The Upper Paraná River and its Floodplain

physical aspects, ecology and conservation

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CHAPTER 10

FISH ASSEMBLAGES

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Abstract

The part of the upper Paraná River basin between the mouth of the Paranapanema River and the Itaipu Reservoir includes at least 153 fish species, recorded in several surveys carried out during fifteen years (1986-1987; 1987-1988; 1992-1993; 1993-1994; 1994-1995; 2000 and 2001). Characiformes and Siluriformes dominate the fish fauna contributing 77% of the total number of species. Native species of the Upper Paraná River floodplain contribute 75.6% of the total number of species. Introduced species from other basins represent 8.4% of the total, whereas the ones dispersed into the Upper Paraná River after the formation of the Itaipu Reservoir, that removed the natural barrier of the Salto de Sete Quedas, represent 15.8 %. Several habitats were sampled and rivers differed relative to fish assemblage from streams and lagoons, which could be attributed to the higher occurrence of small sized species typical of the latter environments. River and channels generally have higher species richness than lagoons. The number of species in a particular combination of month and site (local species richness) varied from 3 to 37. Most common values for richness were 12, 18 and 22 species, indicating a high temporal and spatial species turnover. Most of the spatial variation in the Upper Paraná River floodplain was dependent on the type of environment sampled. Indicator species analysis identified 56 out of 100 species that had significant indicator values: 36 species were typical of rivers, 15 were typical of lagoons, and six were indicators of channels. A lower level of fish assemblage stability was noted in the Paraná River channel, related to the higher degree of hydrological regulation promoted by the dams located upstream.

Introduction

The Sete Quedas Falls formerly constituted a barrier separating two distinct ichthyofaunistic provinces in the Paraná River: the Upper Paraná and the Paraná-Plata (Middle and Lower Paraná) (Bonetto 1986). After the closure of the Itaipu Dam, this barrier was moved some 150 kilometers downstream. As a consequence, more than 15 fish species of the Middle and Lower Paraná invaded the upper stretch (Agostinho *et al.* 1992). Because 15 other species (and probably many more) remained restricted to the stretches downstream from the Itaipu Dam, it appears that despite the dispersions, these provinces are still valid. It should be emphasized, however, that the efficiency of the Sete Quedas as a barrier to the upstream movement of fish before the formation of the reservoir is still uncertain, and it is possible that in years of exceptional floods some species were able to overcome the barrier.

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The fish fauna of the Paraná River basin is composed of about 600 species, most of which are recorded in the Upper Paraguay River (Bonetto 1986). This estimate is preliminary because surveys are still incomplete and there is no consensus on the taxonomic status of several species. The fish fauna in this basin, like others in the neotropical region, is dominated by Othophysi (orders Characiformes, Siluriformes and Gymnotiformes), which constitute more than 90% of total number of species (Britski 1992), divided equally between the orders Siluriformes and Characiformes. Within the present boundaries of the Upper Paraná Province, including the stretches of the Iguaçu River above the Iguaçu Falls (Bonetto 1986), recent surveys have recorded more than 250 species belonging to the orders Characiformes, Siluriformes, Perciformes, Cyprinodontiformes, Myliobatiformes, Pleuronectiformes, Clupeiformes and Synbranchiformes, in addition to the introduced Atheriniformes and Cypriniformes (Agostinho *et al.* 2000). This number is almost twice the 130 species suggested by Bonetto (1986) for the same province. The expansion in the area of this ichthyofaunistic province, entry of species formerly confined to the middle and lower stretches, and more intensive surveys account for the difference (Agostinho & Júlio Jr. 1999).

The stretch of the Paraná River basin between the mouth of the Paranapanema River and the Itaipu Reservoir can be considered, based on the fish fauna, as *slightly modified*, according to the criteria proposed by Welcomme (1979) that classify the state of degradation of floodplains. In the Paraná River floodplain, there are drainage canals to draw off water quickly and efficiently during the receding water stage. The arboreal vegetation has generally been removed. The basin includes pasture land, a small fraction of the basin is used for agriculture (rice plantations), and some human settlements occur on the natural levees and upland areas. However, the local fishery is still based on large species such as pimelodids, principally the pintado *Pseudoplatystoma corruscans* and the jaú *Zungaro zungaro* (formerly called *Paulicea luetkeni*), and a characid, the dourado *Salminus maxillosus* (Agostinho & Zalewski 1996).

The fish fauna of this region is subject to anthropogenic impacts at a local scale (e.g., sand mining, *Pfaffia* harvesting, extensive cattle ranching, rice plantation, subsistence agriculture, and fishing) and at a regional scale (e.g., changes in amplitude, timing and frequency of flooding because of the dams upstream; agriculture with intensive use of pesticides; inadequate soil conservation practices and removal of gallery forests; and large urban and industrial centers in the sub-basins of the tributaries); see chapter 18 for more details. The dimensions of these impacts and their degree of importance to the basin are still unevaluated. It is known, however, that the fish fauna in the upper stretches of the basin has been altered by some of these activities.

In this chapter we describe the fish assemblages of the Upper Paraná River basin. First we characterize the assemblage composition and structure, and discuss its origin and anthropogenic actions that have promoted changes. Next, we ordinate the fish assemblage in an attempt to predict its structure. Lastly, we evaluate temporal (inter-annual) assemblage variations.

Composition and distribution of the fish fauna

The geographical area covered in this study (Upper Paraná River basin between the mouth of the Paranapanema River and the headwaters of the Itaipu Reservoir) has at least 153 fish species, recorded in several surveys carried out during the last fifteen years (Penczak *et al.* 1994, Veríssimo 1994, Pavanelli & Caramaschi 1997, Veríssimo 1999, Agostinho *et al.* 1997, 2000, Abes & Agostinho 2001, Oliveira *et al.* 2001, Pavanelli & Caramaschi 2003, Okada *et al.* 2003). The distribution of these fish species, according to the different environments considered, is shown in Appendix 1.

A correspondence analysis (CA) was applied on the presence/absence data (Appendix 1), to evaluate fish fauna similarities among the environments surveyed. The CA was chosen because of its appropriateness when numerous zero values occur in the data set (Gauch 1994, Olden *et al.* 2001). This analysis provides an ordination where environments closely spaced in a two-dimensional graph are interpreted to have similar fish faunas.

In the ordination, considering axes 1 and 2, the Piquiri River and stream environments exhibited different fish faunas between themselves and among the others environments (Fig. 1). However, the Iguatemi, Paraná, channels, Ivinheima, lagoons, and temporary lagoons share several species given they were positioned close in the ordination space.

The Piquiri River had the lowest number of species, which were typically reophilic with limited distribution. Only *Steindachneridion* cf. *scripta* was exclusive to this river. This pattern could be the result of the presence of numerous rapids and falls, with no associated lentic habitats. Streams had higher species richness. These environments had 16 exclusive species and usually members of the fish fauna were small sized. Streams, similar to lagoons, included their typical set of species and also juveniles of medium and large sized species, particularly in the stretches close to the main river, as demonstrated by Penczak *et al.* (1994), Pavanelli & Caramaschi (1997), and Abes & Agostinho (2001).

Even with the restriction of the arch effect (Gauch 1994) on axis 2 (minimized by the use of the presence/absence data), the ordination clearly identifies the separation of larger water bodies (rivers) from the smaller (streams and lagoons), which could be attributed largely to the occurrence of small-sized species typical of the latter environments.

Characiformes and Siluriformes (Fig. 2) dominate the fish fauna of the Upper Paraná River (representatives of these orders and other are presented in figures 3, 4 and 5). These two orders contributed 77% of the total number of species. This tendency has been observed in other stretches of the Paraná River and other South American basins as well (e.g., Lowe McConnel 1964, Sabino & Castro 1990, Menni *et al.* 1992, Penczak *et al.* 1994, Miquelarena *et al.* 1997, Castro & Casatti 1997, Benedito-Cecílio *et al.* 1997, Garavello *et al.* 1997, Pavanelli & Caramaschi 1997, Sabino & Zuanon 1998, Abes & Agostinho 2001, Oliveira *et al.* 2001, Araújo *et al.* 2001, Súarez *et al.* 2001, Casatti *et al.* 2001). Given the heterogeneity of environments closely associated in the ordination diagram (Fig. 1), it is possible to conclude that the original fauna and not the type of environment determine the fish fauna composition at this taxonomic level.

