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Factors affecting fish diversity and abundance in drying ponds and lagoons in the upper Paraná River basin, Brazil

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Abstract

Monthly samples were taken from April 1992 to March 1993 of fish assemblages present in six permanent lagoons and four ponds, fragmented from them during the drought period and during the terminal phases of desiccation, to evaluate changes in their diversity, abundance and dominance. Their relationships with hydrological and environment conditions were examined. A total of 63 fish species were identified. Species composition and abiotic factors were heterogeneous among the different water bodies. The proportion of piscivores and oxygen concentration were the determining factors for structuring the assemblages. The impact of piscivory upon fish diversity was neutral at the beginning and negative at the end of the dry season. In the terminal phase of desiccation, diversity was higher in ponds that contained a moderate proportion of piscivores than in these containing a higher proportion.

Key words: Paraná River, floodplain, temporary water, fish diversity, density, piscivorous

1. Introduction

In the last 30 years, studies on neotropical fish fauna have intensified. Notwithstanding, there is a scarcity of studies focusing on lagoons and drying ponds which become isolated from the main river in the dry season (eg Lowe-McConnell 1964, 1975; Bonetto *et al.* 1969a, 1969b, 1970; Pignalberi de Hassan, Cordiviola de Yuan 1970; Cordiviola de Yuan, Pignalberi de Hassan 1981, 1985; Winemiller 1989, 1996; Pinto 1994; Veríssimo 1994). In these lagoons, the confined fish are exposed to increased competition, predation by fish, birds, and reptiles, low oxygen concentrations and high temperature (Verissimo 1994). Extreme environmental conditions increase natural mortality during the dry season and natural mortality may exceed fishing mortality by a factor of 4 (Bonetto *et al.* 1969a) in the Middle Paraná.

The Paraná River flows through extensive alluvial plains, including permanent and seasonal floodplain lakes (lagoons, drying ponds). These floodable areas are dynamic as a result of water level fluctuations which are the main determining factor of environment stochasticity (Lowe-McConnell 1987; Junk *et al.* 1989; Sparks *et al.* 1990; Thomaz 1992). The floodplain is the main spawning and nursery area for many fish species including large migratory species, which always dominate commercial fisheries in South America. These highly productive areas also provide food and shelter against predators (Bonetto *et al.* 1970; Goulding 1979; Welcomme 1979; Bayley 1981; Paiva 1983; Oldani, Oliveiros 1984; Lowe-McConnell 1987; Copp, Penáz 1988; Agostinho *et al.* 1992, 1993; Petrere, Agostinho 1993; Okada *et al.* 1996). Without strong seasonal flooding growth and recruitment may be drastically reduced (Barco *et al.* 1993).

This paper analyses the fish assemblages in six separate lagoons and four drying ponds during a complete hydrological period, aiming to establish their variation and relationship with environmental factors, as well as the fish strategies for survival among fish assemblagesin this fluctuating habitat.

The working hypothesis is that fish assemblages of the lagoons and ponds formed by colonisation during the high water season will differ by the end of the dry season because of differences in the periods of connectivity, environmental and biotic factors, particularly predation and macrophyte cover.

2. Material and Methods

The study area

The Paraná River is 4695 km long, draining a total area of about 2 700 000 km^2 of which 47% is in Brazil (Paiva 1982). The study area is located in the high Paraná reach near the Porto Rico village (Fig. 1). The left margin of the river is a 20-km wide inundated area (Agostinho, Zalewski 1995), with different biotopes subject to water level fluctuation. These lentic habitats comprise several lagoons fed by the water table, local rains and by the main river through channels. In the dry season the receding water results in several lagoons which dry up differently throughout the year.

The six lagoons studied were distributed as follows: Canal do Meio and Pontal lagoons are located on Porto Rico Island; Porto Rico, Pau Véio, Tręs Amigos and Mutum lagoons are located on Mutum Island. These islands contain shrub vegetation in the floodable fields, which are used for cattle ranching during the low water period. These lagoons are heterogenous in shape, area, mean depth, shelter, food availability, and

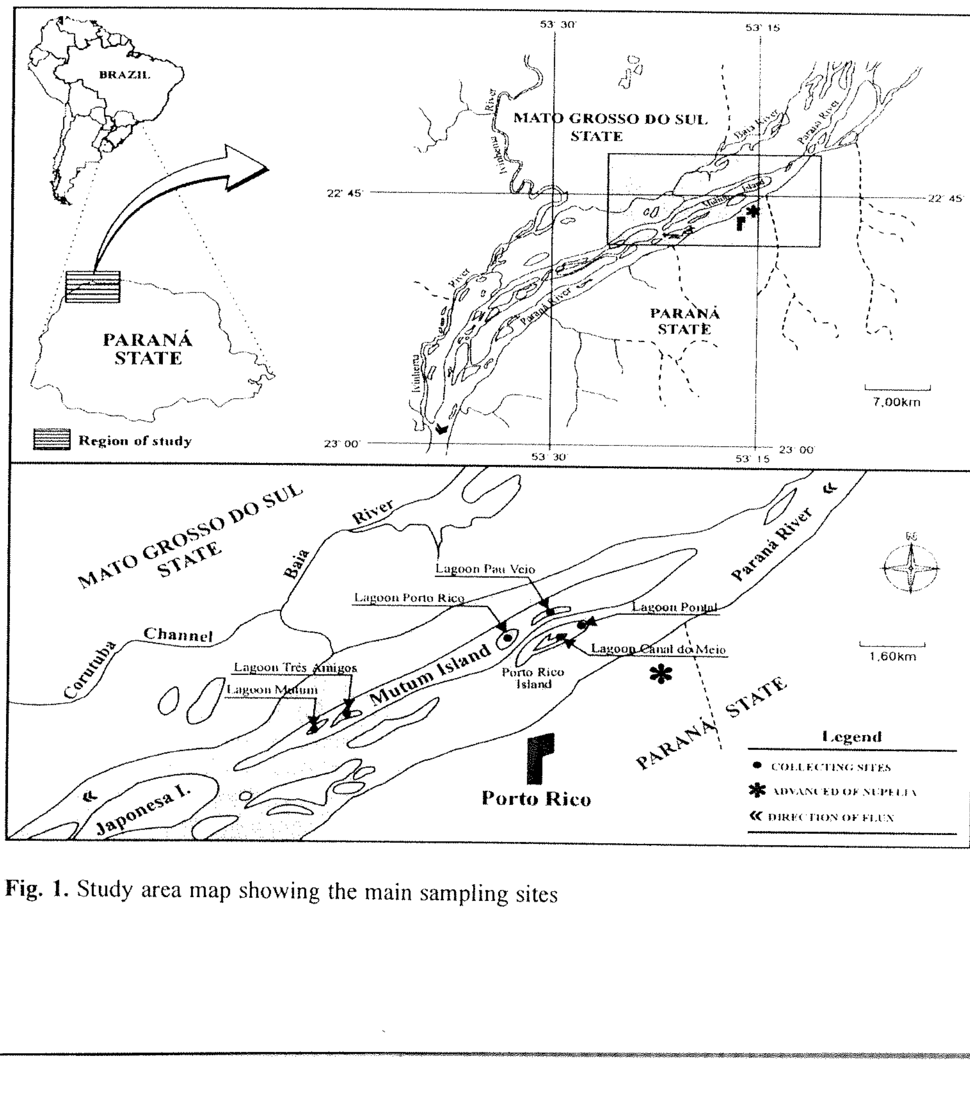


Fig. 1. Study area map showing the main sampling sites

day and month in which they become isolated from the main river. The lagoons have originated from paleochannels of the main river, being elongated during the rainy season. In the dry season, except for Porto Rico lagoon, the lagoons fragment into smaller water bodies, here named drying or isolated ponds, which often dry out.

