

Trophic Aspects of Fish Communities in Brazilian Rivers and Reservoirs

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ABSTRACT

Several studies about the freshwater fish communities of Brazilian river basins have been developed during the last few decades and their results have been published in scientific journals, thesis and internal reports. In this revision we summarise part of the information related to species richness, trophic structure and habitat use reported for streams, rivers and reservoirs. We try to identify patterns between equivalent habitats of the main river basins. Sampling explains most of the variability found between communities, but differences between streams are significantly related to latitude and differences between reservoirs are dependent on their size. The trophic structure of the communities also show common trends. Streams seem to have relatively high diversity and abundance of omnivores and insectivores, while floodplains are dominated by detritivores, and reservoirs and rivers channels have high abundances of piscivores. This structure is probably related to the productivity of the biotopes. The strategy of resource exploitation also show trends between equivalent habitats.

INTRODUCTION

There are approximately 5000 species of freshwater fish in South-America (Böhlke et al 1978) and a large fraction of this fauna is distributed in $8 \cdot 10^6$ km² in the Brazilian network of rivers. This network is divided in eight main river basins: Amazon, Tocantins, Paraná, Uruguai, São Francisco, and three South Atlantic basins (IBGE, 1992). Fish communities in these basins have been surveyed for many years, but the number of studies have been intensified in the last two decades. The increase in the effort was greatly accelerated

by the need to evaluate the impact of dam building in major rivers and the growing social concern on environmental issues.

The accumulated information about the fish fauna is spread in international and Brazilian scientific journals, but is also recorded in many unpublished thesis and reports of limited circulation. In the present paper we try to summarise part of this information, specially those dealing with α -diversity (within habitat accumulated diversity) and trophic inter-relationships. We also try to identify trends in trophic structure of fish assemblages living in equivalent biotopes of different basins.

We understand that the later approach has limitations due to the inadequacy of the data and/or methodological faults (Bayley and Li,

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1989). Fish communities often change their structure in relation to basin components (Barrela and Petrere Jr, 1994) and it is difficult to define the boundaries of these components, which fish populations often migrate across. However, this approach may optimize the large amount of data collected and provide some generalisations that can be tested later.

We divide the basins in 3 main biotopes: streams, rivers and reservoirs (Wellcome, 1985). We also analyse the rivers separated into their main components: the floodplain and the channels. Due to lack of data for many basins we grouped data of those connected. The Amazon basin, for example, comprise water bodies from the Amazon basin and Tocantins basin, and the Paraná basin includes rivers of the Uruguai and Paraná basins. We did not include data from true lakes and estuarine lagoons.

STREAMS

The biotope

Streams have been classified by authors as small rivers of low order, channeled during the dry season and with small floodplains during the rainy season, sometimes not persistent (Knoppel, 1970; Soares, 1979; Uieda, 1984; Garutti, 1988; Viana, 1989; Barrela, 1989; Bertolotti et al., 1990; Sabino e Castro, 1990; Silva, 1992). The water current ranges from 0.1 to 1.7 m·s⁻¹ and a high gradient is common. Rocks and pools often alternate as pool-riffle channel sequences, which together with the marginal vegetation increase the availability of small habitats. Dissolved oxygen is normally high. Temperature variation is seasonal in the southern

basins and dependent on air temperature. Water transparency, pH and conductivity are variable and linked to the geomorphology of the drainage basin. The water courses are at time shaded by gallery forest, but deforested shorelines are common in South and Central regions of Brazil. Marked seasonality occurs in the discharge of tropical and subtropical streams, which increase up to four folds during the wet season (Uieda, 1984; Garutti, 1988) and often with low predicability. Stream floodplains have been addressed in only few cases (Geisler e Annibal, 1986; Garutti, 1988; Prada-Pedreiros, 1992).

Community structure of streams

The structure of fish communities has been surveyed in several Brazilian streams of the major river basins and examples of species composition are available for the Paraná (Uieda, 1984; Caramaschi, 1986; Garutti, 1988; Barrela, 1989; Viana, 1989; Bertolotti et al, 1990; Penczak et al. in press), the Amazon (Knoppel, 1970; Soares, 1979; Silva, 1992) and other smaller basins (Costa, 1987; Malabarba and Isaia, 1988; Sabino and Castro, 1990). Due to their physical complexity and size, fish sampling has involved an array of equipment and techniques, usually used together, such as: traps, handnets, gill nets, hooks, rotenone, beach seine, electric fishing and underwater direct observation.

Fish size distribution has been addressed only in a few streams, where 75% of adult species were smaller than 150 mm. Occasionally, adults of visiting species were also caught (Penczak et al. in press; Borges, 1986; Ribeiro e Petrere Jr, 1990). The species richness is exemplified by a comparison between data of 17 similar sized and independent streams (Horton's order <4; maximum depth

<1.5m; and channel width <9m). Despite the differences in basins, species composition, sampling frequency (a week to 2 years) and area sampled (50m to 14000m), they have shown some remarkable similarities. The diversity ranged from 7 to 52 (Fig. 1). Prada-Pedreiros (1992) reported higher species richness for the stream floodplains of the Rio Negro basin, but he grouped several habitats and therefore was not considered here. Over 50% of the species were characiforms or siluroids, and the former was the most diverse group in 14 out of 16 streams. The remaining two were richer in siluroids gymnotoids and perciforms. A few symbranchids, cyprinodontids and tetraodontids are occasionally found. Over 75% of the species in streams were omnivorous (plant and animal consumer) or carnivores (invertebrate eater) (Fig 2). The remaining 25% species were detritivorous, herbivores and piscivores species. There was strong dominance of three or four species in each community, which totalled 40% of the biomass captured (Tab. 1). In most cases the dominant species differed between streams, but they were mostly omnivorous or carnivores (invertebrate eaters).