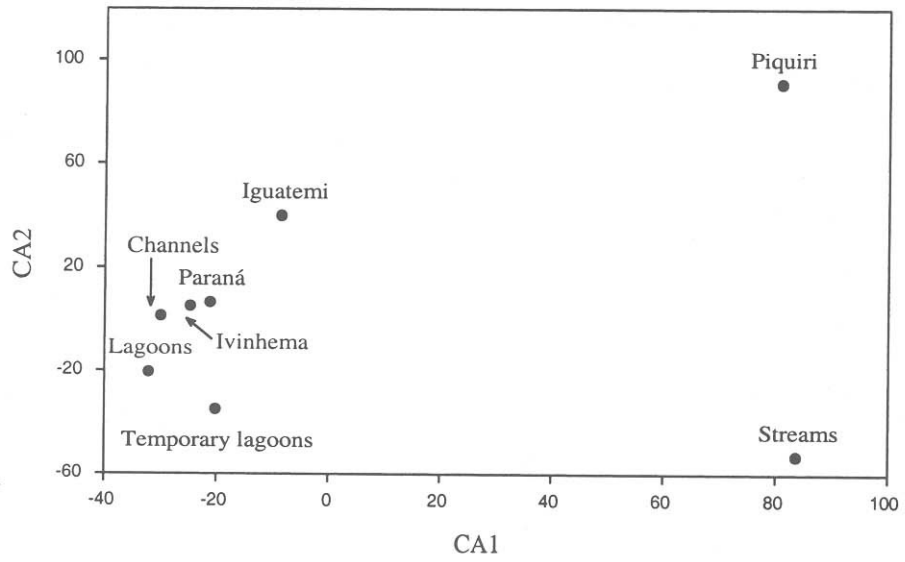

Fig. 1 Ordination of environments based on the species presence-absence data (Appendix 1) using correspondence analysis (CA).

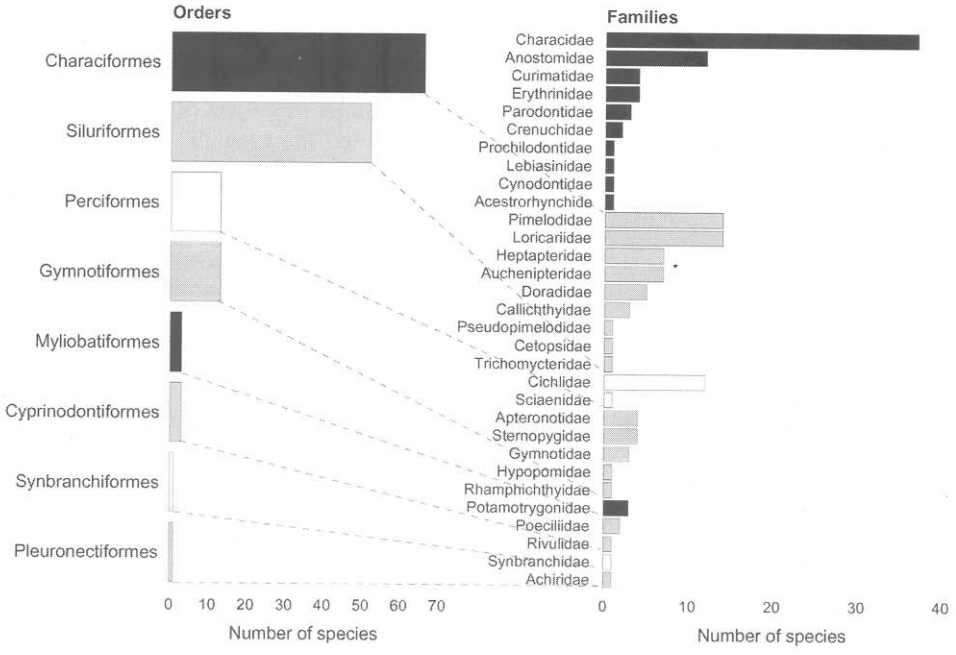

Fig. 2 Frequency of species by order and respective families. Dashed lines delineate families relative to orders.

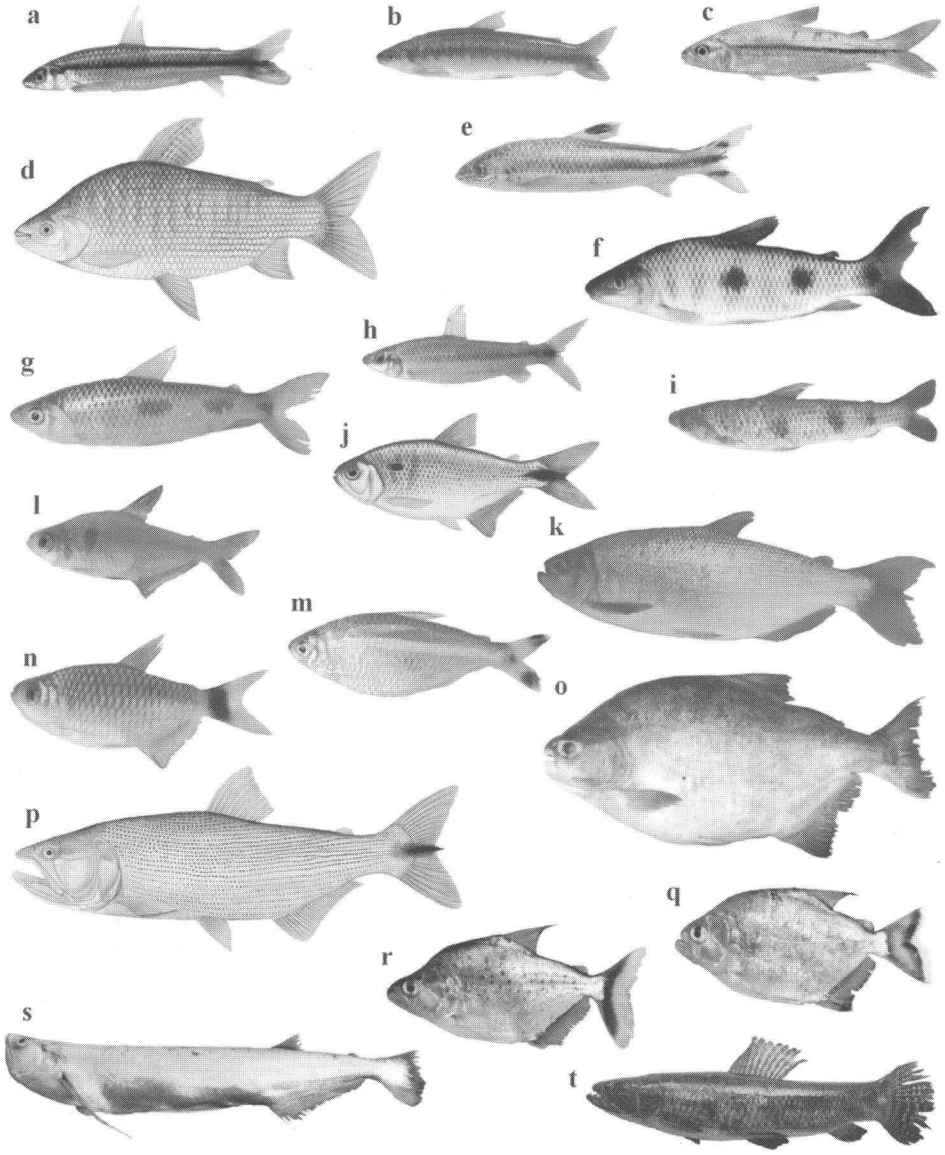

Fig. 3 Representative CHARACIFORMES fish species from the Upper Paraná River floodplain. Numbers in brackets represent the maximum total lengths commonly encountered, in milimiters: (a) *Apareiodon affinis* (150); (b) *Parodon nasus* (155); (c) *Steindachnerina insculpta* (150); (d) *Prochilodus lineatus* (600); (e) *Leporellus vittatus* (300); (f) *Leporinus elongatus* (600); (g) *Leporinus friderici* (370); (h) *Leporinus striatus* (150); (i) *Schizodon borellii* (340); (j) *Astyanax altiparanae* (150); (k) *Brycon orbignyanus* (625); (l) *Hyphessobrycon* cf. *eques* (40); (m) *Moenkhausia intermedia* (85); (n) *Moenkhausia sanctae-filomenae* (70); (o) *Piaractus mesopotamicus* (500); (p) *Salminus maxillosus* (1005); (q) *Serrasalmus maculatus* (230); (r) *Serrasalmus marginatus* (240); (s) *Rhaphiodon vulpinus* (655); (t) *Hoplias* aff. *malabaricus* (350).

