Fish community variation below Yacyretá Dam (Paraná River, Argentina): the relative contribution of microhabitat, hydrology and limnology.

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RESUMO: Variações das comunidades de peixes a jusante da barragem de Yacyretá (Rio Paraná, Argentina): contribução relativa do microhabitat, hidrologia e limnologia. A represa de Yacyretá é uma obra hidroelétrica de grandes dimensões, cujo efeito sobre as comunidades de peixes do rio necessita ser avaliado e mitigado. No entanto, é difícil separar os efeitos naturais, regionais e locais, dos efeitos atribuíveis exclusivamente à operação da represa. Para tal distinção, foi aplicado um método de estudo para avaliar as respostas dos peixes em relação aos fatores ambientais, empregando várias Análises de Correspondência Canônicas (CCA), combinadas com um procedimento de partição da variância. As amostras de peixes foram obtidas em áreas litorâneas a cada 20-30 dias empregando baterias de redes de espera. Selecionaram-se dois locais de amostragem, um deles próximo à represa e outro situado 90 Km à jusante da barragem. As variáveis ambientais foram classificadas em três grupos segundo diferentes escalas de variação espaço-temporal: hidrológicas (bacia), limnologicas (trecho), e microhabitat (local). O estudo foi repetido durante três ciclos hidrológicos, de 1995 até 1998. A variância total explicada oscilou, nos diferentes anos, entre 41% e 56%. A estrutura da comunidade de peixes mostrou ciclos regulares e similares ano após ano, relacionados com as migrações reprodutivas e tróficas. Estes ciclos associaram-se significativamente com as variações nas descargas de água, temperatura e transparência de água. As variáveis ambientais que contribuíram à separação dos locais de coleta foram o tipo de substrato, a taxa de variação do nivel hidrométrico e a profundidade. Em todos os ciclos hidrológicos estudados, os incrementos de vazão d'água turbinada relacionaram-se com aumentos na abundância relativa de peixes ictiófagos, à exceção dos Siluriformes. Os resultados obtidos permitem supor que desde o funcionamento das turbinas em 1994, as comunidades de peixes não apresentaram uma remarcada variaçao nos locais estudados.
Palavras-chave: comunidades de peixes, fatores ambientais, análises de correspondência canônicas, reservatório de Yacyretá, rio Paraná, Argentina

ABSTRACT: Fish community variation below Yacyretá Dam (Paraná River, Argentina): the relative contribution of microhabitat, hydrology and limnology. Yacyretá Dam is a large lowland reservoir, which potential effects on downriver fish communities need to be known and mitigated. However, it is difficult to segregate natural effects from dam effects, which in turn act at different scales in space and time. A methodological approach was adapted to evaluate responses in fish community structure associated to different subsets of environmental variables using Canonical Correspondence Analysis, combined with variance partitioning procedures. The environmental variables were classified in three subsets according to different scales of variation, and the amount of variance explained for each subset was then calculated. Fish were sampled in coastal areas every 20-30 days using a battery of nine monofilament gill net panels. Two sampling

sites were selected; one close to the dam (high impact site) and the other placed 90 km downriver (low impact site). The study was repeated during three hydrologic cycles, since 1995 to 1998. The total variance explained by the selected environmental variables ranged from 41 to 56%. In both sampling sites, fish community structure showed regular and similar cyclical changes related to migration for reproduction and feeding. These cycles were associated to variations in temperature, water transparency and total flow. Sampling sites were clearly distinguished during all the study period. The environmental variables that most contributed to separate sampling sites were substrate (microhabitat), rate of variation in water level (hydrology), and dissolved oxygen (limnology), the two latter being higher at the high impact site. In all of the studied cycles, increments in turbinated discharge were related with augmentations in relative abundance of non-Siluriforms piscivorous fishes. Results suggest that since the beginning of the dam operation in 1994, fish community did not experienced remarkable changes downriver.
Key-words: fish communities, environmental factors, Canonical Correspondence Analysis, Yacyretá Dam, Paraná River, Argentina.

Introduction

The complex ecosystems of the large South American Rivers have been undergoing marked changes because of human activities, including deforestation, pollution, damming and regulation (Quirós, 1990). Long segments of the Paraná River, which belongs to the second largest drainage basin in South America, are presently reduced to a succession of impoundments, especially in Brazil (according to Bonetto *et al.*, 1987, and Petrere, 1996). Yacyretá power facility is located in the reach named High Paraná ("Alto Paraná"), along the border of Paraguay and Argentina. This river is famous for the richness of its fish fauna and the abundance of large-sized sport fishes. Those natural resources support commercial and sport fisheries that are of major social and economical concern for the riparian localities of both countries. After the damming by Yacyretá, the most important fishing activities have been located downriver, due to a reduction in the economically important fish of the reservoir.

The building of the dam, besides flooding a 64-km long reach of the High Paraná, is also expected to affect in some unknown extent, the fish communities inhabiting downriver sections. Some of the predicted and/or observed impacts downriver are: a partial blockage of reproductive migration (only two fish scales allow fish migration upstream), gas supersaturation, abnormal flow fluctuations, increased transparency, increased instream primary production, increased bank erosion processes, deepening of the channel in areas with soft substrates, increases in fishing effort and capture success near to the dam dykes, fish kills by turbines, among others.

The Binational Yacyretá Public Power Utility (EBY) has been supporting uninterrupted survey studies since 1993 to evaluate the state of the fish resources in several fixed sampling sites downriver. The surveys are useful for several purposes. First, they allow for the settlement of a solid scientific knowledge on the biology of the main fish species, by applying the basic principles of fisheries science. Second, they permit a rapid detection of alterations in reproduction, growth or sanitary conditions that would help to take managing decisions in proper time. Finally, they can be eventually useful to answer some of the most poorly known questions concerning the impact, such as: in which manner Yacyretá Dam is affecting fish community structure downriver in time and space. Based on this knowledge, it is expected to produce management suggestions for the operation of turbines, spillways and water levels to mitigate dam effects on fish fauna, and especially on those species of economical interest.