Multiple regression analysis of the α -diversity suggest that latitude and sampling effort explains 56% of the variation between 14 streams ($p=0.0043$). Other variables such as basin (Amazon, Paraná, and South-Atlantic) and total length of the stream are not significant and unfortunately the effect of the number of *piscine* predators, could not be tested, since they were available for a few streams. Sampling effort, estimated as the logarithm of the product of the stream length sampled (km) and sampling period (months) had, as expected, a positive relation to number of species. The latitude was inversely related to the diversity,

as has been shown for many organisms, including fish (Walker, 1989). Latitudinal gradients in diversity is frequently attributed to the less variable environment of the tropics (Lowe-MacConnell, 1987). From the available data on the environmental predictability of the streams it is hard to infer on its effect on diversity. Low latitude streams seems thermally more stable, than the sub-tropical ones, on the other hand rains and stream discharge are highly variable.

The use of space and stream habitats

The community structure changed along streams and time. More variation seemed to exist between different parts of the same stream than between streams of the same drainage basin. Fewer species occurred at the headwaters than at lower reaches (Garutti, 1988; Viana, 1989). Diversity index was higher in pools than in riffles (Soares, 1979; Viana, 1989), and seemed related to habitat diversity (Viana, 1989) and to season (Silva, 1992).

Some species have been associated with stream habitats, such as fast riffles, marginal vegetation and the bottom litter. Silva (1992) found that loricariids algivores were only captured within the vegetation, where as *Hyphessobrycon* were found mostly at mid-stream. Other species, such as the numerous *Astyanax* spp, explored the fast midstream habitats, however, the information available suggests that the majority of the species concentrated in the margins and bottom, where current speed is lower (Soares, 1979; Viana, 1989; Teixeira, 1989; Sabino and Castro, 1990). The species that prefer to explore the fast current sections have to cope with current speeds of up

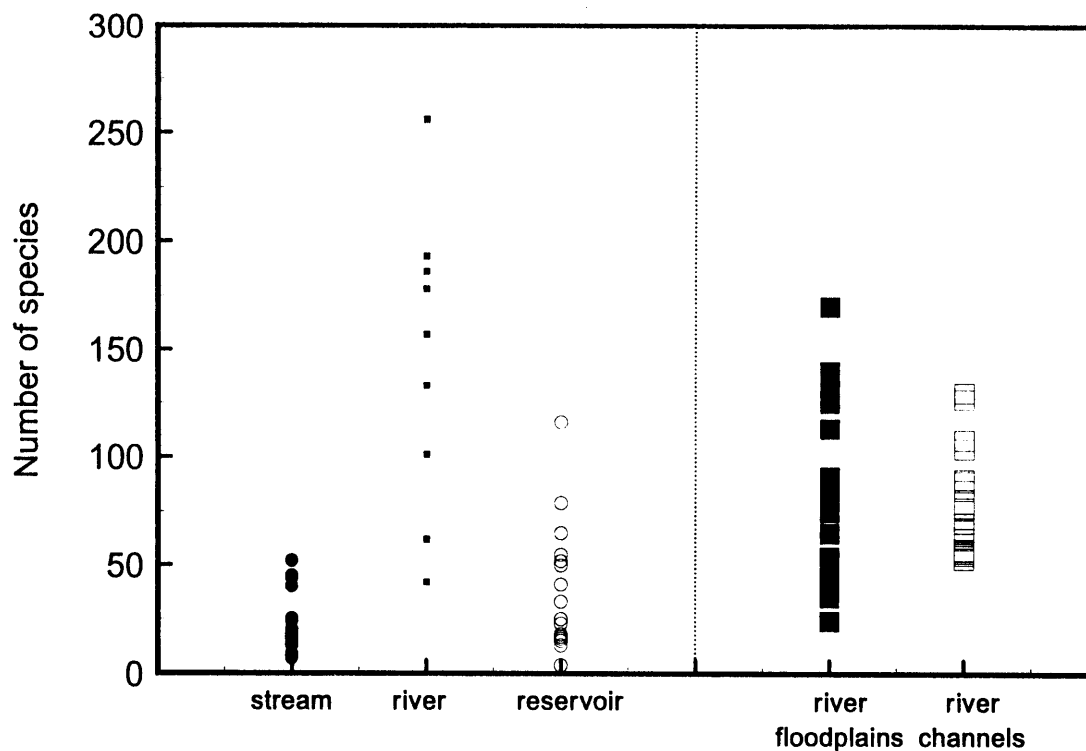
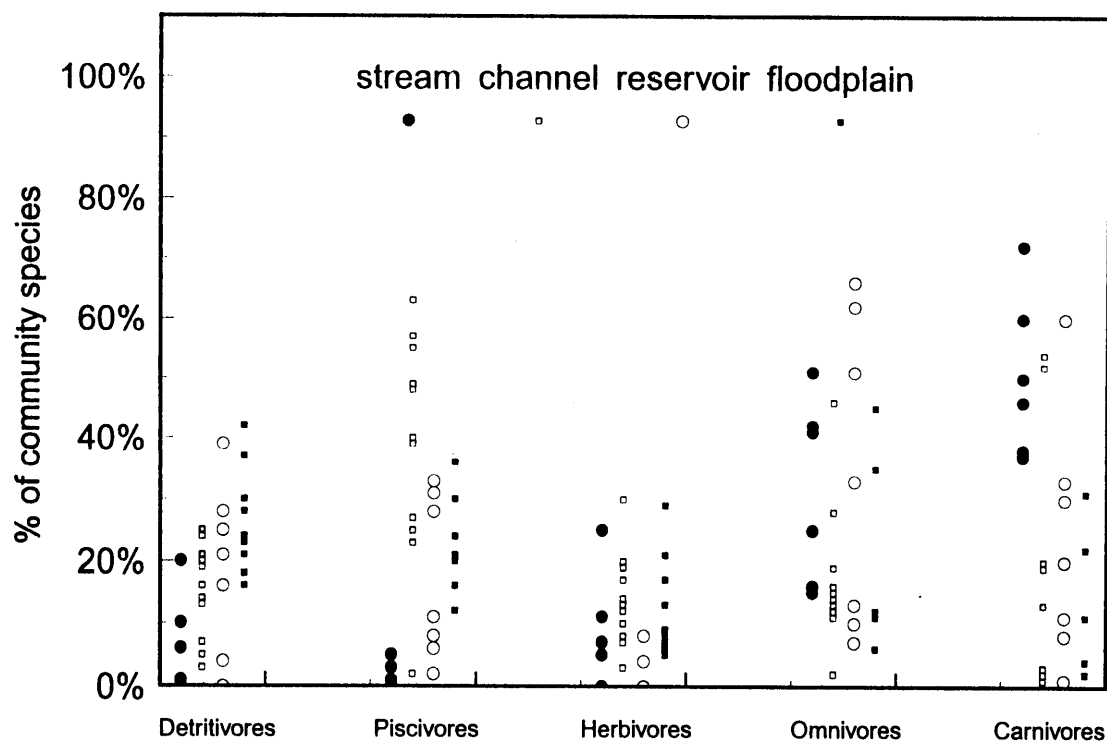