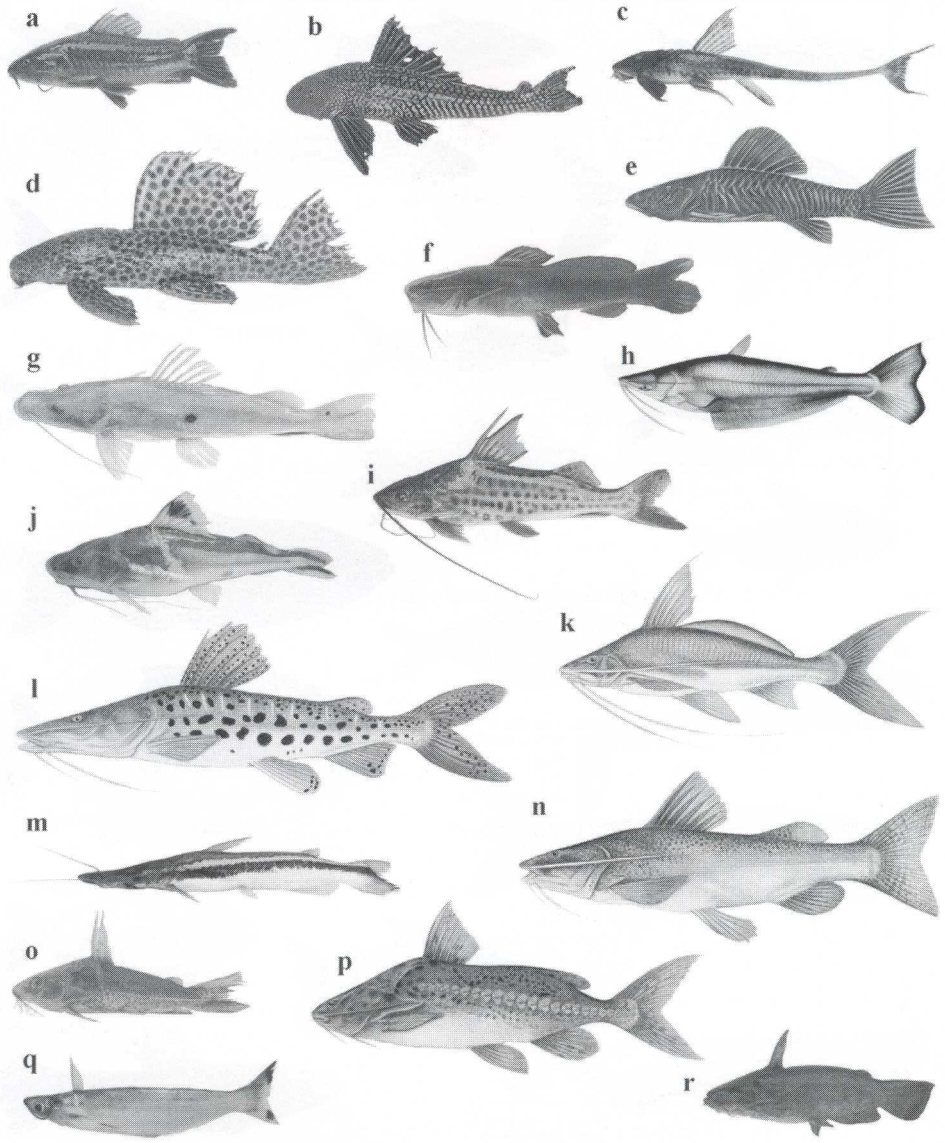

Fig. 4 Representative SILURIFORMES fish species from the Upper Paraná River floodplain. Numbers in brackets represent the maximum total lengths commonly encountered, in milimiters: (a) *Hoplosternum littorale* (195); (b) *Liposarcus* cf. *anisitsi* (400); (c) *Loricariichthys platymetopon* (335); (d) *Megalancistrus parananus* (500); (e) *Rhinelepis* cf. *aspera* (370); (f) *Rhamdia quelen* (300); (g) *Hemisorubim platyrhynchos* (525); (h) *Hypophthalmus edentatus* (600); (i) *Pimelodus maculatus* (360); (j) *Pimelodus ornatus* (385); (k) *Pinirampus pirinampu* (800); (l) *Pseudoplatystoma corruscans* (1360); (m) *Sorubim lima* (505); (n) *Zungaro zungaro* (1100); (o) *Doras eigenmanni* (100); (p) *Pterodoras granulosus* (550); (q) *Auchenipterus osteomystax* (270); (r) *Parauchenipterus galeatus* (200).

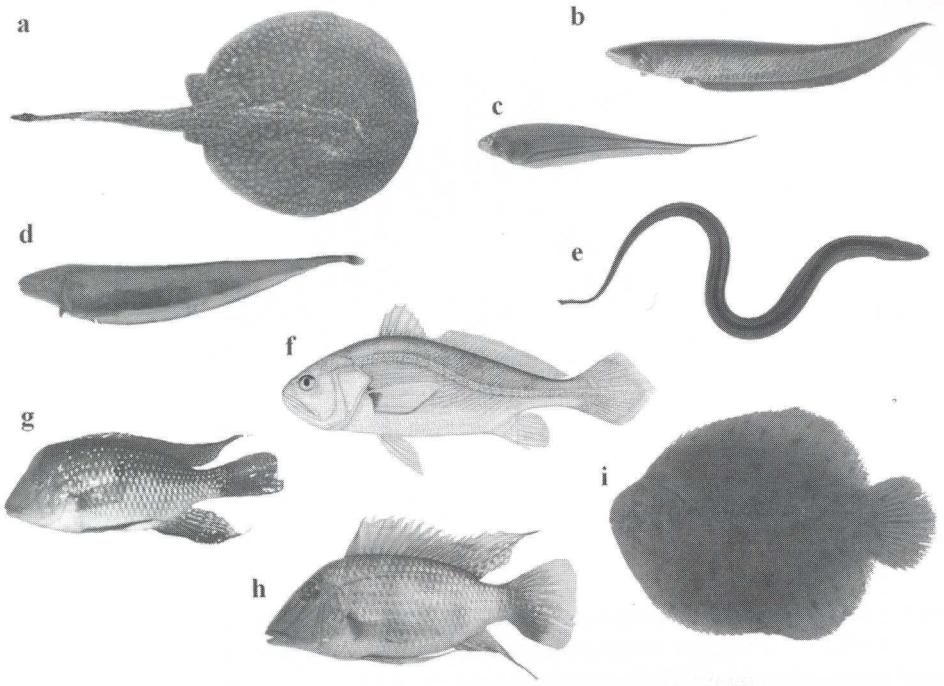

Fig. 5 Representative fish species of other Orders from the Upper Paraná River floodplain. Numbers in brackets represent the maximum total lengths commonly encountered, in milimiters: MYLIOBATIFORMES (a) *Potamotrygon falkneri* (1100); GYMNOTIFORMES (b) *Gymnotus* cf. *sylvius* (330), (c) *Eigenmannia trilineata* (220), (d) *Apteronotus* cf. *brasiliensis* (300); SYNBRANCHIFORMES (e) *Synbranchus marmoratus* (1000); PERCIFORMES (f) *Plagioscion squamosissimus* (480); (g) *Geophagus brasiliensis* (190); (h) *Satanoperca pappaterra* (250); PLEURONECTIFORMES (i) *Catathyridium jenynsii* (250).

The floodplain of the Upper Paraná River in this region has a braided channel with low gradient (0.09 km^{-1}) and high accumulation of sediments on its bed, forming sandbars and small islands. The complex anastomosis in this section of the river involves secondary channels, the Baia River and the lower course of the Ivinheima River on the west margin (Agostinho *et al.* 2000). Fish fauna surveys were conducted in this area during seven years (1986-1987; 1987-1988; 1992-1993; 1993-1994; 1994-1995; 2000 and 2001) and the results of these are presented below.

The number of species found in a particular combination of month and site (local species richness) varied from 3 to 37. Most common values for richness were 12, 18 and 22 species (Fig. 6). These results indicate a high temporal and spatial species turnover, considering that the total species richness in the Upper Paraná River floodplain is relatively high (153 species). Thus, despite the high regional diversity there is low species richness for a single sample of local assemblage. This pattern has been reported worldwide (Matthews 1998).

