

INTERACTIVE EFFECTS OF ABIOTIC, HYDROLOGICAL AND ANTHROPOGENIC FACTORS ON FISH ABUNDANCE AND DISTRIBUTION IN NATURAL RUN-OF-THE-RIVER SHALLOW LAKES

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ABSTRACT

Ecological processes in lowland rivers are mostly dominated by hydrology and its interactions with other environmental factors. Fish–habitat relationships in rivers are also influenced by human impacts.

In this study, we describe patterns of abundance and distribution of fish species in a group of natural lowland river lakes along spatial anthropogenic and abiotic gradients when four hydrologically different summers are compared. We also describe the proportion of the total variances in fish species abundances that can be accounted for by selected abiotic (water conductivity), hydrological (water residence time) and human activity-derived (total phosphorus (TP) concentration and $\text{NO}_3\text{:NH}_4$) variables. Consequently, our main purpose is to explore how abiotic and anthropogenic factors interact to affect fish abundance and distribution together with consistent results across different hydrological conditions. We conclude with a briefly discussion of some management implications.

The anthropogenic impacts on water quality, the extreme hydrological variability and the fluctuating abiotic environment affected fish abundance and distribution. Pampa inland silverside *Odontesthes bonariensis* was benefited from a less human disturbed environment with higher water residence time and total salinity, whereas species as *Cyphocharax voga*, *Parapimelodus valenciennis* and *Cyprinus carpio* found these conditions largely disadvantageous. On the other hand, while most species showed stronger—either negative or positive—response to anthropogenic, hydrological or abiotic factors *Oligosarcus jenynsii* was only slightly affected.

This paper identified the ecological function of a lowland river under its natural flow regime. There are not many opportunities to study unmodified rivers worldwide. Therefore, our findings may help in assessment programmes of fish communities in flow altered and human disturbed aquatic ecosystems. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: Pampa Plain; Salado River; shallow lakes; hydrology; water salinity; anthropogenic impacts; fish abundance

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INTRODUCTION

Natural flow regimes of most rivers worldwide are highly conditioned by the patterns of precipitation in their basins. Although the basic nature of the river is determined by the rocks in the basin, the flow regime largely modifies the physical and chemical conditions within the river (Walling, 1980; Wilby and Gibert, 1996; Wetzel, 2001 among many others). Fishes are mobile organisms that actively select the optimum between a pool of habitats (Karr *et al.*, 1986) provided that a route of water is available between them (Holden, 1963; Schiemer and Spindler, 1989). Therefore, following these changes in the physical and chemical conditions due to the variability of flow regime, river ecosystems usually show marked patterns of changes in fish abundance and distribution along their main course and associated environments (Ryder and Pesendorfer, 1989; Reid and Puckridge, 1990; Quirós and Vidal, 2000). Thus, hydrological disturbance, stressful environments and the ability of fish to cope with abiotic challenges all affect local fish assemblage composition or dynamics (Matthews, 1998), namely patterns in fish abundance and distribution of different species. However, native fish fauna found in a particular river ecosystem is usually well adapted to the natural flow regime variability, and consequently the major changes in the fish

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assemblages of the ecosystem will occur under large departures from the average natural flow patterns (Welcomme, 1985). In the temperate region, natural flow regimes of lotic ecosystems usually show an important hydrological variability, alternating floods and droughts of different intensity both within and between years. These extreme conditions of floods and droughts are disturbing events as they can affect fish both directly and indirectly (Wootton, 1998).

Because the river is only one component of a larger system, the basin, fish communities in rivers are affected not only by events occurring within the channel and its associated waters but by a range of external influences (Welcomme, 1985). Many such influences are the result of natural variability, particularly meteorological conditions, but more frequently such changes are the result of some human intervention (Moss, 1988; Quirós, 1990). Lotic ecosystems provide many valuable services to human well-being including, among others, the purification of urban and industrial wastes. When these effluents exceed the natural carrying capacity of the receiving ecosystem, organic material, nutrients and toxics of different nature accumulate and the risk for the integrity and functioning of the aquatic biota increases sharply (Girardet, 1992). It thus seems worthwhile to investigate fish assemblage attributes in relation to anthropogenic impacts wherever a human threat is present. However, anthropogenic impacts do not operate in isolation, their interactions with environmental factors are which finally influence fish abundance and distribution in freshwater ecosystems. On the other hand, the structure and dynamics of biological communities living in river ecosystems are also largely influenced by hydrologic changes (Petts, 1996; Cowx and Welcomme, 1998).

In the Pampa Plain (Argentina), the Salado River system presents a high number of very shallow lakes. These lakes are highly fluctuating in salinity and water residence time (Quirós *et al.*, 2002) and had been largely modified by man and his use of land and water (Quirós *et al.*, 2006). Rosso and Quirós (2007) used correlative empirical approaches to discern linkages among human disturbance, hydrology and abundance of major fish species at the heavy populated headwaters of this river. Here, we test for differences in fish abundances of these species (*Odontesthes bonariensis*, *Cyphocharax voga*, *Parapimelodus valenciennis*, *Cyprinus carpio* and *Oligosarcus jenynsii*) according to their position along anthropogenic and abiotic gradients when four hydrologically different summers are compared. We also describe the proportion of the total variances in fish species abundance that can be accounted for by selected abiotic, hydrological and human activity-derived variables. Consequently, our main objective is to explore how abiotic and anthropogenic factors interact affecting fish abundance and distribution. Moreover, we look for consistency of results across different hydrological conditions, analysing how spatial patterns in single fish species abundance are still consistent when four hydrologically different summers are compared. There has been a strong recommendation for fish ecologists in order to recognize the importance of interactions across scales in quantifying effects on fishes (Durance *et al.*, 2006). With this paper, we address the way regional scale landscape attributes, namely hydrological variability and human development, interact with the abiotic local environment in order to influence fish abundance and distribution at a smaller local scale. We end by briefly discussing some management implications that emerge from our results.

MATERIALS AND METHODS

Study site

The Salado River is an autochthonous lowland river of 690 km. It heads at 78 m above the sea level and runs along a very smooth plain with an average slope of 0.18 m km^{-1} . The headwater reaches of the river are characterized by the presence of a sedimentary aquifer with high concentrations of sodium chloride, which originated during arid periods of the Pleistocene (Gabellone *et al.*, 2005). The study lakes are very shallow natural impoundments located at the headwaters of this river. They are mostly used for recreational purposes since their high salinity preclude the use for irrigation. With a mean depth around 1 m and an area ranging from 5 to 50 km^2 these lakes have been described as polimictic, eutrophic to hypereutrophic environments (Quirós, 1988).

The climate of this region is warm temperate with a high interannual variability in the precipitation regime (Sierra *et al.*, 1994). Annual precipitation averages around 950 mm most of which occurs during spring–summer months. Flow regime of this river closely follows precipitation patterns which in turn determine the hydrological dynamic of its lakes (Fuschini Mejía, 1994). At the upper reaches of this river mean monthly discharge for spring–

summer period range from 0 to almost $50 \text{ m}^3 \text{ s}^{-1}$ with an overall average for the whole period of $10.1 \text{ m}^3 \text{ s}^{-1}$ (Department of Hydrology, Buenos Aires Province).

The use of arable land of the landscape is mostly devoted to agricultural cultivation (51.5%) and in a lesser extent to livestock breeding (36.2%). Livestock breeding is mostly restricted to marginal zones occasionally flooded by the river. All the study lakes seem to be equally exposed to agricultural impacts. However, not all these lakes seem to be equally exposed to other human perturbations. Large cities (more than 10 000 inhabitants), industries and small villages (less than 1000 inhabitants) are common features of the landscape. The spatial arrangement of these point source effluents along the study site determines that upper reach lake drainages are less populated and industrialized than lower reach lakes (Figure 1). Interestingly, these lakes are also 'sorted' by their total ionic content, with decreasing total salinity as the river flows (Gabbellone *et al.*, 2005). Here, we have considered two main spatial axes along which the lakes may be described: a first axis of landscape human development (Rosso and Quirós, 2007) and a second abiotic axis of total salinity of their waters. The natural fluctuating flow regime of the Salado River represents a third temporal axis of hydrological variability. Therefore, in order to better explore the relationships between fish, human disturbance and environmental variables, five sampling sites were placed at different locations along the river connected lakes. The uppermost site was settled in Mar Chiquita Lake (Mch), two more locations were placed in Gómez Lake named Gómez north (GoN) and Gómez east (GoE) and finally one more in Carpincho (Crp) and Rocha (Rch) Lakes. Three sites (GoN, GoE and Crp) were sampled monthly during four hydrologically different summers (mean, dry, wet and extreme wet), whereas Mch and Rch only were surveyed under dry and wet conditions.