Fish sampling and environmental data

Fish were caught using beach seines 30 m long with 5-mm mesh between opposite knots (stretched mesh). Each lagoon was sampled monthly from April 1992 to March 1993, at sunrise, noon, and sunset, on each sampling occasion. Fishing effort was constant throughout the experiment, and the number of hauls (3) was the same at each fishing site, except for severely drying ponds. Fishing out was possible in four ponds originating from do Canal do Meio (one pond; CM*), Pontal (one pond; PT*) and Tręs Amigos (two ponds; TA*[1] and TA*[2]), utilising beach seines and a large sieve with 2.5 mm mesh, at the end of the dry season. Fish were preserved immediately in 8% formalin for identification and biometry. Fish were identified at species level according to Britski (1972) and Gery (1977).

The area and bathymetric data from the lagoons were estimated for March 1993, using transects 5 m apart. The percentage of shoreline reduction was estimated in August 1992 in the main body of each lagoon. Granulometric sediment analysis was performed just for March 1993, using the Wenthworth granulometric scale (Suguio 1973). The organic sediment content was determined by calcination at 600 °C for three hours. For each sampling occasion, surface and bottom water temperature (°C), dissolved oxygen (mg dm^{-3}) using the Winkler method, conductivity (S cm^{-1}) and pH were recorded. These two last parameters were measured with a portable apparatus in the field. Water transparency (m) was measured by a Secchi disk and also depth (m) and macrophyte coverage (%) were estimated monthly.

Figure 2 shows the water and precipitation levels during the study period. The hydrological cycle had four distinct phases:

1st – April–May period: permanent connection between the lagoons and the Paraná River,

2nd – June–July period: beginning of isolation,

3rd – different stages of full isolation in these habitats: a) December–January in Porto Rico, Pau Véio and Mutum lagoons; b) September-October in Pontal and Tręs Amigos lagoons, and c) October- November in Canal do Meio lagoon,

4th – Februa–ryMarch period: first stages of the connection period with the Parana River.

Phase 3 was characterised by local rains and rising of the water table, denoting the end of this period. In September these rains produced a small rise in river level, enough to re-establish the contact between the adjacent lagoons Canal do Meio and Pau Véio.

Statistical data analysis

The grouping of sampling sites according to the environmental variables (maximum, minimum and mean for each hydrological period), was performed by cluster analysis using Euclidean distance as a metric and UPGMA (Unweighted **P**air – **G**roup **M**ethod **U**sing **A**rithmetic **A**verages) as a link (Ludwig, Reynolds 1988). The similarity of fish assemblages among the lagoons in the final period of isolation (3rd stage) and in the partial isolation period (4th stage) was calculated using the Percentage Similarity (Brower, Zar 1984; Krebs 1989):

$PS = \Sigma$ (p_i or q_i, which is lower)

When comparing two lagoons p_i is the proportion composition of species i in the first lagoon and q_i is the proportion composition of that species in the second lagoon.

The species composition of fish assemblages in the lagoons was analysed using the abundance and constancy in the samples ex-

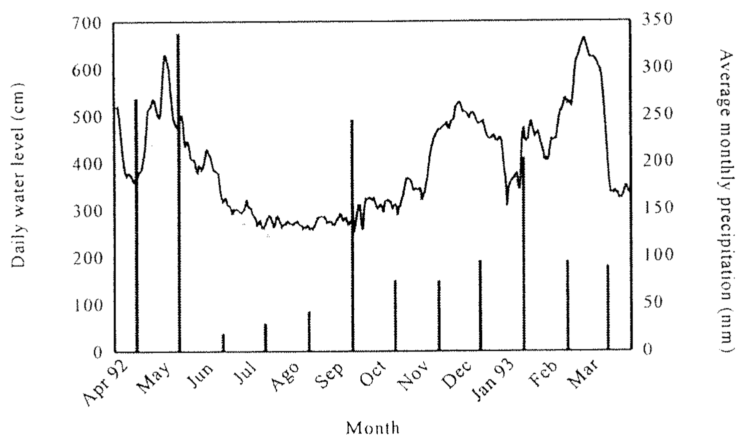


Fig. 2. Daily water level (cm) as continuous line (left scale), and month average precipitation represented by perpendicular lines (mm) (right scale), from April/92 to March/93: DNAEE - Departamento Nacional de Águas e Energia Elétrica).

pressed as the percent in each sample in which each species occurs in relation to the total number of samples.

The fish assemblage attributes considered in the spatial/temporal analysis and in its relation with environmental variables were species richness, species abundance, diversity ($H'=\Sigma p_i.log_2 p_i$) and evenness ($E=H'/H'max$). Canonical correlation analysis was applied to establish the relationship between these attributes and the environmental variables (Manly 1995).

The relationship between the environmental factors in the lagoons and fish assemblage attributes just before desiccation was examined through scatterplots. All the procedures were performed using the package Statistica (1993).

3. Results

Fish assemblages

During the study, 18 968 fish specimens of 63 species included in orders Rajiformes, Characiformes, Siluriformes, Perciformes, Pleuronectiformes and Synbranchiformes were caught (lagoons, 17 246; drying ponds, 1722). Table I shows the abundances and constancies of these species in each lagoon for the whole period. Among the more abundant species were *Astyanax bimaculatus*, *Steindachnerina insculpta* and *Roeboides paranensis* which comprised more than 50% of the catches, except for the Mutum lagoon, where only the first species was important. These species, together with *Astyanax schubarti*, *Prochilodus lineatus* and *Loricariichthys platymetopon*, were constant in the catches of at least five lagoons. The largest number of constant species in the samples was found in Pau Véio (12) and the smallest (7) in Pontal and Mutum lagoons.

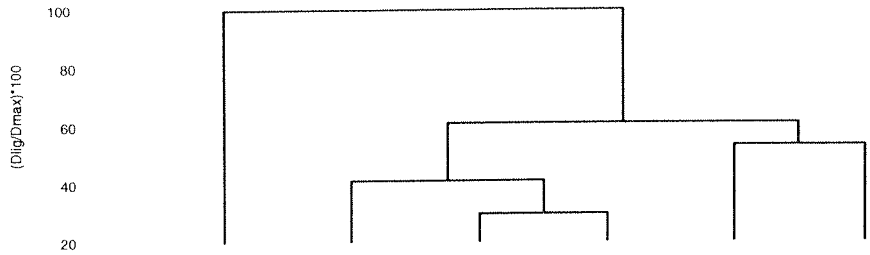
The similarity among the sampled sites (Fig. 3), with respect to environmental variables, was higher between Porto Rico and Pau Véio lagoons than among the other four, of which Tręs Amigos lagoon was more similar to P. Rico and P. Véio, due to the percentage of shoreline reduction, macrophyte cover and electrical conductivity. P. Rico and Pau Véio registered higher diversity and evenness index values and species constancy. The Mutum lagoon was distinguished from all the others by a higher shoreline reduction, smaller depth, macrophyte cover and water transparency. It showed increased variability in dissolved oxygen, electrical conductivity and had a smaller proportion of piscivores. In this lagoon fish were far more abundant but displayed lower species richness, diversity and evenness.

Table II and Fig. 4 show the relationship between the environmental and populations variables, relative to the fish assemblage attributes, examined through canonical correlation analysis; the global correlation is high ($R = -0.916$; $p=0.0043$) for the first canonical root. H' and E were positively related to the proportion of piscivores and lagoon depth and negatively with dissolved oxygen. The redundancy coefficient of this surface was equal to 62.2% for set I, and 36.4% for set II, indicating that canonical surface explains a large part of the total variance of biotic and environmental variables. These high values confirmed that there is a small residual for both sets of data at the multivariate level, which is to be expected because 2 of the 4 characters are significant ($p<0.05$) in set I and 3 of 8 are significant in set II.