Fig. 1 – Species richness in fish assemblages of 17 streams, 9 rivers, 18 reservoirs (left side) and 20 river floodplains and 15 river channels (right side). Data for streams from: Knoppel, 1970; Soares, 1979; Uieda, 1984; Malabarba e Isaia, 1988; Garutti, 1988; Teixeira, 1989; Barreia, 1989; Viana, 1989; Sabino e Castro, 1990; Lowe-McConnell, 1991; Silva, 1992; Penczak et al, in press). Data for rivers from: Vazzoler et al, 1982; Bayley, 1983; Goulding et al, 1988; Merona, 1988; Santos, 1991; Ferreira, 1992; Barletta, 1994; Garcia, 1994; FUEM-NUPELIA/COPEL, 1994a). Data for reservoirs from: CETESB, 1976; Ferreira, 1984a; Castro e Arcifa, 1987; Romanini, 1989; Gehal, 1991; Amaral, 1993; Leite, 1993; Benedito-Cecilio, 1994; FUEM-NUPELIA/COPEL, 1994; Romanini et al, 1994; Santos, 1994; data for river floodplains and channels from: Costi et al, 1977; Vazzoler et al, 1982; Ferreira et al, 1988; Goulding et al, 1988; Merona, 1988; Bertolletti et al, 1990; Galetti et al, 1990; Santos, 1991; Ferreira, 1992; Catella, 1992; Barletta, 1994; Garcia, 1994; FUEM-NUPELIA/COPEL, 1994a; Verissimo, 1994.

to 10 body length•s⁻¹ for long periods, and therefore must have a high metabolic rate.

The dead leaves that accumulate in pools and at stream margins, also shelter a diverse fish fauna. Henderson and Walker (1986, 1990) working in an Amazonian stream found 20 species of fish living in the litter. These fishes, which are quite sedentary,

are distributed horizontally and vertically along the litter, in some cases reaching 0.5 m below its surface. Some of them seem highly specialised to exploit this habitat. *Phreatobius* sp, for example, a very small species living deep in the litter has no visible eyes and its body is bright red, probably due to high haemoglobin levels (Henderson and Walker, 1990).