Several limitations must be overcome when these latter purpose is undertaken, such as the absence of comparable information before the dam building, the presence of a diverse fish fauna (more than 150 species) with complex life cycles, long migratory routes, data available only from gill nets on a restricted number of sampling points, restricted information about environmental variables, among others. Moreover, it is difficult to segregate local (microhabitat) effects from lymnologic (macrohabitat) and basin (hydrologic) effects. Finally, dam effects attributed to the operation of turbines and spillways, as well as to the presence of the reservoir and the dam walls are confounded with natural river effects.

To cope with some of the aforementioned restrictions, the aim of the present work was to analyze short-term (days-months) and long-term (years) responses of fish community structure in relation to selected environmental variables, by applying a multivariate direct gradient analysis technique. To evaluate the relative importance of environmental variables, they were classified in several subsets according to different spatial and temporal scales of variation, and the amount of variance explained for each subset was calculated using a variance partitioning method. The exercise was repeated on each hydrologic cycle to assess long-term responses, and the results of different years were compared to detect regularities and changes.

Material and methods

Study area

The Paraná River at Yacyretá Dam has a 100 years historical mean discharge of about 12,000 $m^3 s^{-1}$, draining an area of about 840,000 km^2. Along a few kilometers below the reservoir, the river flow mainly through basalt bedrock, changing downriver to moving sand bottoms, with extensive areas of sandstone and conglomerate outcrops. Over the rocky bottoms, there is often a massive growth of epilithyc algae (e.g., *Oedogonium, Gomphonema, Lyngbia, Tabellaria, Aulacoseira*) and macrophytes, particularly the reophilic species of the family Podostemonaceae (Varela *et al.*, 1983). Yacyretá Dam and Reservoir are located a few kilometers upstream Ituzaingó Town, in Corrientes Province, Argentina. Placed in a lowland region, it covers a large area (1,600 km^2), operates in a near run-of-the-river regime, and has a limited capacity of flow regulation. However, low scale, abnormal, daily or weekly fluctuations, derived from the optimization of energy production, as well as turbine and spillway operation can be observed. The dam has a length of 63.7 km, with two gated overflow spillways, one of them placed on the Añá Cuá channel (Añá Cuá Spillway, 16 gates), and the remaining on the main channel (Principal Spillway, 18 gates). On a normal operation plan with most turbines functioning, Principal Spillway is scheduled to be operative only during floods, but the Añá Cuá Spillway must release water to ensure a minimum flow of about 1,500 m^3 all along the year.

The powerhouse is located next to the Principal Spillway. The production of electricity began in September 1994. At the beginning of the survey, there were only three turbines running, but its number increased gradually along the three years of the study period. The 20 Kaplan turbines were operative by March 1998. Each turbine can discharge a maximum of 850 $m^3 s^{-1}$, summing together 3,200 MW of total installed capacity (160 MW each turbine). There are also two fish scales equipped with elevators, located on each side of the powerhouse. Elevators operate continuously over the 24 hours, moving migratory fishes from the river to the reservoir, every one to three hours.

The present study was carried out by an agreement between the EBY and the Institute of Ichthyology (INICNE), Faculty of Veterinary Sciences, National University of the Northeastern (UNNE, Argentina). Up to date, four complete hydrologic cycles have been covered, and a fifth is under study. The results of these surveys have been presented in several technical reports (Jacobo *et al.*, 1996; Bechara *et al.*, 1997, 1998), that are available in the EBY offices in Posadas City (Argentina).

Sampling scheme

The sampling scheme involved the capture of fish every 20-30 days, from March 1995 to September 1998, using a battery of nine monofilament gill net panels, with bar measures (distances between contiguous knots) of 20, 25, 30, 35, 40, 60, 70, 80 and 100 mm. This arrangement was chosen to reduce size selectivity effects. The total surface of net panels was of about 400 m^2. Gill nets were placed vertically on the left margin of the river, from the coastline until a distance of 15 to 50 m, always in contact with the bottom. Fish caught were collected every 6-8 hours during a 45-48 hours period. Specimens were identified taxonomically to the specific level, weighted (g), measured (standard length in cm), classified by sex and gonad development, among other routine measurements.

One of the sampling points was located two km below the dam, close to the locality of Ituzaingó (Corrientes Province), and is named hereafter "high impact site". A second sampling point was placed 90 km downriver, near the locality of Itá Ibaté, and is named henceforth "low impact site". A more detailed description of sampling sites and river characteristics can be found in Bechara *et al.* (1996, 1997, 1998).

On each sampling date, microhabitat variables were measured close to the distal end of every gill net. Maximum depth was measured with a weighted rod; water velocity was estimated by registering on three occasions, the time spent by a floating object to travel a distance of five meters. Dominant substrate type (i.e., bedrock, gravel, sand, silt, vegetation) was determined by visual inspection of a bottom sample at each site. Some lymnologic variables were also obtained. Air and water temperature were measured with a thermistor and transparency with a Secchi disk. Calibrated probes were employed for measuring pH (VDSF-Umelttechnik, Germany), conductivity (VDSF-Umelttechnik), and dissolved oxygen (Yellow Spring Instruments, model 55, USA). Total dissolved gases were measured with an electronic saturometer (Common Sensing Inc., USA). Data on water levels and discharges were provided by "Dirección Nacional de Navegación y Puertos" (Argentine Government) and EBY, respectively.

A more detailed description of the methods employed to obtain biological and environmental data can be found in Bechara *et al.* (1997, 1998)

Data analyses and the choice of the statistical model

Data collected were stored in a database and Captures per Unit Effort (CPUE) expressed as fish weight (g) caught in 8 hours by 100 m^2 of net were calculated for each species, at both sites and sampling dates. Weight, instead of number, was chosen as the dependent variable to give more importance to the larger fish, usually of economic interest, but less common in the captures. Fish species were retained for the analyses if present in at least 60% of the total number of samples. The number of species retained on each sampling year varied, depending on the particular structure of the captures, though the most common were present in all years (Tab. I). In addition, the most conspicuous trophic guild had representatives in the selected set of species.

