate its identification by dissection of the soft parts under a stereoscopic microscope.

At each sampling site, physical and chemical variables were monitored immediately before the capture of gastropods. Temperature, pH and conductivity were measured using thermistors, electrode pH-meters, and battery conductivity-meters, respectively. In addition, water samples were taken with a peristaltic pump and transported refrigerated to the laboratory, where the following variables were measured: dissolved oxygen concentration (Winkler method), oxygen percentage saturation, nutrients (nitrites + nitrates, total soluble nitrogen, ammonium and total soluble reactive phosphorus), calcium, hardness, and alkalinity. Chemical analyses where performed according to Standard Methods (1980) and Golterman et al. (1978).

Regarding vegetation, the criterion of relative dominance was employed, based on visual inspection of the sampling area. Plants were coded between 0 and 4 for the data matrix, according to the following scale: 0 = absent (0%); 1 = rare (1–25%); 2 = frequent (25%–50%); 3 = co-dominance (50–99%); and, 4 = complete dominance (100%). The surveyed macrophytes belonged to free-floating covers: *Eichhornia crassipes* (Mart.) Solms. (Pontederiaceae), *Pistia stratiotes* L. (Araceae), *Spirodela intermedia* W. Koch. (Lemnaceae), *Salvinia herzogii* de la Sota, and *S. rotundifolia* Willd. (Salvinaceae); settled with floating leaves: *Victoria cruziana* d'Orbigny (Ninfaceae); settled: *Enhydra anagallis* Gardn. (Compositae), *Hydrocotyle ranunculoides* L. (Umbeliferae), and *Ludwigia peploides* (H.B.K.) Hara (Onagraceae); emergent: *Panicum elephantipes* Nees (Gramineae), *Canna glauca* L. (Cannaceae); and unidentified cespitose hydrophilic Gramineae (Table 3).

Statistical Analyses

Data on gastropod abundance and limnological variables were transformed to decimal logarithm (log(x+1)) to linearize relationships among the variables. The multivariate technique chosen to explore the relationships between environmental variables (independent variables) and snails taxocenosis (dependent variables) was canonical correspondence analysis (CCA) (ter Braak, 1986; ter Braak & Prentice, 1988). The program CANOCO 4 (ter Braak & Smilauer, 1998) was employed to perform the analyses, including adjustment of model parameters, goodness of fit tests, and plotting the results. This canonical ordination technique is a combination of ordination in reduced space and multiple regression. It implies the representation of samples and species constrained by environmental variables in the reduced space of orthogonal axes, which are in turn linear combinations of species relative abundance and environmental gradients. This method assume both unimodal (Gaussian) or linear relationships between species and environmental variables, for long or short environmental gradients, respectively. It shows the major trends of variation of multidimensional data within a reduced space of linearly independent canonical axes, and it is a useful tool to understand community composition in terms of species distribution along different environmental gradients. Therefore, given the unimodal proprieties of CCA, linear relationships between a given environmental variable and species are not required, such as in most canonical multivariate techniques.

The unimodal properties of the model allow the estimation of optimum and tolerances of the species, both indicators of niche attributes. Optimum can be approximated by the CANOCO 4 output named "spaces-by-environmental table", which are weighted averages of species with respect to standardized environmental variables. Results are represented graphically in a reduced space of orthogonal axes, displaying the distribution of species, samples, and/or environmental gradients in the same bidimentional space (biplots and triplots). Since triplots with species scorers and environmental scorers may be in error because they contain the main patterns only, this table is useful to verify that inferences drawn from the plots hold true in the actual data on weighted averages (ter Braak & Smilauer, 1998).

Among the 26 environmental variables surveyed, it was necessary to preselect those of higher contribution to the total variability in snail relative abundance in order to reduce the possibility of an artificial increase in the explained variance by environmental factors, as well as multicolinearity. Stepwise forward selection procedure was employed, using Monte Carlo permutation tests, as implemented in CANOCO 4. A critical rejection level of $P < 0.10$ was applied. The amount of variance explained by the whole model and the first ordination axes was calculated employing Monte Carlo permutation tests, with a critical rejection level of $P < 0.05$.

RESULTS

Planorbid Species

The following planorbid species were found (Table 1): *Biomphalaria tenagophila* (d'Orbigny, 1835), *B. straminea* (Dunker, 1848), *Drepanotrema anatinum* (d'Orbigny, 1835), *D. lucidum* (Pfeiffer, 1839), *D. kermatoides* (d'Orbigny, 1835), and *D. cimex* (Moricand, 1937). In three samples, no planorbids were found; these were omitted from the subsequent statistical analysis.

Biomphalaria straminea occurred more frequently than *B. tenagophila* (48% and 35%, respectively), but the latter showed much higher abundances, especially in 1989. Distributional patterns in space were also different, with *B. straminea* being more common in Negro River and Golf Club Pond, whereas *B. tenagophila* was more abundant in Rural Society and Paikín ponds. Both species are intermediate hosts of schistosomiasis in Brazil.

Species of *Drepanotrema* were much less frequent than *Biomphalaria* (10–16%), but abundances were highly variable in time and space, with values similar in order of magnitude to those of *B. straminea,* and never reaching the high levels of *B. tenagophila. Drepanotrema cimex* and *D. anatinum* were found almost exclusively in Paikín Pond, a biotope where the other species of *Drepanotrema* also showed the highest frequency. In the remaining environments, this genus was rarely found, with *D. anatinun* in Rural Society Pond (one presence), *D. lucidum* in Negro River (two presences), and *D. kermatoides* in Golf Club Pond (two presences).