TROPIC GUILDS

Fig. 2 – Frequency of species per trophic guilds in 6 streams, 12 river channels, 7 reservoirs and 9 floodplains. Data for streams from: Knoppel, 1970; Soares, 1979; Texeira, 1989; Viana, 1989; Sabino e Castro, 1990; Silva, 1992. Data for river channels from: Vazzoler et al, 1982; Ferreira et al, 1988; Goulding et al, 1988; Santos, 1991; Ferreira, 1992; FUEM- NUPELIA/COPEL, 1994a. Data for reservoirs from: Ferreira, 1984a, b; Romanini, 1989; Romanini et al., 1994; Gehal, 1991; Leite, 1993; Benedito-Cecilio, 1994; FUEM- NUPELIA/COPEL, 1994a. Data for floodplains from: Vazzoler et al, 1982; Goulding et al, 1988; Merona, 1988; Santos, 1991; Ferreira, 1992; Meschiatti, 1992.

Food chains and trophic aspects in streams

Stream fishes consumed mostly insects and plant matter. This composite diet, in many cases translated in the large number of omnivores found in the communities. Past reports have stressed the importance of allochthonous food sources for stream fishes (Knoppel, 1970; Welcomme, 1985;

Lowe-McConnell, 1987). Recent ones do not always corroborate these early findings. Algae and larval insects were in many cases equally important food resources (Costa, 1987; Texeira, 1989; Henderson and Walker, 1990; Sabino e Castro, 1990; Lowe-McConnell, 1991; Silva, 1992). However, the foodchain in stream appears to be mostly

TABLE I
Dominant species (summing more 40% of community in weight) and their main food in 32 different streams, river channels, floodplains and reservoirs.
1=abundance in numbers of individuals; 2=dominance based on data from Galleti Jr et al. (1990); 3=probably *Curimata cyprinoides*; 4=probably *Psectrogaster amazonica*; 5=sum only 30% of abundance.

SITE	BASIN	DOMINANT SPECIES	MAIN FOOD	REFERENCES
STREAMS				
Sant' Ana	Paraná	<i>Brycon americanus</i> , <i>Astyanax scabripinnis</i>	insects, plant parts	Viana, 1990
Barro Branco	Amazon	<i>Aequidens tetramerus</i> , <i>Bryconops inpai</i> ¹	insects	Knoppel, 1970
Candirú	Amazon	<i>Farlowella</i> sp., <i>Rinoloricaria</i> sp	algae	Silva, 1992
Porto	Madeira	<i>Astyanax fasciatus</i> , <i>Astyanax</i> sp ¹	insects, plant parts	Soares, 1978
Indaia	S-Atlantic	<i>Deuterodon iguape</i> , <i>Phalloceles caudimaculatus</i> ¹	insects, plant parts	Sabino e Castro, 1990
Bom Jardim	S-Atlantic	<i>Hyphessobrycon luitkeni</i> , <i>Gymnotus carapo</i> , <i>Aequidens</i> sp	insects	Teixeira, 1989
FLOODPLAINS				
Morateiro	Tocantins	<i>Curimata ciliata</i> , <i>Semaprochilodus brama</i>	detritus	Vazzoler et al, 1982
Tauá	Tocantins	<i>C. ciliata</i> , <i>Anodus elongatus</i>	detritus,algae	Vazzoler et al, 1982
Onça	Paraguai	<i>Curimatids</i> , <i>loricariids</i>	detritus,algae	Catella, 1992
Diogo	Paraná	<i>Curimata</i> sp., <i>Prochilodus lineatus</i> ²	detritus,algae	Meschiatti, 1992
Rei	Amazon	38% piscivores spp, 18% detritivores spp	detritus,fish	Merona, 1988
Buiu-açú	Negro	<i>Chilodus punctatus</i> , <i>Curimata plumbea</i> ¹	detritus, insects	Goulding et al, 1988
Tamaquaré	Negro	<i>Curimata</i> sp ¹	detritus	Goulding et al, 1988
Salgado	Trombetas	<i>Pellona castelnaena</i> , <i>Plagioscion squamosissimus</i>	fish	Ferreira, 1992
3 lakes	Madeira	<i>Auchenipterichthys thoracatus</i>	insects	Santos, 1992
4 lakes	Paraná	43% piscivores spp, 39% detritivores spp	detritus, fish	Agostinho et al, 1994
RIVER CHANNELS				
Mamoré	Madeira	<i>Serrasalmus nattereri</i>	fish	Santos, 1992
Maraujá	Negro	<i>Microchemobrycon</i> sp., <i>Hemigrammus mimus</i>	detritus, invertebrates	Goulding et al 1988
Rio Daraá	Negro	<i>Astyanax</i> sp., <i>Hyphessobrycon</i> sp	fish, invertebrates	Goulding et al 1988
Paraná	Paraná	49% Piscivores spp, 25% detritivores spp	fish, detritus	Agostinho et al, 1994
Mucajai	Negro	<i>Boulengerella ocellata</i> , <i>Hydrolicus scomberoides</i>	fish	Ferreira et al, 1988
Breu Branco	Tocantins	<i>Boulengerella maculata</i> , <i>H. scomberoides</i> , <i>Curimata kneri</i> ³	fish, detritus	Vazzoler et al, 1982
Icangui	Tocantins	<i>A. elongatus</i> , <i>Auchenipterus nuchalis</i> , <i>Curimata ciliata</i> ⁴	plankton, insects, detritus	Vazzoler et al, 1982
Itupiranga ⁵	Tocantins	<i>B. maculata</i> , <i>C. kneri</i> ³ , <i>Hemiodus unimaculatus</i>	fish, detritus, algae	Vazzoler et al, 1982
RESERVOIRS				
Itaipú	Paraná	<i>P. lineatus</i> , <i>Hypophthalmus edentatus</i> , <i>P. squamosissimus</i>	fish,detritus,plankton	Benedito-Cecilio, 1994
Volta Grande	Paraná	<i>Steindachnerina insculpta</i> , <i>P. squamosissimus</i> ,	fish, detritus	Santos, 1994
Rosana	Paraná	<i>P. squamosissimus</i> , <i>P. lineatus</i> , <i>Pirinampus pirinampu</i>	fish, detritus	Romanini et al, 1994
Promissão	Paraná	<i>P. squamosissimus</i> , <i>Serrasalmus spilopleura</i>	fish	Amaral, 1993
Alagados	Paraná	<i>Geophagus brasiliensis</i> , <i>Hoplias malabaricus</i>	fish, detritus	Gehal, 1991
Segredo	Paraná	<i>H. malabaricus</i> , <i>Pimelodus ortmanni</i> , <i>Hypostomus myersi</i>	fish, detritus, algae	FUEM-COPEL, 1994
Tucuruí	Tocantins	<i>Serrasalmus rhombeus</i> , <i>Serrasalmus geryi</i>	fish	Leite, 1993
Curua-Una	Amazonas	<i>S. rhombeus</i> , <i>Hemiodus</i> sp	fish, algae	Ferreira, 1984a, b
Marimondo	Paraná	<i>Pimelodus maculatus</i> , <i>P. squamosissimus</i>	fish, insects, detritus	Santos et al, 1994