Environmental and anthropogenic data

In order to study the effects of anthropogenic activity of the landscape on fish abundance and distribution, the human disturbance in these shallow lakes was assessed by measuring the $\text{NO}_3:\text{NH}_4$ ratio and the total phosphorus (TP) concentration (mg L^{-1}). Organic sewage from human populations, industry and agriculture result in excessive nutrient loading and enhanced rate of degradation of organic matter (Wetzel, 2001). Due to the systematic discharge of untreated industrial and human wastes into the Salado River system, the $\text{NO}_3:\text{NH}_4$ ratio and TP were, therefore, assumed to be largely influenced by non-point (human population, agriculture and livestock activities) and point

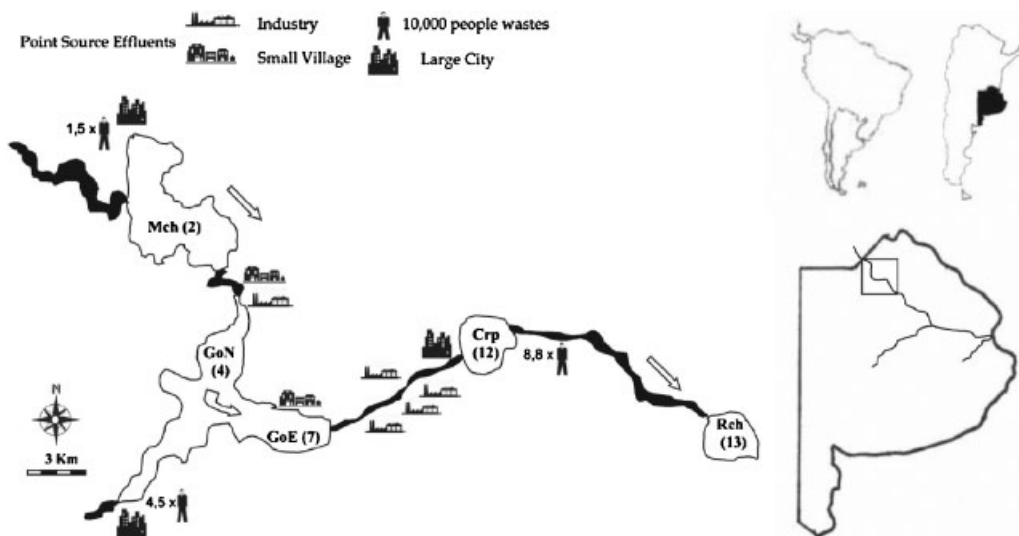


Figure 1. Anthropogenic development of the upper Salado River basin. Legends indicate point sources of human effluents (cities, villages and industries) and graphically display the anthropogenic gradient from the less disturbed Mar Chiquita Lake to the highly impacted Rocha Lake. Study sites are labelled as Mch, Mar Chiquita; GoN, Gómez north; GoE, Gómez east; Crp, Carpincho and Rch, Rocha. Open arrows show main channel flow direction. Numbers in brackets indicate the upstream abundance of point source effluents for each site. Upstream abundance of human population for each site are: Mch, 14 850; GoN, 14 850; GoE, 55 765; Crp, 55 765 and Rch, 144 246

source effluents and hence interpreted as a measure of human activity-derived impacts. The concentration of $\text{NH}_4\text{-N}$ and the proportion of $\text{NH}_4\text{-N}$ in total nitrogen in lake surface waters rise steadily with lake trophic state (measured as TP) for lakes and shallow lakes (Quirós, 2003). Therefore, we also considered both, TP and the $\text{NO}_3\text{:NH}_4$ ratio, as indicators of eutrophication from anthropogenic origin. For nutrient analyses, water samples were taken by duplicate at a depth of 50 cm below the water surface. TP concentrations were determined by the ascorbic acid method corrected for turbidity, following current APHA procedures (APHA, 1995). $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ were quantified using selective electrode methods (APHA, 1995). Probes detection limits were 0.14–1400 mg L^{-1} and 0.03–1400 mg L^{-1} , respectively.

The abiotic environment was explored by quantifying the means of total dissolved oxygen (mg L^{-1}), water temperature ($^{\circ}\text{C}$) and water conductivity ($\mu\text{S cm}^{-1}$) in the water column using a Yellow Spring probe (model YSI 85). Water conductivity had been found to be closely related ($r = 0.934$) with total salinity (measured as the sum of major cations and anions) in these lakes (Rosso and Quirós, unpublished data). Hence, we assume that this variable can be used as a reliable surrogate of salinity. All environmental and human activity-derived variables were explored at monthly intervals in the open waters of study sites.

Hydrological aspects of study sites were explored measuring water column depth (metres) and water residence time (days). Water depth was measured using a weighted scaled rope. The water residence time (T_w) was calculated using lake volumes (based on measurements of surface area (Quirós, unpublished data) and mean depth) and water discharge obtained from the Department of Hydrology (Buenos Aires Province). In order to better describe the hydrological conditions within each summer, precipitation data were gathered from the Servicio Meteorológico Nacional.

Fish sampling

The upper Salado fish fauna includes 18 native and one introduced species. Information on the ecology of these species in the temperate Pampa Plain was gathered as part of a large survey programme of Pampa freshwater ecosystems (Rosso, 2006). Based on their abundances in shallow lakes, five species among the most common Pampa freshwater fish were selected. These were the planktivorous *O. bonariensis* (Atherinopsidae), the small silurid *P. valenciennisi* (Pimelodidae), the detritivorous *C. voga* (Curimatidae), the small carnivorous *O. jenynsii* (Characidae) and the exotic *C. carpio* (Cyprinidae). Fish were caught using two experimental multi-mesh gill nets (15, 21, 25, 30, 35, 40, 52, 60, 75 and 85 mm bar mesh size) set in the open water zone of lakes at night time. All net panels were of equal height (1.4 m) and length (10 m). Fish were identified at species level (Ringuelet *et al.*, 1967; Nelson, 1994) and counted. Fish abundances were standardized to catch per unit of effort (CPUE) prior to analyses. CPUE was calculated as the number of each species collected at each site per hour of netting.

Data analysis

Environmental factors. With all measured physical and chemical attributes of water we constructed a polythetic agglomerative hierarchical clusters analysis, in order to explore the degree of dissimilarity between sites that could arise from differences in their hydrological, anthropogenic and abiotic characteristics when the four summers are compared. Prior to be analysed, data were standardized to zero mean and equal variance to eliminate spurious effects due to unequal variances. We excluded from the cluster analysis the extreme-wet summer sites because there were some missing data in their variables sets.

We used a space-conserving fusion technique (average linkage) in order to better portray the original structure of the data (Jongman *et al.*, 2004). However, before had decided on this option we ran several procedures to get confidence in the cluster solution by comparing results. Even single-linkage, a space-distorting technique, captured the structure of the original data fairly well indicating a rather pronounced structure in the data (McGarigal *et al.*, 2000). Euclidean distance was used as the resemblance measure and the cluster solution was evaluated using the cophenetic correlation. The aim of this analysis is that it should easily display graphically the evidence of the spatial (anthropogenic and abiotic) and temporal (hydrological) axes by means of major abiotic attributes of different sites throughout different hydrological seasons. If different sites of the same hydrological season are grouped together we would expect a greater influence of the hydrological variability on main water attributes, hence on fish.

Conversely, if different hydrological conditions of a single site are grouped together, we might speculate a more important role of local process.

Fish abundance and distribution. We explored patterns of abundance and distribution of single fish species along spatial axes of abiotic and anthropogenic gradient. Then, we look for consistency in the observed patterns of this spatial analysis against a third temporal axis of hydrological variability.

For the spatial analysis, five sites (Mch, GoN, GoE, Crp and Rch) which differ in the human development along their immediate drainages and total ionic content of their waters are explored during two summers with contrasting hydrological conditions. Both summers were analysed separately in order to look for consistency in the observed patterns of fish abundance and distribution. Then, we retest these spatial patterns in fish abundance and distribution with a second data set that includes shorter spatial gradients but a larger temporal hydrological gradient, with three sites (GoN, GoE and Crp) being explored along four hydrologically different summers.