TABLE 1. Abundance of planorbid species (individuals $hour^{-1}$) sampled in the Negro River, Paikín oxbow lake, Rural Society and Golf Club ponds, from Resistencia City in all sampling dates.

Biotopes	Dates	*B. tenagophila*	*B. straminea*	*D. anatinum*	*D. lucidum*	*D. kermatoides*	*D. cimex*
Golf Club Pond	29/02/88	0	21	0	0	0	0
	06/06/88	0	2	0	0	0	0
	23/08/88	9	28	0	0	0	0
	16/11/88	0	36	0	0	0	0
	21/02/89	0	0	0	0	69	0
	05/04/89	573	146	0	0	0	0
	27/07/89	0	195	0	0	0	0
	23/10/89	0	86	0	0	15	0
	Mean	72.8	64.3	0.0	0.0	10.5	0.0
Negro River	29/02/88	0	154	0	62	0	0
	06/06/88	0	10	0	3	0	0
	23/08/88	0	41	0	0	0	0
	21/02/89	0	27	0	0	0	0
	27/07/89	0	8	0	0	0	0
	Mean	0.0	48.0	0.0	13.0	0.0	0.0
Paikín Pond	02/02/88	71	134	91	68	0	14
	06/06/88	0	0	8	0	0	26
	23/08/88	0	0	132	106	0	70
	21/02/89	0	0	14	0	106	14
	05/04/89	144	0	0	0	10	0
	27/07/89	650	0	0	0	0	60
	23/10/89	223	0	0	0	123	0
	Mean	155.4	19.1	35.0	24.9	34.1	26.3
Rural Soc. Pond	29/02/88	72	0	0	0	0	0
	06/06/88	6	12	3	0	0	0
	23/08/88	0	60	0	0	0	0
	16/11/88	536	0	0	0	0	0
	21/02/89	167	0	0	0	0	0
	05/04/89	222	0	0	0	0	0
	27/07/89	179	0	0	0	0	0
	Mean	168.9	10.3	0.4	0.0	0.0	0.0

Environmental Variables

For all sampling periods and sites, physical and chemical variables are shown in Table 2. Water temperature varied between 8°C in June 1988 and 32°C in February 1988. Averages values were similar among sampling sites, being only 1-2°C higher in the Rural Society Pond and Golf Club Pond, respectively. These differences may be partly because sampling hours were not the same for all biotopes. The pH ranged from 6.3 to 8.9 (October 1989 and February 1988, respectively), being alkaline in most sampling dates in Rural Society Pond, and closer to neutral point in the others waterbodies. Specific conductivity showed marked spatial and temporal variations within a range of 90 and 1,600 μS cm^{-1} (August 1988 and November 1988, respectively). The highest conductivities were measured in Golf Club Pond and the lowest in Negro River. Oxygen concentration $[O_2]$ and oxygen saturation percentage $(\%O_2)$ were low or undetectable during the warmest periods, increasing during winter and spring, with figures as high as 8.1 mg l^{-1} and 90% saturation.

Calcium concentration $[Ca^+]$ was also highly variable (Table 2), ranging from 9.5 to 119.4 mg l^{-1} in Paikín Pond (July 1989 and February 1989, respectively). According to Dussart's (1976) classification of mollusk habitat regarding calcium concentration, the highest mollusk abundance generally corresponds to the hardest waters ($[Ca^+] > 40$ mg l^{-1}), while the highest diversity is usually observed in mid-range waters ($[Ca^+]$ between 5-40 mg l^{-1}). Sampled environments of Chaco generally had waters of medium hardness, although hard waters were observed on some occasions (Table 2). Calcium concentration was positively correlated with hardness ($r = 0.677$, $n = 31$, $P < 0.01$), a variable that ranged between 36 and 329 mg l^{-1} (June 1989 and February 1989, respectively). The range of alkalinity due to $[HCO^{-3}]$ was 45-357 mg l^{-1} (October 1989 and August 1988, respectively). Rural Society Pond generally showed the highest levels of alkalinity, while Negro River had the lowest.

Concerning nutrient concentrations (Table 2), nitrates and nitrites $[N\text{-}NO_3 + N\text{-}NO_2]$, were usually below 0.4 mg l^{-1}, reaching exceptionally 9.6 mg l^{-1} on November 1988 in Paikín Pond. Ammonium concentration $[N\text{-}NH_4^+]$ showed maximum levels in Paikín Pond during 1989, and minimum levels in Rural Society Pond most of the time. This nutrient also tended to increase in all waterbodies during the second sampling year. Total soluble nitrogen (N-SOL) followed the same pattern of ammonium. Finally, phosphate concentration $[P\text{-}PO_4]$ was generally below 1.0 mg l^{-1}, reaching exceptionally high levels in one sampling date in Paikín Pond and Rural Society Pond. In Negro River, phosphates had the lowest concentrations of all waterbodies, never being over 0.3 mg l^{-1}.