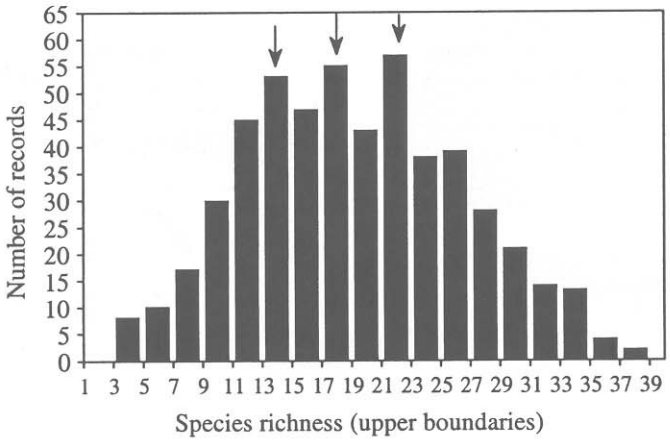

Fig. 6 Histogram representing the frequency distribution of the species richness (number of species) found in month-site combinations (n = 524 fish month-site collections). Arrows indicate most common values.

As expected, there was a positive correlation between species richness and catch per unit of effort (CPUE; an index of abundance) (Fig. 7). Species richness (y-variable) was regressed against CPUE, and the residuals of this regression were used as a new variable to compare environments and years, to take into account the effect of CPUE on species richness.

In the Upper Paraná River floodplain, greater species richness is generally found in rivers and channels than in lagoons (Fig. 7 and 8), despite the higher fish density found in the latter environments. Greater species richness in the main channel of floodplain rivers, when compared to lagoons, was also reported by Winemiller *et al.* (2000) and Agostinho *et al.* (2001). Explanations for this pattern include (i) the effect of area (rivers are larger than lagoons); (ii) the occasional use of the river as a dispersal route by various fish species, other than those that inhabit it permanently (see Appendix 1; Junk *et al.* 1989); (iii) lagoons are "harsh" environments and, only some pre-adapted species are able to cope with habitat instability that is characteristic of these environments, especially the lower dissolved oxygen concentration (see Chapter 4); and (iv) the potential effects of predation and competition, which are higher in lagoons. Agostinho & Zalewski (1996) reported a high proportion of predatory fishes in lagoons, especially in dry years, supporting the latter explanation.

In the three types of environments analyzed, a conspicuous decrease in species richness was observed in the last two years. It is difficult to sort out the main mechanisms that could explain such pattern. We suggest that a potential sampling bias effect (*i.e.*, a possible effect of lower sampling effort in 2000-2001) can be refuted because (1) an analytical control was used to take into account the effect of CPUE (Sale 1996, Griffiths 1999), and (2) the three types of environment were widely sampled in the last two years, especially the lagoons where a decline was also observed.

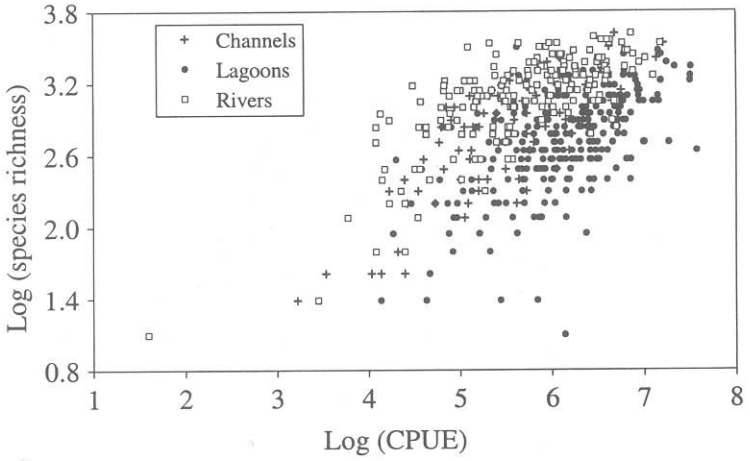

Fig. 7 Comparison of the relationships between species richness and CPUE for assemblages in rivers, channels and lagoons.

For lagoons, there was a significant relationship (Pearson's correlation coefficient) between species richness and annual mean water level ($r = 0.86$, $n = 7$; $P = 0.013$). Also, for rivers and channels, species richness was positively related to annual mean water level, although not significantly ($r = 0.544$, $P = 0.206$ for rivers and $r = 0.625$, $P = 0.133$ for channels). Low water level resulted from a higher hydrological control by operation of dams upstream, and to low precipitation in 2000 and 2001. Agostinho *et al.* (2001) compared the species richness in various types of environments in years with different flood regimes, and found depletion in species richness during dry years. Differences amongst environments in relation to species richness may be attributed to the presence of young of the year of the migratory fishes in lagoons that depend on flood to spawn and to reach them.

Origin of the fish fauna

The native species of the Upper Paraná River floodplain contribute 75.6% of the total number of species (Fig. 9). Introduced species (or exotics) from other basins contribute 8.4% whereas species dispersed after the formation of the Itaipu Reservoir that flooded the natural barrier of the Salto de Sete Quedas contribute another 15.8 %.

Introduced species reached the floodplain from stocking programs promoted since the 1960s in upstream reservoirs (e.g., *Plagioscion squamosissimus* and *Cichla monoculus*), escapes from aquaculture ponds (e.g., *Colossoma macropomum, Leporinus macrocephalus* and *Hoplias lacerdae*), and releases from aquaria (*Phalloceros caudimaculatus, Poecilia reticulata*, *Astronotus ocellatus* and *Laetacara* sp.) or bait (*Hoplerythrinus unitaeniatus* and *Brachyhypopomus* sp.). Agostinho *et al.* (2000) reported that more than 20 fish species were introduced into the upper part of the Paraná River basin, usually with the purpose of improving

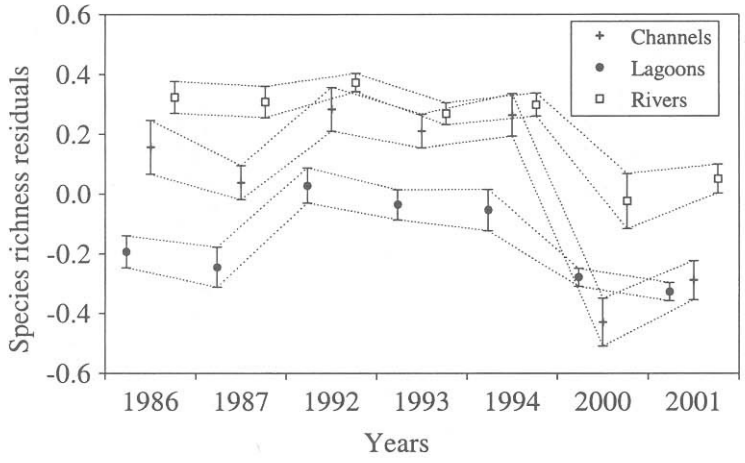

Fig. 8 Species richness residuals derived from a linear regression between species richness (response variable) against CPUE (explanatory variable).

fishery yields. In addition, an unknown number of species escaped from aquaculture facilities. Orsi & Agostinho (1999) reported the escape of more than 1.2 million adult fishes (11 exotic species) during a catastrophic flood (January 1997) in the Tibagi, a medium-sized river in the basin. They attributed this accidental introduction to the illegal occupation of the riparian zone by aquaculture enterprises, and failure to follow measures designed to avoid escapement. Despite the existence of 13 exotic fish species in the Upper Paraná River floodplain, their contribution to the catches is low (1.7% in number and 3.6% in weight; Fig. 9). The most abundant introduced species is *P. squamosissimus* (1.1% by number and 2.6% by weight). This species, native from the Amazon basin, is a successful colonizer of the Paraná River, occupying virtually all habitats of the basin, especially reservoirs. Other species caught during the surveys were *C. monoculus*, *A. ocellatus* and *C. macropomum* (all native to the Amazon basin).

Excluding the exotics species already mentioned, at least 24 species dispersed upstream from the middle stretch of the Paraná River and reached the floodplain when the Itaipu Reservoir submerged the Sete Quedas waterfalls, which according to Bonetto (1986), divided two ichthyofaunistic provinces. Two of these species, *Loricariichthys platymetopon* and *Serrasalmus marginatus* are the most abundant in the floodplain. The great reduction of *Serrasalmus maculatus* concomitant with the proliferation of *S. marginatus* in the floodplain over the last 15 years suggests competition between these congeners (Agostinho *et al.* 2001). Two others species are positioned among the 20 most abundant, a doradid (*Trachydoras paraguayensis*) and an auchenipterid *Parauchenipterus galeatus*. The other species include three stingrays *Potamotrygon* spp. and mapará *Hypophthalmus edentatus* (Júlio Jr & Dei Tós 1995).

