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The importance of floodplains for the dynamics of fish communities of the upper river Paraná

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Abstract

The last free stretch of the River Paraná inside of Brazilian territory, about 230 km of the former 810 km, runs in a wide floodplain, which flood regime is controlled in part by upstream dams. Aim to evaluate the impacts of different levels of hydrological control on the regional fish diversity, nutritional condition, trophic categories proportion, reproduction and young abundance monthly sampling were carried, between 1986 and 1993, during three annual periods with different flood duration and intensity. Lagoons, secondary channels and river channel was sampled with gillnet of different mesh size and standardized effort. Diversity, evenness indexes and number of species increased with the occurrence of floods. The trophic category proportions varied among the periods considered, with a decrease in piscivores participation and an increase of iliophages, herbivores and insectivores (terrestrial) participation in big flood years. The tendencies for piscivores guild were not uniform to every species. The variations on the nutritional condition reveal that the absence of flooding has a negative effect on greater migratory species and positive on sedentary ones. The young abundance shows, however, that fail in the flooding has a strong negative impact on de recruitment of all the reproductive strategies. It's stressed the operational procedures in the upstream dams and the maintenance of the floodplain integrity is essential to preserve the regional biodiversity, fisheries and particularly the greater migratory fishes population.

Key words: floods, fish, biodiversity, neotropical

1. Introduction

The River Paraná has the second largest basin of South America, draining 2.8 × 10^6 km^2 of the entire south-central region of the continent from the Andes to the Serra do Mar close to the Atlantic Ocean. It is the tenth river in the world in water discharge and it is the chief river in the Plata basin, extending 3,780 km from the confluence of the rivers Paranaiba and Grande to the Plata estuary. The River Paraná's upper section (from the confluence of the river Grande as far as the former Sete Quedas Waterfalls in Guaira, Paraná, Brazil, totaling 619 km) and part of the middle stretch (from the former Sete Quedas Waterfalls to the mouth of the River Iguaçu, totaling 190 km) is within Brazil, draining 891,000 km^2 which corresponds to 10.5% of the country's area (Paiva 1982).

The upper River Paraná with an average declivity of 18 cm km^{-1} has an extensive floodplain between Tręs Lagoas, Mato Grosso do Sul, and Guaíra, Paraná (a 480 km stretch). The floodplain may reach up to 20 km wide especially in its right margin. At present the plain is 230 km long since its upper half has been flooded by the hydroelectric reservoir of Porto Primavera. The hydroelectric dam of Ilha Grande (construction halted) would wipe out the last lotic stretch of the River Paraná. In its free stretch the river has a wide braided channel with reduced declivity (10 cm km^{-1}), sometimes with an extensive alluvial plain and a great accumulation of sediments in its bed, producing small islands and sandbanks, sometimes with big islands and a more restricted flooded plain (Agostinho 1994). In this segment the floodplain has a complex anastomosis involving secondary channels, the River Baía and the lower stretches of the Rivers Ivinheima and Amambai. Near Guaíra the river narrows down and enters the Itaipu Reservoir. Here (the site of the former Sete Quedas Waterfalls) the middle River Paraná begins and extends to the confluence of the River Paraguay. The Itaipu dam transferred this natural barrier of fish dispersion some 150 km downstream.

The importance of the ecotonal zones (that may be flooded seasonally) working on the biological cycle of some fish species has been discussed in the literature (Lowe-McConnell 1964, 1987; Welcomme 1979; Machado-Allison 1990; Agostinho *et al.* 1993; Agostinho, Zalewski 1995). However, studies (such as the present) that analyze the effect of different flood intensities and duration on the fish community or group of species with different life history strategies are not common.