supported by allochthonous primary production, since aquatic insects seem to rely on forest litter decomposers (Walker et al, 1990).

Few species have been classified as detritivorous, despite the occasional presence of detritus in the diet of many. Litter has been reported to be abundant in pools of the upper and middle reaches (Soares, 1979; Garutti, 1988; Viana, 1989; Henderson and Walker, 1990; Lowe-McConnell, 1991; Walker, 1993), but detritivorous fish were found mostly in the lower reaches of streams (Garutti, 1988; Viana, 1989).

Fruits and leaves were consumed by many species, but in small amounts (Soares, 1979; Viana, 1989; Silva, 1992). Despite their occurrence in stomach contents little is known about the types of fruits and leaves consumed. The low volume associated with high frequency of occurrence in fish stomachs may reflect their low abundance in streams rather than low demand by fish. *Brycon* sp, for example, forage on fruits and insects in the floodplains, but when visiting low order streams rely on insects, algae and flowers (Borges, 1986).

Filamentous algae are scratched out of rocks and plant surfaces mostly by specialised loricariids (Costa, 1987; Silva, 1992). *Astyanax* spp, *Cheirodon* spp and poecilids species also forage on algae, which they appear to graze on marginal vegetation (Costa, 1987; Viana, 1989; Teixeira, 1989; Sabino e Castro, 1990). Its consumption appears to be higher in communities exploiting open streams, where light incidence favours its growth. No reference to the foraging on *Batrachospermum* spp (Rodophyta) has been made, despite its abundance in Amazonian streams.

The piscivorous species has been poorly stud-

ied in streams. The guild represent 13% and 0.1% of the biomass of primary and secondary consumers in an Amazonian and Paraná streams, respectively (Soares, 1979; Viana, 1989). *Hoplias malabaricus* is the larger common predator reported for streams.

RIVERS

The biotope

Flood rivers can be divided in two main components the channels, the lotic component and the floodplain, the lentic component (Welcomme, 1985). Flood rivers are variable in size and discharge. We considered in this chapter only those rivers of the main hydrographic basins and their tributaries of last but three orders, in which most fisheries studies have concentrated.

Discharge is highly seasonal, depending on the run-off of precipitation in the catchment area (Welcomme, 1985). The flow regime can increase smoothly such as in the Rio Amazonas and Rio Paraná, with a predictable flood peak or irregularly with many small peaks such as in Rio Tocantins, Rio Trombetas and Rio Uatumã. The channel waters carry a variable load of sediments, depending on the geologic characteristics of the drainage basin and land use, which affects the light penetration in the water. Flow in the main channel is often turbulent, reaching velocities above $2 \text{ m} \cdot \text{s}^{-1}$ at midstream, and completely mixing of water column. Secondary currents move the water at speeds higher than $0.3 \text{ m} \cdot \text{s}^{-1}$ in a plane normal to the axis of the primary flow (Thorne et al., 1985). In the central part of the channel, helical skew-induced flow produces inward velocities near the bed, which

sweeps the bedload towards the inner bank (filling bank), and at the outer bank (cutting bank) a small cell of reverse rotation moves towards the surface. Water current reduces near the banks and bottom. Reported currents 2 m off filling banks in the Rio Solimões ranged from 0.1 to 0.4 m •s⁻¹ (Junk, 1973; Araujo-Lima, 1984) and is expected to be much faster in the cutting banks.