Table I: List of species selected in at least one sampling year, classified following the most relevant trophic guilds (stated after unpublished exploratory analyses of gut contents and literature revision). In addition, the most important migratory species are underlined. Regional (Spanish) common names are in parentheses.

Trophic Guild	Species
Plant-Eaters	*Schizodon borellii* (boga fina); *S. nasutus* (boga fina); *S. platae* (boga fina); *Mylossoma duriventris* (pacucito).
Detritivores/ Algivores	*Curimatella dorsalis* (sabalito); *Psectrogaster curviventris* (sabalito); *Prochilodus lineatus* (sábalo); *Cyphocharax platanus* (sabalito); *Hemiodus orthonops* (sardina); *Hypostomus luteomaculatus* (vieja); *Loricaria* spp. (vieja); *Megalancistrus aculeatus* (vieja); *Cochliodon cochlidon* (vieja); *Pterygoplichthys anisitsi* (vieja).
Omnivores	*Leporinus obtusidens* (boga); *L. acutidens* (boga); *Pterodoras granulosus* (armado); *Astyanax* spp. (mojarra).
Invertebrate- Eaters	*Auchenipterus nuchalis* (manduví); *Tetragonopterus argenteus* (relojito); *Platydoras costatus* (armadito); *Iheringichthys labrosus* (bagre); *Trachelyopterus striatulus* (bagre apretador); *Pachyurus bonariensis* (corvina chica); *Pimelodus clarias* (bagre amarillo); *Oxydoras kneri* (armado chancho); *Triportheus paranensis* (cuchilleta).
Scale-Eaters	*Roeboides bonariensis* (dientudo); *R. prognathus* (dientudo).
Small Piscivores (< 40 cm)	*Cynopotamus kincaidi* (dientudo); *C. argenteus* (dientudo); *Galeocharax humeralis* (dientudo); *Serrasalmus nattereri* (piraña); *S. marginatus* (piraña); *Hoplias malabaricus* (tararira); *Lycengraulis olidus* (anchoíta).
Large Piscivores (> 40 cm)	*Ilisha flavipinnis* (lacha); *Salminus maxillosus* (dorado); *Rhaphiodon vulpinus* (pirá-yaguá); *Ageneiosus brevifilis* (manduré); *Hemisorubim platyrhynchos* (manduré); *Pseudoplatystoma coruscans* (surubí); *P. fasciatum* (surubí); *Sorubim lima* (manduré cuchara); *Plagioscion ternetzi* (corvina).

Environmental variables were classified in three subsets (Tab. II). There was a group of hydrologic variables that were chosen to represent the basin and segment effects, which were also influenced by the operation regime of the dam. A second group was constituted by some lymnologic variables, classified as macrohabitat because they represent the segment properties, remaining with little or gradual variations as the fish move. Finally, a third subset consisted in depth, substrate and subsurface water velocity, classified as microhabitat variables, because they usually vary rapidly as fish swim. All variables were transformed to log (x+1), to approximate their distribution to the normal.

The multivariate techniques chosen to explore the relationships between environmental variables and fish community structure were Canonical Correspondence Analysis (CCA) and Partial Canonical Correspondence Analysis (PCCA) (ter Braak, 1996). The program CANOCO 4 (ter Braak & Smilauer, 1998) was employed to perform the analyses. Canonical ordination is a combination of ordination in reduced space and multiple regression. It implies the representation of samples and species constrained by environmental variables in a reduced space of orthogonal axes, which are in turn linear combinations of species relative abundance and environmental variables. These methods assume both, unimodal (Gaussian) or linear relationships between species and environmental variables, for long or short environmental gradients, respectively. Therefore, given the unimodal properties of CCA and PCCA, linear relationships between a given environmental variable and species, are not required such as in most canonical multivariate techniques. The unimodal properties of the model allow the estimation of optimum and tolerances of the species, both indicators of niche attributes. Optimum can be approximated by the CANOCO 4 output named "species-by-environment table", which are weighted

Table II: List of environmental variables employed for the analyses, classified in three subsets, according to their scale of variation. Abbreviations used in the text are in uppercase.

Hydrologic	Limnology	Microhabitat
1. Mean total flow during sampling: QTODUR	1. Transparency (Secchi disk): TRANS	1. Mean depth (gill net location): DEPTH
2. Mean total flow 7 days before sampling: QTOPRE	2. Water temperature during sampling: TEMP	2. Mean sub-surface water velocity: VEL
3. Mean turbinated flow during sampling: QTUDUR	3. pH.	3. % sand: SAND
4. Mean turbinated flow 7 days before sampling: QTUPRE	4. Water conductivity: COND	4. % silt and clay (mud): MUD
5. Mean spillway flow during sampling: QSPIDUR	5. Total dissolved oxygen: SAT.O2	5. % bedrock: BEDROC
6. Mean spillway flow 7 days before sampling: QSPIPRE	6. Total dissolved gases: SAT.GAS	6. % gravel and cobbles: GRAV
7. Mean water level during sampling: WATLEV		7. % aquatic vegetation: VEGET
8. Mean water level 7 days before sampling: WATLEVPRE		
9. Mean absolute rate of change in water level during sampling: WATVAR		
10. Mean absolute rate of change in water level 7 days before sampling: WATVARPRE		

averages of species with respect to standardized environmental variables. This information is adequate to analyze the distribution of species along environmental gradients because biplots usually express only part of the total explained variance. Significant environmental variables can be selected to avoid over-explanation using manual selection or forward stepwise selection. The amount of variance that is explained by the whole model and the ordination axes can be calculated, as well as their statistical significance, employing Monte Carlo permutations tests. Parameters of regression equations relating sample scores of each canonical axis with environmental variables (canonical coefficients) are also calculated by the software. In addition, the most important variables for each canonical axis can be selected using approximate *t*-values of canonical coefficient, which are provided by CANOCO 4 output. Optionally, results can be mapped using sampling points coordinates or represented graphically in the reduced space of orthogonal axes, displaying the distribution of samples and species along different environmental gradients in the same bidimentional space (triplots).