2. Characteristics of the area under analysis

The area under analysis was in the third lower stretch of the upper River Paraná between the mouths of the Rivers Paranapanema and Ivinheima, where the Paraná channel was 3.4-4.0 km wide with an extensive alluvial plain on its right margin. Annual water temperature oscillated between 10.3 and 33.6°C, with an average of 22°C (Stevaux 1994). Average annual rainfall reached 1,200 mm, characterizing the climate of the region as tropical-subtropical. Water discharge measured at River Paranapanema varied between 8,400 m^3 sec^{-1} (from June to September) and 13,000 m^3 sec^{-1} (from November to March). Maximum and minimum values in the last 30 years were 33,740 m^3 sec^{-1} in 1983 and 2,550 m^3 sec^{-1} in 1969.

The vegetation of the plain with 360 identified species was dominated by herbaceous plants. Chief aquatic herbaceae covering variable extensions of lakes, marshes and secondary channels were *Eichhornia azurea, E. crassips, Polygonum acuminatum, P. stelligerum, Nymphea* sp., *Sagittaria montevidensis, Pontederia cordata, Utricularia* sp., *Salvinea* sp. and *Pistia* sp. On the other hand, among the natural terrestrial herbaceous the gramineae (*Panicum prionitis, P. mertensii, P. maximum*), cyperaceae (*Cyperus digitatus, C. difusus*) and amaranthaceae (*Pfaffia glomerata*) predominanted. *Senna pendula, Aeschynomene* sp. and *Sapium bigladulatum* were the commonest shrubs, whilst among the isolated tree forms were *Inga uruguensis* and *Croton urucurana*. In the riparian vegetation, heavily changed by human action and catastrophic floodings, *Cecropia pachystachya, Croton urucurana, Lonchocarpus guilliminianus, L. muhelbergianus* predominated (M.C. Souza-Stevaux, unpubl.).

Although subject to great seasonal and spatial variations in composition, aquatic communities, which occupy the plain, were highly diverse. Incomplete surveys revealed:

(1) more than 300 taxa of planktonic algae among which *Cryptomonas brasiliensis*, *Aulacoseira granulata, Anabaena* spp, *Cyclotella* spp and *Monoraphidium irregulare* were predominant;

(2) more than 150 taxa of algae associated to *Eichhornia azurea*, with special reference to *Cymbella affinis, Achnanthes minutissima, Gomphonema subtile* and *Frustulia rhomboides*;

(3) 286 zooplanktonic taxa with a predominance of rotifers (*Lecane* and *Keratella*), testaceans (*Arcella, Centropyxis* and *Difflugia*), cladocerans (*Bosminopsis, Bosmina* and *Diaphanosoma*) and copepods (*Thermocyclops, Mesocyclops* and *Notodiaptomus*);

(4) gastropods, chironomids, nematodes, tubificids and ostracods among the 28 taxonomic groups of zoobenthos analysed, and which were conspicuously dense, while chironomids were the predominant fauna associated to *Eichhornia* spp. (PADCT-CIAMB/FUEM 1994).