The channel bed may be silty, clayey or sandy and sometimes alternated with rocky pools or rapids. Debris, from the bank vegetation or exported from the adjacent floodplain, are colonised by invertebrates, and accumulate near the bed, even in large rivers such as the Rio Amazonas. Banks are covered by trees and/or macrophytes, which offer shelter and food for fish, specially during the high water season. Rapids are covered with macrophytes and algae. During the low water season muddy or sandy beaches or slopes develop on the banks.

Side channels connect the main channel to floodplain lakes before the main channel overspill. Their flow velocities and direction strongly depend on the hydrological cycle. Different from the main channel, they may not flow at all times of the year and even dry out during the low water season. Detailed descriptions of limnological features of river channels are described elsewhere in this book.

The floodplains are seasonal environments receiving periodically a water inflow from the main channels. Their size depends on the geomorphology of the plain and the main river discharge and therefore changes seasonally. They extend over 92400 km² along the Amazon main stem, 62000 km² along major Amazon tributaries (Sippel, 1992) and 15000 km² in Upper Paraná

(Bonetto e Wais, 1990). Floodplains can be divided in two components: the plain, which is periodically inundated, but dries out during the low water periods and the lakes that hold water during the dry season (Welcomme, 1985). The main floodplain habitats are: flooded forest, floating meadows, open waters, and flooded grassland (champs) (Merona, 1988, Goulding et al., 1988; Garcia, 1994). Floodplain lakes (called lagoons in the Paraná basin) are formed in oxbows, meander depressions or residual channels. Sippel et al. (1992) estimated that the Amazon floodplain lakes occupy only 11% of the area. Small lakes are predominant (90%), but those larger than 2 km² total more than 50% of the total lake area. The floodplain used by the aquatic vegetation (macrophytes and flooded forest) totals a maximum of 60 to 70% of the total area (Junk, 1985a; Sippel et al., 1994), but these proportions change during the year, as well as, between different regions of the basin. Floodplain areas can shrink to less than 20% of total area during dry season (Junk, 1985a; Veríssimo, 1994), what may have potential effects on the density dependent processes acting on populations, such as predation pressure and competition for food and space. Views of system functioning are described in Welcomme (1985) and Junk et al. (1989).

Community structure in rivers

Few studies have surveyed the lentic and lotic components of flood rivers (Vazzoler et al., 1983; Bayley, 1983; Merona, 1987,1988; Santos, 1991; Ferreira, 1992; Goulding et al., 1988; Godinho et al., 1988; Agostinho et al., 1994), and effectively sampled depths below 5 m (Barletta, 1994). The species richness found in ten surveys varied from

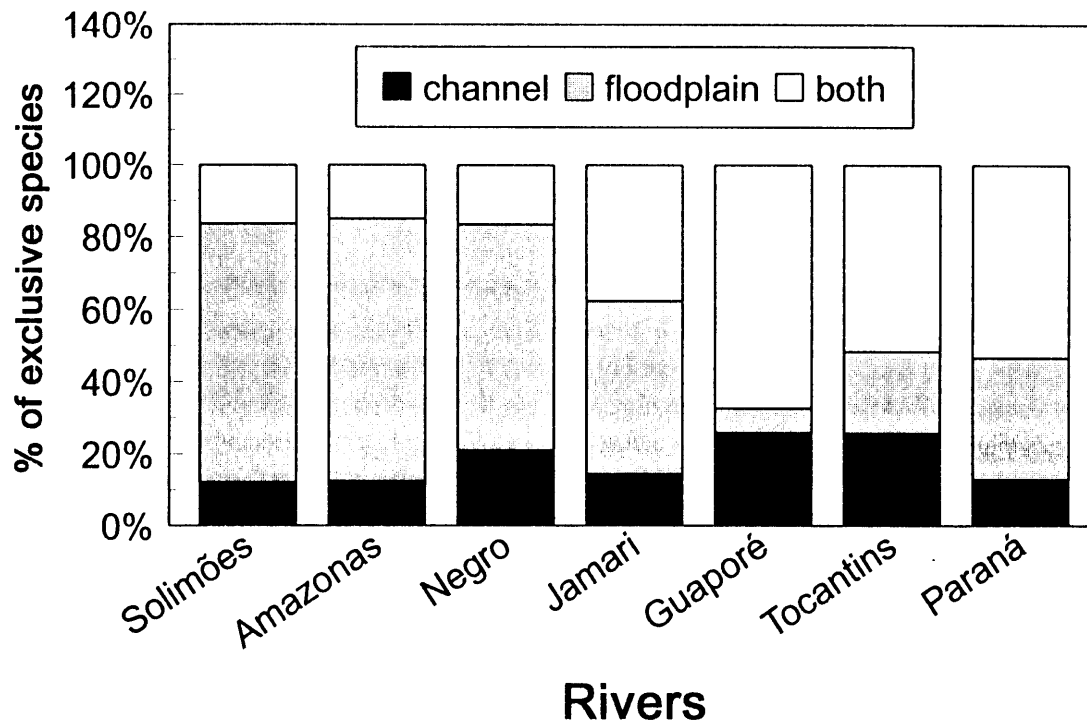


Fig. 3 – Frequency of riverine species occurring exclusively in river channels, floodplains and in both biotopes for 7 rivers communities. Data from: Rio Solimões (Bayley, 1983; Barletta, 1994); Rio Amazonas (Merona, 1988; Barletta, 1994); Rio Negro (Goulding et al, 1988; Garcia, 1994; Barletta, 1994); Jamari and Guapore (Santos, 1991); Tocantins (Vazzoler et al, 1982); and Rio Paraná (FUEM- NUPELIA/COPEL, 1994a).

