Patterns in fish species composition and assemblage structure in the upper Salado River lakes, Pampa Plain, Argentina

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The Pampa Plain, in the central region of Argentina, is mostly drained by the Salado River. The fish fauna of this river is mostly known from field collections in lower reach lakes. Consequently, we aimed to explore the composition and structure of the fish assemblages in the upper Salado River lakes. Patterns in dominance and persistence of species and assemblage level attributes were correlated with environmental and human activity-derived ($NO_3:NH_4$) variables. Overall, 19,913 individuals of 17 species included in 5 orders and 11 families were collected. Several species are first records for the upper Salado River lakes. There was a marked proliferation of species in the family Characidae. Conversely, the remainder 10 families were only represented by one or two species. The species composition along the study lakes changed slightly but their relative contribution to the total fish collected (dominance) varied greatly. Rather few species were present in all collections suggesting an important interannual variability in assemblage stability. The gradient in water conductivity was an important factor for the persistence of particular species in the lakes. The gradients in water conductivity and $NO_3:NH_4$ ratio were associated with particular fish communities dominated by different groups of species. These results suggest that even when broad management and conservation strategies should encompass the system as a whole, lake-specific approaches must also be addressed. Overall, our results highlight that human impacts on surface waters may interact with environmental factors to influence the dynamics of fish species and the structure of their communities.

A planície pampeana, na região central da Argentina, é em grande parte drenada pelo rio Salado. A ictiofauna desse rio é conhecida principalmente pelos estudos conduzidos nos lagos dos segmentos inferiores do rio. Em consequência, procuramos examinar a composição e a estrutura das assembleias de peixes dos lagos do alto rio Salado. Os padrões na dominância e persistência das espécies e os atributos das assembleias de peixes foram correlacionados com variáveis ambientais e variáveis indicadoras de perturbações antropogênicas ($NO_3:NH_4$). Foram coletados 19913 indivíduos de 17 espécies pertencentes a 5 ordens e 11 famílias. Várias espécies foram registradas pela primeira vez para as lagoas do alto rio Salado. Houve uma marcada proliferação de espécies da família Characidae. Em contraste, as 10 famílias de peixes restantes foram representadas por uma ou duas espécies. A composição de espécies variou pouco ao longo dessas lagoas mas sua contribuição ao total de peixes coletados (dominância) foi muito variável. Poucas espécies estiveram presentes em todas as coletas, sugerindo uma importante variação interanual na estabilidade da assembleia de peixes. O gradiente na condutividade elétrica da água foi importante fator para a persistência de algumas espécies nessas lagoas. A condutividade elétrica da água e o gradiente na relação $NO_3:NH_4$ estiveram associados com assembleias de peixes particulares dominadas por diferentes grupos de espécies. Nossos resultados sugerem que, embora as estratégias de conservação e manejo deveriam considerar o sistema por completo, questões particulares a cada lagoa devem também ser consideradas. Em geral, nossos resultados ressaltam que os impactos humanos nas águas superficiais podem interagir com fatores ambientais para influenciar a dinâmica das espécies de peixes e a estrutura de suas comunidades.

Key words: Environmental gradients, Persistence, Dominance, Diversity, Regional biogeography.

Introduction

The most recent biogeographical revision of Argentinean fishes (López *et al*., 2008) classifieds the fish fauna of the Salado River (Buenos Aires province) and its main tributary the Vallimanca stream into the Pampean province, sharing affinities with several drainages of central Argentina. This revision represents a major contribution to fulfil the "blank" in the scenario described in one of the latest synthesis of South America freshwater fish biodiversity (Junk, 2007). In

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[†]In memoriam to Rolando Quirós who worked with me in the first drafts of this paper.

spite of that the southern boundary of the Brazilian subregion is located at the Negro River, in Argentina (Almirón *et al.*, 1997) the Salado River basin already represents the southern range of many Neotropical species (Ringuelet, 1975; López *et al.*, 2002). Hence, updated reliable information about patterns in the composition and structure of fish assemblages in this transitional zone is particularly important. Nonetheless, the Salado River fish fauna (López *et al.*, 2001) is mostly known from field collections in lakes at lower segments of its basin (Gómez & Toresani, 1998). This contrasts with the very few ichthyological investigations that have been conducted at its upper reaches (Mac Donagh, 1934; Ringuelet *et al.*, 1967; Freyre, 1972; Quirós *et al.*, 1988). As consequence, little is known about the actual composition and distribution of the fish fauna in the upper reaches of this river, where major lakes remain largely sub-explored. These lakes are highly fluctuating in salinity and water residence time (Quirós *et al.*, 2002a) and had been largely modified by man and his use of land and water (Quirós *et al.*, 2006).

The assemblage of species that make up fish communities within a river/stream network is attributed mostly to how individual species distributions respond to patterns in vegetated patches (Araujo-Lima *et al.*, 1986; Growns *et al.*, 2003; Pelicice *et al.*, 2008), hydrological connectivity (Amoros & Bornette, 2002; Petry *et al.*, 2003), water transparency (Rodríguez & Lewis, 1997; Reyjol *et al.*, 2008; Melo *et al.*, 2009), physicochemical variables (Koné *et al.*, 2003; Barko *et al.*, 2004), food resources availability (Grenouillet & Pont, 2001), and prey-predator interactions (Piana *et al.*, 2006) among others.