The 170 species of fishes in the floodplain of the upper River Paraná were residents (opportunistic and equilibrium strategies *sensu* Winemiller 1989) which develop their whole life cycle in the area and migrants (seasonal strategy, Winemiller 1989) which utilize the plain merely during a portion of their life cycle. There were different assemblages among the different biotopes. Thus, *Loricariichthys platymetopon* Isbrucker, Nijssen 1979, *Hoplosternum litoralle* (Hancock 1828), *Acestrorhynchus lacustris* (Reinhardt 1874), *Hoplias malabaricus* (Bloch 1794), *Leporinus lacustris* Campos 1945, juvenile *Prochilodus scrofa* Steindachner, 1881 and of other migratory species were predominant in lakes, shallow environments with daily stratification and rich in macrophytes. Besides these, *Iheringichthys labrosus* (Kroyer 1874), *Pimelodus maculatus* Lacépède, 1803, *Trachydoras paraguayensis* (Eigenmann, Ward 1907) and piranhas *Serrassalmus marginatus* (Valenciennes 1847) and *S. spilopleura* Kner, 1860 were common in the secondary semilotic channels. Moreover, *Paulicea luetkeni* (Steindachner 1875) (the biggest fish in the basin), *Raphiodon vulpinus* Agassiz, 1829, *Loricaria* spp, *Salminus maxillosus* Valenciennes, 1840 (the biggest characid) and some apteronotids characterised the River Paraná channel. In the meandering segments of the big rivers anostomids (*Schizodon borelli* (Boulanger, 1895), *Leporinus obtusidens* (Valenciennes 1847)), auchenipterids and doradids predominated with great diversity. Small species characterised fish fauna of small streams sited at the margins of the plain (tetragonopterids, cheirodontids, small pimelodids, loricarids and trychomychtherids) (Agostinho, Julio Jr. 1999). In the small residual water bodies, previous to total desiccation, species such as *Astyanax bimaculatus* (Linnaeus 1758), *Cheirodon notomelas* Eigenmann 1915, *P. scrofa* and *Characidium fasciatus* Reinhardt 1866 (Verissimo 1994) were predominant.

3. Materials and methods

Catches per unit effort (CPUE = number or biomass per 1000m^2 nets per 24hr) were recorded from October 1986 to September 1987; from October 1987 to September 1988 and from October 1992 to September 1993, using gillnets with 3.0–16.0 cm mesh. Fishes were identified and the standard length (SL; cm), total weight (W; g) and stage of gonadal maturation (immature, maturation, ripe and spent) of each were registered. Through analysis of their stomach contents (Hyslop, 1980; Hahn, 1991) fishes were classified as herbivores (HE), planktophagous (PL), iliophagous (IL); detritivores (DE), aquatic insectivores (AI), terrestrial insectivores (TI), benthivores (BE), omnivores (ON), or piscivores (PI).

Classification as residents (complete life cycle in the area), short distance migrants (lateral movements) and long distance migrants (longitudinal displacements) was based on information about reproductive strategies from Miyamoto (1990); Vazzoler, Menezes (1992) and Menezes,

