

DETERMINATION OF PATTERNS OF ICHTHYOFAUNA CO-OCCURRENCE IN THE PARANÁ RIVER BASIN, AREA OF INFLUENCE OF THE ITAIPU RESERVOIR

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In ecology it is of prime importance to know the factors responsible for co-occurrence of species that share the available environmental resources. Associations of species reveal the relationships between the preference of a population for a certain zone and its biological efficiency. According to Fager and McGowan (1963) certain species frequently occur together. Since these groups have special habitats preference, they seem to be constituted by species that present similar reactions to the environment. However, understanding the use that each species makes of the environment's resources and understanding interspecies relationships is normally highly complex since these factors are the result of interactive processes throughout the evolutionary history of each species (Pianka, 1982).

The ability to represent quantitatively the extent in which two species occur together or not is one of the most important tools of ecologists, especially in monitoring (Hurlbert, 1969). Since biological interactions, such as competition and predation determine the success of such procedures, this type of information is also useful in studies aimed at the optimization of fishing potential (Merona, 1981; Penczak *et al*, 1991), in the evaluation of possible

changes in the habitat (Merona, *op. cit.*) and in measures of management which involve species introduction (Wilramanayake and Moyle, 1989; Bruton, 1990). The aim of this research work is to investigate the existence of groups of co-occurring fish species in the basin of the Paraná River, zone of influence of the Itaipu reservoir, and to evaluate the interspecies relationships determining such associations.

Materials and Methods

Eleven sampling stations were established: three stations in the principal body of water of the Itaipu reservoir (Guaíra - GUAI, Santa Helena - SHEL and Foz do Iguaçu - FOZ), four stations in tributaries on the left margin (rivers Ocoí - OCOI, São Francisco Falso - SFFA, São Francisco Verdadeiro - SFVE and Arroio Guaçu - GUAC), two stations on the Paraná river (upstream - MONT and downstream - JUSA of the Itaipu reservoir) and 2 stations in tributaries of the Paraná river (Iguatemi - IGUA and Piquiri - PIQU rivers). The Itaipu reservoir (24°00' to 25°21'S and 54°19' to 54°31'W), was formed along the Brazilian and Paraguayan border in 1982. It comprises an area of 1,460 km² at its maximum level and an extension of

151 km. Volume of the reservoir reaches 29 billion m³. Average depth is 21.5 m with a maximum of 170 m. Residence time of water is 40 days with an average surface velocity of 0.6 m/s in the main current.

A total of 15,656 specimens were caught in monthly samples between September 1987 and July 1988. Gill nets (mesh from 3 to 16 cm), trammel net (6 to 10 cm between opposite knots) were exposed for 24 hours. After the identification of the species, data on standard length (SL), in millimeters, were taken with regard to site. The abundance of each species was expressed by capture per unit effort (CPUE = C * 1000/E). As a capture (C) the number of individuals was taken into consideration; the unit effort (E) being considered 1000 square meters of net in a 24-hour exposure.

Twenty species that occurred in abundance higher than 1% of total capture in all the sampling stations were analyzed to form groups of co-occurring species. The presence and absence of each pair of species, A and B, are listed in 2 x 2 contingency tables. To test the hypotheses that the two species are distributed independently, the χ^2 distribution was applied with the Yates correction for small samples (Legendre and Legendre, 1984). Two types of associa-

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tions were investigated for pairs that rejected the H_0 hypothesis:

Positive, when $a > (a+b)$
 $(a+c) / N$ and negative, when $a \leq (a+b)$
 $(a+c) / N$, where a = the number of combined occurrences of A and B; b = the number of samples in which B occurs and A does not; c = the number of samples in which A occurs and B does not; and d = the number of samples in which both A and B are absent;

Research on groups of relative species followed by giving 0 similarity to negative interactions, as suggested by Krylov (1968), and concluding that the two species are associated if the probability of their χ^2 is smaller than 5%. The similarity measure between species was obtained of the complement of this probability:

$$S_{(A,B)} = 0, \text{ when } (a+b) / N \geq a \text{ and } S_{(A,B)} = 1 - p, \text{ when } (a+b)(a+c) / N < a$$