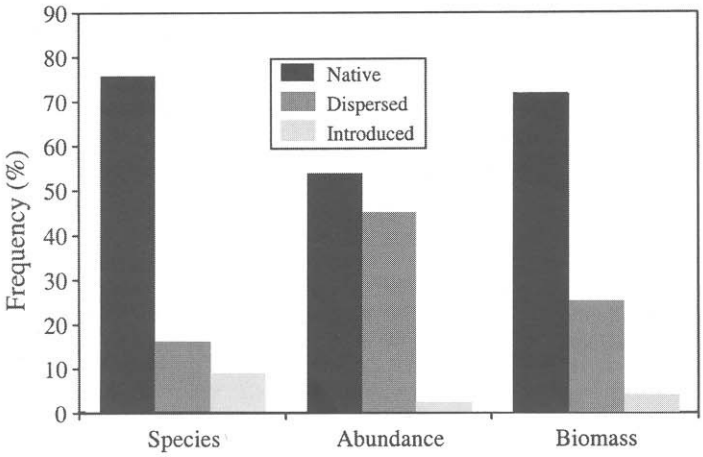

Fig. 9 Contribution (%) of native, dispersed, and introduced species on the species number, individuals number (abundance), and total weight (biomass).

Fish assemblage ordination and classification

Considering the sampling protocol used in this study, two hierarchically-related spatial factors can be used to predict fish assemblage structure in the Upper Paraná River floodplain. First, due to differences in limnology and hydrology, dissimilar fish compositions among river systems (Paraná, Ivinheima and Baia) are expected. Moreover, fish compositions should be more similar within than between river systems due to higher hydrological connectivity (Ward & Tockner 2001 and references therein). Second, and alternatively, type of environment (rivers, lagoons, or channels) within a river system, can be a surrogate variable to indicate environment heterogeneity that influences fish assemblage structure. In this case, higher assemblage similarity should be found within rivers, channels, or lagoons. In other words, fish assemblages will exist as distinctive and repeatable types (sensu Matthews 1998), despite spatial discontinuity caused by sampling in different river systems.

A Detrended Correspondence Analysis (DCA; Hill & Gauch 1980) was used to summarize the data set. Then, sample scores were classified according to year, river system, and environment type. An analysis of variance was subsequently used to estimate the amount of variance in DCA axes scores attributable to year, river system and environment type.

The first two axes of the DCA, based upon 100 species, explained 38.1% of the total data set variance. The first axis contrasts rivers (lower scores) to lagoons (higher scores). Channel scores were positioned between rivers and lagoons (Fig. 10a). This pattern was apparent in the three river systems analyzed. In the Baia River system, however, samples gathered in the river were more similar to those gathered in channels (Fig. 10b).

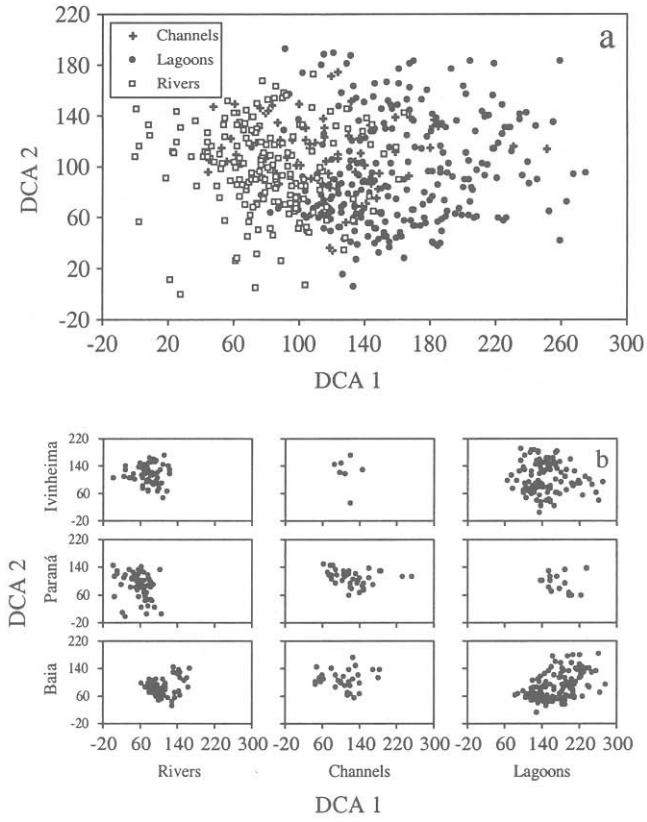

Fig. 10 Results of a Detrended Correspondence Analysis (DCA) applied to the fish assemblage of the Upper Paraná River floodplain (a) and the scores plotted separated for each type of environment within each river (b).

The greatest percent of variation in the scores of the axis 1, as estimated by partitioning of variance component (Fig. 11), was accounted for by type of environment (69.0 %). Thus, much of the spatial variation in the Upper Paraná River floodplain was dependent on the type of environment sampled. Given the small relative variance accounted for by the factors considered (rivers, environment types, and years) the second DCA axis will not be discussed (Fig. 11).

Indeed, according to beta diversity estimates (Harrison *et al.* 1992), species composition of a given environment is, as indicated above, relatively constant from year to year. On the other hand, in all years, intense changes in species composition occur among the environment types analyzed (Fig. 12).

We used the species indicator value method (Dufrêne & Legendre 1997) to typify the fish fauna of each environment type. Of the 100 species analyzed, 56 had significant indicator values, according to the randomization tests. In all, 36 species were typical of rivers, whereas 15 species were typical of lagoons and six species were indicators of channels. *Loricariichthys platymetopon* was identified as the

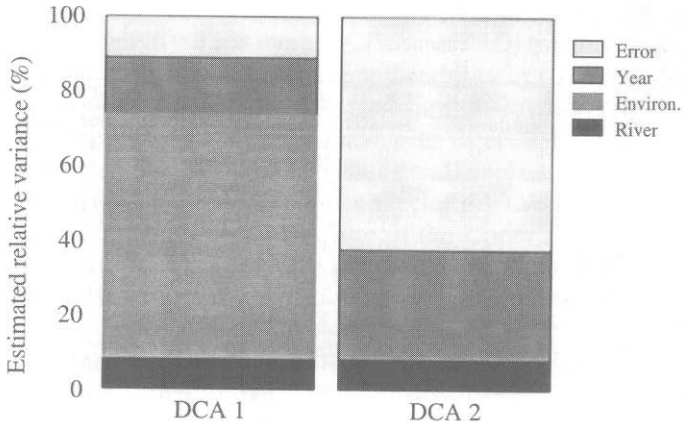

Fig. 11 Percent of the total variance in DCA axes scores that can be attributed to years, rivers and type of environments. Error indicates the variability not explained by these three factors.

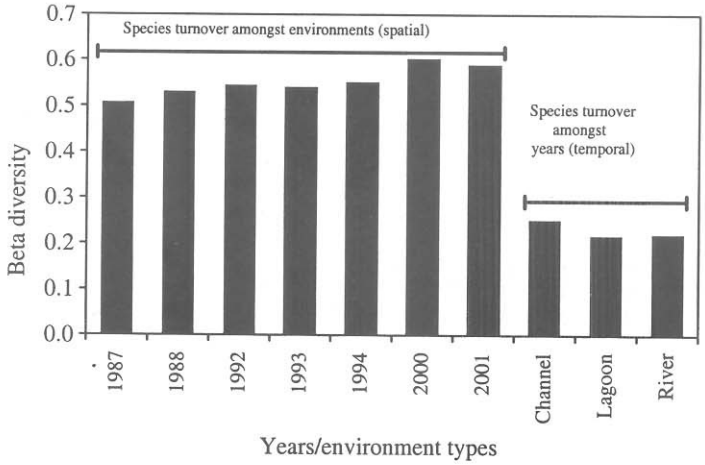

Fig. 12 Spatial (among environment types, within years) and temporal (among years, within environment types) beta diversity estimates in the Upper Paraná River floodplain.

main indicator species of lagoons, followed by *Leporinus lacustris*, *Serrasalmus maculatus* and *Hoplosternum littorale*. Rivers were characterized by *Iheringichthys labrosus*, the armoured catfish *Hypostomus* spp., and several migratory fishes (*Leporinus friderici*, *L. elongatus*, *Raphiodon vulpinus* and *Salminus maxillosus*). *Schizodon borellii* was the main indicator species of channels. Detailed results are presented in Table 1.

Table 1 Relative abundance, relative frequency and species indicator values obtained for the three types of environment analyzed (C = channels, L = lagoons and R = rivers).