The spatial analysis aims to explore how single fish species abundances significantly differ from one site to another. This first test was performed using the Kruskal–Wallis one-way ANOVA on Ranks followed by the Kruskal–Wallis Multiple-Comparison Z-value test in order to find differences between sites (Daniel, 1978). For the temporal analysis, we expand our hydrological gradient while resigning some strength in the spatial spectrum of the analysis. With this test, we attempt to gain confidence in how hydrology influences single fish species abundances to be still different among the three sites (with shorter anthropogenic and abiotic gradients) when the four different hydrological seasons (mean, dry, wet and extreme wet) are compared. At this stage, we also test for differences in fish species abundances between summers of contrasting hydrological conditions. In order to do so, we use sites and seasons alternatively as blocks and treatments and the fish species abundances as the response variable in the Friedman's two-way analysis of variance, using seasons and sites as the main effects. Next, we search for differences between treatments using the Multiple-Comparison procedure suggested by Daniel (1978). Concordance in the 'behaviour' of ranks among different blocks was tested using the Kendall's W of concordance (Conover, 1971) as a complementary measure of difference in fish abundance between 'treatments' (seasons and sites). All statistical analyses were performed using NCSS 2000 statistical software (Hintze, 1998).

Interactive effects on fish abundance. We use canonical correlation analysis (CANCOR) in order to describe the proportion of the total variances in fish species abundance that can be accounted for by selected abiotic (conductivity), hydrological (T_w) and human activity-derived (TP and $\text{NO}_3\text{:NH}_4$) variables. Specifically, we use CANCOR to identify and describe abiotic, hydrological and anthropogenic gradients that are maximally correlated with fish species abundance patterns. The data set consists of nine continuous variables (five fish species abundances plus four selected environmental factors) derived from monthly samples in all study sites during different hydrological seasons. We excluded samples with missing values. The final sample-to-variable ratio was 3.62 which could be considered enough to meet sample requirements in ecological studies (Smith, 1981). Prior to be included in the analysis both variable sets were $\log(x + 1)$ transformed. The resulting variables were inspected for outliers and multicollinearity, both critical elements for the effectiveness of the analysis (McGarigal *et al.*, 2000). Scatter plots of canonical scores for the first canonical variates were used to tested for linearity and normal probability plots of mentioned scores for normality.

In order to assess the importance of canonical analysis we report the squared canonical correlation coefficient (R_c^2), the proportion of a set's variance accounted for by its own canonical variates and finally the product of these two parameters, called redundancy coefficient. Redundancy provides a summary measure of the ability of one set of variables (taken as a set) to explain the variation in the other variables (taken one at time). As such, the redundancy measure is perfectly analogous to the R^2 statistic in Multiple Regression Analysis, and its value as a statistic is similar (McGarigal *et al.*, 2000). In our case, only the redundancy in the fish abundance set was calculated as it is considered to be the dependent variable set.

The number of variates to be retained and therefore the cumulative variance accounted for by the redundancy coefficients were determined using an approximate F -statistic for testing the significance of the Wilk's Lambda test (Hintze, 1998). Ultimately, the interpretation and utility of each canonical solution was grounded on its ecological meaning and redundancy coefficients. The ecological interpretation of the retained variates was performed by analysing its structure coefficients (canonical loadings). These coefficients tell how closely a variable and a canonical variate are related. Hence, we can define a canonical variate on the basis of the structure coefficients by noting the variables that have the largest coefficients. In this way, the canonical structure analysis provides an

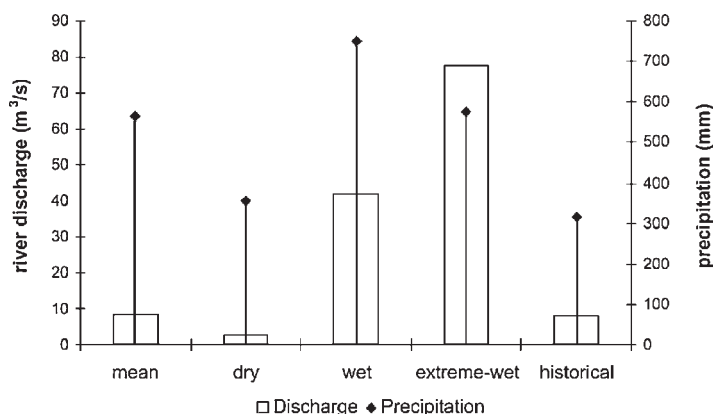


Figure 2. Hydrological characteristics of the four sampled summers by means of river discharge and precipitation variables. The historical summer means of precipitation (100 years) and river discharge (20 years) are reported

ecological interpretation of each canonical function and is one of the most important pieces of information resulting from CANCOR (McGarigal *et al.*, 2000).

In order to assess the validity of the CANCOR analysis, we used the jackknife resampling procedure to judge the reliability of the canonical results and hence the ecological interpretation. We tested the null hypothesis that each observed coefficient from the full data set is equal to the jackknife estimate of the coefficient using a *t*-statistic. Finally, if the null hypothesis is rejected we must conclude that coefficients are unstable and that not really underlying structure exist in the data sets.

RESULTS

Hydrological and environmental dynamics

Summer flows varied widely among sampled years. Summer mean flows ranged from low to extremely high during 1999 through 2002 when compared with the long-term (1978–1998) summer mean of $8.1 \text{ m}^3 \text{ s}^{-1}$. As expected this variation followed closely the precipitation regime of the region. Using flow and precipitation variables (Figure 2), we classified sampled summers into four hydrologically different seasons as mean (1999), dry (2000), wet (2001) and extreme wet (2002). Environmental characteristics of lakes largely reflected (Table I) this oscillation in mean flow patterns. Harsh dry conditions of summer 2000 produced the greatest environmental contrast between sites. This low flow summer maximized the spatial gradient of water conductivity and also increased sharply the water residence times for all sites. The conductivity of the water reached the maximum of the whole period during this dry summer with $9818 \mu\text{S cm}^{-1}$ in Mar Chiquita Lake and $6804 \mu\text{S cm}^{-1}$ in Rocha Lake. The persistence of the water in the environment, as measured by the T_w , ranged from less than a month (19.6 days) in Rocha Lake to almost a year (347.9 days) in Gómez Lake. Differences in the $\text{NO}_3:\text{NH}_4$ ratio among sites was also enhanced during the driest summer showing a strong negative relationship with the abundance of human impacts (cities and industries) of the landscape. There were not evident gradients in water temperature, dissolved oxygen, TP nor water depth during the dry summer.

Wet summer of 2001 made even the major environmental gradients lowering the values of water conductivity, $\text{NO}_3:\text{NH}_4$ ratio and T_w in all sites. Similarly, water depth and TP were increased. Extreme-wet summer of 2002 further decreased the conductivity of the water and the T_w to the lower levels ever registered. Mean summer water temperatures were slightly lower during the wet summer and further decreased by more than 3°C in the extreme-wet summer of 2002. Mean summer of 1999 displayed, as expected, average values for almost all measured variables excepting the $\text{NO}_3:\text{NH}_4$ ratio that was higher during this summer.

Table I. Monthly mean (range) of environmental variables at each study site across four summers (1999–2002) for GoN, GoE and Crp and two summers (2000–2001) for Mch and Rch

Site	N	Depth	Conductivity	Temperature	Oxygen	NO ₃ :NH ₄	TP	T _w
Mch	6	1.18 (0.6–1.8)	5925 (2019–9818)	24.3 (17.8–28)	7.5 (4.1–10.7)	2.38 (0.006–5.32)	1.19 (0.82–1.85)	76.3 (7.7–326.8)
GoN	12	1.59 (1.4–1.9)	5062 (2390–8955)	24.2 (17.6–29.7)	8.1 (5.4–11.5)	1.79 (0.006–3.96)	0.93 (0.42–1.32)	118.5 (8.1–829.4)
GoE	12	1.71 (1.4–1.9)	4813 (2296–8449)	23.5 (17.8–28.1)	9.2 (5.1–12.7)	1.34 (0.02–3.11)	0.78 (0.39–1.47)	118.5 (8.1–829.4)
Crp	12	1.27 (1.1–1.6)	4460 (2202–7524)	24.3 (18.5–28.7)	10.4 (6.1–13.1)	0.78 (0.007–1.85)	0.81 (0.38–1.24)	12.8 (0.9–88.1)
Rch	6	1.19 (0.9–1.5)	5200 (3545–6804)	24.6 (18–28.7)	8.2 (5.8–10.9)	0.52 (0.09–1.64)	1.11 (0.96–1.27)	10.2 (0.6–47.1)

Notes: Codes of sites correspond to Mch, Mar Chiquita; GoN, Gómez north; GoE, Gómez east; Crp, Carpincho and Rch, Rocha. TP, total phosphorus; T_w, water residence time. N, indicates the number of monthly samples at each site. Note the marked environmental gradient when analysing the NO₃:NH₄ ratio and water conductivity. The lack of sampling in Rch Lake during the extreme-wet summer disrupts the natural gradient in water conductivity displayed in this table due to the high lower value of the range.