The steps followed in the present study included first, the application of a CCA to each subset of environmental variables and the selected fish species. Environmental variables were retained using a manual forward stepwise procedure with a rejection probability of $P<0.05$, as implemented in CANOCO 4. This procedure intends to overcome some undesirable properties of the model, such as over-explanation and multicolinearity. Some apparently important variables may be eliminated, but they remain explained by others that are retained in the model. Thus, the model obtained is the best in statistical terms, but not the only possible. In other cases, the excluded variables are simply those that do not have any significant relationship with community structure. In addition, some variables employed in the present study, such as conductivity or transparency, can be considered as surrogates of other more important that were not included (i.e., dissolved solids, nutrients, organic matter, and phytoplankton).

In a second step, the amount of variance explained for each subset of environmental variables, as well as the shared variance, and the unexplained variance, were estimated by a modification of the method described by Borcard *et al.* (1992) and Magnan *et al.* (1994). The total variance was decomposed into five components: (1) variance explained by hydrologic variables, (2) variance explained by lymnologic variables, (3) variance explained by microhabitat variables, (4) shared variance, (5) unexplained variation and stochastic fluctuation. Items (1) to (3) were estimated by statistical removal, by PCCA, of the remaining subsets (e.g., for the hydrologic subset, lymnologic and microhabitat variables were set as covariables, and so on). Item (4) was estimated as total variance explained by all of the retained environmental variables together minus quantities (1), (2) and (3). Item (5) was estimated as the remaining variation in species ordination after removal of the four previously calculated variances.

Finally, the results of the CCA using all of the environmental variables retained in the different analyses were employed to interpret the spatial and temporal pattern of variation in community structure. All of the environmental variables retained in each subset were employed in this latter step in order to preserve variables representing each subset, that could be otherwise eliminated by the forward selection procedure. Models were retained if the relationships between environmental variables and species were significant at $P<0.05$, using the Monte Carlo permutation tests, as implemented in CANOCO 4. Canonical coefficients with significant *t*-values for the first four axes were retained for interpretation, employing a critical rejection level of $P<0.05$. These axes corresponded to 70-94% of the explained variance.

Because the relative abundance of some species varied greatly from year to year, it was preferred to divide the analysis in several river hydrologic cycles (March 1995-March 1996, June 1996-September 1997, October 1997-September 1998) instead of combining all of them in just one matrix, to avoid a distortion of the results. Similarity between sampling years was verified using several Mantel tests with Monte Carlo permutations. Euclidean Distances among ordination scorers constrained by environmental variables for the four first axes were employed to build the resemblance matrix. Null hypothesis of no significant correlation between distance matrices was tested by employing the Z statistic, with a critical rejection level of $P<0.05$ (Legendre & Legendre, 1998).

Results

The relative contribution of microhabitat and macrohabitat variables.

Partitioning the total variance

The results of the three hydrologic cycles analyzed up to date are summarized in Tab. III. Only 6-9 environmental variables were retained by the forward selection procedure from the original 23 employed at every year. In addition, the species included in the analyses increased from 26 in 1995-96 to 42 in 1997-98. The total variance explained by the selected environmental variables ranged from 41,0 to 55,5% (Tab. III).

For the first year, the most important subset was microhabitat (substrate and depth), but it lost their relative importance afterward (39 to 15% of the total explained variance, Fig. 1). In turn, hydrologic variables replaced microhabitat in relative importance (17 to 31% of the total explained variance). Lymnologic variables were never the most important, but its relative contribution to total explained variance increased in the last hydrologic cycle (17 to 25% of the total explained variance). For each subset of variables, most of the fish-environment relationships were significant when tested alone using Monte Carlo permutations, considering both, the overall test and the first axis test ($P<0.05$). The variance shared for the three subsets remained

Table III: Summary of the results for the three sampled hydrologic cycles. See Tab. II for abbreviations of environmental variables.

Variables	1995-96	1996-97	1997-98
Number of env. variables	6	7	9
Number of species	26	37	42
% explained	46.0%	41.0%	55.5%
Significant variables (t-values of canonical coefficients, P<0.05)	TEMP-SAND -QTUPRE-DEPTH- QTOPRE	MUD-TEMP-WATVAR-DEPTH-QSPIPRE-QTUDUR-QTOPRE	BEDROC-TEMP- TRANS-DEPTH-WATVAR-QTUPRE-SAT.O2- QTOPRE-WATLEV
Dam operation related variables retained in forward selection	QTUPRE	QTUPRE-WATVAR-QSPIPRE	QTUPRE-SAT.O2-WATVAR-TRANS
Trophic guild typical of high impact site	Herbivores, detritivores, small piscivores.	Large piscivores, herbivores, detritivores.	Herbivores, detritivores, large and small piscivores.
Trophic guilds typical of low impact site	Detritivores, invertebrate-eaters, scale-eaters.	Invertebrate-eaters, detritivores, scale-eaters.	Invertebrate-eaters, large and small piscivores, detritivores.
Main trophic guilds related to increases in turbinated flow	Large and small piscivores (non-Siluriforms).	Large and small piscivores (non-Siluriforms).	Large and small piscivores (non-Siluriforms).