Species	C	L	R	C	L	R	C	L	R	Probability
	Relative abundance			Relative frequency			Indicator value			
I.labrosus	6	24	70	36	25	71	2	6	**49**	0.000
Hypostomus sp.	28	14	57	59	28	78	17	4	**45**	0.000
L.friderici	39	8	53	60	23	83	24	2	**44**	0.000
L.elongatus	21	29	50	51	43	81	11	12	**41**	0.000
R.vulpinus	27	22	51	59	42	77	16	9	**39**	0.000
S.maxillosus	21	7	73	19	7	54	4	0	**39**	0.000
P.squamossimus	15	31	55	31	27	69	5	8	**38**	0.000
T.paraguayensis	24	24	52	59	22	72	14	5	**37**	0.000
S.insculpta	15	33	52	44	42	61	7	14	**32**	0.004
A.osteomystax	10	51	39	33	51	73	3	26	**29**	0.024
H.platyrhynchos	20	34	46	37	30	59	7	10	**27**	0.001
Loricaria sp.	28	3	68	14	5	34	4	0	**23**	0.000
P.pirinampu	12	13	75	5	5	30	1	1	**22**	0.000
C.nagelli	5	42	52	17	38	42	1	16	**22**	0.018
P.granulosus	45	10	45	31	10	44	14	1	**20**	0.000
L.elongatus	37	18	45	29	8	35	11	2	**16**	0.004
G.knerii	16	0	84	8	0	18	1	0	**15**	0.000
B.orbignyanus	27	22	51	15	12	29	4	3	**15**	0.002
H.edentatus	3	51	46	4	20	28	0	10	**13**	0.043
M.parananus	43	1	56	14	1	22	6	0	**12**	0.004
A.affinis	0	0	100	0	0	8	0	0	**8**	0.001
P.motoro	30	7	63	8	1	12	2	0	**8**	0.005
C.jenynsi	14	30	56	4	3	13	1	1	**7**	0.018
R.dorbignyi	53	2	45	5	1	16	3	0	**7**	0.043
L.vittatus	0	0	100	0	0	6	0	0	**6**	0.003
C.haroldoi	20	0	80	4	0	8	1	0	**6**	0.006
P.ornatus	18	19	63	1	2	10	0	0	**6**	0.011
A.ellisi	20	4	75	5	0	8	1	0	**6**	0.026
A.schubart	13	31	56	3	3	11	0	1	**6**	0.028
M.platanum	0	0	100	0	0	5	0	0	**5**	0.001
A.valenciennesi	29	18	53	4	2	10	1	0	**5**	0.037
A.fasciatus	0	19	81	0	0	4	0	0	**3**	0.031
L.prolixa	25	0	75	3	0	4	1	0	**3**	0.050
H.regaini	11	0	89	1	0	4	0	0	**3**	0.015
L.octofasciatus	0	0	100	0	0	3	0	0	**3**	0.007
L.platymetopon	15	63	21	85	96	83	13	**61**	18	0.000
L.lacustris	12	74	14	22	63	28	3	**47**	4	0.000
S.maculatus	5	68	27	45	63	48	2	**43**	13	0.000
H.littorale	10	82	8	21	50	24	2	**41**	2	0.000
S.marginatus	24	46	30	88	85	87	21	**39**	26	0.030
A.lacustris	12	60	28	44	57	38	5	**34**	11	0.001
H.malabaricus	34	45	21	73	75	66	25	**33**	14	0.030
P.galeatus	25	50	25	73	57	57	19	**28**	14	0.029
C.modestus	6	85	9	5	31	11	0	**26**	1	0.000
Gymnotus sp.	14	76	10	13	32	11	2	**24**	1	0.000
*L.*cf.*anisitsi*	4	83	12	5	28	5	0	**23**	1	0.000
H.unitaeniatus	40	56	4	6	15	4	3	**9**	0	0.024
A.ocellatus	9	85	6	1	8	1	0	**7**	0	0.003
C.paranaense	16	64	21	3	10	4	0	**6**	1	0.033
*M.*cf.*maculatus*	0	94	6	0	4	1	0	**4**	0	0.029
S.borellii	61	20	19	90	78	83	**55**	15	16	0.000
S.pappaterra	57	36	7	38	23	14	**22**	8	1	0.000
S.lima	50	17	33	27	12	34	**13**	2	11	0.036
D.eigenmanni	65	29	6	13	3	2	**8**	1	0	0.000
A.brevifilis	74	2	25	8	0	5	**6**	0	1	0.008
C.monoculus	48	24	28	10	3	3	**5**	1	1	0.050

Inter-annual variability in relative species abundance

There are different ways to measure temporal stability in fish assemblage composition and structure (Matthews 1998). If, for example, species abundance ranks are temporally stable over years, it is reasonable to infer that the assemblage is predictable (stability hypothesis). On the other hand, unpredictability or instability is assumed when it is not possible to predict species relative abundance.

How predictable is the fish assemblage of the Upper Paraná River floodplain? To answer this question it is necessary to take into account that this floodplain has been impacted, upstream and downstream, by the construction of several dams. Other impacts have occurred on the floodplain itself (e.g., cattle ranching, deforestation, sand extraction, fire and draining; Agostinho & Zalewski 1996). In addition, due to the extreme hydrological and climatic temporal variation that occurs in tropical floodplains, a high temporal variability in fish assemblage structures should be expected (Rodríguez & Lewis Jr. 1997, Tejerina-Garro *et al.* 1998). Indeed, recent studies have challenged the traditional assumption of temporal stability of fish assemblages (Winemiller 1996 and references therein). Then, to analyze the stability of fish structure in the Upper Paraná River, the following analytic protocol was used. First, an annual mean was estimated based on CPUE values, according to species and environment type. Then, we computed Pearson's correlation coefficients using species values paired by year.

In the Upper Paraná River floodplain, the high among-years similarity in the patterns of species relative abundances was a rather unexpected result (Table 2). Other than the effects aforementioned (*i.e.*, hydrological variability and human impacts), low similarity or predictability was expected because there are a large number of possible alternative states in systems with many species (Sale 1996, more below). The observed environmental variability in tropical floodplains, although predictable, incite expectations that perhaps overstate the effects of abiotic factors on biotic communities.As demonstrated here and in other floodplains, these changes are considered predictable on an annual or seasonal basis but unpredictable in shorter terms (Winemiller 1996). Even in the unpredictable environment of reservoirs, long-term stability was detected in fish assemblage structure (Gido & Matthews 2000, Gido *et al.* 2000). Matthews (1998) reviewed numerous published stability analyses for stream fish assemblages and concluded that "On balance, and at the time scale of many years, most stream fish assemblages seem relatively resistant to change or oscillate about some relatively stable condition, barring human intervention or introductions of exotic species." Our preliminary results are in concordance with these findings, but more important, provide a consistent baseline to test the effects of natural and anthropogenic disturbances. Nevertheless, there were subtle declines in the coefficients of correlation between the first year (1986) and the successive years analyzed (Table 3). This pattern can be partially attributed to the cumulative environmental impacts affecting the Upper Paraná River floodplain, a hypothesis that will be evaluated below.

Table 2 Pearson's correlations for catch per effort (CPUE) over seven years based on 100 species at each environment

Lagoons						
	1986	1987	1992	1993	1994	2000
1986						
1987	0.882					
1992	0.755	0.893				
1993	0.730	0.880	0.951			
1994	0.701	0.771	0.829	0.864		
2000	0.718	0.764	0.835	0.835	0.786	
2001	0.696	0.746	0.816	0.820	0.752	0.934
Channels						
	1986	1987	1992	1993	1994	2000
1986						
1987	0.833					
1992	0.746	0.786				
1993	0.759	0.820	0.958			
1994	0.723	0.800	0.906	0.940		
2000	0.669	0.735	0.805	0.841	0.807	
2001	0.670	0.753	0.804	0.831	0.833	0.868
Rivers						
	1986	1987	1992	1993	1994	2000
1986						
1987	0.926					
1992	0.759	0.843				
1993	0.771	0.848	0.944			
1994	0.777	0.856	0.879	0.918		
2000	0.650	0.751	0.781	0.812	0.801	
2001	0.638	0.693	0.700	0.743	0.728	0.836

Assemblages that seem stable at large spatial scales may be unstable at smaller scales (Rahel 1990 and references therein). This hierarchical nature of assemblage stability is a testable hypothesis. Thus, we analyzed the patterns of assemblage stability, as before, using the data set for each river separately. The prediction of lower level of fish assemblage stability observed in the intensely regulated Paraná River was also evaluated. The results were unambiguous. A relatively high level of stability was found for the Baia and the Ivinheima rivers, being similar to the pooled river data (Table 3); on the other hand, lower stability was noted in the Paraná River.

Despite the relatively stable assemblage when pooled data were analyzed, continued monitoring over successive years gives additional information on the response of the fish assemblage to disturbances, mainly those related to hydrological regulation.

Table 3 Pearson's correlations based on catch per effort data (CPUE) for seven years based on 100 species at each river.