Temporal variation

Figure 5 does not show any consistent pattern of H' variability in the four distinct phases of the hydrological cycle. The sharpest drop in diversity, except for Mutum, occurred in phase 2, due to the increase in abundance and a drop in species richness. Medium size fish species, such as *Brycon orbignyanus*, *Leporinus friderici*, *Salminus maxillosus*, *Pimelodus maculatus*, *Leporinus elongatus* with generalised occurrence during the connection period, were not registered after that. The opposite occurred for small Characiformes. In the Mutum lagoon, where diversity increased in phase 2, there was a decrease in richness and increase in equitability, due to a drastic decrease in the abundance of *Astyanax schubarti*, the dominant fish species in this lagoon during the high water season.

Decreases in diversity during phase 3 were detected in Mutum and Pontal lagoons, whose biotope areas contracted most, with smaller macrophyte cover and shallower depth during the dry season. The proportion of piscivores in these lagoons was also low during the dry season (0.5% and 2.0% respectively) when compared to the other lagoons for the same period (between 5.7% and 23.5%). The decrease in species number occurred in four lagoons, except Canal do Meio and Pau Véio, for which a slight increase in water level, due to local rains, enabled the contact reestablishment. It is remarkable that the evenness increased after these lagoons became isolated, the increase being maximal under intermediate conditions of piscivory (%PISC: Pau Véio = 5.5%; Canal do Meio = 8.0%) rather than in lagoons showing higher or lower percentage of piscivores (Tręs Amigos = 22.6%; Porto Rico = 3.7%; Pontal = 2.0% and Mutum = 0.5%).



	MUTUM	T.AMIGOS	P.VÉIO	P.RICO	PONTAL	C.MEIO
POPULATIONS VARIABLES						
s=number of species	*35*	37	36	41	**42**	38
N=number of individuals	**4.371**	3.303	*1.922*	3.315	2.254	2.081
const=No of constant species	*7*	11	**12**	10	*7*	10
H'=Shannon diversity index	*2.534*	3.196	3.415	**3.458**	3.161	3.192
E=evenness	*0.494*	0.614	**0.661**	0.645	0.586	0.608

ENVIRONMENTAL VARIABLES		MUTUM	T.AMIGOS	P.VÉIO	P.RICO	PONTAL	C.MEIO
Lagoon Area (ha)		3.0	3.3	**8.2**	7.6	*0.9*	5.5
Rmx=%		**95.0**	75.0	*60.0*	70.0	90.0	85.0
DCR (months)		2	**7**	2	2	**7**	6
M.O. (%)		18.0	16.3	15.6	**20.9**	*4.4*	6.4
Share of Piscivores	X(S)	*0.045*(0.036)	0.109(0.090)	0.123(0.169)	0.049(0.034)	**0.131**(0.166)	0.099(0.135)
	Min-Max	0.00-0.12	0.00-0.27	**0.00-0.67**	*0.01-0.11*	0.00-0.60	0.00-0.53
Type of bottom		**medium sand**	*fine sand*	*fine sand*	*Fine sand*	*fine sand*	*fine sand*
Depth (m)	X(S)	*1.30*(0.802)	1.52(0.769)	1.66(0.878)	**1.99**(0.711)	1.56(0.874)	**1.99**(0.732)
	Min-Max	0.38-2.60	*0.55-2.60*	**0.47-3.50**	1.07-3.60	0.45-3.30	1.00-3.55
Transparency (m)	X(S)	*0.31*(0.242)	0.72(0.458)	0.70(0.503)	**1.13**(0.339)	0.71(0.527)	0.61(0.448)
	Min-Max	*0.07-0.85*	0.08-1.70	0.10-1.60	0.65-1.80	**0.08-1.90**	0.05-1.60
Macrophyte cover (%)	X(S)	*12.2*(17.1)	44.6(25.4)	**58.3**(21.7)	53.3(12.1)	30.5(25.7)	33.8(30.4)
	Min-Max	0.0-60.0	15.0-90.0	20.0-95.0	*40.0-80.0*	0.1-70.0	**1.0-90.0**
MeanTemperature(°C)	X(S)	**24.9**(3.6)	24.5(3.0)	23.9(4.0)	23.9(3.4)	23.5(3.5)	23.8(3.7)
	Min-Max	18.0-34.0	*18.5-30.0*	**15.5-34.0**	16.5-31.5	15.0-30.0	17.0-34.5
O_2 concentr. (mg dm^{-3})	X(S)	6.43(3.1)	**7.38**(1.4)	3.74(2.7)	4.22(1.8)	6.50(1.5)	4.28(2.8)
	Min-Max	**0.00-14.60**	4.64-11.11	0.49-11.17	*0.47-7.71*	2.86-11.13	0.06-10.39
Conductivity(µs.cm^{-1})	X(S)	**79.2**(39.8)	41.1(9.9)	47.9(17.5)	*39.1*(10.0)	54.5(12.1)	46.2(23.0)
	Min-Max	**31.0-231.0**	*27.0-59.0*	22.0-84.0	24.0-67.0	22.0-81.0	21.0-120.0
pH	X(S)	*6.4*(0.5)	6.8(0.5)	*6.4*(0.3)	*6.4*(0.2)	**6.9**(0.4)	*6.4*(0.3)
	Min-Max	**5.1-8.0**	5.9-8.4	5.9-7.7	*5.9-7.0*	5.9-8.2	5.8-7.7

Rmx=% of area reduction in relation to the peak of the high water season;
DCR=duration of the lagoon contact with the main river (months);
MO= % of the organic content of the sediment;
X(S) = mean and standard deviation.

Fig. 3. Dendrogram of the lagoons using the Euclidean distance and UPGMA distance based on the populations and environmental variables

The fish fauna just before desiccation

The composition of the remaining fish fauna in the drying ponds was distinct from the one present during phase 3 of the lagoons that gave rise to the ponds. Except for the pond TA*[1] (Table III), originating from Trȩs Amigos lagoon, the sum of the relative frequencies of each species shared by the isolated pond and its lagoon was smaller than 50%. In Trȩs Amigos lagoon the first isolated pond, TA*[1], had a fish fauna more similar to that in the other water bodies (Table III).

The characteristics of the drying ponds and the species assemblage data are shown in Table IV. Among the dominant species in each isolated pond we may distinguish three which occurred in three out of the four ponds: *Astyanax bimaculatus*, *Steindachnerina insculpta*, _and *Cichlasoma paranaense*. As the ponds dried up, juveniles of two species were abundant only: *Leporinus obtusidens* and *Prochilodus lineatus*. The majority of

Table I. Species abundance (n) and constancy (cons) in each lagoon (bold = most abundant)