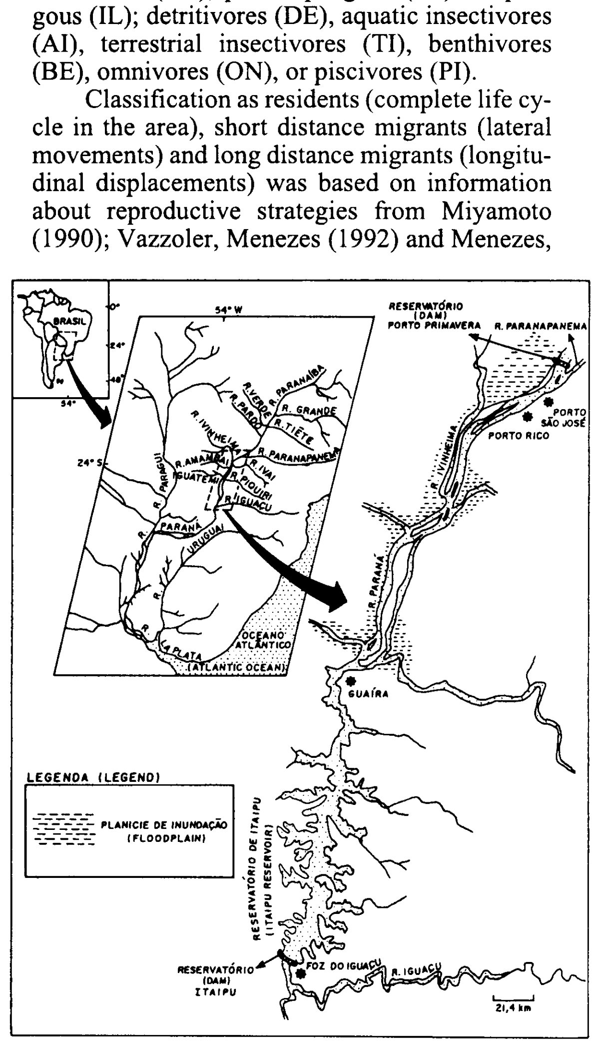

Fig. 1. Map of the region with sampling sites

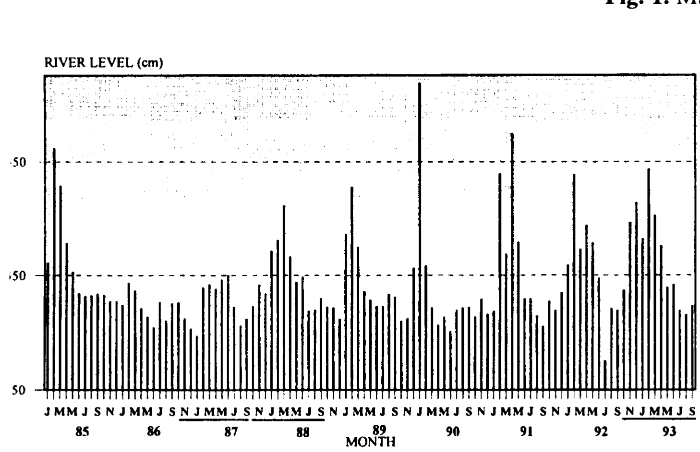

Fig. 2. Average monthly river levels in the River Paraná, in the municipality of Porto São José, Paraná, Brazil (marked months = sampling periods)

Vazzoler (1992). Classification of individuals as juveniles or adults was based on the standard length at which 100% of individuals in each species reached maturity (Suzuki, unpubl.).

Fluviometric levels of the River Paraná from 1985–93 were given by DNAEE (National Department of Water and Electric Power) collected from registers obtained at the Hydrometric Station of Porto São José (Fig. 1 and 2). The fluviometric level of 3.5 m was considered an overflooding level (Verissimo 1994) since the hydrometric index (Ihi) was determined from this level taking into consideration the area below the annual level curve on a standard scale (Valderrama Barco, Petrere Jr. 1994).

The diversity of species and eveness were evaluated according to Shannon's Diversity Index (Krebs 1989). The condition factor used for inference with regard to the nutritional state was calculated according to Ricker's (1975) proposal, selecting the size interval in which the variations of the condition factor per class size were smallest.

4. Results

Flood regime

Generally, the levels of the River Paraná are minimal from July to September, rising to a maximum from January to March (Fig. 2). Taking 3.5 m as critical flooding level (Verissimo 1994) and the monthly average levels, flooding was nil in 1986–1987 (Ihi = 0), moderate in 1987–1988 (Ihi = 199 mm^2) and high in 1992–1993 (Ihi = 592 mm^2). The amplitudes of annual variation were 1.68–4.62 m, 2.32–5.84 m and 2.42–6.64 m respectively. The floods lasted for 28 days in the first year, 136 days in the second and 168 days in the third. Maximum levels occurred in May 1987, March 1988 and February 1993. In the last two years peaks were coincident with the months of greater duration of floods, while in the first year the greatest number of days with floods occurred in June.

Diversity and abundance

In the floodplain, the Diversity Index (H'), Eveness (E) and the number of species increased gradually during the period with the occurrence of floods (Fig. 3). There were opposite tendencies in the annual variations of the Diversity Index and Eveness in the three principal categories of the floodplain's environment and a more pronounced increase in the number of species (Table I).