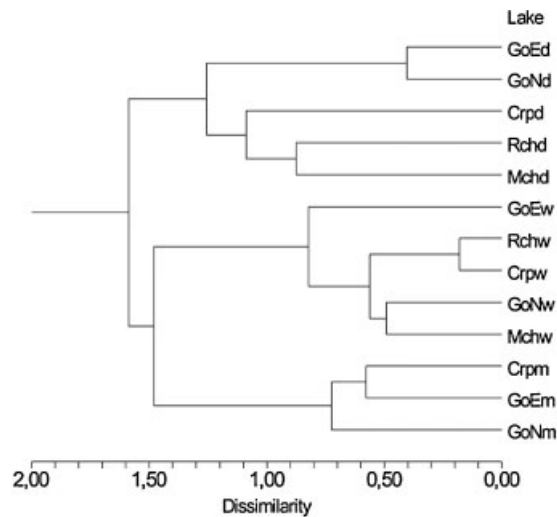


Figure 3. Dendrogram of UPGMA cluster analysis of sampling sites at different hydrological seasons by measures of hydrological variability, abiotic environment and human activity-derived variables. Sampling entities labelled by study site codes as in Figure 1 plus the corresponding letter for each hydrological season: d, dry summer; w, wet summer and m, mean summer

Overall, cluster solution sufficiently accounted for these fluctuations in the environmental features of the study sites, reflecting a marked structure of the data. The cluster analysis (cophenetic correlation of 0.75) perfectly grouped together different sites of the same hydrological season (Figure 3). This suggests that hydrological variability probably overcome abiotic (water temperature and dissolved oxygen) and human activity-derived variables ($\text{NO}_3\text{:NH}_4$ ratio and TP) in representing the main source of variation for the spatial and temporal dynamics of these shallow lakes. Cluster analysis also captured the pronounced spatial gradient observed during the driest conditions. At a dissimilarity cut-off value of 1 distinctive clusters were already formed (wet and mean sites), whereas the dry sites cluster finally fused well above this value. This demonstrates how study sites differ most, in relation to the major physical and chemical conditions, during a harsh dry summer. Indeed, at a value of 1 the Crp site of the dry summer cluster still was a single entity. Cluster of the dry summer sites finally jointed the remainder sites at a dissimilarity value greater than 1.5.

Fish abundance along the anthropogenic and abiotic spatial gradients

Dry summer. During dry summer, when fish abundances were explored against anthropogenic and abiotic spatial gradients, almost all species displayed significant among-site differences in their population sizes (Table II). There was a marked tendency of bottom-dwelling fishes as *C. voga* and *C. carpio* to be more abundant at highly human disturbed sites with lower salinities and T_w . Conversely, *O. bonariensis* showed the opposite pattern being more abundant as the human activity of the landscape decreased and the total salinity of the water increased. The small silurid *P. valenciennis* was also more abundant at lower sites during this summer. *O. jenynsii* showed only marginally significant differences in its spatial abundance patterns.

Wet summer. When the same five sites were explored under a high river discharge summer, there were still three species with consistent spatial patterns in fish abundance and significant differences among sites (Table II). *C. voga* and *C. carpio* still were significantly more abundant in lower Carpincho and Rocha Lakes. *O. bonariensis* also preserved the tendency to be more abundant at upstream sites. For the remainder two species, *P. valenciennis* and *O. jenynsii*, patterns of the dry summer disappeared and more evenness was recorded in their spatial patterns of fish abundance with a tendency to display higher abundances in the former saltier lakes when compared with the dry season patterns (Figure 4). However, irrespective of the hydrological conditions, *O. jenynsii* was always less abundant at the saltier, less disturbed Mar Chiquita Lake (Table II).

Table II. Among-site differences in fish abundances at the upper Salado River study sites, 2000–2001

Species	Dry season (2000)		Wet season (2001)			
	Among-site differences (Kruskal–Wallis Z-value test)		Among-site differences (Kruskal–Wallis Z-value test)			
	One-way ANOVA χ^2	<i>p</i>	One-way ANOVA χ^2	<i>p</i>		
<i>Parapimelodus valenciennis</i>	10.44125	0.033616	GoE, Crp, Rch > Mch and GoE, Rch > GoN	2.633333	0.62093	None
<i>Cyprinus carpio</i>	11.33333	0.023063	Crp, Rch > Mch, GoN and Rch > GoE	9.6	0.047733	GoN, Crp, Rch > GoE and Rch > Mch
<i>Oligosarcus jenynsii</i>	9.1	0.058648	GoN, GoE, Crp, Rch > Mch	7.433333	0.114685	GoN, GoE, Crp, Rch > Mch
<i>Odontesthes bonariensis</i>	9.833333	0.043331	GoN > GoE > Crp, Mch, Rch	9.784139	0.044225	Mch, GoE, Crp > Rch and Mch > GoN
<i>Cyphocharax voga</i>	9.83394	0.04332	Crp, Rch > Mch, GoN, GoE	10.61235	0.031284	Crp, Rch > Mch, GoE and Rch > GoN

Notes: Codes of sites correspond to Mch, Mar Chiquita; GoN, Gómez north; GoE, Gómez east; Crp, Carpincho; Rch, Rocha.

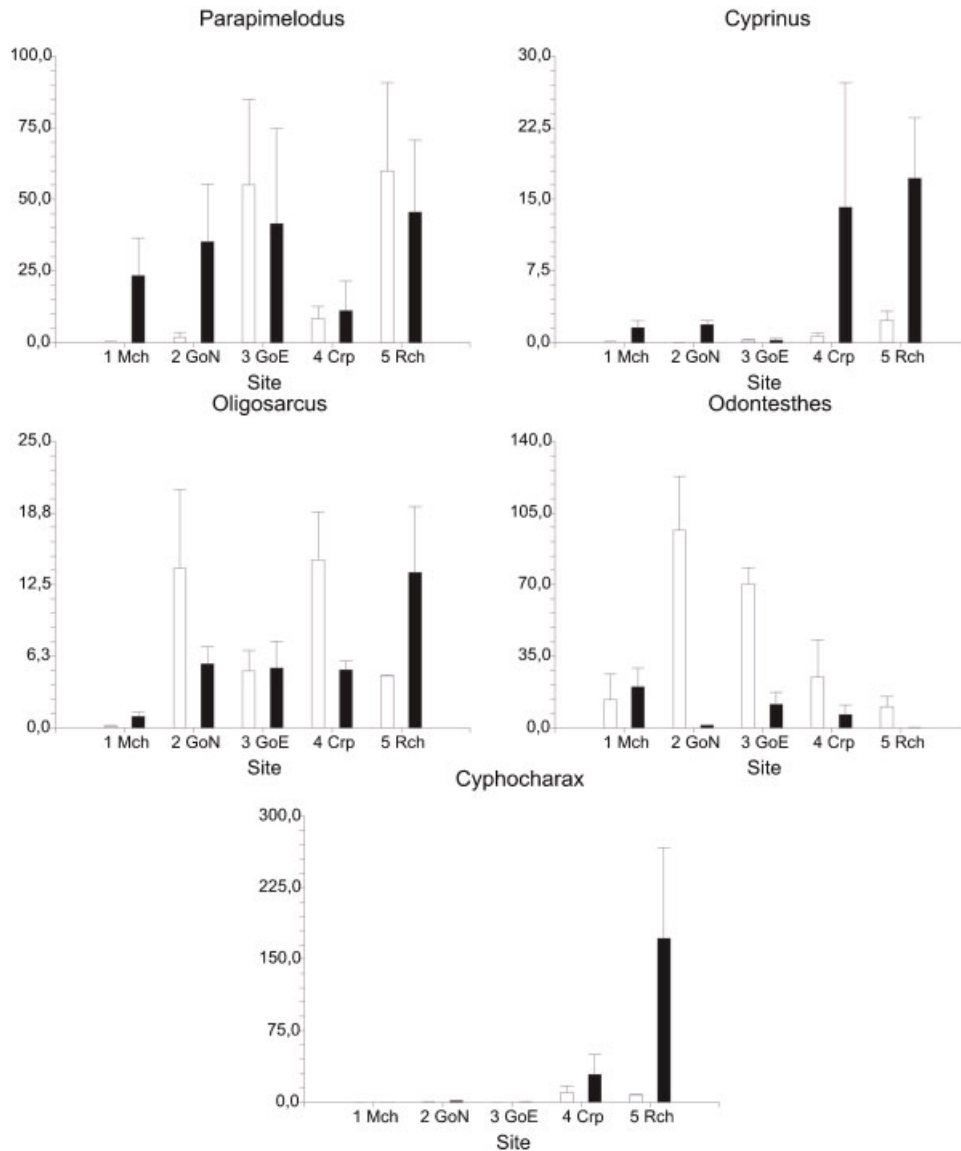


Figure 4. Bar charts showing mean summer abundances (as CPUE) of major fish species in the upper Salado River sites during dry and wet summers. To ease the interpretation, site labels in the x-axis are ordered following their longitudinal position along the anthropogenic and abiotic gradients. Open bars, dry summer; filled bars, wet summer. Crossing lines represent the upper limits of standard errors. This figure is available in colour online at www.interscience.wiley.com/journal/rra