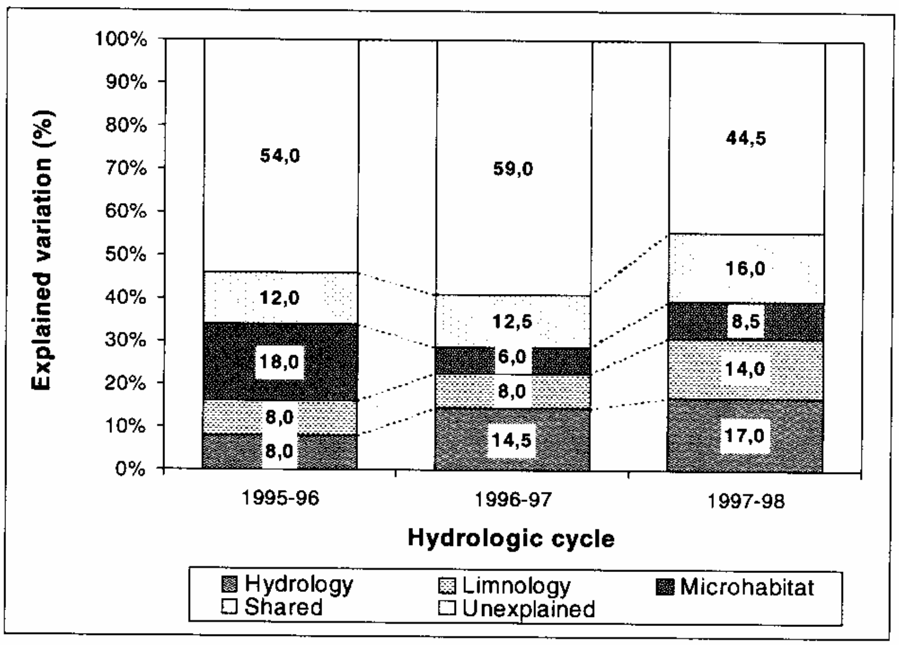

Figure 1: Decomposition of the total variation in fish community structure into five independent components: "pure" hydrologic, "pure" lymnologic, "pure" microhabitat, variance shared for all subsets, and unexplained. Results for each hydrologic cycle are shown in separate bars.

with little variations along the hydrologic cycles, being about 26-31% of the total explained variance. Substrate type (sand, mud or bedrock) and water temperature appeared as the two single most important variables during all the study period (Tab. III), given the high *t*-values of the canonical coefficients, that correlated significantly ($P<0.05$) with the first canonical axis in all hydrologic cycles.

ʼish community structure and environmental variables. Ordination liagrams

The results of the CCA carried out with the selected variables are showed in letail for the 1997-98 study period (Tab. IV, Fig. 2). In previous years, the results vere approximately similar, with variations in relative importance of species and environmental variables (Figs. 3 and 4). This fact is supported by Mantel tests (Tab. V), vhich show significant positive correlation among ordination scorers obtained in the hree study periods. The lower Mantel correlations were observed between 1997-98 ınd the other hydrologic cycles.

In the 1997-98 study period, the two first axes represent 54% of the total explained 'ariance and are the most useful for the interpretation of results (Fig. 2, Tab. IV). In ›oth sampling sites, fish communities showed clear, regular and similar cyclical :hanges related to migration for reproduction and feeding. These cycles were chiefly ıssociated with variations in limnology (TEMP, TRANS), and in a lesser extent to flow

ſable IV: Summary results of Canonical Correspondence Analysis for the seven retained environmental variables and the 37 selected species of the 1997-98 hydrologic cycle. Significant variables are underlined according to the *t*-value of the canonical coefficients, with a critical value of P = 0.05

Axes	1	2	3	4	Total Inertia
Eigenvalues	0.094	0.056	0.038	0.026	
Species-environment correlations	0.94	0.93	0.91	0.87	
Cumulated variance of species data	18.7	29.9	37.6	42.8	
Species-environment cumulated variance	33.8	53.8	67.7	77.2	
Sum of all unconstrained eigenvalues					**0.499**
Sum of all canonical eigenvalues					**0.277 (55.5%)**
Inter set correlations of environmental variables with canonical axes					
Mean total flow before sampling (QTOPRE)	-0.474	-0.444	0.334	0.279	
Mean turbinated flow (QTUPRE)	0.471	0.526	0.333	-0.327	
Water level (WATLEV)	0.188	-0.592	0.243	-0.329	
Rate of variation in water level (WATVAR)	-0.431	0.373	0.288	0.490	
Water temperature (TEMP)	-0.429	-0.502	-0.445	-0.260	
Secchi disk (TRANS)	0.273	0.603	-0.397	-0.191	
Saturation dissolved oxygen (SAT.O2)	-0.624	-0.015	0.283	0.155	
Mean depth in sampling area (DEPTH)	-0.624	-0.015	0.283	0.155	
Frequency of bedrock (BEDROC)	-0.548	0.617	0.189	-0.141	

ſable V: Summary results of Mantel test for association between Euclidean distance matrices of the first four constrained sample scorers of the CCA ordination; *r* statistics and P levels for null hypothesis of no correlation between years are shown. Significance was tested using Monte Carlo permutations with 1,000 runs, employing the Z statistics.

Hydrologic cycle	1995-96	1996-97	1997-98
1995-96	1		
1996-97	0.473 (P<0.001)	1	
1997-98	0.423 (P<0.001)	0.403 (P<0.001)	1

QTOPRE). One of the inflection points of the cycle corresponded to middle winter June-July), at the beginning of the migratory period, associated to high water ransparency, high rates of turbinated water, and low total flow. The second change ›ccurred during the summer-autumn transition, coincident with the end of the eproductive period, the return of the adults downriver, and the recruitment of juveniles ›orn in spring and early summer. Therefore, fish communities presented different