In the upper Salado River lakes, the abundance and distribution of dominant fish species have been shown to mostly follow spatial gradients in water conductivity and anthropogenic factors (Rosso & Quirós, 2009). However, it was not explored yet whether patterns in dominance and persistence of all fish species in response to these directive gradients may finally influence the richness, diversity and structure of fish assemblages in these lakes. Hence, in this paper our main objective was to addressed two main aspects of the fish fauna of upper Salado River lakes that are still mostly uncover. Firstly, we updated the information about the composition and distribution of the fish fauna. Then, patterns in dominance and persistence of species and assemblage level attributes in relation with major environmental and anthropogenic gradients of the system were explored. These results have strong implications for management and conservation purposes which are discussed accordingly at the end of the paper.

Material and Methods

Study area

The Salado River is a lowland river with 690 km running from 89 meters above sea level in El Chañar Lake (Santa Fe province) and flowing out into the lower reaches of the Paraná-Plata basin, at the Samborombón Bay. Together with its main tributaries, the Samborombón River and the Vallimanca Stream,

the Salado River encompasses one of the major ecoregions of Central Argentina (López *et al.*, 2002), comprising an area of 179,000 km². The study lakes are very shallow interconnected natural impoundments located at the headwaters of this river between 34°21' and 34°42'S, and 60°39' and 61°15'W (Fig. 1). With a mean surface area ranging from 2 km² to 50 km² (Table 1), these lakes are wind mixed, eutrophic to hypereutrophic environments (Quirós *et al.*, 2002a). Due to the high primary productivity by phytoplankton, the extreme turbidity and the habitual anoxia of the water-sediment interface, plant cover in these lakes is minimal and restricted to shallow littoral habitats (Quirós *et al.*, 2002b). Structural complexity (composition and density) of plant cover along shoreline habitats of study lakes is similar (Rosso, pers. obs.) Connectivity between lakes, albeit variable, was always enough to assume a free dispersion of fish among them. Consequently, for the purposes of this paper we disregarded the study of plant cover and connectivity patterns as templates for fish assemblage structure. Conversely, we considered the two main spatial axes along which these lakes may be described; a first axis of landscape human development (Rosso & Quirós, 2007) and a second abiotic axis of total salinity of their waters (Gabellone *et al.*, 2005). Accordingly to these directive gradients, these lakes display a spatial variation in the NO_3:NH_4 ratio and water conductivity respectively (Rosso & Quirós, 2009).

Fig. 1. Schematic diagram of the study area in the upper Salado River, Pampa Plain, Argentina.

Fish sampling

In order to explore the fish fauna of the upper Salado River lakes monthly samples were taken during two subsequent summers (January to March, 2000 and 2001). Sampling in summer months is aimed to reduce biases in the estimation of species composition due to changes in the seasonal behavior of fishes in relation to the thermal dynamics of waters and photoperiod. Fish collections were made with several fishing gears including seine nets, gill nets and hook-lines. Sampling was conducted simultaneously at the littoral and limnetic regions of lakes. In the limnetic areas two multifilament experimental gill nets of ten panels (15, 21, 25, 30, 35, 40, 52, 60, 75 and 85 mm bar mesh size) of equal height (1.4 m) and length (10 m) were set during the first two hours of darkness. To capture species in the littoral areas we deployed hook-lines during 4 to 6 hs and hauled a bag seine net constructed with 20 m long wings (10 mm mesh) and a 2 m long bag (5 mm mesh) covering 1000 m² just before sunset.

Table 1. Mean morphometric and limnological attributes of upper Salado River lakes. Sources: Quirós *et al*. (1988), Rennella (2007), and Rosso (2008).

Lake	Area (km^2)	Depth (m)	Secchi (cm)	Chlorophyll-a (µg/l)	Conductivity (µS/cm)	$NO_3:NH_4$
Mar Chiquita	50	0.9	11	150.98	5925	1.13
Gómez	40	1.2	19	98.88	5873	0.81
Carpincho	5	1.0	21	103.12	5341	0.49
Rocha	3.6	0.8	18	139.27	5200	0.28

The effectiveness of these fishing gears as well as the sampling strategy adopted was successfully tested before for these types of lakes (Quirós *et al*., 1988). Nonetheless, using a large subsequent monthly sampling program in this system (Rosso, 2008) covering seasonal and interannual variation we evaluate if samplings yielded consistent estimates of species composition and relative abundances in all study lakes. All captured fishes were identified in the field (Ringuelet *et al*., 1967) and counted. The systematic arrangement presented here follows Nelson (2006). Taxonomic synonymies and current status of valid species were checked using the Catalog of Fishes (Eschmeyer & Fricke, 2008). Comments on geographical distribution of fish species are based on Ringuelet *et al*. (1967) but updated in accordance to recently published information (Liotta, 2006). Voucher specimens were deposited in the Museo Municipal de Ciencias Naturales "Lorenzo Scaglia" (MMPEAA), at Mar del Plata, Argentina.

Data analysis

Species composition of each lake was reported as the total number of fish species collected in repeated monthly samples in order to account for eventual variation in patterns of occurrence. With these findings, we discuss the presence and distribution of species in relation with historical reports for these lakes and within the context of regional biogeography. At each lake we computed the total specimens collected of each species as a measure of abundance. Data from hook-lines were only used to complete information on species composition and were not included in the calculation of species abundances. The relative contribution of each species to the total amount of fish collected (expressed in percentage) and their frequencies of occurrence in the samples were estimated. The relative contribution of each species was used as a measure of dominance (Medeiros & Maltchik, 2001). The frequency of occurrence (as percentage) of each species at each sampling site was computed by dividing the number of samples in which the species was present by the total samples and multiplying by 100. This was used as a measure of persistence. Fish assemblage richness and diversity (Shannon & Weaver, 1949) at each lake was also reported.