Fish abundance and the temporal hydrological variability

Season effect. When the effect of the hydrological variability on fish abundances was explored at the three sites (GoN, GoE and Crp) of the second data set, the abundance of *C. voga* and *O. bonariensis* were significantly different between summers showing a noteworthy response to particular hydrological conditions (Table III). These two species showed an opposite behaviour in their population dynamics. Whereas *C. voga* was more abundant during the wettest periods, *O. bonariensis* displayed higher abundances under low to average summer flows (Figure 5). *O. jenynsii* and *C. carpio* showed a marginal tendency to be affected by the hydrological season. As *C. voga*, *C. carpio* tend to be more abundant when wet conditions prevailed. *O. jenynsii* resembled *O. bonariensis* in

Table III. Effects of longitudinal position of sites and hydrological seasons on fish abundances at three sites of the upper Salado River basin

Species	Season			Site		
	Friedman's <i>Q</i>	Kendall's <i>W</i>	Comparisons	Friedman's <i>Q</i>	Kendall's <i>W</i>	Comparisons
<i>Parapimelodus valenciennis</i>	1	0.111111		3.5	0.4375	
<i>Cyprinus carpio</i>	5.8*	0.644444	wet > mean, dry	2	0.25	
<i>Oligosarcus jenynsii</i>	5.8*	0.644444	dry > mean, wet, exwet	0.5	0.0625	
<i>Odontesthes bonariensis</i>	7.4**	0.822222	mean, dry > wet, exwet	0.2	0.032	
<i>Cyphocharax voga</i>	8.2***	0.911111	exwet > mean, dry	6.5***	0.8125	Crp > GoN, GoE

Notes: The *Q* statistics are all corrected for ties. For Friedman's results, df: 3 for season and 2 for site; exwet, extreme wet. Codes of sites correspond to GoN, Gómez north; GoE, Gómez east and Crp, Carpincho.

* $p < 0.15$; ** $p < 0.10$; *** $p < 0.05$.

that its population size tend to be more abundant under dry conditions. *P. valenciennis* was not clearly affected by the hydrological condition when GoN, GoE and Crp sites were explored along this temporal axis.

Site effect. When the spatial patterns of fish abundances were explored during four summers of contrasting hydrological conditions, only *C. voga* showed significant differences in its population sizes. The abundance of this species was always higher in Carpincho Lake regardless extreme variation in summer mean flows (Table III). On the other hand, the Friedman's sum of ranks summary (Table IV) indicated that the abundance of *C. carpio* also tend to be higher in Carpincho Lake. Similarly, the sum of ranks test showed that *P. valenciennis* tend to be more abundant at GoE, where a small village otherwise almost unpopulated, receive thousands of visitors each day during summer months. One interesting result is that among-site differences in abundance of *O. bonariensis* were maximized under the harsh abiotic conditions of the dry summer (Figure 5).

CANCOR analysis

The first pair of canonical variates was the most closely related (Table V). Indeed, almost 70% of the variance in the first fish variate was accounted for by the variance in the environmental variates and *vice versa*. This percentage is reduced in the subsequent variates. However, the strong linear relationship between scores of fish and environmental variates reflects the high canonical correlation between all these canonical solutions (Figure 6). The results of the significance test indicate that the data set contains canonical correlations significantly ($p < 0.05$) different from zero until after the third pair of canonical variates have been extracted (Table V). The redundancy analysis indicates that, collectively, all three environmental variates explain 44.4% of the variance in the fish abundance data. The first environmental variate alone accounts for almost 20% of the variation in fish species abundances (Table VI). However, the second variate explains slightly less than 10% of the fish abundance.

Based on redundancy and significance analyses, we choose to retain the first and the third pairs of canonical variates for subsequent ecological interpretation (Table VII). The cumulative redundancy for these two environmental variates is 35.1%, which represents almost 80% of the total redundancy (44.4%) in the fish abundance data.

The correlations between the environmental variables and the first environmental variate indicate that Factors 1 represents gradients in hydrological and trophic conditions. Specifically, Factors 1 represents gradients in T_w and TP concentration with sites richer in phosphorous (TP = 0.72) loading high on one end of the gradient and sites characterized by larger water residence times ($T_w = -0.81$) loading high on the opposite end of the gradient. The correlations between fish species abundances and the first fish variate (Fish 1) identify a gradient in species

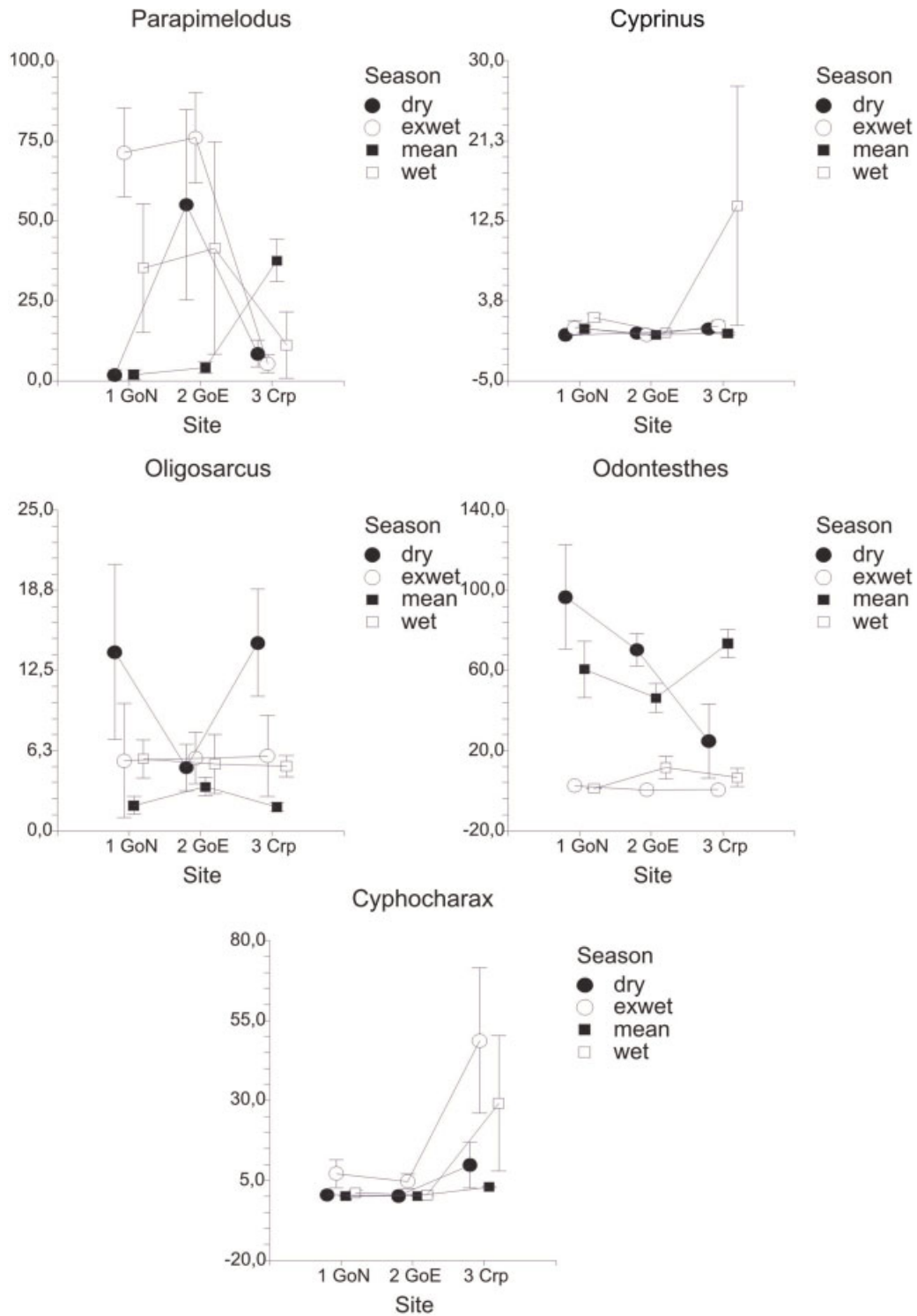


Figure 5. Means of abundances (as CPUE) of major fish species at three sites of the upper Salado River, when the anthropogenic and abiotic gradients were explored against four hydrologically different summers. Crossing lines represent the limits of standard errors. This figure is available in colour online at www.interscience.wiley.com/journal/rra

Table IV. Friedman's sum of ranks summary for season and site effects

	Parapimelodus	Cyprinus	Oligosarcus	Odontesthes	Cyphocharax
Exwet	9	7	9	4	12
Wet	8	12	8	5	9
Mean	7	5	3	10	4
Dry	6	6	10	11	5
Crp	7	10	8	8	12
GoE	11	6	7	8	5
GoN	6	8	9	8	7

Notes: Codes of sites correspond to GoN, Gómez north; GoE, Gómez east and Crp, Carpincho; Exwet, extreme wet.