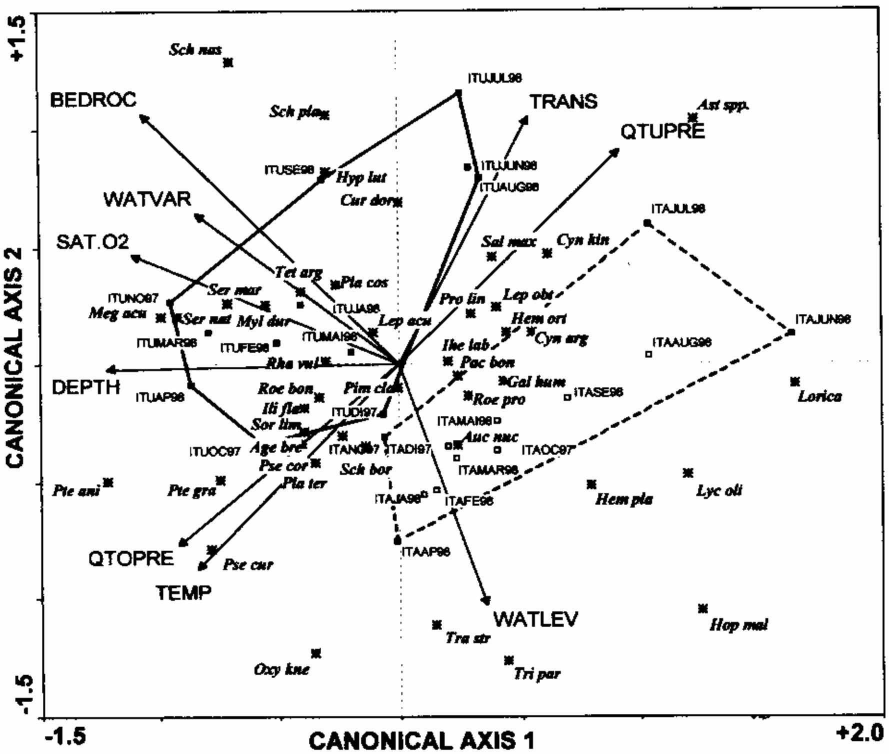

Figure 2: Ordination diagram (triplot) corresponding to the 1997-98 hydrologic cycle. The two first axes of the Canonical Correspondence Analysis (CCA) are plotted. Abbreviations for environmental variables (vectors) can be found in Tab. II. The three first letters of genera and species are in *Italics* (see Tab. I). Samples are denoted by boxes with labels indicating site, month and year. ITA= low impact site (empty squares); ITU= high impact site (filled squares). Lines connect outer observations for each sampling site. Dashed lines low impact site; solid lines= high impact site.

configurations: summer, winter and transitional. Some species were present most of the time, being those placed near the center of the plot (Figs. 2-4). It is important to note that the 1997-98 hydrologic cycle corresponds to the well-known El Niño episode (ENSO), characterized by higher water temperatures and discharges than previous years. During that period, fish community structure showed a shift of the inflexion point to April, when a typical summer configuration in fish fauna was observed. During April, the second most important extraordinary flow during the century was registered. In previous years, the same inflection point was observed during December-February.

In spite of similarities in the cycles of their fish fauna, both sampling sites were clearly distinguished during all of the hydrologic periods. Actually, they almost never overlap in the plots, being only slightly more similar in December (Fig. 2), at the end of the migratory period. In the 1997-98 hydrologic cycle, the environmental variables that most contributed to separate both sampling stations were bedrock (microhabitat), rate of variation in water level (hydrology), and dissolved oxygen (limnology). Total dissolved gases had supersaturated levels at high spillway discharge, but were in general not related to community structure, except in the 1997-98 study year. Their importance was explained by dissolved oxygen, a variable highly correlated with total dissolved gases, and retained in the forward selection procedure (Tab. IV). In the remainder hydrologic cycles, the situation was similar (Figs. 3 and 4), with differences due to the increasing amount of turbinated water released by the dam, as

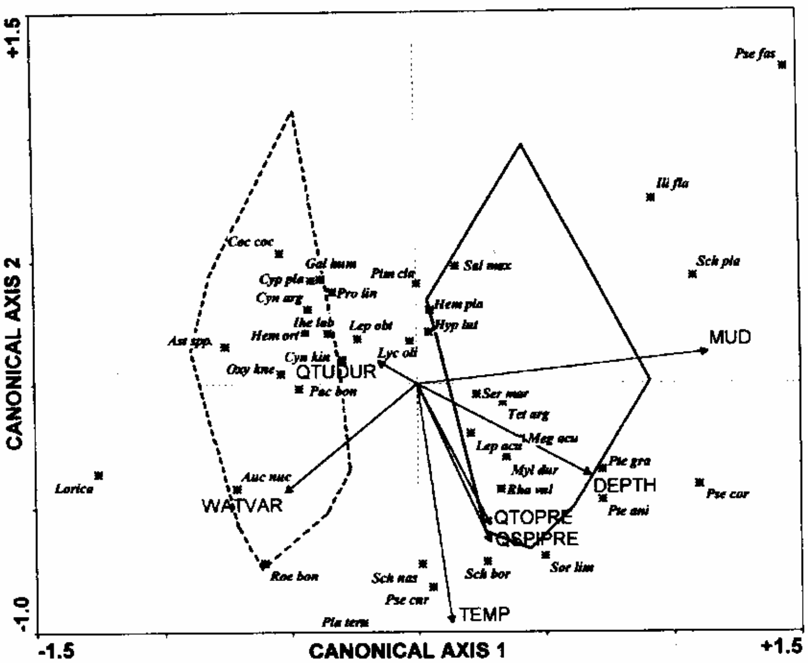

Figure 3: Ordination diagram (triplot) representing the two first axes of CCA corresponding to the 1996-97 hydrologic cycle. Abbreviations for environmental variables (vectors) can be found in Tab. II. The three first letters of genera and species are in *Italics* (see Tab. I). Lines connect outer observations for each sampling site. Dashed lines= low impact site; solid lines= high impact site.

well as the selection of different types of substrates (mud or sand), as the main gradient dividing sampling sites. Water variation also took its major importance to explain difference between sites during the last study period, when almost all planned power units were in operation.