Relative abundances of aquatic plants are shown in Table 3. Among the most important emergent macrophytes, *Panicum elephantipes* was frequent and dominant in Golf Club Pond and Negro River, but absent in the other waterbodies. On the other hand, *Canna glauca* was always dominant in Paikín Pond, and completely absent from the other biotopes. Among other settled macrophytes, *Enhydra anagallis* was frequent and important in Paikín and Rural Society ponds, while *Hydrocotile ranunculoides* was present only on some dates in Rural Society Pond and Paikín Pond. Of free-floating plants (Table 3), *Pistia stratiotes* was dominant in Rural Society Pond and during 1989 in Golf Club Pond. *Eichhornia crassipes* was completely absent from Negro River, and present in variable abundance and frequency in the remainder of the waterbodies.

Other gastropods that were present with planorbids (Table 3), were *Heleobias spp.* (Hydrobiidae), *Stenophysa marmorata* (Guilding, 1828) (Physidae), *Gundlachia moricandi* (d'Orbigny, 1835) (Ancylidae), and species of the family Ampullariidae, mainly *Pomacea canaliculata* (Lamark, 1801) and *P. scalaris* (d'Orbigny, 1835). All the gastropods found with planorbids were eliminated in the stepwise forward selection of independent variables. *Pomacea canaliculata* was the most frequent gastropod considering all samples. This species has also a wide distribution in del Plata Basin, especially in the Argentinean area.

Canonical Correspondence Analysis

Seven of the 26 environmental variables used in the canonical correspondence analysis (CCA, Table 4) were retained in the stepwise forward selection procedure. For all of the selected variables, the variance inflation factor (V.I.F.) was below 5, the level suggested for

TABLE 2. Values of physical and chemical variables measured in the Negro River, Paikín oxbow lake, Rural Society and Golf Club ponds from Resistencia City in all sampling dates. n/d = not detectable; * = data not available

Biotopes	Dates	Water temp (°C)	pH ([H$^+$])	Conductivity (□S cm^{-1})	D.O. (mg l^{-1})	D.O. (%)	HCO$_3^+$ (mg l^{-1})	Hardness (mg l^{-1})	Ca+ (mg l^{-1})	NO$_3$+NO$_2$ (mg l^{-1})	N-NH$_4^+$ (mg l^{-1})	N-SOL (mg l^{-1})	P-PO$_4$ (mg l^{-1})
Golf Club Pond	29/2/88	29	7.7	120	4.4	57.0	178	121.0	28.4	0.073	0.025	0.098	0.080
	6/6/88	8	7.8	1200	8.1	70.0	200	222.6	49.4	0.036	0.049	0.085	0.136
	23/8/88	28	7.7	1200	3.3	42.0	238	132.7	30.4	0.290	0.063	0.353	0.152
	16/11/88	30	7.2	1600	n/d	n/d	*	99.0	22.0	n/d	0.250	0.250	0.026
	21/2/89	28	7.2	1000	n/d	n/d	185	153.0	45.2	0.010	0.550	0.560	0.832
	5/4/89	27	6.8	385	4.0	50.5	124	57.2	17.0	0.010	2.750	2.760	0.488
	27/7/89	16	7.0	650	4.1	41.5	165	36.0	12.0	0.030	1.000	1.030	0.648
	23/10/89	31	6.3	850	5.8	78.5	45	47.2	13.4	0.025	0.250	0.275	0.600
	Mean	24.8	7.2	876	4.9	56.6	162	220.1	27.2	0.068	0.617	0.676	0.370
Negro River	29/2/88	32	7.45	215	5.3	73.0	164	75.6	16.4	0.081	0.050	0.128	0.150
	6/6/88	13	7.0	600	3.0	28.3	88	58.8	13.3	0.050	0.290	0.340	0.082
	23/8/88	24	7.8	350	4.2	50.0	262	272.2	61.0	0.344	0.238	0.582	0.300
	21/2/89	23	6.7	600	6.7	78.0	78	61.0	15.0	0.015	0.450	0.465	0.260
	27/7/89	21	6.9	700	1.5	17.0	98	50.0	15.0	0.010	1.750	1.760	0.220
	Mean	20.3	7.1	563	3.8	43.3	132	110.5	26.1	0.105	0.682	0.787	0.216
Paikín Pond	29/2/88	28	7.0	380	5.3	68.5	160	45.0	11.8	0.005	0.067	0.072	0.240
	6/6/88	11	7.2	700	8.1	74.0	307	100.8	23.5	0.090	0.131	0.221	0.136
	23/8/88	24	7.4	200	4.5	53.5	357	134.4	32.0	0.019	0.132	0.151	0.208
	21/2/89	24	6.5	1300	2.2	26.5	75	329.0	119.4	9.600	8.000	17.600	0.664
	5/4/89	22	6.9	380	1.4	17.0	170	85.0	18.0	0.014	6.000	6.014	2.320
	27/7/89	22	6.8	470	1.8	20.5	203	36.0	9.5	0.100	1.100	1.200	0.180
	23/10/89	28	8.4	420	1.8	23.0	202	33.8	10.6	0.030	1.100	1.130	0.158
	Mean	22.7	6.9	550	3.6	40.4	211	109.1	32.1	1.408	2.361	3.770	0.558
Rural Soc. Pond	29/2/88	31	8.9	95	6.7	90.0	220	85.6	18.0	0.018	0.021	0.039	0.100
	6/6/88	13	8.4	1000	8.1	76.5	241	92.4	19.0	0.350	0.090	0.440	0.070
	23/8/88	21	8.6	90	3.3	36.0	278	63.8	17.6	0.182	0.081	0.263	0.152
	16/11/88	29.9	6.6	750	n/d	n/d	*	109.0	37.0	0.012	0.253	0.265	3.800
	21/2/89	24	8.4	1200	5.3	63.0	332	61.0	19.2	0.030	0.450	0.480	0.240
	5/4/89	25	6.7	700	3.8	46.0	208	148.5	35.4	0.010	2.500	2.510	0.090
	27/7/89	20.5	7.0	700	3.4	38.5	200	99.0	33.0	0.010	0.440	0.450	0.020
	Mean	23.5	7.8	648	5.1	58.3	247	94.2	25.6	0.087	0.548	0.635	0.639