Patterns in dominance and persistence of species as well as in richness and diversity of fish assemblages in relation with gradients in water conductivity and $NO_3:NH_4$ ratio were explored with Spearman rank correlation coefficients. Summer means of species dominance, assemblage richness and diversity (n = 8) plus overall persistence of each species at each lake (n = 4) were used for correlation analyses. Information of water conductivity and the $NO_3:NH_4$ ratio was

gathered from Rosso & Quirós (2009). Data were log (x+1) transformed prior to analysis.

In field studies, the length of the sampled gradient is important to decide which index of fauna similarity should be applied. The relative weight that is given to abundance information should be larger for short gradients (Lambert & Dale, 1964). Hence, in order to explore similarity in terms of relative abundance of each species (assemblage structure) we quantified the magnitude of resemblance between fish assemblages of these lakes by performing a similarity percentages analysis (SIMPER) using the Bray-Curtis dissimilarity index as the distance coefficient between two samples. To achieve this we used the corresponding routine in the PRIMER.5 (Plymouth Routines In Multivariate Ecological Research) package. This test also allowed us to identify those species that contribute most to explain dissimilarities between lakes. The relationships between fauna dissimilarity and distance between lakes were explored.

Results

Overall, 19,913 individuals of 17 species included in 5 orders and 11 families were collected during the surveys. The dominant orders in terms of number of species were Characiformes (41.2%), and Siluriformes (35.3%), with seven and six species respectively. Cyprinodontiformes ranked third, with two species (11.7%) collected in two families, whereas the remainder two orders, Cypriniformes and Atheriniformes, were represented by a single species into a single family, Cyprinidae and Atherinopsidae respectively (Table 2). There was a marked proliferation of species in one family. Conversely, the remainder 10 families were only represented by one or two species. By number of species, the dominant family was Characidae with five members (29.6%) followed by Heptapteridae and Loricariidae with two (11.7%) species. Hence, there were as few as 1.54 species per each family in these freshwater environments of the temperate Pampa Plain.

With this survey, the fish fauna of Rocha Lake was explored for the first time. Furthermore, *Cnesterodon decemmaculatus* is recorded for the first time in the upper Salado River lakes. This is also the first time that some species are cited for Mar Chiquita, Gómez and Carpincho Lakes. *Astyanax fasciatus*, *Astyanax eigenmanniorum*, *Bryconamericus iheringii*, *Cheirodon interruptus*, *Jenynsia multidentata* and *Loricariichthys anus* are reported for the first time for Mar Chiquita Lake. Three species, *Cnesterodon decemmaculatus*, *Astyanax fasciatus* and *Astyanax eigenmanniorum* are new reports for Gómez Lake whereas *Cnesterodon*

Table 2. Systematic list of fish species found in the upper Salado River lakes. MMPEAA: catalog numbers of voucher specimens deposited at the Museo Municipal de Ciencias Naturales "Lorenzo Scaglia".

Order	Family	Fish Taxa	Species Code	MMPEAA
Siluriformes	Heptapteridae	*Pimelodella laticeps* Eigenmann, 1917	Pl	517
		Rhamdia quelen (Quoy & Gaimard, 1824)	Rq	518
	Pimelodidae	*Parapimelodus valenciennes* (Lütken, 1874)	Pv	519
	Callichthyidae	*Corydoras paleatus* (Jenyns, 1842)	Cp	520
	Loricariidae	*Loricariichthys anus* (Valenciennes, 1836)	La	521
		Hypostomus commersoni Valenciennes, 1836	Hc	522
Characiformes	Characidae	*Astyanax fasciatus* (Cuvier, 1819)	Af	523
		Astyanax eigenmanniorum (Cope, 1894)	Ae	524
		Bryconamericus iheringii (Boulenger, 1887)	Bi	525
		Cheirodon interruptus (Jenyns, 1842)	Ci	526
		Oligosarcus jenynsii (Günther, 1864)	Oj	527
	Curimatidae	*Cyphocharax voga* (Hensel, 1870)	Cv	528
	Erythrinidae	*Hoplias malabaricus* (Bloch, 1794)	Hm	529
Cypriniformes	Cyprinidae	*Cyprinus carpio* Linnaeus, 1758	Cc	530
Cyprinodontiformes	Anablepidae	*Jenynsia multidentata* (Jenyns, 1842)	Jm	531
	Poeciliidae	*Cnesterodon decemmaculatus* (Jenyns, 1842)	Cd	532
Atheriniformes	Atherinopsidae	*Odontesthes bonariensis* (Valenciennes, 1835)	Ob	533

decemmaculatus is the only species that we added to the richest Carpincho Lake. These findings represent an increase of 66, 21 and 6% for the known ichthyofauna of Mar Chiquita, Gómez and Carpincho Lakes respectively. In these lakes, the diversity of fish assemblages and the species richness varied considerably and were highly related with the gradient in the $NO_3:NH_4$ ratio (Fig. 2). Fish assemblages were significantly richer (-0.72; $p < 0.05$) and more diversified (-0.93; $p < 0.01$) as the $NO_3:NH_4$ decreased.