By examining the ordination diagrams of Figs. 2-4, it is possible to find out which species are typical of each sampling site in different seasons of the year. Since samples of both sites are clearly distinguished, the species placed at the ends of the gradient separating sites can be considered as those that contributed most to the scorers of those sites. During the 1997-98 hydrologic cycle, the warmest period in the low impact site was characterized by *T. paranensis*, *T. striatulus* and *O. kneri*, all of them invertebrate-eaters. The rest of the year, the most typical species were *H. malabaricus*, *H. platyrhynchos*, *L. olidus* (piscivores) and several species of Loricariinae (detritivores/algivores). In the high impact site, typical winter species were *S. nasutus*, *S. platae*, *C. dorsalis*, and *H. luteomaculatus*, whereas the most characteristic summer species were *M. duriventris*, *S. marginatus*, *S. nattereri*, *P. anisitsi* and *M. aculeatus*. Excluding the two piranha species, the remaining are plant-eaters or detritivores/algivores. Using the same procedure with the ordination diagrams of other hydrologic cycles, it can be seen that this latter trophic guild, along with piscivorous species was important in all sites, but plant-eaters were more important in the high impact site and invertebrate-eaters in the low impact site (Tab. III). The presence of extensive basaltic bedrock supporting dense populations of macrophytes growing in fast-flowing waters (Podostemonaceae) in the high impact site may be the reason for these differences. Unpublished gut contents analyses carried out by the authors indicate that many fish species feed actively on these aquatic plants.

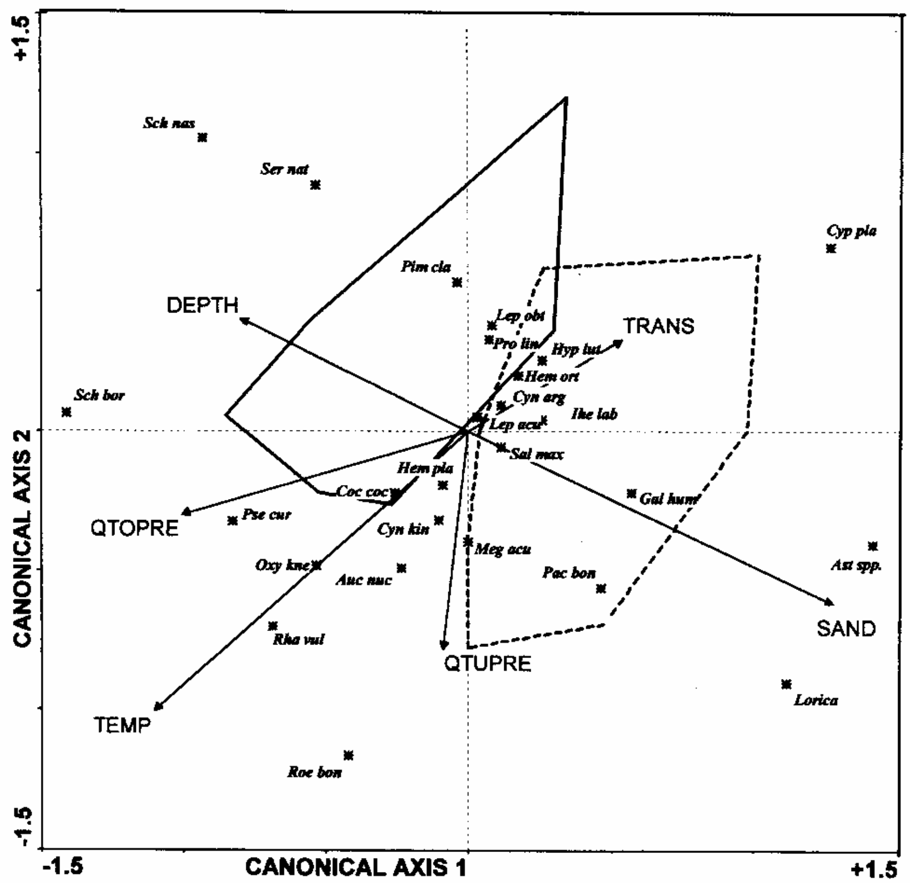

Figure 4: Ordination diagram (triplot) representing the two first axes of Canonical Correspondence Analysis (CCA) corresponding to the 1995-96 hydrologic cycle. Abbreviations for environmental variables (vectors) can be found in Tab. II. The three first letters of genera and species are in *Italics* (see Tab. I). Lines connect outer observations for each sampling site. Dashed lines= low impact site; solid lines= high impact site.

In all of the studied cycles, increases in turbinated water (QTUPRE) were mainly related to increments in the relative abundance of non-Siluriform piscivorous fish (Tab. III). The weighted averages provided by CANOCO indicate that in 1995-96 those fish were *S. maxillosus*, *R. vulpinus* and *C. kincaidi*; in 1996-97, *C. argenteus*, *I. flavipinnis*, *S. marginatus* and *P. ternetzi*; finally in 1997-98, *S. maxillosus*, *C. kincaidi*, and *L. olidus*. Other trophic guilds were less common and showed less consistency from year to year at high levels of turbinated waters. In contrast, some Siluriform piscivores, such as *P. coruscans*, *P. fasciatum*, *H. platyrhynchos* and *S. lima*, were relatively more abundant at low levels of turbinated waters in all hydrologic cycles. In the two last hydrologic cycles, this environmental variable appeared as a distinct gradient that acquired a greater importance during low water periods, when little or no flow was passing through spillways, and high water transparency was observed (Figs. 2 and 3). The relative importance of turbinated water is more clearly observed in the third and four orthogonal axes (Tab. IV).

Discussion

The resulting model shows that about half variability in community composition can be explained by a reduced set of environmental variables. This relatively large amount of variance, considering the substantial number of species included, indicates how strongly related is fish community structure to variables such as discharge, transparency, temperature, substrate and depth in the Paraná River. In a similar way, Quirós (1990), employing multiple regression techniques, obtained good fits between commercial fish landings in the Lower Paraná River and hydrology, climate, river regulation and pollution variables.