TABLE 3. Relative dominance observed in macrophytes and non-planorbid mollusks, measured in the Negro River, Paikín oxbow lake, Rural Society and Golf Club ponds from Resistencia City, in all sampling dates. Macrophytes: *Eichhornia crassipes, Pistia stratiotes, Spirodela intermedia, Enhydra anagallis,* Gramineae, *Ludwigia peploides, Panicum elephantipes, Victoria cruziana, Hydrocotyle ranunculoides* and *Canna glauca.* Mollusks: *Heleobias* sp., *Stenophysa marmorata, Gundlachia moricandi, Pomacea canaliculata* y *P. scalaris.*

		Macrophytes										Freshwater mollusks				
Biotopes	Dates	E. cr.	P. st.	Spir.	E. an.	Gram.	L. pe.	P. el.	V. cr.	H. ra.	C. gl.	Hel.	S. ma.	G. mo.	P. ca.	P. sc.
Golf Club Pond	29/02/88	0	0	0	0	0	3	4	2	0	0	1	0	0	3	0
	06/06/88	0	0	0	0	0	3	4	2	0	0	0	0	0	0	0
	23/08/88	0	0	0	0	0	3	4	2	0	0	4	0	0	3	4
	16/11/88	0	3	0	0	0	0	4	0	0	0	0	0	0	0	0
	21/02/89	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
	05/04/89	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0
	27/07/89	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0
	23/10/89	4	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Negro River	29/02/88	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
	06/06/88	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
	23/08/88	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
	21/02/89	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
	27/07/89	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Paikín Pond	02/02/88	3	0	0	0	4	3	0	0	0	4	0	0	0	4	0
	06/06/88	3	0	0	0	4	3	0	0	0	4	0	2	1	2	0
	23/08/88	0	0	0	0	4	0	0	0	3	4	0	4	0	0	0
	21/02/89	0	0	0	4	0	0	0	0	0	4	0	0	0	0	0
	05/04/89	0	0	0	4	0	0	0	0	0	4	0	4	0	0	0
	27/07/89	0	4	0	3	0	0	0	0	0	0	0	4	0	2	0
	23/10/89	0	0	4	0	0	0	0	0	0	3	0	0	0	0	0
Rural Soc. Pond	29/02/88	1	2	0	3	0	0	0	0	2	0	0	0	0	0	0
	06/06/88	1	2	0	3	0	0	0	0	2	0	0	0	4	0	0
	23/08/88	1	2	0	3	0	0	0	0	2	0	0	0	0	0	0
	16/11/88	0	4	0	3	0	0	0	0	0	0	0	0	0	0	0
	21/02/89	0	4	0	3	0	0	0	0	0	0	0	0	0	0	0
	05/04/89	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0
	27/07/89	0	4	0	1	0	0	0	0	0	0	0	0	0	4	0

TABLE 4. Summary of major results of the canonical correspondence analysis relating planorbid species to the selected environmental variables.

Canonical Axes	I	II	III
Eigenvalues	0.469	0.401	0.354
Cumulative percentage of variance of species data	23.4	43.4	61.0
Cumulative percentage variance of species-environment relation	37.6	69.8	98.2
Species-environment correlation	0.840	0.837	0.838
Correlation of the environmental variables with the axes			
P. elephantipes	–0.543	–0.346	–0.190
C. glauca	0.095	0.684	0.413
H. ranunculoides	–0.139	0.461	–0.036
E. crassipes	–0.221	–0.006	–0.068
P. stratiotes	0.385	–0.274	–0.587
[N-NH4$^+$]	0.408	–0.133	0.310
%O_2	–0.291	0.268	–0.237
Total of unconstrained eigenvalues			2.006
Total of canonical eigenvalues	1,247 (62% of explained variance)		

avoiding multicolinearity and over-explanation (ter Braak and Smilauer, 1998). Ammonium [N-NH_4^+] and percentage saturation of D.O. (%O_2) were the water quality variables retained. The remaining environmental variables were all macrophytes, including *P. stratiotes, E. crassipes, H. ranunculoides, P. elephantipes,* and *C. glauca.* The selected environmental variables explain 62% of the total variation in planorbid species relative abundance. Moreover, the first three canonical axes account for 98% of the variance explained by these variables. The species-environment relationship was highly significant, according to the Monte Carlo permutational test ($F = 4.46$; $P < 0.001$; 999 permutations), as well as the first canonical axis ($F = 5.80$; $P < 0.01$; 999 permutations). In three samples from Negro River and one from Rural Society Pond, planorbids were not found, being excluded by the CCA program.