On the other hand, relative density (CPUEn)

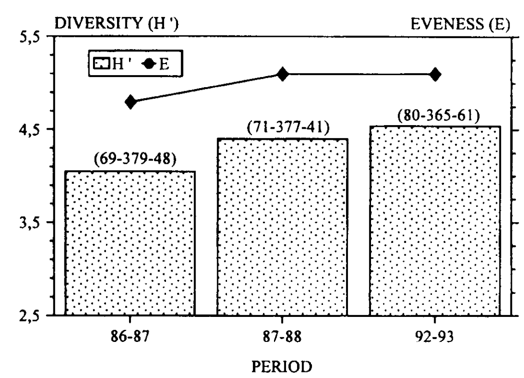

Fig. 3 Shannon's Diversity Index (H) and Eveness (E) estimated for the community of fishes in the floodplain of Porto Rico, Paraná, Brazil. Numbers in parantheses = (number of species – number of individuals per 1000 m^2 gillnet per 24 hr – weight per 1000 m^2 gillnet per 24 hr)

decreased with the increase of the flooded area. Biomass (CPUEw) increased from 48 kg (in 1986–1987) to 61 kg per 1000 m^2 nets per 24 h (in 1992–1993). The increase in living space and a greater capture of larger species may explain variations in relative density and biomass respectively.

Proportion among trophic categories

Among the eight trophic categories, detritivores species (iliophagous and true detritivores) were dominant (34–47% of individuals; 30–43% of biomass), followed by piscivores (30–31% of individuals; 31–53% of biomass). In the drought year (1986–1987) piscivores fish contributed

Table I. Number of species (s), Shannon's Diversity Index (H), Eveness (E), Density (CPUEn=no./1000 m^2 nets/24 hr) and Biomass (CPUEw=Kg/1000 m^2 nets/24 hr) per environmental category

	Lagoons			Channels			Rivers		
	86-87	87-88	92-93	86-87	87-88	92-93	86-87	87-88	92-93
s	47	49	56	43	51	52	54	58	68
H'	3.57	4.01	4.22	3.86	4.10	4.27	4.76	4.47	4.50
E	0.64	0.71	0.73	0.71	0.77	0.75	0.83	0.76	0.74
CPUEn	522.02	440.53	526.71	417.36	442.46	285.9	144.09	197.71	282.2
CPUEw	60.97	39.88	90.52	43.92	46.93	33.61	36.05	38.40	60.25

more than half the biomass captured (Fig. 4). Annual variations in density and in relative biomass increased towards the years of the biggest floods among herbivores, terrestrial insectivores and omnivores guilds, zooplanktivores and aquatic insectivores species decreased. Iliophagous species, dominated by *P. scrofa,* were infrequent during moderate floods (1987–1988). Probably due to recruitment failure following the drought of 1986–1987. But predominated in the year of the biggest floods (41% of the biomass). Detritivores fish, dominated by *L. platymetopon*, were more abundant in the first two years when floods were absent or moderate. However, all detritivores species are sedentary, show parental care and are largely independent of floods. Piscivore, prevalent in drought years, did not vary uniformly among their 23 species. *Hypophthalmus edentatus* Spix, 1829, the only zooplanktivore in the floodplain, had the greatest relative biomass in the first year in contrast to the benthivore.