Table V. Canonical correlation coefficients and significance test

Variate number	Canonical correlation	R-squared	F-value	Prob. level	Wilks' Lambda
1	0.83374	0.695123	4.04	0.000008	0.073102
2	0.764411	0.584324	3.33	0.001089	0.239775
3	0.649867	0.422328	2.32	0.049229	0.576833

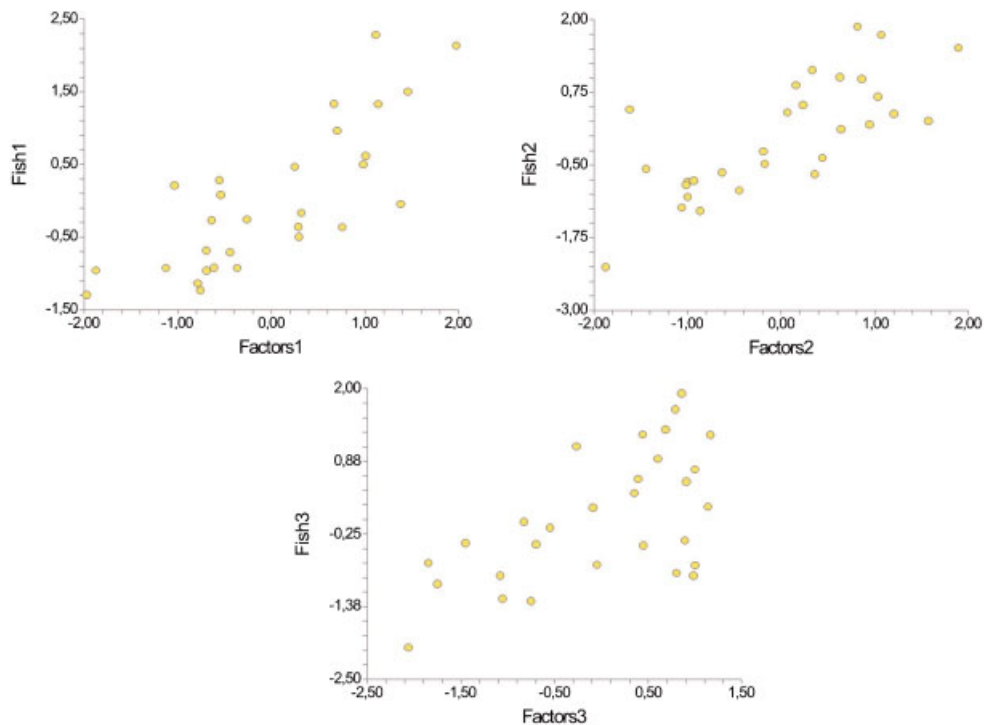


Figure 6. Score plots between the first three pairs of fish and environmental variates. Both fish and environmental factors are described in Table VII. This figure is available in colour online at www.interscience.wiley.com/journal/rra

Table VI. Variation explained section (Redundancy Analysis)

Canonical variate number	Variation in these variables	Explained by these variates	Individual per cent explained	Cumulative per cent explained	Canonical correlation squared
1	Fish	Fish	28.3	28.3	0.6951
2	Fish	Fish	15.9	44.2	0.5843
3	Fish	Fish	36.5	80.7	0.4223
Redundancy					
1	Fish	Factors	19.7	19.7	
2	Fish	Factors	9.3	29	
3	Fish	Factors	15.4	44.4	

Table VII. Canonical structure coefficients for the first three pairs of canonical variates

Variables	Variates		
	Fish 1	Fish 2	Fish 3
Parapimelodus	-0.125466	-0.064734	-0.788591
Odontesthes	-0.851473	0.032445	0.334752
Cyphocharax	0.554218	0.510169	-0.483266
Cyprinus	0.497559	0.131268	-0.806174
Oligosarcus	-0.34483	0.437153	-0.457518
	Factors 1	Factors 2	Factors 3
Conductivity	-0.370059	0.410421	0.713985
NO ₃ /NH ₄	0.121922	-0.102171	0.97564
TP	0.722397	-0.423458	-0.301406
T _w	-0.806711	-0.188292	0.545482

abundance that closely parallels the environmental gradients displayed by the first environmental variate ($R_c = 0.83$; $R_c^2 = 0.69$; $p < 0.00001$). Three species show a strong correlation with Fish 1 variate. *Odontesthes* was strongly and negatively correlated with the first fish variate while *Cyphocharax* and *Cyprinus* were positively correlated with this variate. These three species are therefore closely aligned with the hydrological and trophic gradients defined by the first environmental variate.

Factors 3 represents gradients in water conductivity and NO₃:NH₄ ratio and to a lesser extent in T_w. Those sites with higher NO₃:NH₄ ratio (NO₃:NH₄ = 0.97) water conductivity (conductivity = 0.71) and water residence time (T_w = 0.54) loaded high on the positive end of the gradient. This represents an interactive gradient in anthropogenic, abiotic and hydrological conditions. The gradient in fish species abundances extracted by the third fish variate (Fish 3) is significantly correlated with the third environmental variate ($R_c = 0.65$; $R_c^2 = 0.42$; $p < 0.05$). *Parapimelodus*, *Cyphocharax* and *Cyprinus* are closely and negatively related with the third fish variate, therefore, loading high on sites with lower NO₃:NH₄ ratio, water conductivity and water residence time.

The two sample *t*-test revealed that the observed canonical coefficients and those calculated with the jackknife resampling procedure did not differ significantly ($t = -0.2827$ and $p = 0.779888$). Therefore, the ecological interpretation of the canonical variates based on its structure coefficients is found to be satisfying.

DISCUSSION

The anthropogenic impacts on water quality (TP, NO₃:NH₄), the extreme hydrological variability and the concomitant fluctuating abiotic environment all affected fish abundance and distribution.

During summers of contrasting hydrological characteristics, fish faced extreme variation in river discharge and other abiotic conditions and some species showed important changes in their abundances associated with this variability. However, some other fish species have been less intensely modified by hydrology and abiotic environment fluctuations and only show slightly changes in their abundances and practically no response in their distribution. The higher salinity of the upstream sites, more evident during the driest conditions, might explain the absence of some species and the low abundance of many others. Usually spatial distribution of fish reflects the response of individuals to several intrinsic qualities of a location, including the main physical and chemical factors (Wootton, 1998). It is highly probable that harsh abiotic conditions precluded *P. valenciennis*, *C. voga* and *O. jenynsii* to be present in the upper saltier Mar Chiquita Lake during the dry summer. Moreover, when dry conditions established, *C. voga*, *C. carpio* and *P. valenciennis* were all significantly more abundant in downstream sites with lower total salinity. In addition, our results showed that abundance of *C. voga* was significantly and *C. carpio* marginally higher during summers with less stressful abiotic conditions and higher flows (Table III; Figure 5). The adverse effects of high total salinity on all these species were extracted by the third canonical variate, whereas the first variate sufficiently account for the negative relationship between abundance of these species and the T_w .

O. bonariensis showed a unique pattern of abundance and distribution, opposite to those found for the remainder species. This species was significantly more abundant at saltier upstream sites during the dry summer and also displayed larger population sizes during the low to average mean flows with higher salinity and T_w . This positive relationship between abiotic and hydrological gradients and abundance of *O. bonariensis* was revealed by both selected canonical solutions. High abundances in ionic rich waters are possible due to the broad salt tolerance (Gómez, 1996) of this euryhaline species. On the other hand, macrozooplankton biomass in these lakes is negatively affected by low T_w (Rennella and Quirós, 2006), suggesting that abundance of *O. bonariensis* may have been also favoured during low flow conditions through the improvement of food availability.