The graphic representation of the species positions along the environmental gradients in the reduced space of the first three canonical axes, yielded the following results (Figs. 2, 3):

(1) Axis I separates *B. straminea* and *D. lucidum* from *B. tenagophila* and *D. kermatoides,* along an increasing gradient of [N-NH_4^+] and *P. stratiotes,* as well as a decreasing gradient of %O_2 and *P. elephantipes.* The remaining species of *Drepanotrema* occupy intermediate positions along the first axis gradient.

(2) Axis II separates *D. lucidum, D. anatinum* and *D. cimex* from the species of *Biomphalaria* and *D. kermatoides,* mainly through a decreasing gradient of *H. ranunculoides* and *C. glauca,* as well as an increasing gradient of *P. elephantipes.*

(3) Finally, along axis III, species of *Drepanotrema* appear more clearly distributed, with *D. kermatoides* on the top, *D. anatinum* and *D. cimex* in the middle, finishing with *D. lucidum* at the opposite end, close to *B. straminea. Biomphalaria tenagophila* is placed on the opposite negative side of the planorbid distribution along the third axis. This axis is mainly related to the independent variables *C. glauca* and [N-NH_4^+] (positively) and *P. stratiotes* (negatively).

In addition, employing the environment-by-species table provided by the program CANOCO 4 (Table 5), the position of the optimum of planorbid species along gradients of environmental variables can be better analyzed, independently of their correlations with canonical axes. With this alternative analytical approach, the following results were obtained:

(1) *Canna glauca* was the most important independent variable in the stepwise forward selection. All species of *Drepanotrema* appear on the positive side of the gradient, with *D. anatinum* and *D. cimex* placed at the edge. *Biomphalaria* species were on the negative side, with *B. straminea* at the outermost end of the gradient.