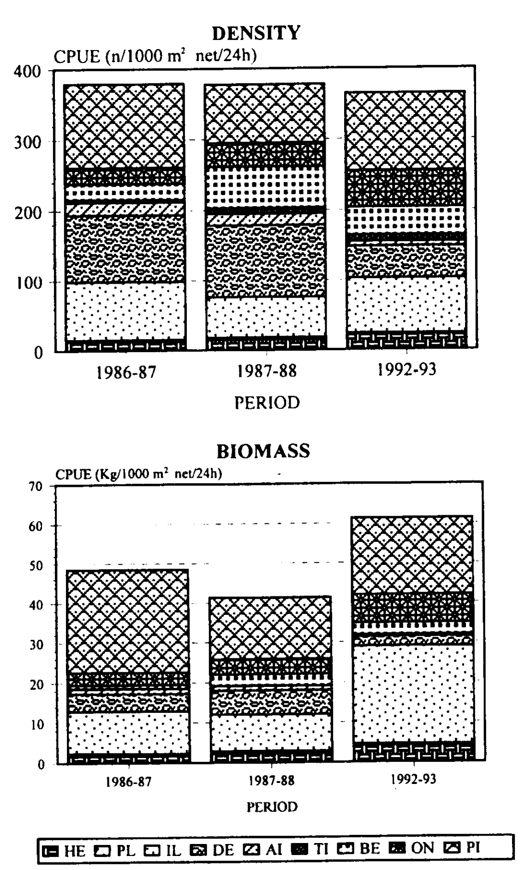

Fig. 4. Proportion between captures per unit of effort of the different trophic categories for each year (1986–1987 – overflow absent; 1987–1988 – moderate flood; 1992–1993 – high flood). (HE – herbivores, PL – planktivores, IL – iliophagous, DE – detritivores, AI – aquatic insectivores, TI – terrestrial insectivores, BE – benthivores, ON – omnivores, PI – piscivores)

Indicators of the nutritional state

During the years without floods (1986–1987), with moderate floods (1987–1988) and big floods (1992–1993) condition factors increased among herbivores (*S. borelli*), iliophages (*P. scrofa*) and omnivores (*P. maculatus*), but decreased among aquatic insectivores (*Auchenipterus nuchalis* (Spix, 1829)) and zooplanktivores (*H. edentatus*) (Fig. 5). These tendencies coincided with the CPUE variation of these groups. Among the piscivores there were distinct variation among the chief species. Condition factors of *H. malabaricus*, a middle sized species extremely abundant in the last year, increased; and of *S. spilopleura*, smaller in size and more abundant in the drought year, decreased. Condition factor of *I. labrosus*, a typical benthivores of the basin, decreased in the flood years; and of *H. littorale*, a less restricted benthivores, did not vary. Fishes with a terrestrial insects diet and detritivores, did not vary in condition factor.

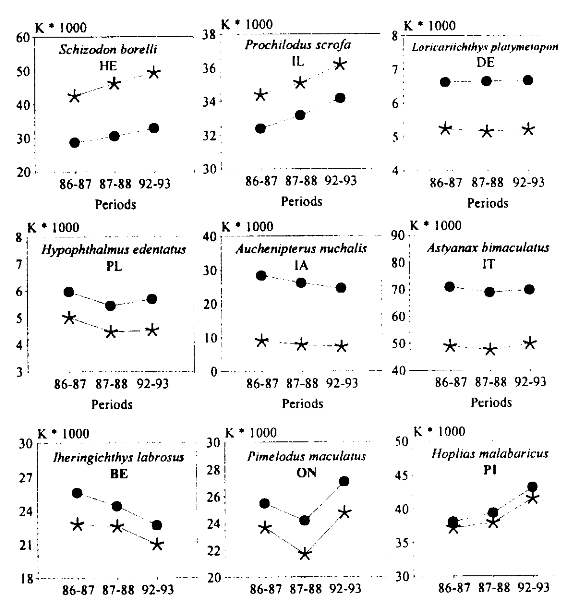

Fig. 5. Annual average values of the condition factor (K) for species of different trophic categories (• – males; * – females). (HE – herbivores, PL – planktivores, IL – iliophagous, DE – detritivores, AI – aquatic insectivores, TI – terrestrial insectivores, BE – benthivores, ON – omnivores, PI – piscivores)

Reproduction and abundance of juvenile forms

The mean annual CPUE of ripe and/or spent individuals of sedentary species was greater in the drought periods. The great difference between the years may have been caused by a larger flooded area in the last two years affecting absolute density and capturability (Fig. 6A). On the other hand, "reproducing" individuals of migratrory species were more abundant in the year of the biggest flood (1992-1993). Species with such a strategy do not spawn on the floodplain, but pass through it to spawn at the highest points of the basin, and so relatively few were caught. Short-distance migrants varied in an intermediate way.