The fish fauna of these lakes was dominated by open waters planktivore species (Table 3). The most abundant species was the visual planktivore *Odontesthes bonariensis* followed by the filter planktivore *Parapimelodus valenciennis*. Both species comprised almost 40% of total fish collected. These lakes were characterized by a striking low abundance of large piscivores. The top predator *Hoplias malabaricus* was extremely rare. Similarly, the abundance of *Rhamdia quelen* was also very low. Conversely, the small carnivore *Oligosarcus jenynsii* was the most abundant species among the elements that may usually exert some piscivory. Altogether, the abundance of potentially piscivore individuals (carnivores plus piscivores) represented slightly more than 5% of total fish captured in this river-lakes system. However, if we considered the piscivore *Hoplias malabaricus* by its own, it only represented on average 0.25% of total fish collected. Only one species, *Cyprinus carpio*, is exotic to these temperate waters of Pampa Plain.

Most of the species collected but *Hypostomus commersoni*, *Hoplias malabaricus* and *Cnesterodon decemmaculatus* were present in all lakes. However, their spatial patterns in abundance distribution were highly variable (Fig. 3). Whereas some species seem to be evenly distributed along the study lakes (located around the center of Fig. 3) most of them are highly skewed to either Mar Chiquita and Gómez or Carpincho and Rocha Lakes. Similarly, the dominance of certain species within an assemblage varied from lake to lake. The majority of the species collected dominated most in those lakes where they were more abundant. More than 80% of the individuals of *Odontesthes bonariensis* were collected in Mar Chiquita and Gómez Lakes.
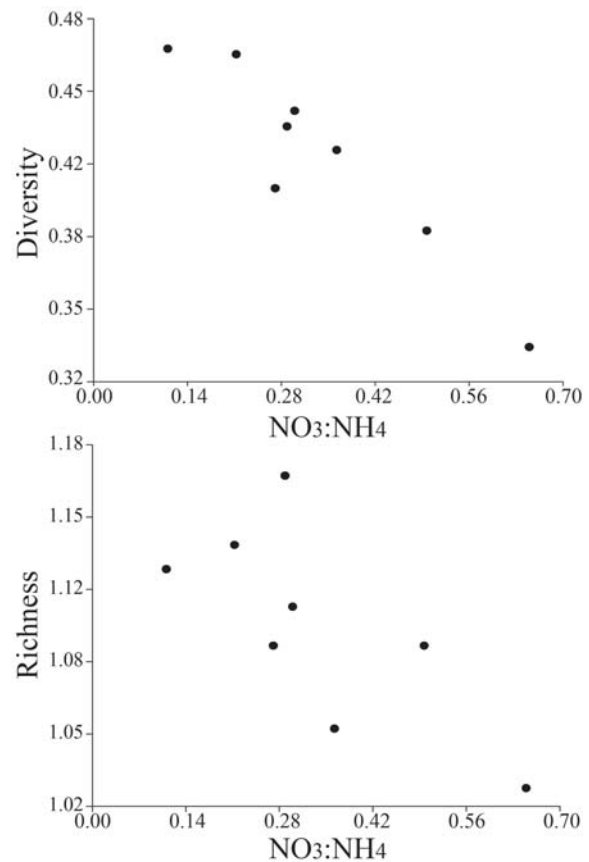

Fig. 2. Relationship between diversity and species richness in fish assemblages and the $NO_3:NH_4$ ratio.

Accordingly, dominance of this species in fish assemblages decreased from Mar Chiquita to Rocha Lakes (Table 3). Similarly, *Jenynsia multidentata* was extremely skewed to Mar Chiquita and Gómez Lakes with 98% of their total individuals collected in these environments and contributing with a dominance of more than 10%. The third most abundant species of the system, the detritivorous *Cyphocharax voga*, was mostly (99%) captured in Carpincho and Rocha Lakes. Accordingly, the dominance of this species in Mar Chiquita

Table 3. Number of individuals collected (N), dominance (D) and persistence (P) of fish species in the upper Salado River lakes during summers 2000 and 2001. Dominance and persistence are expressed in percentage. Mch = Mar Chiquita, Go = Gómez, Crp = Carpincho, and Rch = Rocha.

Species	Mch			Go			Crp			Rch			Total	
	N	D	P	N	D	P	N	D	P	N	D	P	N	D
Parapimelodus valenciennes	309	5.60	66	967	13.84	91	294	10.22	100	1,085	23.93	100	2,655	13.33
Pimelodella laticeps	16	0.29	50	9	0.12	25	32	1.11	50	49	1.08	33	106	0.53
Rhamdia quelen	4	0.07	50	4	0.05	41	5	0.17	50	1	0.02	16	14	0.07
Corydoras paleatus	742	13.45	66	53	0.75	41	1	0.03	16	9	0.19	33	805	4.04
Loricariichthys anus	2	0.03	16	8	0.11	58	48	1.66	100	3	0.06	33	61	0.30
Hypostomus commersoni	0	0	0	0	0	0	1	0.03	16	0	0	0	1	0.01
Astyanax fasciatus	68	1.24	100	113	1.61	100	189	6.56	100	436	9.61	100	806	4.04
Astyanax eigenmanniorum	199	3.61	100	292	4.17	100	119	4.14	100	99	2.19	100	710	3.56
Bryconamericus iheringii	332	6.02	100	690	9.87	100	199	6.90	100	170	3.75	100	1,391	6.98
Cheirodon interruptus	930	16.86	100	820	11.74	100	159	5.52	100	327	7.21	100	2,235	11.22
Oligosarcus jenynsii	142	2.57	83	285	4.07	100	299	10.39	100	257	5.66	100	983	4.93
Cyphocharax voga	4	0.07	50	16	0.22	50	680	23.64	100	1,579	34.82	100	2,279	11.44
Hoplias malabaricus	0	0	0	1	0.01	8	9	0.31	50	40	0.88	66	50	0.25
Cyprinus carpio	33	0.59	66	29	0.41	66	208	7.23	100	187	4.12	100	457	2.29
Jenynsia multidentata	1,074	19.47	50	990	14.17	75	32	1.11	83	13	0.28	50	2,109	10.59
Cnesterodon decemmaculatus	0	0	0	102	1.46	100	4	0.13	50	7	0.15	50	113	0.56
Odontesthes bonariensis	1,659	30.08	100	2,609	37.34	100	598	20.79	100	272	5.99	100	5,138	25.80
Species richness	14			16			17			16			17	
Diversity	1.41			1.59			1.81			1.74				
Total fish collected	5,515			6,987			2,877			4,534			19,913	