Ivinheima						
	1986	1987	1992	1993	1994	2000
1986						
1987	0.916					
1992	0.763	0.838				
1993	0.753	0.846	0.887			
1994	0.738	0.843	0.827	0.934		
2000	0.683	0.791	0.724	0.834	0.865	
2001	0.650	0.696	0.733	0.783	0.791	0.730

Baia						
	1986	1987	1992	1993	1994	2000
1986						
1987	0.939					
1992	0.796	0.843				
1993	0.760	0.785	0.946			
1994	0.800	0.828	0.874	0.901		
2000	0.654	0.672	0.770	0.800	0.774	
2001	0.693	0.711	0.740	0.796	0.786	0.897

Paraná						
	1986	1987	1992	1993	1994	2000
1986						
1987	0.902					
1992	0.661	0.698				
1993	0.637	0.735	0.922			
1994	0.581	0.714	0.853	0.865		
2000	0.357	0.390	0.450	0.454	0.389	
2001	0.386	0.398	0.505	0.572	0.479	0.590

The correlation coefficients between 1986 and the consecutive years sampled indicate that more recent fish structures differed from the first year studied. However, this pattern was stronger for the Paraná River data (Fig. 13). Thus, there is little doubt that the lower level of fish assemblage stability in the Paraná River is related to the higher degree of hydrological regulation in this river (Table 3). In fact, the Ivinheima and the Baia rivers are not dammed, unlike the Paraná River, and the main force function on this stretch of the basin is the hydrological regime (Agostinho *et al.* 1995).

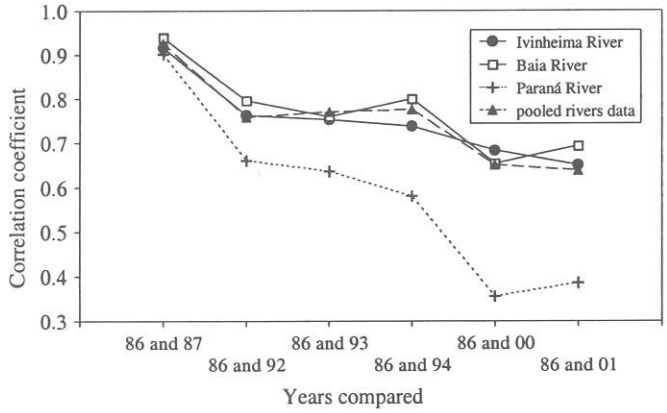

Fig. 13 Pearson's correlation coefficients for catch per effort between 1986 data and consecutive years sampled.

We suggest that the reservoirs located upstream from the study area should be managed to minimize the regulation of discharges into the Paraná River main channel. Appropriate management of discharges could be used to simulate floods. This practice has potential to increase the level of stability in the river and favor recruitment by allowing reproduction of migratory species.

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Appendix 1 Species recorded in different environments of the part of the upper Paraná River basin, between the mouth of the Paranapanema River and the Itaipu Reservoir (PAR = main channel of the Paraná River; IVI = Ivinheima River; PIQ = Piquiri River; IGU = Iguatemi River; CHN = side channels in the floodplain; STR = streams; LAG = lagoons (perennial); TLG = temporary lagoons; [I] = species introduced from other basins; [D] = species dispersed from the middle Paraná River after the formation of the Itaipu Reservoir, others are native species). The classification is based on Reis *et al.* (2003).

SPECIES / ENVIRONMENT	PAR	IVI	PIQ	IGU	CHN	STR	LAG	TLG
CHONDRIICHTHYES								
MYLIOBATIFORMES								
Potamotrygonidae								
Potamotrygon falkneri Castex & Maciel, 1963[D]	+	+			+			
Potamotrygon motoro (Müller & Henle, 1841) [D]	+	+		+	+	+	+	+
Potamotrygon sp. [D]	+	+				+		
OSTHEICHTHYES								
CHARACIFORMES								
Parodontidae								
Apareiodon affinis (Steindachner, 1879)	+	+	+	+	+	+	+	
Apareiodon piracicabae (Eigenmann, 1907)	+		+		+	+		
Parodon nasus Kner, 1859	+					+		
Curimatidae								
Cyphocharax modestus (Fernández-Yépez, 1948)	+	+	+	+	+	+	+	+
Cyphocharax nagelii (Steindachner, 1881)	+	+	+	+	+		+	+
Steindachnerina brevipinna (Eigenmann & Eig., 1889) [D]	+	+		+	+	+	+	+
Steindachnerina insculpta (Fernández-Yépez, 1948)	+	+	+	+	+	+	+	+
Prochilodontidae								
Prochilodus lineatus (Valenciennes, 1836)	+	+	+	+	+	+	+	+
Anostomidae								
Leporellus vittatus (Valenciennes, 1850)	+		+		+	+		+
Leporinus amblyrhynchus Garavello & Britski, 1987			+			+	+	
Leporinus elongatus Valenciennes, 1850	+	+	+	+	+	+	+	
Leporinus friderici (Bloch, 1794)	+	+	+	+	+	+	+	+
Leporinus lacustris Campos, 1945	+			+	+	+	+	+
Leporinus macrocephalus Garavello & Britski, 1988 [I]	+					+	+	
Leporinus obtusidens (Valenciennes, 1836)	+	+	+	+	+	+	+	+
Leporinus octofasciatus Steindachner, 1915	+		+	+		+		
Leporinus striatus Kner, 1858	+		+		+	+	+	+
Schizodon altoparanae Garavello & Britski, 1990	+	+		+	+	+	+	+
Schizodon borellii (Boulenger, 1900)	+	+	+	+	+	+	+	+
Schizodon nasutus Kner, 1858	+		+	+	+	+		
Crenuchidae								
Characidium aff. *zebra* Eigenmann, 1909	+	+			+	+	+	+
Characidium sp.						+		
Characidae								
Aphyocharax anisitsi Eigenmann & Kennedy, 1903	+	+			+	+	+	+
Aphyocharax dentatus Eigenmann & Kennedy, 1903[D]	+							
Aphyocharax sp.	+	+				+		+
Astyanax altiparanae Garutti & Britski, 2000	+	+	+	+	+	+	+	+
Astyanax eigenmaniorum (Cope, 1894)						+		
Astyanax fasciatus (Cuvier, 1819)	+		+	+	+	+		
Astyanax marionae Eigenman, 1911 [D]	+							
Astyanax scabripinnis paranae Eigenmann, 1914						+		
Astyanax schubarti Britski, 1964	+	+	+		+	+	+	+
Astyanax sp.						+		
Brycon orbignyanus (Valenciennes, 1850)	+	+	+	+	+		+	+
Bryconamericus iheringi (Boulenger, 1887)						+		
Bryconamericus stramineus Eigenmann, 1908	+	+	+	+	+	+	+	+