Groups of species were distinguished by non-hierarchical groupings of complete linkage clustering (Fager, 1957), modified by Krylov (1968). In the analysis of resulting co-occurring groups the abundances of component species grouped by site and season of the year were investigated according to the following relationships (Fager, 1957):

a) **dominance among the species** - were evaluated by Kendall's Coefficient of Concordance (W) which varies from 0 (no concordance) to 1 (perfect concordance) (Siegel, 1975). Value of significance observed in W was obtained by test "F" at a 5% level (Fager, 1957).

b) **relative abundance** - differences among relative abundances were tested according to the null hypothesis in which two species (A and B) would have the same spatial distribution. Mann-Whitney test was applied; to determine the value of significance observed in U_1 value z was used (Siegel, 1975).

c) **concordance of species with regard to preferential habitat** - relationship among species of the same group and the capture sites was investigated by the use of Kendall's Coefficient of Concordance (W), described in dominance relationships. However, the difference lies in the structure of the analysis table which is now placed in an inverted position (Fager, 1957).

Results

Pairs of species associated positively and negatively were identified

by significant values of χ^2 . From positive associations three groups of co-occurring species were established (Figure 1, Table I). Satellite species, or rather, species in association with only some members of the specific groups, were also determined.

Group I is made up of 10 species associated to similarity levels higher than 0.95 and representing various trophic levels. In general, they are characterized by constancy of sampling in the reservoir and in its left margin tributaries, with low to moderate water velocity, where the development of juveniles predominantly occurs. They are also recorded in JUSA, MONT and IGUA, but never in PIQU. *Loricariichthys* sp and *Schizodon borelli* are associated with this group: the former showed affinities to seven species and the latter to only one of the ten components of this group. Groups II and III are made up of 3 species each and their similarities are higher than 0.95 and 0.99, respectively. Species of Group II were constant in RES, TRIB, MONT and PIQU, with juveniles recorded in all environments. Species of Group III were constant in RES and PIQU, with juveniles recorded exclusively in big lotic areas (PIQU and MONT).

Steindachnerina insculpta associates itself only to one species of each of Groups II and III. *Acestrorhynchus lacustris* is related only to the above satellite species. Including from their most juvenile phases, both species are constant in samplings made in lotic environments.

Analysis of interspecies relationship in each group showed that in Group I significant values for W were obtained for species of the same feeding habit (insectivorous and piscivorous) at a 5% probability level. This means that the species have essentially the same patterns of abundance (high or low density) in relation to the other species of the same trophic category in most seasons of the year and in collecting sites (Table II). Within the insectivorous species, *A. nuchalis* is constantly dominant with regard to *Parauchenipterus galeatus* and *Ageneiosus ucayalensis*, while *P. galeatus* is dominant with regard to *A. ucayalensis*. Among the piscivorous species, *Plagioscion squamosissimus* is predominant with regard to other species of the same feeding habit, while *Serrasalmus marginatus* predominates also over *Rhaphiodon vulpinus*.

The same analysis concerning position of species in the water column for Groups II and III reveals a relationship of constant dominance only among those of Group III. In this case, *Astyanax bimaculatus* presented the smallest total sum of ranks, which indi-