41 to 256 (Fig. 1). Approximately 11% to 27% of the species occur exclusively in the channels (Fig. 3). The proportions of species occurring only in the floodplain and in both, floodplain and channel, are highly variable between rivers (Fig. 3). This difference may be caused by sampling bias. The channel of the Rio Amazonas, Rio Negro and Rio Solimões have been sampled up to 30 m depth, contrasting to the other river channels that have been fished only near the banks. Despite those possible bias, it seems to exist a difference between both fish assemblages, since the number

of species exclusive of rivers channels were quite stable. Therefore their diversity were addressed separately.

RIVER CHANNELS

Channel communities have been studied in the Amazon basin (Costi, 1977; Santos e Carvalho, 1982; Vazzoler et al., 1982; Merona, 1987; Ferreira et al., 1988; Goulding et al., 1988; Santos, 1991; Ferreira, 1993; Barletta, 1994) and the Paraná basin (FUEM-NUPELIA/Itaipu-Binacional, 1990a; Bertoletti et al., 1990;

Agostinho et al., 1994). Most of these studies aimed to evaluate the impact of hydroelectric dam building on river fish communities. Sampling has been done, chiefly, with gill nets, long lines, traps, seines and cast nets, and in two cases with trawls, as well.

Size distribution is still unknown, but small (~5 cm) and very large sized adults have been recorded in channels of the Amazon and Paraná basin (Goulding, 1980; Barletta, 1994). Eggs, larvae and juveniles are also present (Araujo-Lima, 1984; Petry, 1989; Araujo-Lima et al. in press). Species number in ten channels sections ranged from 55 to 127 (Fig. 1). An analysis of the differences between channels did not show significant effects from basin, latitude and sampling frequency. Otophisians (Characiformes, Siluroidei, Gymnoidei) totalled 87% of the species, but the proportion of each one of these groups changed markedly in relation to habitats. Few species of other groups, such as perciforms, clupeiforms, tetraodontiforms, pleuronectiforms, are also present. Piscivory is not only the most diverse guild in the channels of the Amazon and Paraná basins, but in many cases comprised also the highest fish biomass (Tab. 1).

The higher diversity and biomass of piscivores in river channels are probably related to their low autochthonous production. Piscivorous may prey upon floodplain foragers and detritivorous and carnivorous be supported by exported floodplain carbon (Junk et al., 1989). However, some rivers, with low turbidity, are important caveats to this argument, since they seem to have enough primary production to support high biomasses of algivores, even during high water season when the plain habitats are avail-

able (Vazzoler et al., 1982).

RIVER FLOODPLAINS

Examples of floodplain fish assemblages are available for the Pantanal (Catella, 1992; Palmeira, 1993), Paraná (Galetti Jr et al., 1990; Agostinho et al., 1994; Verissimo, 1994), Amazon (Junk et al., 1983; Goulding et al., 1988; Ferreira et al., 1988; Garcia, 1994), and São Francisco basins (Sato et al., 1987). The fish were sampled with assorted gear, such as sets of gill nets, dipnet, seine net, trawls, rotenone, line and pole, trap and hand net. Seines were used to survey the assemblages of the floating meadows, open shores and of shallow lakes (Junk et al., 1983; Araujo-Lima et al., 1986b; Ferreira et al., 1988; Bayley, 1988) and trawls to sample the midwater and bottom of open water habitats (Garcia, 1994). Both gear allowed the authors to estimate habitat biomass. Gill nets have been useful in sampling the flooded forest and other structurally complex habitats. Size distribution of adults has been barely reported in community studies and the amount of the small species has been underscored by sampling gear. It ranges from adults measuring 20 mm, such as *Microphilypnus* sp, one of the smallest vertebrates, to over 1800 mm in *Arapaima gigas* in the Amazon and *Pseudoplatystoma corruscans* in the Paraná basin. The limited data shows that 75% of the species are smaller than 200 mm tl (Goulding et al., 1988), a figure close to that presented for the streams. The floodplains are also exploited by juveniles and larval fish from local spawning populations or emigrants from adjacent rivers (Bayley, 1983; Araujo-Lima, 1984, 1994;

Sato et al., 1987; Goulding et al., 1988; Petry, 1989; Galetti Jr et al., 1990; Agostinho et al., 1993, 1994).

Species richness varied from 36 to 180 (Fig. 1). Amazonian floodplains have significantly higher a diversity (ANCOVA; $N=16$; $p=0.0014$) than Parana basin floodplains. This effect is probably related to the size of the basins or the floodplain which could no be accessed from available data. Sampling frequency was not significant. The highest number of species was found in the floodplains of the Rio Amazonas and is probably underestimated, since most sampling has been done with gillnets (Zaret, 1984; Merona, 1988). The lowest value (37 spp) was reported for 9 floodplain lakes of the Rio São Francisco (Sato et al, 1987), and the richness of individual laggons may be lower. Characiforms and siluroids dominated 15 communities totalling over 70% of the species. These were followed by the cichlids, gymnotoids, clupeids, scianids, osteoglossids, lepidosirenids, cyprinotids, tetraodontids, soleids and belonids. Similar results were also found in floodplains of Rio Madeira (Goulding, 1980), and São Francisco basins. The only exception was the Upper Paraná basin, where siluroids have more taxa (Agostinho et al., 1994).