Appendix 1 Continued

SPECIES / ENVIRONMENT	PAR	IVI	PIQ	IGU	CHN	STR	LAG	TLG
OSTHEICHTHYES								
Bryconamericus spp.	+	+	+		+	+	+	
Colossoma macropomum (Cuvier, 1818) [I]	+	+		+	+		+	
Galeocharax knerii (Steindachner, 1879)	+	+	+	+	+	+		
Hemigrammus marginatus Ellis, 1911	+	+			+	+	+	+
Hemigrammus sp.	+	+			+	+	+	
Hyphessobrycon cf. *eques* (Steindachner, 1882)	+				+	+	+	+
Hyphessobrycon sp.						+		
Metynnis cf. *maculatus* (Kner, 1858) [D]	+				+		+	
Moenkhausia intermedia Eigenmann, 1908	+	+	+	+	+	+	+	+
Moenkhausia sanctae-filomenae (Steindachner, 1907)	+	+		+	+	+	+	+
Myleus tiete (Eigenmann & Norris, 1900)	+	+	+	+	+	+	+	+
Mylossoma orbignyanum (Valenciennes, 1850)				+				
Odontostilbe sp.	+	+	+	+	+	+	+	+
Oligosarcus pintoi Campos, 1945						+		
Piabina argentea Reinhardt, 1867			+			+		
Piaractus mesopotamicus (Holmberg, 1887)	+	+		+	+		+	
Roeboides paranensis Pignalberi, 1975	+	+		+	+	+	+	+
Salminus hilarii Valenciennes, 1850		+	+	+		+		
Salminus maxillosus Valenciennes, 1849	+	+	+	+	+	+	+	+
Serrapinnus notomelas (Eigenmann, 1915)	+	+			+	+	+	+
Serrapinnus sp.1	+	+			+	+	+	+
Serrapinnus sp.2	+	+			+	+	+	+
Serrasalmus maculatus Kner, 1858	+	+	+	+	+	+	+	+
Serrasalmus marginatus Valenciennes, 1847 [D]	+	+		+	+	+	+	+
Acestrorhynchidae								
Acestrorhynchus lacustris (Lütken, 1875)	+	+	+	+	+	+	+	+
Cynodontidae								
Rhaphiodon vulpinus Agassiz, 1829	+	+		+	+	+	+	
Erythrinidae								
Erythrinus cf. *erythrinus* (Bloch, 1801) [I]							+	+
Hoplerythrinus unitaeniatus (Agassiz, 1829) [I]		+			+	+	+	
Hoplias lacerdae Ribeiro, 1908 [I]		+	+	+		+		
Hoplias aff. *malabaricus* (Bloch, 1794)	+	+	+	+	+	+	+	+
Lebiasinidae								
Pyrrhulina australis Eigenmann & Kennedy, 1903						+	+	+
SILURIFORMES								
Cetopsidae								
Pseudocetopsis gobioides (Kner, 1858) [D]				+		+		
Trichomycteridae								
Trichomycterus spp.			+			+		
Callichthyidae								
Callichthys callichthys (Linnaeus, 1758)	+	+		+	+	+	+	+
Corydoras aeneus (Gill, 1858)						+		
Hoplosternum littorale (Hancock, 1828)	+	+		+	+	+	+	+
Loricariidae								
Ancistrus cirrhosus (Valenciennes, 1836)						+		
Farlowella sp.	+	+				+		
Hypostomus ancistroides (Ihering, 1911)	+					+		
Hypostomus cf. *microstomus* Weber, 1987	+				+			
Hypostomus regani (Ihering, 1905)	+	+			+	+		
Hypostomus spp.	+	+	+	+	+	+	+	+
Liposarcus cf. *anisitsi* (Eigenmann & Kennedy, 1903)	+	+			+		+	
Loricaria prolixa Isbrücker & Nijsen, 1978	+	+			+			+
Loricaria sp.	+	+		+	+	+	+	

Appendix 1 Continued

SPECIES / ENVIRONMENT	PAR	IVI	PIQ	IGU	CHN	STR	LAG	TLG
OSTHEICHTHYES								
Loricariichthys platymetopon Isbrücker & Nijsen, 1979 [D]	+	+		+	+	+	+	+
Loricariichthys rostratus Reis & Pereira, 2000 [D]	+			+	+		+	
Megalancistrus parananus (Peters, 1881)	+	+	+		+		+	+
Microlepidogaster sp.						+		
Rhinelepis cf. *aspera* Agassiz, 1829	+	+		+	+			
Pseudopimelodidae								
Pseudopimelodus mangurus (Valenciennes, 1835)	+	+	+	+				
Heptapteridae								
Cetopsorhamdia iheringi Schubart & Gomes, 1959						+		
Imparfinis mirini Haseman, 1911						+		
Imparfinis schubarti (Gomes, 1956)						+		
Phenacorhamdia tenebrosa (Schubart, 1964)						+		
Pimelodella gracilis (Valenciennes, 1835)	+	+	+	+	+	+	+	+
Pimelodella sp.	+	+			+	+	+	
Rhamdia quelen (Quoy & Gaimard, 1824)		+	+	+	+	+	+	
Pimelodidae								
Hemisorubim platyrhynchos (Valenciennes, 1840)	+	+		+	+	+	+	
Hypophthalmus edentatus Spix, 1829 [D]	+	+		+	+		+	+
Iheringichthys labrosus (Lütken, 1874)	+	+	+	+	+	+	+	
Megalonema platanum (Günther, 1880)	+	+	+	+	+	+	+	
Pimelodus heraldoi Azpelicueta, *2001*	+		+					
Pimelodus maculatus Lacépède, 1803	+	+	+	+	+	+	+	+
Pimelodus ornatus Kner, *1858*	+	+		+	+	+	+	
Pimelodus paranaensis Britski & Langeani, 1988	+				+		+	
Pimelodus sp.					+			
Pinirampus pirinampu (Spix, 1829)	+	+		+	+		+	
Pseudoplatystoma corruscans (Agassiz, 1829)	+	+	+	+	+	+	+	+
Sorubim lima (Schneider, 1801) [D]	+	+		+	+	+	+	+
Steindachneridion scripta (Ribeiro, 1918)			+					
Zungaro zungaro (Humboldt, 1821)	+	+		+				
Doradidae								
Doras eigenmanni (Boulenger, 1895) [D]	+	+			+		+	
Platydoras armatulus (Valenciennes, 1840) [D]	+	+						
Pterodoras granulosus (Valenciennes, 1821) [D]	+	+		+	+		+	+
Rhinodoras dorbignyi (Kner, 1855)	+	+		+	+		+	
Trachydoras paraguayensis (Eig. & Ward, 1907) [D]	+	+		+	+	+	+	
Auchenipteridae								
Ageneiosus brevifilis Valenciennes, 1840 [D]	+	+		+	+			
Ageneiosus ucayalensis Castelnau, 1855 [D]	+	+		+	+		+	
Ageneiosus valenciennesi Bleeker, 1864	+	+		+	+		+	
Auchenipterus osteomystax (Ribeiro, 1918) [D]	+	+	+	+	+	+	+	+
Parauchenipterus galeatus (Linnaeus, 1766) [D]	+	+		+	+	+	+	+
Tatia neivai (Ihering, 1930)			+			+		
Trachelyopterus cf. *coriaceus* Valenciennes, 1840 [D]				+	+		+	
GYMNOTIFORMES								
Gymnotidae								
Gymnotus cf. *carapo* Linnaeus, 1758	+	+	+	+	+	+	+	+
Gymnotus cf. *sylvius* Albert & Fernandes-Matioli, 1999	+	+	+	+	+	+	+	+
Gymnotus inaequilabiatus (Valenciennes, 1839) [D]		+					+	
Sternopygidae								
Eigenmannia trilineata López & Castello, 1966	+	+			+	+	+	+
Eigenmannia virescens (Valenciennes, 1836)	+	+		+	+	+	+	
Eigenmannia sp.							+	
Sternopygus macrurus (Bloch & Schneider, 1801)	+	+	+	+	+	+	+	

Appendix 1 Continued

SPECIES / ENVIRONMENT	PAR	IVI	PIQ	IGU	CHN	STR	LAG	TLG
OSTHEICHTHYES								
Rhamphichthyidae								
Rhamphichthys hahni (Meinken, 1937)	+	+		+	+	+	+	+
Hypopomidae								
Brachyhypopomus sp. [I]							+	
Apteronotidae								
Apteronotus albifrons (Linneus, 1766)	+	+	+	+	+	+	+	
Apteronotus cf. *brasiliensis* (Reinhardt, 1852)	+		+	+	+	+	+	
Apteronotus ellisi (Arámburu, 1957)	+				+		+	
Sternarchorhynchus britskii Campos-da-Paz, 2000	+							
CYPRINODONTIFORMES								
Rivulidae								
Rivulus sp.							+	+
Poeciliidae								
Phalloceros caudimaculatus (Hensel, 1868) [I]						+		
Poecilia reticulata Peters, 1859 [I]						+		
SYNBRANCHIFORMES								
Synbranchidae								
Synbranchus marmoratus Bloch, 1795			+		+	+	+	+
PERCIFORMES								
Sciaenidae								
Plagioscion squamosissimus (Heckel, 1840) [I]	+	+		+	+	+	+	
Cichlidae								
Astronotus ocellatus (Agassiz, 1831) [I]	+	+		+		+		
Cichla monoculus Spix, 1831 [I]	+			+	+	+	+	
Cichlasoma paranaense Kullander, 1983		+	+	+	+	+	+	+
Cichlasoma sp.					+		+	
Crenicichla britskii Kullander, 1982	+	+	+	+	+	+	+	+
Crenicichla haroldoi Luengo & Britski, 1974	+	+	+		+	+		
Crenicichla nierderleinii (Holmberg, 1891)			+		+		+	
Crenicichla sp.	+	+	+	+	+	+	+	
Geophagus brasiliensis (Quoy & Gaimard, 1824)		+				+	+	
Laetacara sp. [I]					+	+	+	+
Oreochromis niloticus (Linnaeus, 1758) [I]						+	+	
Satanoperca pappaterra (Heckel, 1840)	+	+			+		+	+
PLEURONECTIFORMES								
Achiridae								
Catathyridium jenynsii (Günther, 1862) [D]	+	+		+	+	+	+	+
TOTAL NUMBER OF SPECIES	**111**	**97**	**56**	**78**	**107**	**111**	**103**	**63**