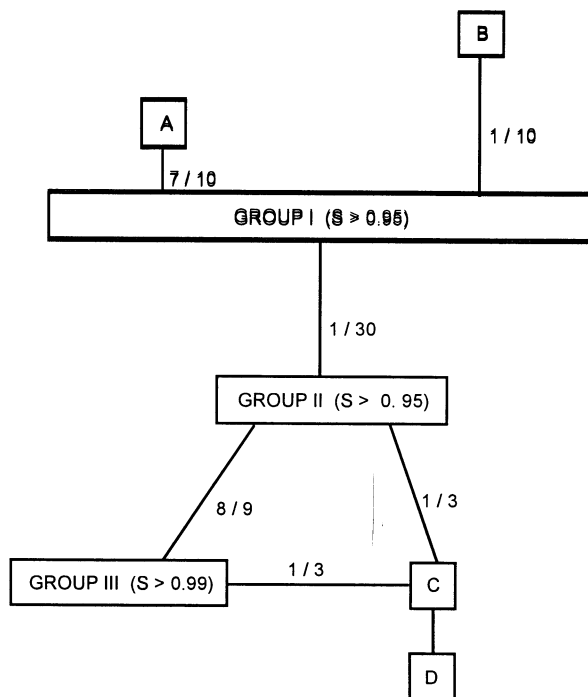


Figure 1. Relationship between co-occurring groups (S = similarity level of group; fractions show the number of affinities observed in relation to maximum number of pairs of possible species; A = *Loricariichthys* sp; B = *S. borelli*; C = *S. insculpta*; D = *A. lacustris*).

TABLE I
Biological characteristics of group members of co-occurring species and of associated satellite species
(SL max = maximum standard length in millimeters; RES = stations of the principal body of the Itaipu reservoir;
TRIB = tributaries of the left margin of the Itaipu reservoir).

Groups	Species	SLmax	habitat of adults ¹	feeding habitat	habitat of juveniles ¹
I	<i>H. edentatus</i>	446	RES	planktophagous ²	RES
	<i>Loricaria sp</i>	374	RES-TRIB	ileophagous ²	RES-TRIB
	<i>A. ucayalensis</i>	324	RES-TRIB-IGUA	insectivorous ²	RES
	<i>T. paraguayensis</i>	120	RES-TRIB-IGUA	benthophagous ²	RES
	<i>P. galeatus</i>	220	RES-TRIB-JUSA-IGUA	omnivorous ⁵	RES
	<i>P. granulosus</i>	532	RES-TRIB-JUSA-IGUA	omnivorous ²	TRIB
	<i>A. nuchalis</i>	270	RES-TRIB-JUSA-IGUA	insectivorous ²	RES-TRIB
	<i>P. squamosissimus</i>	479	RES-TRIB-JUSA-MONT-IGUA	piscivorous ²	RES-TRIB
	<i>R. vulpinus</i>	640	RES-TRIB-JUSA-MONT-IGUA	piscivorous ²	RES-TRIB-JUSA
	<i>S. marginatus</i>	219	RES-TRIB-JUSA-MONT-IGUA	piscivorous ²	RES-TRIB-MONT
II	<i>I. labrosus</i>	262	RES-TRIB-MONT-PIQU	benthophagous ²	JUSA-MONT-PIQU
	<i>Hypostomus sp</i>	436	RES-TRIB-MONT-PIQU-IGUA	detritivorous ³	TRIB-JUSA-PIQU
	<i>P. maculatus</i>	360	RES-TRIB-JUSA-MONT-PIQU-IGUA	omnivorous ²	RES-TRIB-MONT
III	<i>G. knerii</i>	240	RES-PIQU	piscivorous ⁴	PIQU
	<i>A. bimaculatus</i>	136	RES-TRIB-MONT-PIQU-IGUA	omnivorous ²	PIQU-MONT
	<i>P. lineatus</i>	487	RES-JUSA-MONT-PIQU-IGUA	ileophagous ²	MONT
S A T E L L I T E S	<i>A. lacustris</i>	264	RES-TRIB-PIQU-IGUA	piscivorous ²	PIQU
	<i>S. insculpta</i>	198	TRIB-MONT-PIQU-IGUA	ileophagous ²	TRIB-PIQU
	<i>Loricariichthys sp</i>	330	TRIB	detritivorous ²	TRIB
	<i>S. borelli</i>	240	RES-TRIB-MONT-IGUA	herbivorous ²	IGUA

¹ Benedito-Cecilio (1994); ²Agostinho and Julio Jr. (1993); ³FUEM/PADCT-CIAMB (1993); ⁴Hahn (1991); ⁵Andrian (1991)

TABLE II
Results in terms of Kendall's Coefficient of Concordance (W) and of Test F for species of the same feeding habit (Group I) and behaviour (Groups II and III)
(R_j = sum of ranks given to each species; n₁ and n₂ = degree of freedom; * significance at 5%).