When abiotically stressful low flow conditions were diluted by higher river discharges, some patterns in fish abundance and distribution changed accordingly. Wetter summers with lower total salinity and T_w enhanced abundance of *C. voga* and *C. carpio* and allowed individuals of *P. valenciennis* to colonize upstream former abiotically stressful sites. However, the same abiotic and hydrological conditions largely depleted populations of *O. bonariensis* mainly during the extreme-wet summer. During the wet summer, even when depleted, populations of *O. bonariensis* preserved a similar spatial pattern in fish abundance as the observed during the dry summer. Thus, *O. bonariensis* was still more abundant at upstream less disturbed sites during the wet summer even when this species showed a significant tendency to be less abundant as river discharge increased (Table III; Figure 5). Similarly, during the wet summer, *C. voga* and *C. carpio* were still significantly more abundant at downstream sites as they were during the dry summer. Cyprinids are primary freshwater species with a long evolutionary history in fresh waters but still have high tolerances to salinity (Wootton, 1998). However, our results showed a clear tendency of the cyprinid *C. carpio* to be enhanced under wet, fresher conditions.

We are not able to completely disregard biotic mechanisms as regulating factors of these fish assemblages, but our results suggest that they might be of minor importance when compared with the effects of the abiotic and hydrological factors. Indeed, biotic factors influence distributions of animals in benign environments but in harsh environments, the ability of organisms to tolerate or avoid physicochemical stressors may be more critical to their success (Matthews, 1998). Fluctuating flow regimes usually play a 'keystone' effect preventing the dominance of any particular species at any site and thus enhancing persistence of ecological communities and increasing diversity (Power *et al.*, 1995). The positive changes of many fish species in the study sites following the increase in river discharge during the wetter seasons agree with the intermediate disturbance concept (Connell, 1978; Chesson, 1986). Indeed, the drop in total salinity of the water during floods might be interpreted as a form of disturbance which permitted a higher number of species to coexist in former saltier sites than would be possible if harsh osmotic conditions prevailed. This was particularly true for *P. valenciennis* and *O. jenynsii* whose after the flooding of the wet and extreme-wet summers colonized the upstream former abiotically stressful sites. Consequently, downstream sites should be considered as refuges for these species during the dry periods of the hydrological regime. Probably these two species have solved the problem of 'when to stay and when to go'? (Matthews, 1998). High salt concentrations also may hamper *C. voga* and *C. carpio* to thrive during low flow conditions. Food digestibility, consumption rate and growth of *C. carpio* are inversely related with water salinity (Wang *et al.*, 1997). Moreover,

when comparing contrasting hydrological seasons, this species displayed better yields under wet conditions with lower water conductivity (Fernández and Navarrete Salgado, 1998). On the other hand, the fecundity of *C. voga* is usually lower in environments with high levels of water salinity (Schifino *et al.*, 1998). Hence, water salinity may act as an important environmental constraint for the optimum development of populations of these two species.

Cities and industries emit large amounts of substances to the surface waters and these releases occur in element ratios far different from those of natural ecosystems leading to alteration of major biogeochemical cycles and subsequent changes in species composition (Austin *et al.*, 2003). Where cities release untreated sewage into river, the high organic carbon loads stimulate respiration leading to an anoxic environment (Ballester *et al.*, 1999) in which nitrification is inhibited and direct denitrification of nitrate is enhanced (Wetzel, 2001). Therefore, nitrates concentrations are lowered and ammonia accumulates in the water (Martinelli *et al.*, 1999). In Latin America and the Caribbean, rivers are exposed to an ever-growing pressure by human activities (Pringle *et al.*, 2000). Agriculture and urbanization are the human activities that mostly threaten aquatic ecosystems in Europe and North America (Paul and Meyer, 2001). Lake Tai, the third largest freshwater body in China, had recently succumbed to industrial and agricultural waste (World Economic Forum, 2008).

In this study, we found intimate inverse relationships between abundance of both human population and point source effluents and the $\text{NO}_3\text{:NH}_4$ ratio (Table I and Figure 1) which in turn, was more evident during the dry summer. Following canonical solutions, *C. voga*, *C. carpio* and *P. valenciennis* were found to be negatively related with the $\text{NO}_3\text{:NH}_4$ ratio, suggesting that these species might be positively influenced by organic releases from both human and industrial sources. Conversely, *O. bonariensis* seems to be negatively influenced by human activity. The first canonical solution significantly correlated (Figure 6) the gradient in abundance of this species with the gradient in TP concentration, with increasing abundance of *O. bonariensis* as TP decrease. The present study also reveals that this negative effect would be maximum when harsh dry conditions prevail. Indeed, among-site differences in abundance of *O. bonariensis* were extremely enlarged under the harsh abiotic conditions of the dry summer (Figure 5).

When dry conditions prevail and connectivity between sites still allows fish movement, the fish assemblage structure in lowland river units might be showing an approximate view of how environmental gradients interact to influence fish abundance and distribution (Rodríguez and Lewis, 1997; Zeug *et al.*, 2005). Following this rationale we might ask why fish species (e.g. *O. bonariensis*) that tend to be more abundant at saltier less polluted sites are there because their intolerance to human disturbance, their preference for these ionic rich waters or both reasons. The same applies for those fish species (*C. voga*, *C. carpio* and *P. valenciennis*) that showed the opposite pattern of distribution, being more abundant at downstream sites, with increasing human disturbance and lower total salinity.

In this study, we demonstrated that interactive effects from hydrological, abiotic and human activity-derived variables were accurately extracted by the selected pairs of canonical variates (Table VII). Overall, the canonical solutions suggest that interactive effects of T_w , TP, the $\text{NO}_3\text{:NH}_4$ ratio and water conductivity on abundance and distribution of some fish species are present. *C. voga* was significantly more abundant in sites with lower total salinity under dry conditions and in wetter 'diluted' summers. On the other hand, it was the only species that showed to be significantly affected by site position in the landscape, being always more abundant in Carpincho Lake, a highly impacted site. Hence, we can conclude that abundance of *C. voga* is not only strongly affected by the natural variation in river discharge and the consequent changing abiotic environment but also by the degree of anthropogenic impact which in turn depends on site position within the landscape. Combined effects of anthropogenic, hydrological and abiotic factors on dynamics of *C. voga* lead to a distribution of this detritivorous species that may be considered largely invariant regardless extreme environmental variability and closely related with the $\text{NO}_3\text{:NH}_4$ ratio and TP. This persistence of the curimatid *C. voga* at downstream highly disturbed sites regardless extreme hydrological and environmental variability, might mask a deterministic effect of organic releases from anthropogenic sources on dynamics of this species. This is not an isolated local pattern. In the lower Paraná River, the abundance of the curimatid *Prochilodus platensis* is intimately related with the organic matter content of the water (Quirós, 1990). Similarly, occurrence of curimatid species in the floodplain creeks of the Cinaruco River, in the Orinoco River drainage, is partially explained by dense accumulation of decomposing organic matter (Hoeinghaus *et al.*, 2003). In the upper Paraná River, *Cyphocharax modestus* together with other bottom-dwelling fishes were associated to high values of chemical demand of oxygen irrespective of the strong

seasonality of this system (Fialho *et al.*, 2008). All these findings suggest the possibility of a causal link between organic releases and abundance of these detritivorous species.

As precipitation regime is currently an unpredictable event in the Pampa Plain and Salado River discharge closely follows this climatic phenomenon, fish assemblages of this ecosystem should be considered mostly stochastic (Grossman *et al.*, 1982). Indeed, cluster analysis results suggest that hydrological variability probably overcome anthropogenic impacts on water quality in regulating the main physical and chemical conditions of these lakes (Figure 3). Nevertheless, there is enough evidence in southern temperate and tropical freshwater ecosystems to hypothesize that abundance of bottom-dwelling detritivorous species (as curimatid) is intimately linked to anthropogenic activities. If further empirical and experimental approaches validate it, these species could be used as biological indicators for the evaluation of anthropogenic impacts and health status in freshwater ecosystems.

Similarly to *C. voga* strong patterns were found between the abundance of *O. bonariensis* and several anthropogenic, hydrological and abiotic aspects, but with the opposite direction. This inland atherinid was significantly more abundant at sites with higher total salinity under dry conditions and during low to average flow summers. On the other hand, our results show that during the wet summer, even when abiotic stressful environment was largely diluted, this species was still significantly less abundant at downstream highly impacted sites. Interactive effects of hydrological and human activity-derived variables on abundance of this species were mostly represented by the first canonical solution (T_w and TP).