Species (native names are in brackets)	Lagoons											
	CMeio		Pontal		PRico		PVeio		TAmigos		Mutum	
	n	Const	n	const	n	const	n	Const	n	cons	n	const
Astyanax bimaculatus (tambiu)	**905**	100.0	218	91.7	**622**	100.0	**427**	100.0	**684**	75.0	**1944**	91.7
Astyanax schubarti (lambari)	118	66.7	31	58.3	51	50.0	137	66.7	108	75.0	276	58.3
Astyanax fasciatus (lambari)	---	---	1	8.3	1	8.3	---	---	1	8.3	---	---
Bryconamericus stramineus (pequira)	---	---	---	---	63	41.7	---	---	---	---	---	---
Hyphessobrycon callistus (mato-grosso)	26	25.0	1	8.3	4	25.0	2	8.3	13	33.3	23	41.7
Hemigrammus marginatus (piaba)	---	---	---	---	23	41.7	6	8.3	---	---	---	---
Moenkhausia intermedia (piqui)	94	41.7	155	83.3	372	83.3	164	91.7	**233**	100.0	45	33.3
Moenkhausia sanctae-filomenae (piqui)	3	25.0	5	25.0	2	8.3	5	25.0	6	25.0	1	8.3
Aphyocharax nasutus (piqui)	---	---	1	8.3	---	---	---	---	---	---	1	8.3
Cheirodon notomelas (pequira)	77	75.0	4	33.3	21	41.7	---	---	9	16.7	7	25.0
Cheirodon sp (pequira)	3	25.0	1	8.3	79	58.3	1	8.3	1	8.3	1	8.3
Odontostilbe sp (pequira)	---	---	---	---	---	---	1	8.3	---	---	---	---
Characidium fasciatus (piquira)	---	---	---	---	3	16.7	---	---	1	8.3	---	---
Serrasalmus marginatus (piranha)	15	25.0	8	33.3	10	33.3	5	16.7	7	16.7	1	8.3
Serrasalmus spilopleura (piranha)	25	50.0	21	66.7	32	75.0	18	41.7	25	66.7	---	---
Myloplus levis (pacu-prata)	---	---	---	---	7	8.3	1	8.3	---	---	---	---
Piaractus mesopotamicus (pacu)	1	8.3	---	---	---	---	---	---	---	---	20	33.3
Acestrorhynchus lacustris (lambiá)	2	16.7	55	50.0	67	91.7	62	75.0	96	83.3	20	16.7
Oligosarcus sp (peixe-cadela)	---	---	1	8.3	---	---	2	16.7	---	---	---	---
Brycon orbignyanus (piracanjuba)	1	8.3	2	16.7	1	8.3	2	8.3	1	8.3	9	25.0
Salminus maxillosus (dourado)	3	8.3	---	---	---	---	---	---	---	---	3	8.3
Roeboides paranensis (dentudo)	92	91.7	**708**	91.7	**450**	83.3	**453**	83.3	222	91.7	47	25.0
Cyphocharax nageli (saguiru)	2	16.7	1	8.3	5	16.7	20	58.3	14	25.0	1	8.3
Cyphocharax modesta (saguiru)	2	16.7	4	25.0	9	25.0	38	33.3	7	33.3	6	8.3
Steindachnerina insculpta (saguiru)	**148**	66.7	**466**	83.3	**831**	100.0	**280**	83.3	**1108**	83.3	20	33.3
Apareiodon affinis (canivete)	---	---	---	---	41	33.3	4	8.3	15	16.7	---	---
Apareiodon piracicabae (canivete)	---	---	---	---	1	8.3	---	---	---	---	2	8.3
Leporellus vittatus (solteira)	---	---	---	---	1	8.3	---	---	---	---	---	---
Leporinus elongatus (piapara)	---	---	---	---	1	8.3	7	8.3	---	---	---	---
Leporinus lacustris (corró)	3	16.7	---	---	1	8.3	6	33.3	---	---	1	8.3
Leporinus friderici (piau)	---	---	1	8.3	2	8.3	3	16.7	12	25.0	4	8.3
Leporinus obtusidens (piau)	8	41.7	13	33.3	30	25.0	28	58.3	32	66.7	107	66.7
Leporinus striatus (canivete)	1	8.3	---	---	2	16.7	---	---	6	16.7	---	---

Schizodon altoparanae (piava)	2	16.7	---	---	1	8.3	12	50.0	7	33.3	2	16.7
Schizodon borelli (piava)	1	8.3	20	41.7	2	16.7	43	66.7	29	50.0	15	41.7
Hoplias malabaricus (traíra)	105	75.0	84	41.7	11	50.0	28	83.3	217	75.0	168	66.7
Hoplerytrinus unitaeniatus (jejú)	1	8.3	---	---	---	---	---	---	---	---	2	16.7
Prochilodus lineatus (curimba)	**132**	58.3	140	50.0	102	58.3	79	66.7	177	58.3	**755**	83.3
Pyrhulina australis (charutinho)	1	8.3	---	---	---	---	---	---	---	---	---	---
Rhaphiodon vulpinus (dour. Cachorro)	---	---	1	8.3	---	---	---	---	---	---	---	---
Auchenipterus nuchalis (surumanha)	1	8.3	1	8.3	---	---	---	---	---	---	---	---
Parauchenipterus galeatus (morrudo)	1	8.3	8	41.7	---	---	2	8.3	---	---	---	---
Pimelodella gracilis (chorão)	15	58.3	2	16.7	151	41.7	1	8.3	---	---	---	---
Pimelodus maculatus (mandi)	---	---	11	16.7	1	8.3	---	---	---	---	---	---
Pseudoplatystoma corruscans (pintado)	---	---	---	---	6	25.0	---	---	---	---	1	8.3
Sorubim cf *lima* (chinelo)	---	---	1	8.3	---	---	---	---	---	---	---	---
Calichthys callichthys (tamboatá)	---	---	---	---	---	---	---	---	---	---	1	8.3
Hoplosternum littorale (caboja)	91	41.7	2	8.3	1	8.3	8	8.3	2	16.7	**784**	66.7
Corydoras aenius (armadinho)	---	---	---	---	---	---	---	---	1	8.3	---	---
Hypostomus aff *derbyi* (cascudo)	---	---	5	16.7	---	---	---	---	---	---	---	---
Loricariichthys platymetopon (chinelo)	126	66.7	**231**	58.3	202	75.0	36	66.7	165	66.7	5	33.3
Gymnotus carapo (morenita)	4	25.0	---	---	---	---	3	16.7	---	---	4	8.3
Rhamphichthys rostratus (peixe-espada)	---	---	3	16.7	---	---	---	---	3	25.0	---	---
Eigenmannia trilineata (tuvira)	1	8.3	1	8.3	---	---	---	---	3	25.0	1	8.3
Eigenmannia virescens (tuvira)	---	---	3	16.7	---	---	---	---	---	---	---	---
Cichla monoculus (tucunaré)	---	---	2	16.7	---	---	---	---	2	8.3	---	---
Cichlasoma paranaense (cará)	33	58.3	11	25.0	20	50.0	11	50.0	69	50.0	83	58.3
Crenicichla britskii (joaninha)	4	8.3	2	8.3	2	16.7	---	---	11	41.7	3	25.0
Satanoperca pappaterra (cará)	15	41.7	17	16.7	56	91.7	17	33.3	13	41.7	---	---
Laetacara sp (cará)	18	33.3	4	16.7	28	50.0	9	41.7	1	8.3	8	25.0
Catathyridium jenynsii (lingüado)	---	---	6	25.0	---	---	---	---	1	8.3	---	---
Synbranchus marmoratus (muçum)	1	8.3	2	16.7	---	---	1	8.3	---	---	---	---
Potamotrygon motoro (raia)	---	---	---	---	---	---	---	---	1	8.3	---	---
Total	2081		2254		3315		1922		3303		4371	