Groups	Species	R _j	W	F	n ₁	n ₂
I	<i>A. nuchalis</i>	80.5				
	<i>P. galeatus</i>	94	0.180	10.32*	2	92
	<i>A. ucayalensis</i>	113.5				
	<i>P. squamosissimus</i>	83.5				
	<i>S. marginatus</i>	98	0.090	4.65*	2	92
	<i>R. vulpinus</i>	106.5				
II	<i>I. labrosus</i>	90				
	<i>Hypostomus sp</i>	99	0.014	0.67	2	92
	<i>P. maculatus</i>	99				
III	<i>A. bimaculatus</i>	82.5				
	<i>P. lineatus</i>	91.5	0.150	8.29*	2	92
	<i>G. knerii</i>	114				

cates predominance over the other species of the group, with *Prochilodus lineatus* constantly dominant over *Galeocharax knerii*.

The study on spatial distributions of the two populations, independently of dominance constancy, are shown in Table III. Similar distributions were evidenced for pairs *R. vulpinus* x *S. marginatus*, *Pimelodus maculatus* x *Hypostomus sp*, *A. bimaculatus* x *G. knerii* and *G. knerii* x *P. lineatus*. On the other hand, U value significance (Mann-Whitney) at a 5% level has been observed for *Auchenipterus nuchalis* x *A. ucayalensis*, *A. nuchalis* x *P. galeatus*, *P. galeatus* x *A. ucayalensis*, *P. squamosissimus* x *R. vulpinus*, *P. squamosissimus* x *S. marginatus*, *Iheringichthys labrosus* x *Hypostomus sp*, *I. labrosus* x *P. maculatus*, *A. bimaculatus* x *P. lineatus*, with the first species of each pair more abundant than the second.

Only Group I obtained significant Kendall's Coefficient of Concordance ($p < 0.001$) (Table IV). The order of ranks shows that the most favourable habitats of this group are some tributaries of the left margin, chiefly SFVE, the Paraná River reservoir downstream, besides the dammed area. The most unfavourable stations are SFFA, GUAC, MONT and PIQU.

Discussion

Knowledge of the correlations which synthetize the characteristics of the biological cycle is useful in foreseeing the answer of populations to different anthropomorphic disturbances and also in determining the basis for a comparison between answers of different species to the same disturbance (Wine-miller and Rose, 1992).

From significant values of χ^2 the three identified groups of species are distinguished with regard to the biological characteristics of their members and to their respective environmental exigencies. Groups are specific units in which an interspecies relationship is inferred, even though components of one group may be present in other environments (Fager and McGowan, 1963).

With the exception of *P. squamosissimus* and *Loricaria* spp, all the other species of Group I occupied exclusively the lower segments of the Paraná River before damming and reached the upper stretches after the flooding of Sete Quedas. However, they did not reach the Piquiri River and this was probably due, besides unfavourable biotic and abiotic conditions, to the great velocity of water in some parts.

Species of Group II have a distribution area larger than those of Group III and occur in all the sampled environments. Another characteristic of these groups is the position of their members in the water column: species of Group II explore the bottom and those of Group III position themselves above this zone. Probably, such patterns are of fun-

TABLE III
Results of significance tests of Mann-Whitney (U) for species of the same feeding habit (Group I) and behaviour (Groups II and III) ($Z =$ standard value for $N_{0.1}$, $p =$ probability associated to Z ; * significant at 5%).

Groups	Species	U	z	p
I	<i>A. nuchalis</i> x <i>A. ucayalensis</i>	438.0	3.57	*0.0003
	<i>A. nuchalis</i> x <i>P. galeatus</i>	613.0	2.70	*0.0035
	<i>A. ucayalensis</i> x <i>P. galeatus</i>	338.5	1.70	*0.0440
	<i>P. squamosissimus</i> x <i>R. vulpinus</i>	184.0	3.67	*0.0002
	<i>P. squamosissimus</i> x <i>S. marginatus</i>	229.0	2.83	*0.0023
	<i>R. vulpinus</i> x <i>S. marginatus</i>	351.0	1.27	*0.1020
II	<i>Hypostomus</i> sp x <i>I. labrosus</i>	450.5	1.89	*0.0294
	<i>P. maculatus</i> x <i>Hypostomus</i> sp	666.0	0.58	0.2810
	<i>P. maculatus</i> x <i>I. labrosus</i>	386.5	2.91	*0.0018
III	<i>A. bimaculatus</i> x <i>G. knerii</i>	284.0	1.23	0.1093
	<i>A. bimaculatus</i> x <i>P. lineatus</i>	308.0	1.93	*0.0268
	<i>G. knerii</i> x <i>P. lineatus</i>	224.0	0.37	0.3557