and Gómez Lakes was less than 1%. The exotic *Cyprinus carpio* and the top predator *Hoplias malabaricus* were mostly confined to Carpincho and Rocha Lakes where their dominances were higher. Dominance of *Hoplias malabaricus* ranged from 0.01% in Gómez Lake to 0.88% in Rocha Lake.

Abundance distributions of other species were also highly skewed to some lakes but their dominance within an assemblage did not changed accordingly. *Corydoras paleatus* and *Pimelodella laticeps* showed an opposite spatial distribution (Fig. 3), being the former comparatively more abundant at Mar Chiquita and Gómez Lakes and the latter in Carpincho and Rocha Lakes. Nevertheless, their dominance in any fish assemblage rarely surpassed 1% (Table 3). The dominances of some species were related with gradients in water conductivity and the
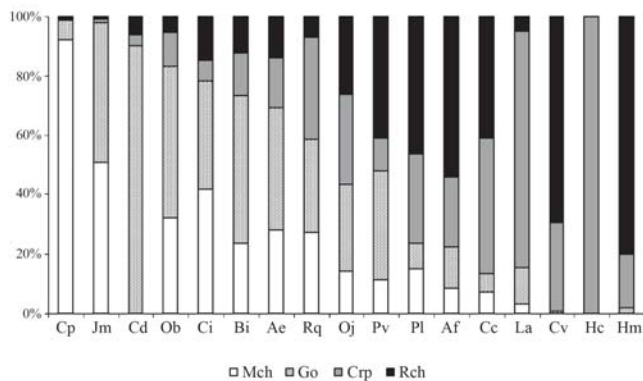

Fig. 3. Bar chart showing the distribution of total fish collected of each species within the upper Salado River lakes. Species codes as listed in Table 2. Species are intentionally sorted by means of their spatial distribution to ease the interpretation. From left to right, from clear to dark filled bars: Mch = Mar Chiquita, Go = Gómez, Crp = Carpincho, and Rch = Rocha.

$NO_3:NH_4$ ratio (Fig. 4). Dominance of *Jenynsia multidentata* was higher (0.88; $p < 0.01$) as water conductivity increased whereas the dominance of species such as *Cyprinus carpio* (-0.73; $p < 0.05$) and *Cyphocharax voga* (-0.83; $p < 0.05$) were higher when the $NO_3:NH_4$ ratio was lower.

The inland silverside *Odontesthes bonariensis* together with the small characins *Astyanax fasciatus*, *Astyanax eigenmanniorum*, *Bryconamericus iheringii* and *Cheirodon interruptus* were present in all collections of each lake (Table 3). The number of species that showed a persistence of 100% during sampling increased from 5 in Mar Chiquita to 10 and 9 in Carpincho and Rocha Lakes respectively. This increase almost linearly follows the increase in species richness and less intimately in assemblage diversity. Variability in the persistence of some species was related with the gradient in water conductivity. Particularly, persistence in a lake of *Cyphocharax voga* (-0.89; $p < 0.10$), *Parapimelodus valenciennis* (-0.94; $p < 0.05$), *Hoplias malabaricus* (-0.99; $p < 0.01$) and *Cyprinus carpio* (-0.89; $p < 0.10$) decreased as the water conductivity increased.

The species composition along the study lakes changed slightly but the relative contribution of each species to the total fish collected varied greatly. Dissimilarities in the fish assemblage structure between lakes increased as distance between lakes increased and ranged from as few as 23.48% (Mar Chiquita - Gómez) to almost 70% (Mar Chiquita - Rocha). Accordingly, average dissimilarity between Mar Chiquita and Carpincho was intermediate (52.43%). Average dissimilarity between Gómez and Carpincho (44.48%) was smaller than Gómez and the more distant Rocha Lake (59.82%). Finally, percentage dissimilarity between Carpincho and Rocha averaged 30.38%. The percentage dissimilarity between Carpincho and Rocha Lakes with the remainder lakes was always best explained by the relative abundance of