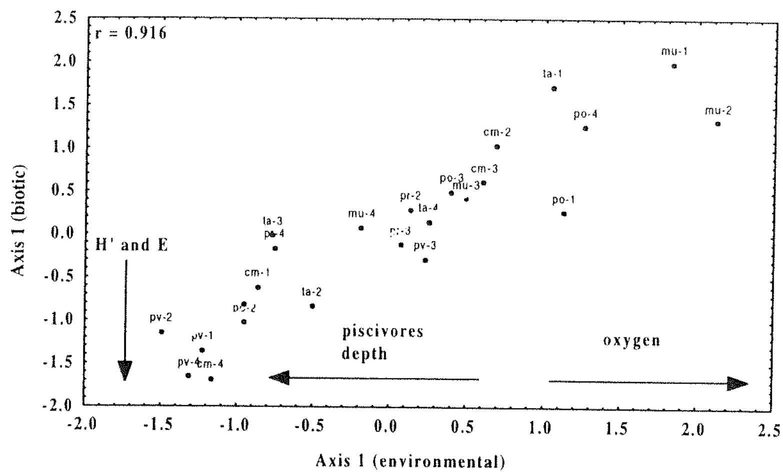


Fig. 4. Plot between the first canonical axis from biotic and first canonical axis from environmental variable. The arrows indicate the direction of the correlation of the most important component variables of each axis. Lagoons: pv = Pau Veio, ta = Tres Amigos, pr = Porto Rico, po = Pontal, cm = Canal do Meio, mu = Mutum. Numbers = phases of hydrological cycles

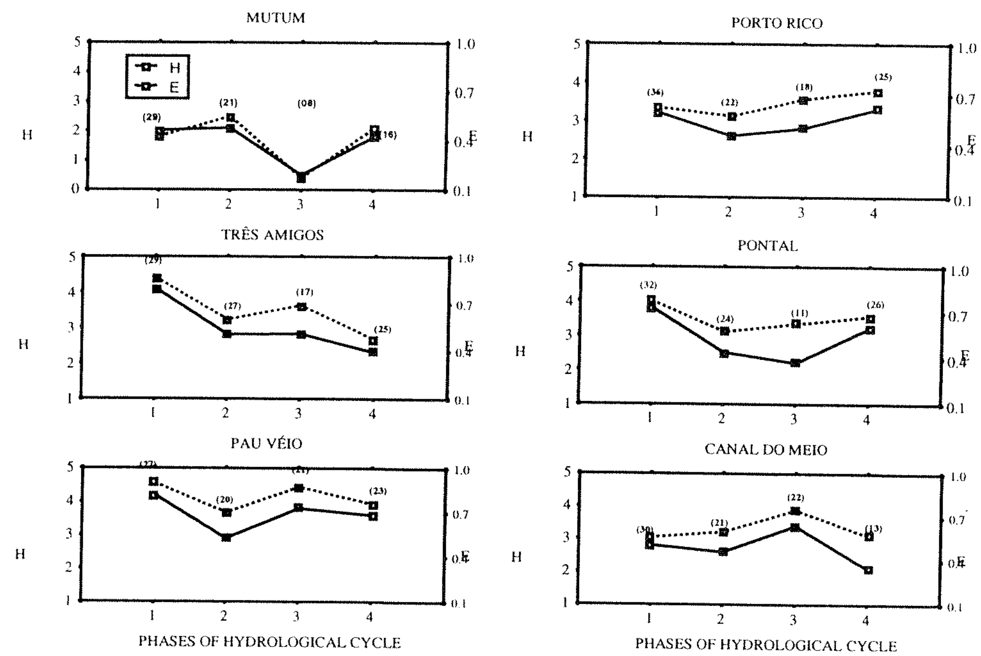


Fig. 5. Specific diversity for each hydrological phase and lagoon (continuous line = diversity; dashed line = equitability; see text for hydrological phase).

Table II. Canonical factors related to abundance, diversity and abiotic variables of the lagoons. Bold indicates (P<0.05)

SET I (ASSEMBLAGE OF FISH)		SET II (ENVIRONMENT)	
Variable	**Canonic Factor**	**Variable**	**Canonic Factor**
Number of species	0.0114	EC(μs.cm^{-1})	0.1251
Number of indiv.	0.4835	O_2(mg dm^{-3})	**0.5567**
Diversity index H'	**-0.7606**	pH	0.3604
Equitability	**-0.9159**	Depth(m)	**-0.5892**
		TRANSP(m)	-0.1826
		T(^{o}C)	-0.1126
		MACR(%)	-0.4759
		PISC	**-0.7460**
Redundance	62.19%		36.46%

Table III. Proportional Similarity matrix between the fish fauna from pools just before the desiccation and the original lagoon during the final period of isolation (phase 3)
*fragmented pond; [1] and [2] different time of fragmentation).

	CM	CM*	PT	PT*	TA	TA*[1]
Canal do Meio **CM***	35.6					
Pontal **PT**	28.3	4.5				
Pontal **PT***	50.4	50.8	40.5			
Três Amigos **TA**	59.4	9.4	35.4	31.2		
Três Amigos **TA***[1]	57.6	28.3	31.8	56.4	55.4	
Três Amigos **TA***[2]	22.4	7.8	10.3	15.3	31.8	27.4

Table IV. Environmental and biotic variables just before the pools desiccation.
*fragmented pond; [1] and [2] different time of fragmentation).

		Canal do Meio **CM***	Pontal **PT***	Três Amigos **TA***[1]	Três Amigos **TA***[2]
Area (m^2)		3.7	2.0	3.5	2.0
Depth (m)		0.10	0.10	0.13	0.20
Macrophytes cover (%)		100.0	2.0	0.0	20.0
Dissolved Oxygen	8:00 hs	1.76	6.18	6.46	6.84
($mg\ dm^{-3}$)	14:00 hs	2.34	8.25	11.33	18.21
	20:00 hs	1.58	6.32	6.37	8.31
pH	8:00 hs	5.62	6.98	6.08	6.34
	14:00 hs	5.66	6.74	6.55	8.38
	20:00 hs	5.54	6.46	5.82	6.37
Electric Conductivity	8:00 hs	32	67	60	96
($\mu S.cm^{-1}$)	14:00 hs	35	70	50	80
	20:00 hs	27	72	53	86
Proportion of Piscivores		0.013	0.055	0.15	0.808
Number of species		19	18	14	10
Density (ind. m^{-2})		298	100	99	36.5
H'		2.46	2.78	2.72	1.29
E		0.58	0.67	0.72	0.39
Dominant species	1	*A.bimaculatus*	*A.bimaculatus*	*S.insculpta*	*H.malabaricus*
	2	*C.notomelas*	*R.paranensis*	*A.bimaculatus*	*S.insculpta*
	3	*H.callistus*	*S.insculpta*	*R.paranensis*	*C.paranaense*
	4	*C.paranaense*	*C.paranaense*	*H.malabaricus*	*H.littorale*

the species ranged from small to medium size Characiformes, totalling 59% of the species and 88% of the individuals.

Inspection of the scatter plots in Fig. 6, between the environmental variables and the parameters of the fish assemblages, indicates that the proportion of piscivores is inversely related to diversity, species richness, number of individuals and evenness. Inverse relationships were also observed between fish density and minimum dissolved oxygen. Evenness is correlated with the proportion of piscivores, but not with any environmental variables.