(2) *Pistia stratiotes,* the second most im-

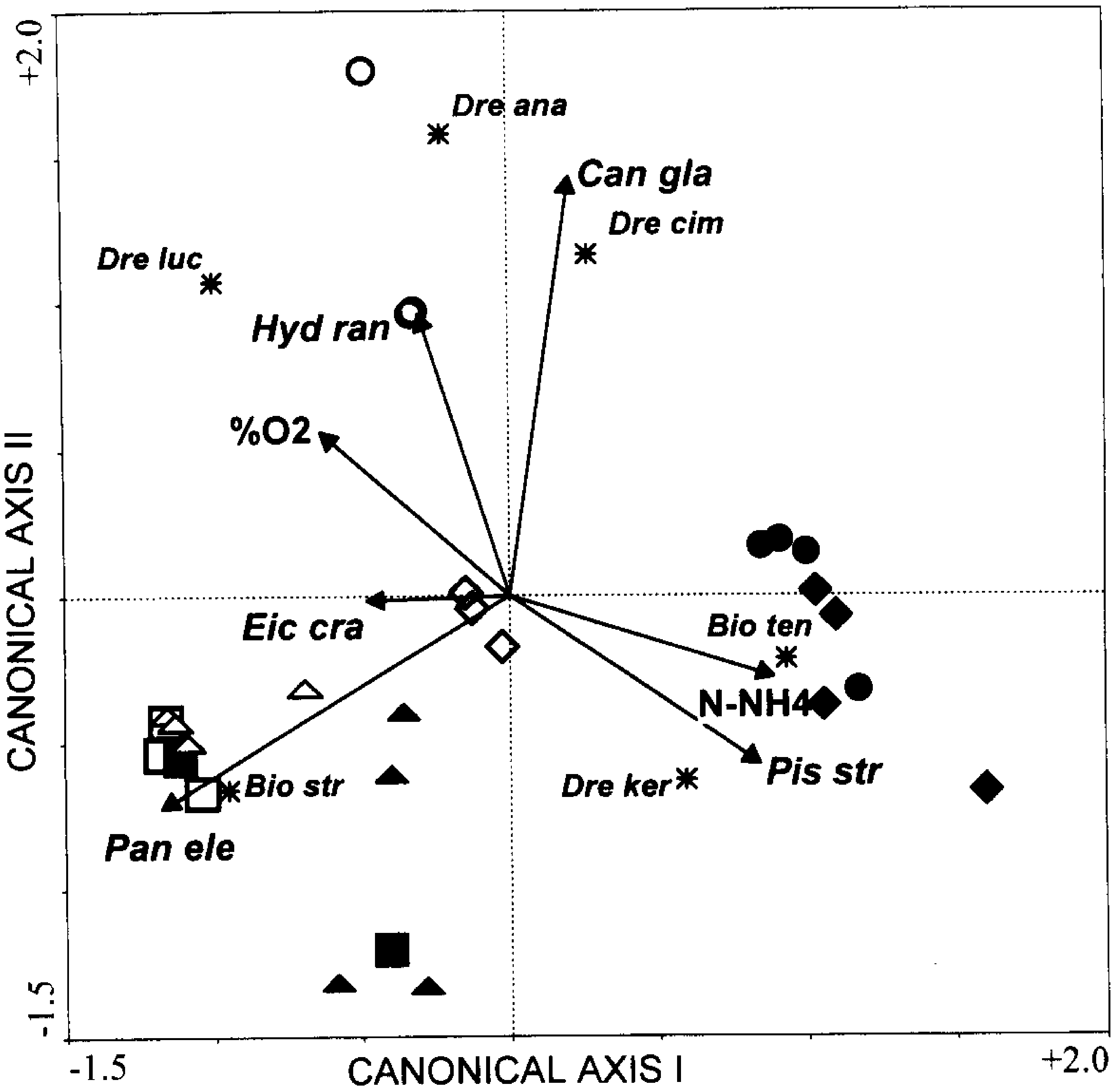

FIG. 2. Spatial representation of the samples, species and environmental variables in the space defined by the two first canonical axes. Circles: Paikín pond. Diamonds: Rural Society Pond. Squares: Negro River. Triangles: Golf Club Pond. Empty symbols: 1988. Filled symbols: 1989. Arrows: environmental variables. Stars: planorbid species. *Bio str: Biomphalaria straminea; Bio ten: B. tenagophila; Dre ana: Drepanotrema anatinum; Dre cim: D. cimex; D. ker: D. kermatoides; Dre luc: D. lucidum; Can gla: Canna glauca; Eic cra: Eichhornia crassipes; Hyd ran: Hydrocolyle ranunculoides; Pan ele: Panicum elephantipes* and *Pis str: Pistia stratiotes.*

portant independent variable, had *B. tenagophila* at the positive end of the distribution, whereas all species of *Drepanotrema* were on the negative side. *Biomphalaria straminea* was placed close to the center of the distribution.

(3) Along the gradient of [N-NH_4^+], both species of *Biomphalaria* were clearly segregated, with *B. tenagophila* having its optimum at higher concentrations, together with *D. kermatoides*. Moreover, *B. straminea* was placed on the opposite end, close to *D. lucidum,* while *D. cimex* occupied the center of the distribution.

(4) With respect to %O_2, planorbid species responded inversely as [N-NH_4^+].

(5) Dense stands of *P. elephantipes* supported the highest abundances of *B. straminea,* together with *D. lucidum.*

(6) *Hydrocotile ranunculoides* had a tendency to house populations of *D. anatinum, D. lucidum* and *D. cimex* preferably, while *Biomphalaria* species and *D. kermatoides* were at the negative side of the gradient.

(7) Finally, along the *E. crassipes* gradient, *B. straminea* and *B. anatinum* were on the positive side, *D. cimex,* close to the center, and the remainder on the negative side.

With respect to sample distribution in the reduced space of the first three axes, four groups were observed, each one characterized by a kind of vegetation and a particular planorbid assemblage (Figs. 2, 3):

(1) Samples in Paikín in 1988, characterized mainly by *C. glauca* and *H. ranuncu-*