damental importance in niche occupation and in the sharing of environmental resources. Luk'yanenok (1991) establishes 5 principal associations of mesopelagic fish. All these associations include species with distinct geographic distributions, differing in the vertical distribution at night. On the other hand, Wikramanayake and Moyle (1989) suggest that the microhabitat, or rather, the position in the water column, is the basis for species segregation.

The existence of satellite species which present affinity with only some members of co-occurring groups reflects the organizational complexity of biological communities (Legendre and Legendre, 1984). *Loricariichthys* sp and *Schizodon borelli*, satellite species of Group I, are very different in distribution area. While the former is constant in the tributaries of the reservoir and is related to seven out of the ten species of Group I, the latter has a much larger distribution. It is constant in samplings in the reservoir, in its tributaries, upstream of the reservoir and in the Iguatemi River. It is related to *R. vulpinus* only. Al-

though the distribution area of the latter is evidently greater, the small size of its population, besides other biotic and abiotic factors which certainly exist, obstructs a greater relationship of this species with the group.

On the other hand, *Steindachnerina insculpta* was a satellite for Group II and Group III since it occurred in all the sampled stations. *Acestrorhynchus lacustris* had relationship only with the latter species since it was not found in samplings at SFVE and JUSA, the stations recording a higher number of species of the identified groups. Both species are constant in samplings of lotic areas as from the most juvenile phases.

According to Balirwa and Bugenyi (1988) and Lake *et al.* (1988), biological communities are structured along trophic hierarchies which influence many aspects of the ecosystem's mechanism. Thus, the structure of freshwater assemblages is the result of biotic interactions such as predation and competition and the environment which functions through reciprocal feedback mecha-

TABLE IV

Values of sum of ranks given to each collecting station based on the abundance of species in each co-occurring group and results of Kendall's Coefficient of Concordance (W) and test "F" (n_1 and $n_2 =$ degrees of freedom; * significant at 5%).

group	Sampling Stations											W	F	n_1	n_2
	Sfve	jusa	guai	foz	ocoi	shel	igua	sffa	guac	mont	piqu				
I	32.0	47.5	48.0	49.0	50.0	52.0	59.0	63.5	82.0	70.5	106.5	0.31	*4.04	10	88
II	9.0	23.0	23.0	29.0	9.0	18.0	23.0	16.0	17.0	15.0	16.0	0.38	1.23	9	19
III	24.5	18.5	19.0	24.0	26.0	19.0	10.0	22.0	12.5	10.0	12.5	0.36	1.13	9	19

nisms. However, patterns of distribution and abundance of some of the species seem to reflect mechanisms based on autecological answers too (ability and preference in the use of resources) besides synecological mechanisms. According to Giller (1984) coexistence among species is kept within certain limits as a function of the number of available resources in the environment and/or maximum tolerable overlapping of niches.

The absence of a constant character in dominance among species of Group II shows that the structure of these populations is governed by abiotic forces which are changed in an unforeseeable way, impeding a certain species from being dominant over another as has been suggested for other groups. For example, the piscivorous species of Group I are constantly dominated by *P. squamosissimus*, a species introduced in the Paraná River basin in 1967 and with an extremely high participation in fish hauling in almost all the reservoirs of the basin (Torloni *et al.*, 1993). In the area of the Itaipu reservoir this species is among the ten most frequent species in the environment.