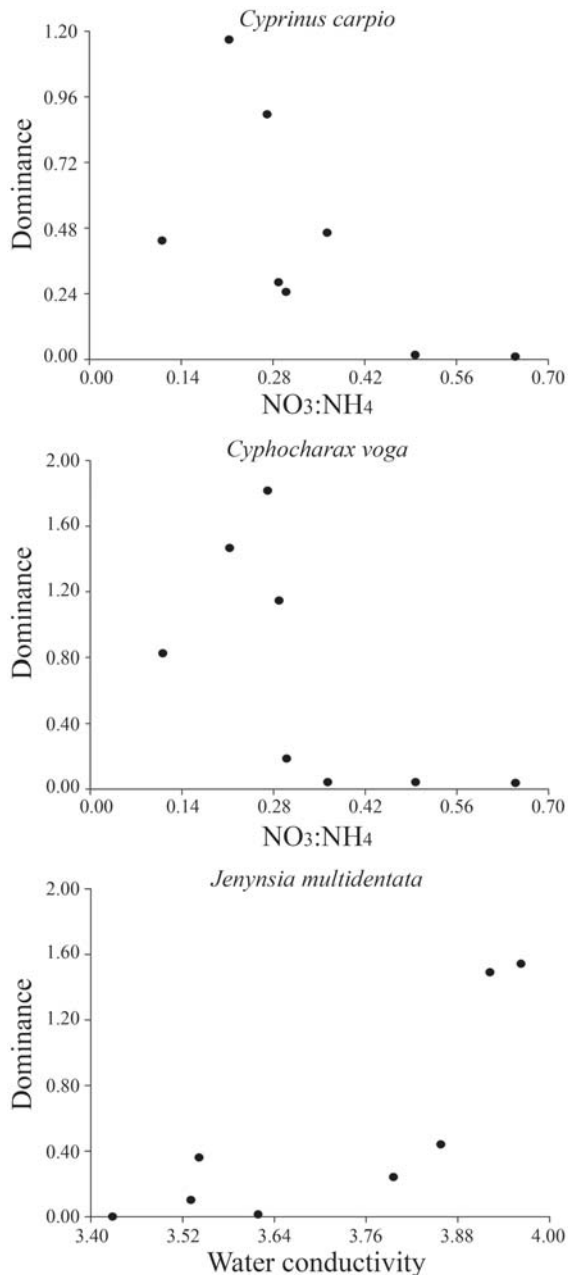**Fig. 4.** Relationship between dominance of fish species and gradients in water conductivity and the NO_3:NH_4 ratio.

Cyphocharax voga. This species contributed to the total amount of dissimilarity with a percentage ranging from 22.47 to 28.92%. *Corydoras paleatus* and *Jenynsia multidentata*, two abundant species in Mar Chiquita Lake, were important elements to explain dissimilarities between this lake and the remainder lakes. All these three species together with *Odontesthes bonariensis* were the most important elements in explaining dissimilarities between any pair of lakes (Table 4). Combining the individual percentage of these four species it raised to a cumulative contribution averaging near 60% of the total dissimilarity between lakes. Nevertheless, none species was able to account for more than 30% of the percentage dissimilarity between lakes.

Discussion

In the upper Salado River lakes, species from Characiformes and Siluriformes orders made up more than 75% of the total fish fauna. This is a constant pattern of fish assemblage organization for most freshwater environments of South America (Lowe-McConnell, 1987; Rodríguez & Lewis, 1990; Pouilly *et al.*, 1999). Nonetheless, when entering into the Pampa Plain, the contribution of Characiformes and Siluriformes to fish assemblages diminishes sharply. In the Salado River basin as a whole both orders represent the 64% of total species (López *et al.*, 2001) but further inland, when occasional visitors from lower Salado River are "filtered", its contribution to the whole assemblage drops to 53% (Rosso, 2006). This has been considered as a transitional process of change in assemblage organization towards the Austral subregion (Ringuelet, 1975).

Historical records and regional biogeography of species
The pioneer study of Mac Donagh (1934) and later contributions of Ringuelet *et al.* (1967), Quirós *et al.* (1988), López *et al.* (2001), plus a series of unpublished reports available at Dirección Provincial de Pesca (2008), constitute the reference for the known ichthyofauna of the upper Salado River lakes. Overall, these studies reported 9 species in Mar Chiquita Lake, 14 in Gómez Lake and 16 in Carpincho Lake. None effort had ever been directed until this paper to study the fish fauna of Rocha Lake. Besides the presence of *Hypostomus commersoni* in Mar Chiquita and Gómez Lakes (Dirección Provincial de Pesca, 2008), all species previously cited for the upper Salado River lakes were registered in our samples.

Most of the species that we collected in the upper Salado River lakes are widely distributed along the entire Pampa Plain (López *et al.*, 2002). Conversely, *Parapimelodus valenciennis*, *Loricariichthys anus* and *Hypostomus commersoni* are mostly restricted to the Salado River basin (Rosso, 2006). *Parapimelodus valenciennis*, which nowadays represents the second most abundant species in the upper Salado River lakes, was cited for the first time in this system by the year 1934 in Carpincho Lake (Mac Donagh, 1934). However, subsequent samplings during the next decades did not report this species in these lakes (Ringuelet *et al.*, 1967; Quirós *et al.*, 1988). By the year 2000 this species was reported again for the upper Salado River lakes when was collected in Gómez Lake (Dirección Provincial de Pesca, 2008). The intermittent presence of *Parapimelodus valenciennis* in the upper Salado River lakes could be the result of the use by this species of the main course of the Salado River as an important corridor for displacements between lakes. For instance, an upstream migration from lower reaches lakes as a source of this species for the upper river lakes might be possible. Indeed, when Ringuelet *et al.* (1967) explored the Salado River basin this silurid was absent in the upper lakes but was conspicuously found in lower reaches lakes. This suggest that in the past it is quite probable that lower reach lakes behaved as "source habitats" (*sensu* Pulliam, 1988) for *Parapimelodus*

Table 4. Similarity Percentage Analysis detailing individual (Contrib %) and cumulative (Acum %) contribution of each species for all between lakes comparisons. Mch = Mar Chiquita, Go = Gómez, Crp = Carpincho, and Rch = Rocha. Species codes as listed in Table 2.