The abundance of juveniles of reproductive types was low in the floodless year (1986–1987) (Fig. 6B).

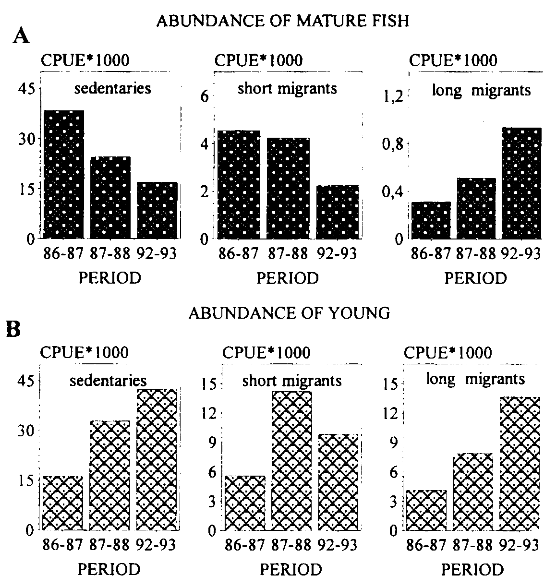

Fig. 6. Capture per unit of effort of mature individuals (A) and juveniles (B) per category of reproductive strategy and year. (See text for the definition of categories)

5. Discussion

Although the 48 great dams upstream diminish and delay the flood peaks, the chief influence on the community using this area is still the fluviometric regime (Thomaz 1991). In the last ten years levels insufficient to overflow the floodplain occurred due insufficient rain in 1984–1985, and 1985–1986 to water retention from the reservoir because of the previous year's depletion (Agostinho, unpubl.).

Since floods annex large extensions of the terrestrial environment to the water bodies seasonally (ecotonal zones), they produce great environmental fluctuations which affect the biological processes and the structure and functioning of present communities. For fish these fluctuations determine to a variable extent the availability of shelter and food, reproduction, growth and mortality rate, and the relationships in competition, predation and parasitism in the community. However, the incorporation of a great biomass by the aquatic environment may restricts availability of dissolved oxygen causing emigration or death of many fishes (Agostinho, Julio Jr. 1999). During the retracting water period, the desiccation of remaining pools and the predation by birds may also cause massive mortalities. Bonetto *et al.* (1969a) estimated that this mortality rate may be four times that due to the professional fishery in the lower River Paraná. Many species were selected by these stressing conditions and showed a high tolerance to variations in these environments. Verissimo (1994) found 21 species, with juveniles of big migratory species, in a 5 cm deep pool in the high River Paraná floodplain. During the period of retracting water many species, specially juveniles of big migratory species, abandon shallow areas and return to the river or confine themselves to permanent water bodies. Then, predation at the points of discharge is intensified (Agostinho, Julio Jr. 1999). More lasting floods act favourably on fish survival, allowing large individuals during the water retraction period and reducing the threat of predators on them.

Annual variations during the period, intensity and duration of floods should affect species with different life strategies differently, determining variations in the composition and structure of fish communities. A greater complexity in the structure of the environment in flood years should increase the colonization rate and may explain the increasing number of species in the floodplain during the study. The absence of floods (harshness condition) should affect negatively the richness of the species. However, variations in intensity and duration should increase species richness (intermediate level of disturbance) since they might prevent a competitively dominant species from excluding other species (Wootton 1990). The increase in richness of the species did not affect the diversity index of the floodplain's different environments uniformly. Diversity may become lower as a result of a lesser eveness in the distribution of individuals among the species (dominance), similar to that found in rivers. In this case, water retraction after the flood periods puts into the river a great number of juveniles of some species, which produce a rise in the dominance level. Because of their relative character biomass and density data estimated in this study restrict the possibility of conclusions, especially with regard to lagoons and channels whose areas were very variable during the years. However, in spite of a smaller area and of an expected greater absolute density in the first year, a propensity of greater relative density and biomass in the year of an average higher level was verified.