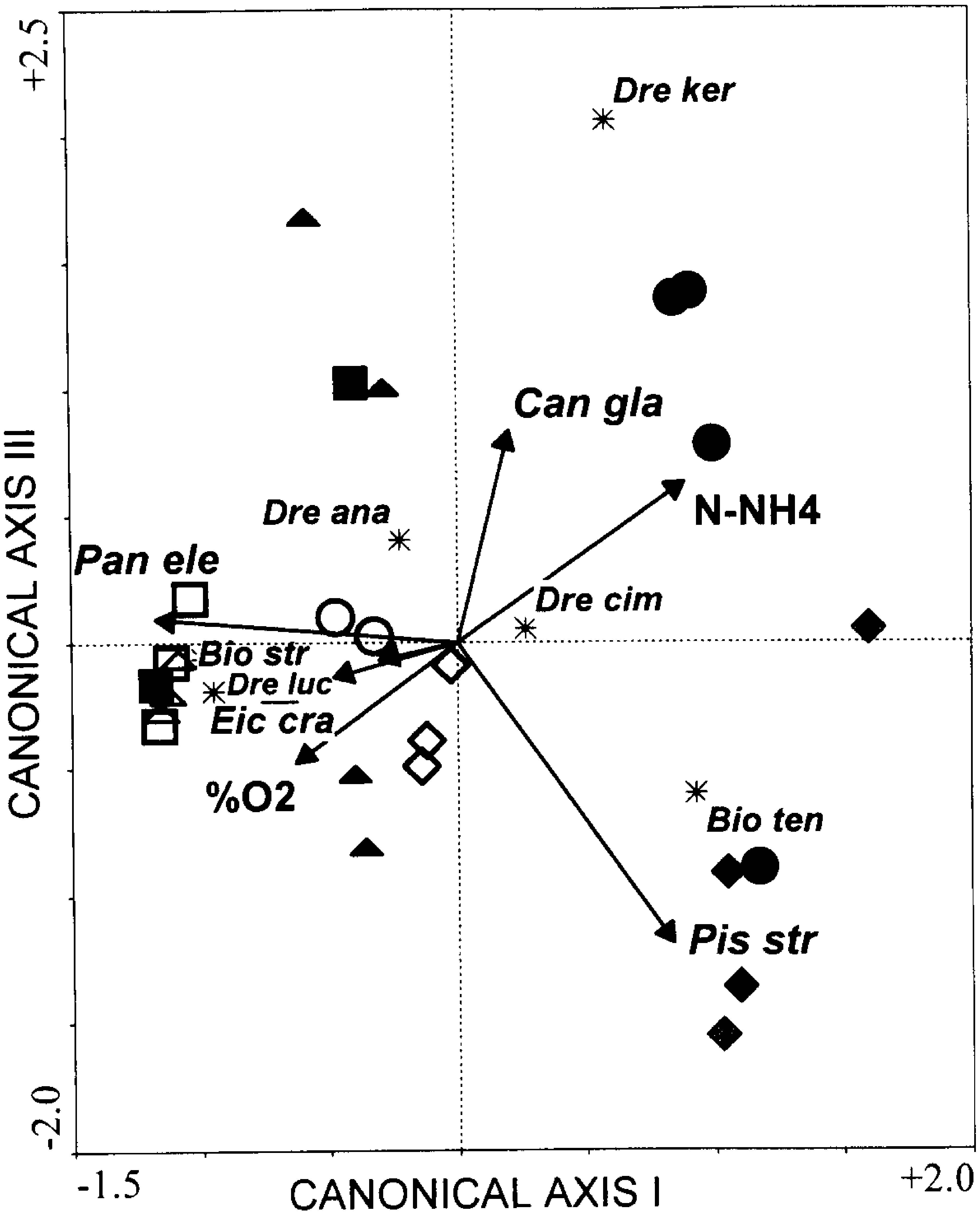

FIG. 3. Spatial representation of the samples, species and environmental variables in the space defined by canonical axes I and III. Circles: Paikín oxbow lake. Diamonds: Rural Society Pond. Squares: Negro River. Triangles: Golf Club Pond. Empty symbols: 1988. Filled symbols: 1989. Arrows: environmental variables. Stars: planorbid species. *Bio str: Biomphalaria straminea; Bio ten: B. tenagophila; Dre ana: Drepanotrema anatinum; Dre cim: D. cimex; D. ker: D. kermatoides; Dre luc: D. lucidum; Can gla: Canna glauca; Eic cra: Eichhornia crassipes; Pan ele: Panicum elephantipes* and *Pis str: Pistia stratiotes.*

loides. The most common species were *D. anatinum, D. lucidum* and *D. cimex.* The genus *Biomphalaria* was rare.

(2) Samples from Rural Society Pond and from Paikín Pond in 1989, characterized by the presence of *P. stratiotes* and the highest concentrations of ammonium, with *B. tenagophila* and *D. kermatoides* as the most common planorbid species.

(3) Samples from Rural Society Pond in 1988, with low-density stands of *E. crassipes,* and the presence of *B. straminea* and *B. tenagophila* also in low densities.

(4) Samples from Negro River and Golf Club Pond, characterized by the presence of *P. elephantipes,* and the highest concentrations of %O_2. *Biomphalaria straminea* was the most typical species, while the other planorbids were negatively related to this kind of vegetation. Within this group, two separated clusters of samples can be observed, one of them more

TABLE 5. Environment-by-species table showing weighted means and standard deviations of environmental factors, weighted averages of planorbid species with respect to the seven standardized variables ("optima"), and back-transformed data to original format as in Tables 2 and 3 (in parentheses). Note that for limnological variables, original data were transformed to decimal logarithm.

	Mean	Stand dev.	*B. tenagophila*	*B. straminea*	*D. anatinum*	*D. lucidum*	*D. kermatoides*	*D. cimex*
C. glauca	1.460	1.881	−0.288 (0.9)	−0.584 (0.4)	1.163 (3.6)	0.536 (2.5)	0.426 (2.3)	0.839 (3.0)
H. ranunculoides	0.393	0.930	−0.196 (0.2)	−0.158 (0.2)	0.772 (1.1)	0.622 (1.0)	−0.423 (0.0)	0.3826 (0.7)
P. elephantipes	0.884	1.648	−0.434 (0.2)	0.688 (2.0)	−0.536 (0.0)	0.393 (1.5)	0.009 (0.9)	−0.5361 (0.0)
E. crassipes	1.055	1.558	−0.185 (0.8)	0.274 (1.5)	0.203 (1.4)	−0.112 (0.9)	−0.301 (0.6)	−0.0004 (1.1)
P. stratiotes	1.325	1.775	0.726 (2.6)	−0.068 (1.2)	−0.646 (0.2)	−0.745 (0.0)	−0.745 (0.0)	−0.2038 (1.0)
[N-NH4$^+$]	0.238	0.276	0.211 (0.977)	−0.328 (0.403)	−0.136 (0.586)	−0.709 (0.102)	0.884 (2.034)	0.0696 (0.807)
%O_2	1.534	0.493	−0.193 (26.5)	0.158 (39.9)	0.435 (55.0)	0.499 (59.2)	−0.789 (13.0)	0.2062 (42.2)

clumped, belonging to 1988, and the other more dispersed, from 1989.

These results indicate that there is not a clearly defined seasonal variation in the structure of planorbid assemblages. The most important patterns were spatial or inter-annual, as is shown in the triplot of axes I and II (Fig. 2). There is a defined tendency of most samples from all waterbodies to move in a top-left to bottom-right direction from 1988 to 1989, following a gradient of increasing ammonium concentration and decreasing oxygen saturation.