Mch *vs*. Go	Contrib %	Acum %	Go *vs*. Crp	Contrib %	Acum %	Rch *vs*. Crp	Contrib %	Acum %
Cp	27.01	27.01	Cv	26.31	26.31	Ob	24.33	24.33
Pv	17.53	44.55	Ob	18.60	44.91	Pv	22.56	46.89
Ob	15.43	59.97	Jm	14.67	59.58	Cv	18.42	65.31
Jm	11.31	71.29	Cc	7.66	67.24	Oj	7.78	73.09
Ci	10.93	82.22	Oj	7.10	74.34	Bi	5.21	78.30
Bi	8.20	90.43	Ci	6.98	81.32	Cc	5.11	83.41
Oj	3.20	93.63	Af	5.58	86.90	Af	5.01	88.42
Cd	3.11	96.73	Pv	4.07	90.97	Ae	3.21	91.63
Ae	1.21	97.95	Bi	3.32	94.29	Ci	2.77	94.40
Af	0.79	98.73	La	1.75	96.04	La	2.64	97.04
Cc	0.39	99.12	Cd	1.48	97.52	Jm	1.36	98.40
Pl	0.34	99.47	Pl	1.11	98.63	Hm	0.94	99.34
Cv	0.33	99.80	Cp	0.83	99.46	Cp	0.27	99.61
La	0.17	99.97	Hm	0.34	99.80	Rq	0.25	99.86
Hm	0.03	100	Rq	0.11	99.91	Hc	0.06	99.92
Rq	0	100	Ae	0.05	99.96	Pl	0.05	99.97
Hc	0	100	Hc	0.04	100	Cd	0.03	100
Mch *vs*. Crp	Contrib %	Acum %	Go *vs*. Rch	Contrib %	Acum %	Rch *vs*. Mch	Contrib %	Acum %
Cv	22.47	22.47	Cv	28.92	28.92	Cv	24.85	24.85
Jm	17.51	39.98	Ob	26.19	55.11	Ob	17.22	42.07
Cp	12.80	52.78	Jm	11.60	66.71	Jm	13.72	55.79
Ci	10.81	63.59	Pv	8.44	75.15	Pv	13.10	68.89
Ob	8.87	72.46	Af	6.70	81.85	Cp	9.48	78.37
Oj	7.46	79.92	Bi	5.12	86.97	Ci	6.90	85.27
Cc	6.32	86.24	Ci	3.78	90.75	Af	5.99	91.26
Af	5.09	91.33	Cc	3.10	93.85	Cc	2.52	93.78
Pv	4.40	95.73	Ae	1.67	95.52	Oj	2.21	95.99
La	1.56	97.29	Oj	1.33	96.85	Bi	1.62	97.61
Bi	0.85	98.14	Cd	1.09	97.94	Ae	1.02	98.63
Pl	0.78	98.92	Pl	0.80	98.74	Hm	0.63	99.26
Ae	0.50	99.42	Hm	0.73	99.47	Pl	0.57	99.83
Hm	0.30	99.72	Cp	0.48	99.95	Cd	0.11	99.94
Cd	0.13	99.85	Rq	0.04	99.99	Rq	0.04	99.98
Rq	0.10	99.95	La	0.04	100	La	0.02	100
Hc	0.03	100	Hc	0	100	Hc	0	100

valenciennis. The same could be happening in the present with *Hypostomus commersoni*, a commonly abundant species in lower basin lakes. A very few individuals of this species had been collected for the first time in the upper reach lakes lately (Dirección Provincial de Pesca, 2008; this paper). The expansion in the distribution of this species within the middle and lower Salado River reaches from 1957 to present was suspected to be related with changes in pluviosity, temperature and channelization (Gómez, 2008). In the case of *Parapimelodus valenciennis*, it has been shown that temporal variability in the water residence time and water salinity affect the distribution range of this species (Rosso & Quirós, 2009).

With this work we enlarge the distribution range of several species that have been cited for the first time in the upper Salado River lakes. Particularly, this is the first time that *Cnesterodon decemmaculatus* is collected in these lakes. This small cyprinodontiform was cited three times in the Salado River, but always at lower reaches of the basin in Chascomús, Vitel and Lobos Lakes (López *et al*., 2001). This species seems to be more conspicuous in the southern Atlantic drainages of the Pampa Plain (Casciotta *et al*., 1999).

From source to sea, there is a worldwide pattern of gradual increase in fish species richness in riverine environments, intimately associated to a longitudinal gradient in environmental, hydrological and topographic conditions. This was early highlighted for steeped temperate rivers in North America (Burton & Odum, 1945), Europe (Huet, 1949) and South America (Petry & Schulz, 2006). This pattern was also revealed in tropical fluvial ecosystems where altitudinal gradient seems to be one of the most important factors determining fish species distribution (Hoeinghaus *et al*., 2004; Súarez & Petrere Júnior, 2007). Under such conditions, in spite of the higher number of species at lower reaches, some fish species occur exclusively at headwaters whereas others occur exclusively at downstream. Comparing the updated taxonomic list that we presented here with the fish fauna of middle and lower reach lakes of the Salado River (López *et al*., 2001) allowed us to realize that species composition along the longitudinal axis of this river changes exclusively by species addition instead of substitution. This finding contrasts with the worldwide pattern observed in lotic ecosystems. Nonetheless, if we consider the fish fauna of the Quinto River, which in the past was connected with the headwaters of the Salado River (Siragusa, 1964), the traditional scenario of longitudinal distribution of fish species is achieved with the exclusive presence of *Trichomycterus corduensis* and *Trichomycterus tenuis* (Ringuelet, 1975).