4. Discussion

Tropical floodplain lagoons are submitted to seasonal floodings, which connect them with the main river at least once a year. The connecting period with the river, the sluggishness of receding waters and late floodings may re-establish the communication and determine the profile of the fish assemblages in these confined biotopes. According to Bonetto *et al.* (1965), such lagoons do not have a peculiar and stable fish community, and one whose connection with the main channel is ephemerous has a different assemblage when

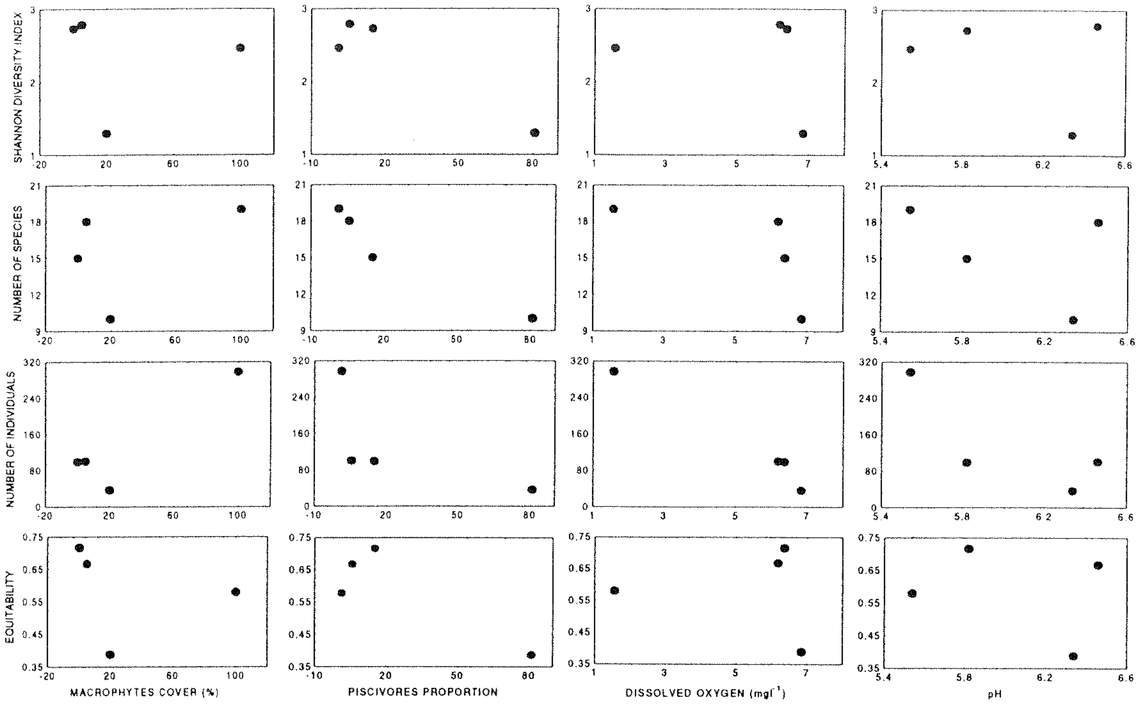


Fig. 6. Scatterplot matrix for the four pools before desiccation, based on the biotic and environmental variables

compared with those more isolated. Water level and local topographic conditions regulate the exchanges between these two biotopes and after the isolation, predation, competition and other biotic factors will play a major role in assemblage organisation.

Lowe-McConnell (1987) suggests that stochastic processes must be involved in the composition of fish assemblages in floodplains of Rupununi and Paraná. Which events therefore play a major role in the drying ponds? In them the assemblages were primarily deterministic, in which case resources are partitioned through competition (and predation which somewhat lessens competition between prey species), which is the driving force affecting coexistence in the community. These assemblages are also stochastic (without equilibrium) and species abundance is determined mainly through unpredictable environmental changes, instead of biological interactions. These random changes might reduce populations to levels at which competitive exclusion does not occur, or they may make a limited resource randomly available again.

Walter and Reartes (1975), who studied lagoons in Los Sapos Island in the Middle Paraná, reported that the habitat presented a great influence upon the biotic structure, the most important aspect being the gradual reduction in area during desiccation. Biotic interactions may become critical due to territory reduction and vanishing refuges.

Junk *et al.* (1989) concluded that stochastic flood pulses control population size. Consequently, under these conditions biotic interactions would be less determinant in structuring fish communities.

Chapman and Chapman (1993) report that despite the extreme annual alterations in the landscape of the Sokoto River (Nigeria), species composition in the seasonal ponds is similar in the dry season of different years. Lowe-McConnell (1964) found that different kinds of ponds tended to have the same species composition in different years, perhaps being a result of habitat selection by the species or due to their sedentary behaviour.

The canonical correlation analysis between the environmental variables and the parameters of fish assemblages suggests that diversity and equitability have a strong association with the proportion of piscivores. In lagoons with higher diversity, equitability and richness formed a cluster with increased similarity in relation to the environmental factors. In Mutum lagoon, extreme variations in dissolved oxygen, pH and conductivity and scarcity of piscivores decreased species richness and allowed resistant prey fish to dominate (*Astyanax bimaculatus* - 45%), even with low macrophyte density, although Cordiviola de Yuan (1980) detected a negative correlation between macrophyte cover and species richness in the Middle Paraná.

Species richness in the lagoons was somewhat reduced after they became detached from the main river, as many species left them before the separation (*Brycon orbignyanus, Leporinus friderici, L. elongatus, Salminus maxillosus,* and *Pimelodus maculatus*). These are migratory species and their adults prefer lotic habitats, colonising the lagoons only in their early life cycles (Veríssimo 1994). Other migratory species, such as *Prochilodus lineatus* and *Leporinus obtusidens*, remain in these lagoons till maturity and/or when water allows them to swim back to the main river. For *Prochilodus lineatus* Agostinho *et al.* (1993) reported a relationship between body length and its movements between different biotopes.

Decreases in species diversity during the dry season were registered only in Mutum and Pontal lagoons where water surface retraction exceeded 90% (when compared to the maximum area in the rainy season) and with minimum macrophyte cover. These decreases, which occurred despite the low incidence of piscivores, may be explained by limiting environmental conditions (Mutum), and by the predominance in the other seasons, of a small piscivore *Acestrorhynchus lacustris* which was particularly sensitive to low dissolved oxygen concentrations (Pontal). Augmented natural mortality and scarcity of food could explain the decrease in species richness in the dry season in these lagoons, except to the piscivores. Shallowness would also enhance predation by birds.

Reduction of dominance was observed in five lagoons. This fact may be ascribed to the piscivores, which are generally not selective, preying upon those items which are more abundant (Hahn 1991; Almeida *et al.* 1997).

Although the fish assemblage at the time of isolation was derived from the composition of species present, its similarity with the original fauna was low. The similarity between the assemblages retained in different drying ponds was also low. Different environmental conditions in these ponds may explain this.

Among the dominant species two were iliophagous (*Steindachnerina insculpta* and *Prochilodus lineatus*), one piscivorous (*Hoplias malabaricus*) and two omnivorous (*Cichlasoma paranaense, Astyanax bimaculatus*); of these species, only *S. insculpta* has not been mentioned as dominant in previous studies, although the dominance of these three trophic categories occurred in other places. For example, Veríssimo (1994) in a survey of some drying ponds in one of our areas recorded *A. bimaculatus, H. Malabaricus, P. lineatus, Cheirodon notomelas, Characidium fasciatus, Hyphessobrycon callistus, Crenicichla britskii, Satanoperca papaterra* and *Cichlasoma paranaense.* Kullander (1983), analysing the retained assemblage in the drying ponds of the Tietę River, a major affluent of Paraná, reported the occurrence of *Cichlasoma paranaense, Hoplias malabaricus, Cheirodon notomelas, Pyrhulina australis, Astyanax* spp. and *Characidium fasciatus.* Pinto (1994), who studied artificial ponds along roads in the Pantanal, registered three species, *Hoplias malabaricus, Astyanax bimaculatus* and *Synbranchus marmoratus* and representatives of three genera (*Cichlasoma dimerus, Laetacara dorsigera* and *Hoplosternum* sp), in common with our work. Winemiller (1989) found similar results in the Venezuelan llanos. The fauna composition reported by these authors is similar to that of Canal do Meio, which also has extensive macrophyte cover, low incidence of predators, low dissolved oxygen and pH. Under these conditions, species such as *Cheirodon notomelas, Hyphessobrycon callistus*, sporadic or absent in the other ponds, were dominant.