The high biomass of iliophagous species (mud-feeders) in water bodies with a high level variation has been observed by many authors (Bonetto *et al.* 1969a; Goulding, Ferreira 1984; Lowe-McConnell 1987; Agostinho, Zalewski 1995). This guild (dominated by *P. scrofa*) stood out as the greatest biomass in the big flood years, but it was preceded by piscivores in low flood years. Feeding at the bottom or at the branches or trunks of inundated vegetation, iliophagous species are favoured by the expansion of water bodies, as are herbivores, terrestrial insectivores and omnivores. Detritivores distinguished from mudfeeders by eating thicker detritus particles (Fugi *et al.*, 1996), varied inversely to iliophages. The apparent contradiction may be explained by the greater reproductive success for each species of this group in the drought years. This happens because these sedentary species, with parental care, reproduce independently of flood regimes. The same explanation may account for specific differences within the groups, as in aquatic insectivores and benthivores. Piscivores (with a high biomass and density during the three years under analysis) contributed more than half the biomass in the low flood year (1986-1987). When they and their prey were in restricted environments, shelter (permanent aquatic areas) was less available, and predation was favoured. The predominance of piscivores during low water in the floodplain has been discussed in the South American fauna (Bonetto *et al.* 1969b; Mago-Leccia 1970; Agostinho, Zalewski 1995) and in other continents (Welcomme 1979). The piscivores feeding spectrum is very wide: the great majority feeds alternatively on invertebrates (shrimps and Odonata nymphs) but preferences are regulated by prey size (Almeida *et al.* 1997). In the drought period, however, a prey variety decrease and specialization increased (Lowe-McConnell 1964; Winemiller 1989; Machado-Allison 1990).

Allochthonous organic material in the aquatic environment during floods allows some species to build up great energetic reserves to survive the drought periods and to elaborate gonadal tissues for reproduction in the next flood period (Welcomme 1979). In each trophic category the principal species increased their mean annual condition as abundance and relative biomass increased, except for terrestrial insectivores which did not vary and benthivores and piscivores which decreased. Gomes and Agostinho (1997) found low condition factor, visceral-somatic relationships and growth of *P. scrofa* juveniles in drought years or seasons. Food availability should not limit mud-feeding species (Sverlij *et al.* 1993), even in very prolonged droughts, but floods improve the nutritional quality of food rather than make food more available. Bowen (1983) found that detritus consumed by *Sarotherodon mossambicus* varied in aminoacid content from inadequacy to sufficiency for fast growth.

Similar to other South American basins (Welcomme 1979; Lowe-McConnell 1987; Machado-Allison 1990; Machado-Allison 1992; Vazzoler, Menezes 1992; Menezes, Vazzoler 1992) recruitment success in the high River Paraná basin is correlated with the time, duration and intensity of the floods (Agostinho *et al.* 1993; Agostinho 1994; Gomes, Agostinho 1997). This dependence is least in sedentary species with parental care, and greatest in migratory species which spawn at the highest points of the basin and whose young develop first in the flooded areas.

Vazzoler (1992) and Agostinho *et al.* (1993) found that high levels in summer correlated with spawning success of most species. Gomes, Agostinho (1997) concluded that recruitment levels were more dependent on flood duration (r=0.74) than on level reached (r=0.50). Floods were specially favourable to recruitment if they occurred during summer and autumn (r=0.84). The latter authors found that recruitment of *P. scrofa* failed in the Itaipu Reservoir stock when there were no floods in 1986–1987.

The maintenance of fish diversity in the last free segment of the River Paraná in Brazil, especially among the great migratory species, depends on the integrity of the land-inland water ecotones represented by the floodplain. The maintenance of this integrity should necessarily be linked to the disruption of human occupation in the region and to a greater rationalization of the operation of the dams upstream.

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