Patterns in species richness and assemblage diversity

The species richness in a particular freshwater environment may be interpreted as the result of a process in which the global pool of fish species must face a series of filters (Smith & Powell, 1971). Following this concept we may assume that once the species "reached" the upper Salado River lakes in the past, they dispersed among them following major environmental gradients in relation with their autoecology. Indeed, one striking feature of this system is its unusual high concentrations of sodium chloride derived from a sedimentary aquifer located in its headwaters, which originated during arid periods of the Pleistocene (Gabellone et al., 2005). It is quite probably, therefore, that this factor had historically filtered much of the potential regional fauna and forced those species able to reach these waters to disperse in accordance with their tolerance to salinity. Further in the present, the interactive effects of salinity with anthropogenic impacts and hydrological variability impose additional directive forces for some species (Rosso & Quirós, 2009). Precisely, this study shows that the effects derived from anthropogenic releases (as indicated by the $NO_3:NH_4$ ratio) are highly important for the richness and diversity of the fish assemblage at a particular locality.

In this study we also found evidence that linked persistence of species with richness and to a lesser extent with diversity of fish assemblages. Particularly, our results suggest that assemblages where more fish species seem to be highly persistent (100%) are prone to be richer and more diverse or *vice versa*. These findings partially agree with an historical view in ecology that postulated that diversity begets stability (Odum, 1953; Elton, 1966). In this sense, richer and more diverse assemblages of these lakes should be more stable since they have a larger number of species with high persistence in the environment. However, persistence of species is just one component of stability. Stability is really a meta-concept that covers a range of different properties and components of the ecosystem (Loreau et al., 2002). In our study, regardless the relative few sampling months, rather few species were present in all collections at any lake (Table 3) suggesting an important interannual variability in assemblage stability as indicated by persistence of species.

Dominance, persistence and assemblage structure

Following observed patterns in persistence and dominance of species, we may assume that not all these lakes seemed to be equally favorable environments to most of the fish species present in the upper Salado River basin. Fishes are mobile organisms that actively select the optimum between a pool of habitats (Karr, 1981). It could be expected, therefore, that the abundance of each species should be larger near its optimum suite of environmental conditions. Similarly, for those species with wider tolerance for environmental variables, we should expect they would dominate most near the limit of its distribution range, where the suite of more extreme environmental conditions probably exclude less tolerant species. Indeed, the significant association between dominance of *Jenynsia multidentata* and gradient in water conductivity is in accordance with the well known tolerance of this Cyprinodontiformes to high salinity (Thormälen de Gil, 1949; Menni et al., 1996). Similarly, the finding that dominances of *Cyphocharax voga* and *Cyprinus carpio* were negatively aligned with gradient in $NO_3:NH_4$ ratio, agrees with previous results that highlighted how these two species are favored by organically impacted (low $NO_3:NH_4$) environments, whereas other species found these conditions largely disadvantageous (Rosso & Quirós, 2009). The present paper also revealed how these environmental gradients are important for the persistence of particular species at particular sites. In northern temperate streams (see review in Matthews, 1998) the more abundant species at a locality are typically persistent and only some rarer species are nonpersistent. Similarly, in the upper Salado River lakes, the persistence of species as *Parapimelodus valenciennis*, *Cyprinus carpio*, *Cyphocharax voga* and *Hoplias malabaricus* varied greatly between lakes but was higher in those lakes where these species were more abundant and tended to dominate most. Particularly, the persistence of these four species in a lake seemed to be negatively affected by water conductivity.

In spite of the high proximity between lakes and the short spatial gradient explored, different patterns in dominance and persistence of many species leaded to an important variation in fish assemblage structure. Exploration of fish assemblages along a short spatial scale in the uppermost part of the Paraná River also demonstrated a great ichthyofauna heterogeneity (Fialho et al., 2007). In our study, with only four species, the similarity percentage analysis was able to explain almost 60% of the total dissimilarity between any pair of lakes. Thus, *Corydoras paleatus*, *Jenynsia multidentata*, *Cyphocharax voga* and *Odontesthes bonariensis* may be considered as key species for the distinctiveness between the upper Salado River lakes.

Overall, we have shown that the gradient in water conductivity is an important factor for the persistence of particular species in a particular location. This study also highlighted that gradients in water conductivity and the $NO_3:NH_4$ ratio set up particular conditions that were associated with particular fish communities dominated by different groups of species. All these results show that human impacts on surface waters may interact with environmental factors to influence the dynamics of fish species and the structure of their communities. In comparison, the extremely low abundance of piscivores suggests that predation would play a minor role in these fish assemblages.

Implications for management and conservation

In this paper, we identified those species that contribute most to the distinctiveness of each lake in the upper Salado River basin. These findings are of practical interest for management and conservation purposes. Particularly, the contracted spatial distribution of locally abundant species, as *Odontesthes bonariensis* and *Cyphocharax voga*, should be addressed as an important issue for fisheries regulations.

Similarly, conservation efforts should be enforced towards those less abundant species that are, as well, mostly confined to a shorter spatial habitat. Among these species major efforts should be focused on *Cnesterodon decemmaculatus* in Gómez Lake, loricariids in Carpincho Lake and finally, on the top predator *Hoplias malabaricus* which was almost exclusively found in Rocha Lake. Likewise, control plans for the exotic *Cyprinus carpio* should be mostly centered around Carpincho and Rocha Lakes, where this species is more abundant. These results demonstrate that even when broad management and conservation strategies should encompass the system as a whole, lake-specific approaches must also be addressed.

Acknowledgements

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