The inverse relationship between the proportion of piscivores and fish diversity, species richness, number of individuals and equitability in desiccating ponds, suggesting that this proportion plays a decisive role in assemblage structuring.

In the present study piscivores reached 81% of the total number of species present in the pond (TA*2), corresponding to 30 individuals m^{-2}. This phenomenon has also been observed in the Orinoco (Mago-Leccia 1970) and in the Paraná (Bonetto *et al.* 1969b).

Hoplias malabaricus, a stalker piscivore, was the dominant piscivore in all drying ponds, and the only piscivore in two. This species has special morphological adaptations to hypoxia such as large size, wide mouth, elastic stomach, concealing coloration pattern (Loureiro 1994). It also has physiological adaptations to endure hypoxia (Rantin, Johansen 1984; Dickson, Graham 1986) as well as parental care (Suzuki 1992; Almeida *et al.* 1997). In this case, there is evidence that the abundance of *Hoplias malabaricus* in the four ponds tends to be negatively correlated with depth, which is corroborated by observation. Its low abundance in drying pond CM* was probably a consequence of high macrophyte cover (100%), low dissolved oxygen (1.58 mg dm^{-3}) and low pH (5.5).

Veríssimo (1994) suggested that in the small-sized prey species, *Astyanax bimaculatus, A. Bimaculatus, Cheirodon notomelas, Cheirodon* sp., the presence of spots and the general coloration pattern helps them to elude predators, thereby enhancing their survival in desiccating ponds. This was also observed in this work, but only in isolated ponds with high macrophyte abundance.

During the dry season, low depth, absence of shelter, and the behaviour of seeking more oxygen at the surface make fish more susceptible to bird predation (Lowe-McConnell 1964; Bonetto *et al.* 1969a; Veríssimo 1994) and we observed numerous *Egretta* sp., *Ceryle torquata, Chloroceryle* sp., *Phalacrocorax olivaceous* and *Pitangus sulphuratus* in the study area.

Scatterplots showed inverse relationship between dissolved oxygen and fish density. The small Characiformes, responsible for a high abundance in three out of the four drying ponds, seem not to be affected by low dissolved oxygen, as they colonise the upper layers, like those recorded by Winemiller (1996) in the Cano Maraca (Venezuela). The majority of piscivores are highly affected by oxygen concentration (Bonetto *et al.* 1967; Welcomme 1979), so this lessens natural mortality. The higher susceptibility of the prey to avian predators when they are at the surface, is compensated for the protection of macrophytes which tend to be negatively correlated with dissolved oxygen.

Diversity and evenness were lower under extreme conditions (% of piscivores, pH, dissolved oxygen and electrical conductivity). Intermediate proportions of piscivores exerted an efficient control upon the dominant species. Area reduction maximises density dependent effects, so it is to be expected that besides predation, competition and probably parasitism play major roles, due to territory reduction, fish concentration and vanishing refuges. Under such adverse conditions abiotic factors only become relevant when critical tolerance limits are exceeded.

Terminal dried-outponds exhibit an even more diverse fauna. In the largest pond (minimum depth of 10 cm and area of 3.7 m^2) 30 of the 63 fish species were recorded for the whole period, and reached a density of about 300 individuals/m^2. These kinds of biotope are scattered throughout the floodplain in the dry period (May to September), resulting in massive fish mortalities. Delays in the natural flooding period, or short-term pulses in the drainage of the main river imposed by turbine operation, enhance fish mortality.

Despite the adverse conditions in the isolated ponds and lagoons, global fish diversity is very high, due to heterogeneous environment conditions and varying biotic and abiotic factors. The proportion of piscivores and oxygen conditions were the most relevant traits structuring the fish assemblage in isolated waterbodies at different phases of desiccation. Nevertheless, predation showed contrary effects when considering total habitats in lagoons and isolated ponds in the terminal phase of desiccation. In the former it had a positive effect upon diversity, due to the reduction of dominant species, and in the latter it was negative due to reduction in diversity.

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5. References

Agostinho, A.A., Zalewski, M. 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Paraná River, Brazil. *Hydrobiologia* **303**, 141-148.

Agostinho, A.A., Júlio. H.F., Jr Borghetti J.R. 1992. Considerações sobre os impactos dos represamentos na ictiofauna e medidas para sua atenuação. Um estudo de caso: reservatório de Itaipu. [Considerations about the impacts of the impoudment on the fish fauna and its mitigation. A case history: Itaipu Reservoir.] *Revista Unimar*, Maringá **14,14,** 89-107 [Engl. summ.].

Agostinho, A.A., Vazzoler, A.E.A., de M, Gomes, L.C., Okada, E.K. 1993. Estratificacion espacial y comportamiento de *Prochilodus scrofa* en distintas fases del ciclo de vida, en la planicie de inundación del alto rio Paraná y embalse de Itaipu, Paraná, Brasil. [Spatial distribution and behaviour of *Prochilodus scrofa* during its life cycle, in the High Paraná river floodplain and Itaipu Reservoir, Paraná, Brazil] *Rev. Hydrobiol. Trop.* **26,** 79-90 [Engl. summ.].

Agostinho, A.A.; Gomes, L.C.; Suzuki, H.I.; Júlio Jr., H.F. (*in press*) Migratory fish from the upper Parana river basin, Brazil. In: J. Carolsfeld; B. Harvey; A. Baer; C. Ross [Eds] Migratory Fishes of South America: Biology, social Importance and Conservation Status. UNEP-*World Fisheries Trust.*

Almeida,V.L.L., Hahn, N.S., Vazzoler, A.E.A. de M 1997. Feeding patterns in five predatory fishes of the high Paraná River floodplain (PR, Brazil). *Ecol. Fresh. Fish.* **6**, 123-133.

Barco, M.B.V., Petrere. M. Jr, Villareal, M.Z., Vera, G. 1993. Parámetros poblacionales (mortalidad, rendimento máximo sostenible) y estado de explotación del bocachico (*Prochilodus magdalenae* Steindachner, 1878; Prochilodontidae) del Bajo Rio Magdalena (Colombia). [Population parameters (mortality, maximum sustainable yield) and exploitation status of the bocachico (*Prochilodus magdalenae* Steindachner, 1878; Prochilodontidae) from lower Magdalena river (Colombia)] *Bol. Cientifico INPA* **1**, 43-60 [Engl. summ.].

Bayley, P.B. 1981. Fish yield from the Amazon in Brazil: comparisons with African river yields and management possibilities. *Trans. Am. Fish. Soc.* **110**, 351-359.

Bonetto, A.A., Pignalberi, C., Cordiviola de Yuan, E. 1967. Las palometas o pirañas de las aguas del Paraná medio. [The palometas or pirañas from the middle Paraná]. *Acta. Zool. Lilloana* **23**, 45-65 [Engl. summ.].

Bonetto, A.A., Cordiviola de Yuan, E., Pignalberi, C., Oliveros, O. 1969a. Ciclos hidrologicos del rio Parana y las poblaciones de peces contenidas en las cuencas temporarias de su valle de inundacion. [Hydrological cycles of middle Paraná River and the fish populations contained in temporary basins of its flood valley]. *Physis* (Buenos Aires) **29**, 213-223 [Engl. summ.].

Bonetto, A.A., Dioni, W., Pignalberi, C. 1969b. Limnological investigations on biotic communities in the Middle Paraná River valley. *Verh. Internat. Verein. Limnol.* **Stuttgart 17**, 1035-1050.

Bonetto, A.A., Cordiviola de Yuan. E., Pignalberi, C. 1970. Nuevos datos sobre poblaciones de peces en ambientes leniticos permanentes del Paraná Medio. [Further information about fish populations inhabiting permanet lenitic water bodies in the middle Paraná river]. *Physis* (Buenos Aires) **30**, 141-154 [Engl. summ.].