Fish community showed fairly constant cyclical changes during the three periods considered, a fact observed in both sampling sites. Some species migrated for reproduction and were commonly captured in spring and summer, while others moved in search of food, being most frequently found in autumn and winter. In the Middle Paraná River, Quirós & Vidal (1999) found that potamodromous migratory fish maintained their seasonal position in the river main channel independently of historical changes in water level. Though water temperature was more consistent with fish cyclical behavior, the authors hypothesize that factor other than flood and water temperature are responsible for triggering fish migrations in large rivers. In the present work, temperature was consistently and tightly related to community structure along the study period, while the importance of discharge or water level variations was variable. Moreover, Rodríguez & Lewis Jr. (1994), studying fish communities of floodplain lakes of the Orinoco River (Venezuela), found a remarkable regularity in the pattern of among-year variation. In that study, water transparency was noted to be a good predictor of fish community structure, in contrast with dissolved oxygen and temperature.

Rodríguez & Lewis Jr. (1994) found some evidence supporting deterministic mechanisms as responsible of rapid assemblage recovery after floods in floodplain lakes. The authors propose some plausible mechanisms of regulation, that include site-dependent winnowing or culling of prey species by piscivores, habitat selection by fish when flood water recedes, and selection of spawning sites by mature female. The present study shows that cyclical changes in community structure maintained its general pattern in spite of large among-years differences in environmental variables, that were mainly related to climatic oscillations (e.g., ENSO), as well as changes in dam operation regime. These results suggest that deterministic regulatory mechanisms may be also operating in Paraná River, to maintain fish communities within a limited range of variation.

The microhabitat characteristics of the sites of gill net emplacement seem to have a great effect in the resulting composition of the captures. Nevertheless, some microhabitat variables (substrate) and dam operation related variables (oxygen saturation and water level) were highly correlated, which makes difficult to determine their relative importance in explaining differences in community composition between low impact site and high impact site. The method employed allowed to estimate relative contribution to the explained variance of each subset as a whole. The results suggest that as time passes, microhabitat variables decrease in relative importance. However, if microhabitat was not included in the analyses, the observed differences in fish composition could have been solely attributed to some kind of impact related to the proximity of the dam.

The non-Siluriform piscivores were an important and abundan trophic guild positively related to a particular feature of the dam, the turbinated water flow. It could be shown that the condition factor of those piscivorous fishes was better or similar in the high impact site, relative to the low impact site (Jacobo *et al.*, 1996). On the other hand, many prey species such as *P. lineatus*, *H. orthonops* and *L. obtusidens* had significantly better condition factors in the low impact site. These results suggest that predators may have been taking some profit of the agglomeration of available prey along the dam walls. According to Rodríguez & Lewis Jr. (1994), piscivorous fishes in floodplain lakes may play a major role in community assemblages both, directly through predation, and indirectly by influencing selection of predator-free areas by fish prey. This pattern could also be important in the river main channel, especially in coastal areas. These results also suggest that migratory fish species responded in different ways to turbinated water, because Siluriform fish were less commonly found in captures at high discharge by turbines, and some others such as *P. lineatus* and *L. obtusidens* did not show a clear negative or positive association.

Some methodological limitations must be carefully considered in the interpretation of the results. Due to the passive methods of fish capture employed, certain observed responses may be mainly related to the variability in effectiveness of capture of the gill nets on different times of the year. It implies that more mobile fish species may be over-represented. Thus, the non-explained variance may be related to factors inherent to the capture device, and not necessarily to fish community structure or the lack of explanatory power of environmental variables. A second limitation to be considered are the time lags in the fish responses to short term variations in environmental variables such as discharge, as were mentioned by Bini *et al.* (1997), in a study on fish communities and environmental variables of a reservoir of the Iguazú River in Brazil. In this sense, it is interesting to note that in the present study, many of the hydrologic variables retained in the forward selection procedure were those averaged during one week before sampling. Gradients found significant in all hydrologic cycles, as for example substrate and temperature, confronted with those retained in the model in latter years, such as water level variations and oxygen saturation, permit to better determine short term and long term responses related to dam. According to Petts (1984), fish populations and communities can take several years or decades to reach stable conditions in river segments below dams. The present study was carried out shortly after the filling of the reservoir. Therefore, some of the observed patterns may be transitional, and will only be steady when the river corridor and the whole ecosystem finally achieve a new state, dynamically equilibrated with the modified river conditions. Finally, the selected environmental variables were not necessarily those that best explained fish community structure, but their choice was limited by the constraints of an intensive survey program. Perhaps, including other variables such as particulated or dissolved organic matter would result in better explanations of community structure, as it was found by Quirós & Balgún (1985) for the rivers of Del Plata Basin (South America), and Bini *et al.* (1997) for the Iguazú River (Brazil).

The present approach is an alternative way of looking at complex systems in which natural effects at different spatial and temporal scales are confounded with impacts of human activities. In spite of the limitations in the number of study sites, the sampling devices, and the restricted number of environmental variables employed, a great amount of valuable information could be finally obtained. However, the results are always interpreted in terms of significant explanatory variables and should never be taken as causal explanations, which would be possible if inferential statistics were applied. Indeed, the inherent characteristics of dams force the use non-conventional methods, while keeping scientific postulates. It has been suggested that a better approach for this kind of endeavor is to employ principles applied in epidemiology, a discipline confronted with comparable methodological limitations. In particular, the lack of replications and randomization that impose restrictions to inferential statistics. A series of assembly rules such as strength, consistency and specificity, have been proposed as causal arguments replacing inferential statistics in these situations (Beyers, 1998). Linking some of the postulates advocated by the aforementioned approach with the techniques described in the present paper would eventually help to find out causal arguments in future studies.

In spite of its limitations, the proposed procedure is a valuable tool to reduce the complex data matrices representing community structure and environmental variables in large rivers. It can help in the interpretation of changes in community structure, evaluating the relative importance of natural river variables and dam-related variables, at different scales of time and space. The technique can be employed as a heuristic approach to generate verifiable hypotheses about the impact of dams in research conditions that otherwise would avoid any clear conclusion. Furthermore, the accumulation of information of several hydrologic cycles increases the strength and consistency of the interpretations, allowing to discriminate natural river trends from others related to the reservoir itself.

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