Combined effects of analysed variables were less evident for *P. valenciennis* and *C. carpio* but still show a clear pattern. Both species were largely restricted to downstream less saltier sites during the harsh dry summer (Table II) at the same time that they showed a tendency to be more abundant at downstream anthropogenic disturbed sites regardless hydrological conditions (Table IV). Interactive effects of low T_w , decreased total salinity, reduced $\text{NO}_3:\text{NH}_4$ ratio and in a lesser extent high TP on abundance of these two species were clearly extracted by the third pair of variates (Table VII).

CONCLUSIONS

Following our findings we should conclude that there exist three main axes which govern fish assemblage dynamics in lowland river ecosystems. Two spatial axes of anthropogenic and abiotic gradients and one temporal axis of hydrological variation.

However, one of these axes is not a universal component of river ecosystems. As many temperate lowland rivers worldwide, the Salado River is expose to both a temporal axis of hydrological variability and an ever-increasing spatial gradient of human impact. Conversely, a striking gradient in total salinity at upper reaches of a lowland river as well as the presence of a euryhaline species with brackish water affinity (*O. bonariensis*) as one of the major elements of the fish assemblages is a particularity of this system.

Besides *O. bonariensis* any other species are thought to be resistant to high salinity since they belong to families with a long evolutionary history in freshwaters. Among these families bottom-dwelling species feeding on organic rich sediments and its associated biota seemed to be favoured by organic releases from anthropogenic origin.

We found a strong dichotomy in how fish species responded to the hydrological, anthropogenic and salinity gradients. Fundamental differences in the acquisition of life history strategies during the evolutionary and adaptive process may be accounting for that (Southwood, 1977, 1988). For instance, recent investigations suggest that both hydrology and habitat heterogeneity interact with fish life history strategy to determine optimal conditions for recruitment (Zeug and Winemiller, 2008).

Our results show that a particular set of variables that was beneficial for some particular species resulted detrimental for many others. At one extreme is the visual planktivore *O. bonariensis* that was benefited from a less human disturbed environment with high water residence time and salinity and at the other extreme are detritivorous, filter feeding and bentophagous fish species as *C. voga*, *P. valenciennis* and *C. carpio*, respectively, that found these conditions largely disadvantageous. As expected, not all the species showed such as evident response. Whilst most species displayed strong either negative or positive response to anthropogenic, hydrological or abiotic factors, *O. jenynsii* was only slightly affected.

Basically, the observed patterns of fish abundance and distribution in relation to anthropogenic impacts and hydrological variability might be at some extent generalized to other lowland rivers with impoundments or natural lakes. In contrast, the outstanding influence of salinity on fish dynamics mostly resemble patterns described for dryland and coastal aquatic ecosystems. This complex conjunction of basic ecological patterns makes the Salado River a useful framework that allowed us to simultaneously evaluate the interactive effects of hydrology, salinity and human impacts on fish abundance and distribution.

Absolute extremes, diel fluctuations or unpredictable changes of abiotic and hydrological conditions are common events in dryland (Boulton and Brock, 1999; Bunn *et al.*, 2006) and coastal (Herke and Rogers, 1999) aquatic ecosystems, and usually establish stressful or lethal physical or chemical conditions (Moyle and Cech, 2004). Interactive effects from environmental factors are important contributors to interannual variation in the abundances of estuarine fish stocks (Rose and Summers, 1992). Salinity by its own was reported as a structuring factor in some inland 'freshwater' ecosystems (Echelle *et al.*, 1972; Miquelarena and López, 1995). Some studies have approached the ecological response of aquatic biota to both changing water regime and salinity (Brock *et al.*, 2005). Nevertheless, the interactions between salinity, water regimes and other stressors associated with human activity impacts have been less intensely approached. This is a noteworthy element in order to better understand the ecological dynamics in aquatic ecosystems since the fish-habitat relationships are also influenced by anthropogenic activities (Wiens, 2002).

Our results showed that the Salado River system is a good example of how both abiotic and hydrological variability may be of major importance in regulating fish communities in ecosystems others than those found in dryland and coastal regions. On the other hand, we also added a human component to the analysis by exploring the effects of anthropogenic development of the landscape on water quality.

The first tenet of the *riverine ecosystem synthesis* (RES) states that species distributions in a river network are associated primarily with the distribution of small to large spatial patches formed principally by hydrogeomorphic forces and modified by climate and vegetation (Thorp *et al.*, 2006). These authors claim that the RES describes the functioning of pristine river networks, but it could be used to test effects of human activities. With this paper, we hope to make a modest contribution to this heuristic and comprehensive 'riverscape' model. Our findings provide strong evidence that spatial patterns of human impacts may be considered as an additional element in modifying the species distribution in those river networks where human development of the landscape are important.

There is enough evidence, therefore, that are abiotic environment, human disturbance and hydrology that mostly will influence fish assemblages dynamics in human disturbed lowland rivers by affecting the abundance and distribution of their major species. In this study, the variation in fish species abundance and distribution along abiotic, hydrological and anthropogenic gradients was significantly accounted for by the interactive effects of T_w , TP, the $\text{NO}_3:\text{NH}_4$ ratio and water conductivity.

Perhaps, one of the most important outcomes from this study is that we found strong evidence of the way several factors that rarely are found to 'operate' together in freshwater environments interact to affect fish abundance and distribution.

Flow management implications

By the year 2003, the Salado River system was modified by channelization and damming of different reaches at the upper section of the basin, altering its natural flow regime. River fisheries depend largely on natural flow regimes (Zalewski *et al.*, 1997; Welcomme and Halls, 2002) and management strategies of flow altered rivers should also incorporate a provision of minimum flows to prevent deleterious biological impacts (Stalnaker *et al.*, 1989; Walker *et al.*, 1995; Poff *et al.*, 1997). Our findings provide further evidence that both extreme minimum and maximum flows as well as impacts of anthropogenic releases would differently affect the major fish species of river ecosystems. Our results also suggest that where hydrological and anthropogenic gradients may interact with a gradient of total salinity (usually estuaries, lower reaches of rivers or coastal and dryland ecosystems), particular attention should also be focussed on how fish species differ in their respond to the osmotic constraints of the water.

Overall, a hydrological schedule that generates extensive low flow periods with consequent increase in evaporation rates and water salinity would improve populations of most tolerant species, as *O. bonariensis*. Our study also suggest that this response may be of minor importance in highly organically loaded environments if

tolerant fish species are prone to be negatively affected by organic enrichment of surface waters. On the other hand, a harsh abiotic environment would hamper the establishment of less tolerant species as was the case of *C. voga*, *P. valenciennis* and *C. carpio* and probably increase further the success of those species that are able to cope with this environmental constraint. Nonetheless, it is not everything about water salinity. Fish communities tend to be mostly either limnophilic or rheophilic, depending on the type of water regime prevalent in the river reach in which they live (Welcomme, 1985). More stable hydrological conditions during low flows probably also select to a fish community dominated by limnophilic open waters species, as *O. bonariensis*. Conversely, the provision of higher volumes of water per unit of time would select towards the rheophilic components of the fish community.

The marked dichotomy reported in this paper regarding fish response in relation to hydrological and environmental variability mostly agrees with the environmental guilds classification proposed by Welcomme *et al.* (2006). Whilst *O. bonariensis* may easily be placed into the brackish estuarine water guild, species as *C. voga*, *C. carpio* and *P. valenciennis* should be better encompassed within some of the lowland river (potamonic) guilds.

With this study, we also suggest that particular attention should be focussed on the effects from anthropogenic releases during water scarcity periods since its concentration and 'availability' would tend to its maximum. Under these conditions, insolation on the reduced volume of water would increase water heating leading to a higher metabolic rate of aquatic organisms and in consequence a higher probability to uptake toxics and pollutants.

Finally, a major contribution of this paper is that we have identified the ecological function of a lowland river under its natural flow regime. This kind of information is crucial to the effectiveness of re-establishing a relatively natural regime in flow altered rivers (Bayley, 1991; Richter *et al.*, 1997; Amoros and Bornette, 2002). The ability to model the biological response of fish to the restoration of river flows depends on the capacity to establish clear relationships between natural changes in river hydrology and the fish assemblages (Gowns, 2008). There are not many opportunities to study unmodified rivers worldwide. Therefore, our findings may be useful in approaches planning the management and conservation of fish populations in flow altered and human disturbed aquatic ecosystems.

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