The dominance of *A. nuchalis* over *P. galeatus* and *A. ucayalensis* may be explained by the former being insectivorous while the other species including other items in their diet (Hahn, 1991), thus tends to concentrate *A. nuchalis* in all areas of greatest density of insects with great success. *A. ucayalensis* and *P. galeatus* disperse to other areas in their search for food. This condition is proved by the identification of spatial distributions in the significantly different abundance among other species.

A certain species may be constantly dominant with regard to another and yet its relative abundance may not be significantly different since they distribute themselves in a similar way (Fager, 1957). This condition is verified for the species of Group I (*S. marginatus* x *R. vulpinus*) and III (*A. bimaculatus* x *G. knerii*; *P. lineatus* x *G. knerii*). It should be emphasized that the dominance of the first species over the second one in each pair, identified by the sum of the ranks, is extremely evident. This fact is evidenced by Ribbink and Eccles (1988) when they state that in many cases species present apparently identical requirements, but distinct territorial behaviour and particular trophic specialization which allow them to use the different available resources of the environment. Sturmbauer *et al.* (1992) also concedes that sympatric species are capable of coexisting because of their slightly different feeding habits. This dif-

ference is also emphasized for coexisting species studied by Rinne (1992).

If one admits that areas with a greater abundance of a certain species comprise the most suitable habitats and that a lesser abundance means unsuitable habitats for the species, therefore the relative abundance among samples may be used to determine whether each group as a whole shows any concordance within its component species with regard to the "better" or "worse" habitat (Fager, 1957). The species of Group I showed a high coincidence in environmental exigencies and presented concordance among them in their choice of the "best" habitat and the refusal of the less suitable.

The importance due to the role of interspecies competition is found in the structure of natural communities (Hanski and Ranta, 1983; Lake *et al.*, 1988). Although Hastings (1987) questions data of co-occurrence of species in the investigation of competitive forces, among omnivorous (*Astyanax bimaculatus* x *Parauchenipterus galeatus*; *A. bimaculatus* x *Pterodoras granulosos*) and piscivorous species (*Galeocharax knerii* x *Plagioscion squamosissimus*; *G. knerii* x *Rhaphiodon vulpinus*; *G. knerii* x *Serrasalmus marginatus*) a negative significant association has been recorded. This fact suggests the existence of feeding competition and environmental preferences. In spite of the lack of knowledge on the evolutionary history of each species, there is evidence of a strong relationship of the former's absence when the latter species is present in the majority of the samples.

Begon *et al.* (1996) emphasize that pairs of species, predator-prey, co-evolve, too, in proportion to the predator's perfecting his ability in capturing its food and the prey's capacity in avoiding or resisting the predator. Negative associations of this type seem to occur between *P. squamosissimus* x *A. bimaculatus*, *R. vulpinus* x *A. bimaculatus*, *P. squamosissimus* x *S. insculpta*, since the second species of each pair corresponds to one of the feeding items explored by the first (Hahn, 1991).

Fager (1957) emphasizes the fact that the absence of any significantly negative correlations between pairs of similar species shows that the increase in the number of individuals of one species is not followed by a reduction in number of the other. This fact holds for piscivorous species of Group I where a relationship of competition would be expected. Although *Plagioscion squamosissimus* is constantly dominant over all the other species of Group I, even disclosing

a distinct distribution, it does not show any negative association with the same species, or rather, there is no significant competition among them. In certain cases competitive interactions may lead to structural forces that decrease such interaction in due time. This has been verified by Norton (1991) when competitors were introduced in the rivers of Sri Lanka.

Amensalist interactions as defined by Pianka (1982) seem to predominate between the following species, *A. bimaculatus* x *A. nuchalis*, *A. bimaculatus* x *A. ucayalensis*, *A. bimaculatus* x *H. edentatus*, *A. nuchalis* x *S. insculpta*, *A. nuchalis* x *Hypostomus* sp, *S. insculpta* x *P. galeatus*, *H. edentatus* x *Hypostomus* sp and *Loricariichthys* sp x *P. lineatus*, since one population is not frequent in the presence of the other even though they are probably not harmful to one another. However, definite conclusions with regard to such interactions need to be proved by more detailed field and experimental studies. Their relevance as an assistance in management, especially in impacted environments, would justify an additional effort.

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