Brower, J.E., Zar, J.H. 1984. *Field and laboratory methods for general ecology*. 2nd ed. Wm. C. Brown Publisher, Dubuque, Iowa, USA.

Chapman, L.J., Chapman, C.A. 1993. Fish population in tropical floodplain pools: a re-evaluation of Holden's data on the River Sokoto. *Ecol Fresh Fish* **2**, 23-30.

Copp. G.H., Penáz, M. 1988. Ecology of fish spawning and nursery zones in the flood plain, using a new sampling approach. *Hydrobiologia* **169,** 209-224.

Cordiviola de Yuan, E. 1980. Campaña limnológica "Keratella I" en el rio Paraná Medio: Taxocenos de peces de ambientes leníticos. [Keratella I limnological cruise along the middle Paraná river: Fish taxocenosis from lenitic environments.] *Ecologia (Buenos Aires)* **4**, 103-113 [Engl. summ.].

Cordiviola de Yuan, E., Pignalberi, C. 1981. Fish populations of the Paraná River. II. Santa Fé and Corrientes areas. *Hydrobiologia* **77**, 261-272.

Cordiviola de Yuan, E., Pignalberi, de Hassan C. 1985. Fish population in the Middle Paraná River: Lentic environment of Diamante and San Pedro Areas (Argentine Republic). *Hydrobiologia* **127,** 213-218.

Dickson, K.A., Graham, J.B. 1986. Adaptations to hypoxic environments in the erythrinid fish *Hoplias microlepis*. *Environ. Biol. Fishes* **15,** 301-308.

Goulding, M. 1979. *Ecologia da pesca do Rio Madeira. [Fishery ecology of Madeira River]* Trad. de Naércio Menezes. INPA, Manaus, AM, Brasil.

Hahn, N.S., Agostinho, A.A., Gomes, L.C., Bini, L.M. 1998. Estrutura trófica da ictiofauna do reservatório de Itaipu (Paraná-Brasil) nos primeiros anos de sua formação. [Throphic ecology of fishes from the Itaipu reservoir (Paraná-Brazil) in the first years after impoundment.] *Interciçncia, Venezuela*, **23** (5), 299-305 [Engl. summ.].

Junk, W.J., Bayley, P.B., Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems. In: Dodge, D.P. [Ed.] Proceedings of the International Large River Symposium. *Can. Spec. Publ. Fish. Aquat. Sci.* **106**, 110-127.

Krebs, C.J. 1989. *Ecological Methodology*. Harper & Row, N.Y., USA.

Kullander, S.O. 1983. *A revision of the South American cichlid genus Cichlasoma*. The Swedish Museu of Natural History, Stockholm, Sweden.

Loureiro, V.E., Hahn, N.S. 1996. Dieta e atividade alimentar da traíra *Hoplias malabaricus* (Bloch 1794) (Osteichthys – Erythrinidae) nos primeiros anos de formação do reservatório de Segredo – PR. [Diet and feeding activity of "traíra", *Hoplias malabaricus* (Bloch, 1794) (Osteichthyes, Erythrinidae), in the following years after the construction of Segredo reservoir (PR)]. *Acta Liminologica Brasiliencia*. **8**, 195-205 [Engl. summ.].

Lowe-McConnell, R.H. 1964. The fishes of the Rupununi savana district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. *J. Linn. Soc. Lond. Zool.* **45** (304), 103-143.

Lowe-McConnell, R.H. 1975. *Fish Communities in Tropical Freshwaters. Their Distribution, Ecology, and Evolution.* Longman, London.

Lowe-McConnell, R.H. 1987. *Ecological Studies in Tropical Fish Communities*. Cambridge University Press, Cambridge.

Ludwig, J.A., Reynolds, J.F. 1988. Statistical *Ecology. A Primer on Methods and Computing.* Wiley, New York.

Mago-Leccia, F. 1970. Estudios preliminares sobre la ecologia de los peces de los llanos de Venezuela. [Preliminary studies on ecology of fishes from the llanos of Venezuela]. *Acta Biol Venez* **7**, 71-102 [Engl. summ.].

Manly, B.F.J. 1995. *Multivariate Statistical Methods*. Chapman & Hall, New York.

Okada, E.K., Agostinho, A.A., Petrere, M. 1996. Catch and effort data and the management of he commercial fisheries of Itaipu reservoir in the upper Paraná river, Brazil. In: Cowx, I.G. [Ed.] *Stock Assessment in Inland Fisheries*. Fishing News Books, Bodman, UK, pp. 155-161.

Oldani, N.O., Oliveros, O.B. 1984. Estudos limnologicos en una seccion transversal del tramo medio del rio Parana. XII: Dinâmica temporal de peces de importância econômica. [Limnological studies in a cross-section of the middle reach of Paraná river, XII: Temporal dynamic of commercial fish.] *Rev. Asoc. de Cienc. Nat.* **15,** 175-183 [Engl. summ.].

Paiva, M.P. 1982. *Grandes represas do Brasil [Brazilian Large reservoirs]*. Editerra, Brasilia, DF, Brasil.

Paiva, M.P. 1983. *Peixes e pesca de águas interiores do Brasil [Fishes and inland fisheries in Brazil.]*. Editerra, DF, Brasil.

Petrere Jr., M., Agostinho, A.A., Okada, E.K., Julio Jr., H.F. 2002. Review of the Fisheries in the Brazilian Portion of the Paraná/Pantanal basin. In: Cowx, I. [Ed.] *Management and Ecology of Lake and Reservoir Fisheries*. Fishing News Books, London. pp.123-143

Pignalberi de Hassan, C., Cordiviola de Yuan, E. 1970. Fish population in the Paraná River. I. Temporary water bodies of Santa Fé and Corriente areas. (Argentine Republic). *Stud. Neotrop. Fauna Environ.* **20**, 15-26.

Rantin, T.F., Johansen, K. 1984. Responses of the teleost *Hoplias malabaricus* to hypoxia. *Environ. Biol. Fishes* **11**, 221-228.

Sparks, R.E., Bayley, P.B., Kohler, S.L., Osborne, L.L. 1990. Disturbance and recovery of large floodplain rivers. *Environ. Manage.* **14**, 699-709.

Suguio, K. 1973. *Introdução ŕ Sedimentologia. [Introduction to Sedimentology].* Edgard Blüscher/Universidade de São Paulo, São Paulo, Brasil.

Thomaz, S.M. 1992. Seasonal variation of some limnological factors of lagoa do Guaraná, a varzea lake of the High Rio Paraná, State of Mato Grosso do Sul, Brazil. *Rev. Hydrobiol. Trop.* **25**, 269-276.

Walter, D., Reartes, J.L. 1975. Susceptibilidad de algunos peces del Parana medio expuestos a temperaturas extremas en condiciones de campo y laboratorio. [Susceptibility of some fishes of the Middle Parana River exposed to extreme temperatures in field and laboratory conditions.] *Physis (Buenos Aires)* **34**, 129-137 [Engl. summ.].

Welcomme, R.L. 1979. *Fisheries ecology of floodplain rivers.* Logman, London, England.

Winemiller, K.O. 1989. Development of dermal lip protuberances for aquatic surface respiration in South American Characid fishes. *Copeia* **2**, 382-90.

Winemiller, K.O. 1996. Dynamic diversity in fish assemblages of tropical rivers. In: Cody, M.L., Smallwood, J.A. [Eds] *Long-Term studies of vertebrate communities.* Academic Press, San Diego. U.S.A, pp. 99-132.