DISCUSSION

The empirical model developed in this paper explains a relatively high percentage of observed variance compared with other community studies (Borcard et al., 1992), and is in addition highly significant. As a general pattern, the multivariate model shows that *Biomphalaria straminea* tends to be relatively more important in well-oxygenated environments with reophilic vegetation, such as *Panicum elephantipes.* Junk (1973) also found that this planorbid species was abundant in the roots of "floating meadows" (*Paspalum repens* Berg, and *Echinochloa polystachya* (H.B.K.)) in várzea lakes of the Amazon River. Conversely, *Biomphalaria tenagophila,* the other potential transmitter of schistosomiasis, is more common in less oxygenated waters and higher ammonium concentrations, conditions that, together with pH over 8 and temperatures higher than 25°C, may be extremely toxic for aquatic animals due to the high proportion of ammonia (NH_3) (Boyd, 1990). These particular limnological features are generally associated with continuous floating covers of *Pistia stratiotes,* with roots that would function as substratum and refuge for *B. tenagophila. Drepanotrema kermatoides* follows a similar pattern to that of *B. tenagophila,* while the association of *B. straminea* with species of *Drepanotrema* was unclear, except for *D. lucidum.* This latter species was also found by Junk (1973) occupying the same habitat as *B. straminea.* In this sense, the dominance of *Canna glauca* and *Hydrocotyle ranunculoides* also indicates the dominance of *Drepanotrema* species, as well as lower densities of *Biomphalaria* species, particularly *B. straminea.*

Among the environmental factors taken into account in the CCA, the regulatory effect of water temperature on population dynamics was already known, as was the importance of calcium concentration related to pH, hardness and macrophytes, on the distribution and abundance of mollusks (Dussart, 1976; Pigott & Dussart, 1995; Thomas, 1982; Rumi & Hamann, 1992). However, only ammonium concentration and percentage of oxygen saturation were retained as significant limnological variables in the process of forward selection, and they were negatively correlated with each other. *Biomphalaria tenagophila* and *D. kermatoides* were distributed along this limnological gradient, mainly at the highest ammonium concentrations, with optima at 0.98 and 2.00 mg l^{-1}, respectively, as well as the lowest oxygen saturation, with optima at 26.6% and 13.0%, respectively. These results suggest that the variance explained by the excluded variables was either unimportant to be selected in the stepwise procedure, or that this variation was better explained by oxygen and ammonium, or even aquatic plants, which were retained first by the statistical method employed, due to their larger explained variance. Therefore, these results do not necessarily mean that variables not retained were not relevant for planorbids.

The lack of clear seasonal trends in planorbid communities may be explained because the environments in which this study was carried out are of permanent waters, unlike others of tropical areas, with well-defined seasonality in rainfall. These observations agree with Rumi & Hamann (1992), who compared, in another permanent pond of eastern Chaco in Corrientes Province, rainfall pattern with the relative abundance of *Biomphalaria occidentalis* Paraense, 1981, finding also a very low correlation between those variables. However, in this region of Chaco, inter-annual variability in water availability can be very important, particularly the surplus after evaporation, soil infiltration and scouring (Bruniard, 1997). Since environmental variables as well as planorbid population dynamics are related to climatic changes, large variations in planorbid composition and abundance in samples of the same biotopes from one year to the next may be due to different rainy and drought periods. For example, different amounts of precipitation can affect total biotope area, producing an increase in planorbid density during dry periods due to retraction in pond area, or an opposite decrease during wet periods due to dilution effects. Furthermore, although ponds are physically isolated most of the time, extensive superficial interconnections among wetlands always take place during rainy episodes or river floods. Thus, migration events in snail populations would be expected at those times. These two processes could provoke rapid changes in abundance, and could partially explain the marked seasonal modifications in snail capture observed in the present paper.

Until not long ago, the urban ponds were employed for rubbish deposits, which affected the water quality and planorbid population size, especially during dry climatic events. In addition, populations of *B. straminea* were much more abundant during the first year, while *B. tenagophila* showed an increase in population densities during the second year.

The non-explained variability in planorbid relative abundance could be attributed to a rather extensive list of possibilities, including the colonization patterns in space and time, sampling biases, and environmental variables not included (i.e., fish and invertebrate predators). First, given the limited capacity of planorbids to disperse and the time required for settled populations to grow, it is possible that even with suitable environmental conditions, populations could not reach maximum or stable densities within the sampling period. Second, the observed variation range of environmental variables and of planorbid assemblages could be related to the specific environments selected for sampling, as well as the sampling technique employed. Thus, including more biotopes and making a greater sampling effort could have resulted in a larger explained variance or in a somewhat different distributional pattern. Finally, the role of predators as controls of planorbid populations cannot be ignored, given that eastern Chaco environments usually hold an abundant and diverse fish fauna (Menni et. al., 1992), with large proportions of invertebrate-eating, including mollusc-eating, species, such as small to medium-sized silurids, characins, cichlids and gymnotids. Therefore, given similar environmental conditions, the presence or absence of predatory fishes could result in different planorbid densities and species composition.

From a sanitary standpoint, it is remarkable that the species *B. tenagophila* and *B. straminea,* living in urban environments in the Chaco, are natural transmitters of schistosomiasis in Brazil. Because the presence and abundance of these two planorbid species is explained chiefly by some species of aquatic macrophytes, these variables may be employed as indicators for a rapid assessment of potential sites of proliferation of *B. tenagophila* and *B. straminea.* However, these results must be supplemented with new samplings, as well as experimental field and laboratory tests, to confirm the observed trends.

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