Most trophic guilds were well represented (Fig. 2), except the planktivorous, which were never more than 7% of the species. Communities were dominated by one species (>30%) and the abundance of three to four species totalled more than 45% of the community biomass (not considering the bias introduced by undersampling small fishes). Detritivorous species were the highest ichthyomass in eight out of ten floodplains with clear species dominance (Tab. 1). Bayley (1983)

and Sato et a., (1987) estimated that detritivorous biomass represents 25% and 42% of the communities of Solimões and São Fransisco basin lakes, respectively.

The use of space and river habitats

RIVER CHANNELS

Species richness (S) and composition seems to change in relation to habitats. Sampling sites with lower current, such as bays and deposition banks rocky pools and areas near rapids have shown a higher number of species ($67 < S < 130$) than the midstream bottom ($53 < S < 77$). Characiforms diversity seems higher in rapids and near the banks (>54%). Inversely the Siluroidei and Gymnotoidei proportions in the communities appear to be higher near river beds (Santos e Carvalho, 1982; Barletta, 1994; Agostinho et al., 1994), where they totalled 80% of the species (Barletta, 1994). The species of these groups, however, were concentrated in the 10 to 30 m deep sections of the channel. Mid-channel seems to be occupied mostly by the large catfish predators, such as *Phractocephalus hemioliopterus* and *Brachyplatystoma* spp (Zuanon, 1990). Agostinho et al., (1994) also reported the presence of large siluroids in the main channel of River Paraná. Long term trawling studies are being conducted now along the whole Amazon river (Cristina Fernandes and John Lundberg, pers. com.), but sampling, is still needed to check if this trend occurs in other channels. The fast water current in the midstream of large rivers probably limits the use of this habitat to small fishes, this may explain why species concentrate near the banks, where the current is slowest.

The main channels are an important route for migrations used by many floodplain and riverine species. River migrations have been intensively studied in the Paraná basin (Godoy, 1957, 1959, 1975). The best known case is *Prochilodus scrofa* (*P. lineatus*), whose migration was studied by tagging in the rivers of the Upper Paraná basin (Godoy, 1959; Toledo et al., 1986). *P. scrofa* migrate upriver to spawn in the tributaries and then downriver back to their feeding grounds. Equivalent movements were reported for other populations of this species (Agostinho et al., 1993). Tagging experiments undertaken in the Rio São Francisco and its tributaries, has shown movements of 50- 530 km upstream and downstream of *Prochilodus* spp and *Duopalatinus emarginatus* (Paiva and Bastos, 1982). In the rivers of the Amazon the migratory movements are more complex. They migrate twice a year for reproduction, feeding and dispersion purposes. At least 19 species have been identified leaving the floodplain and low nutrients tributaries, migrating upstream in white water channels during the falling water period and dispersing again (Goulding, 1980; Zaniboni Filho, 1985; Fernandes, 1989; Ribeiro e Petrere Jr, 1990). The schools return to white water channels to spawn in the beginning of the flood. Among them are important species to local fisheries such as: *Semaprochilodus* spp, *Brycon* spp, *Prochilodus* spp, *Mylossoma* spp, *Colossoma macropomum* and others. Hypotheses about the adaptive significance of these complex movements are presented by Goulding (1980), Fernandes (1989) and Ribeiro e Petrere Jr (1990). A different pattern was, however, described for two species of the Rio Tocantins, where

migrations are similar to those of the Paraná basin (Carvalho e Merona, 1986). Siluroids, such as *Brachyplatystoma vaillantii*, *B. flavicans*, *B. filamentosum* and *Paulicea luetkeni* also move along the river yearly (Barthem et al., 1991), mainly during falling waters. Their migration, however is less understood.

Larval fish drift occurs in the channels during most of the year. Araujo-Lima (1984; in press) recorded the drift of characiform and tetraodontiform larvae in the Amazon river which peaks during the beginning of the annual flood. Larvae densities were, however, 2 to 3 orders of magnitude higher in specific sites of the banks of the Amazon (Araujo-Lima, 1984; Nascimento, 1992), near river and lake mouths. These patches were probably caused by the spawning of floodplain fish and/or transport by secondary currents. The larvae stay in the river for a short period (Araujo-Lima, 1984) and only juveniles of siluroids, *Plagioscion* spp and *Raphiodon* spp stay in the channel longer (Barletta, 1994). Nascimento (com. pers.) also observed siluroids, characiforms and gymnotoids larvae drifting in the Rio Paraguai in the beginning of the flood.

RIVER FLOODPLAINS

The habitats of floodplains have different species composition and abundance. During the high water season in Lago do Rei, Central Amazon, for example, the fish biomass in the open waters was significantly higher than in the flooded forest and flooded champs, but similar to the floating meadows (Merona, 1988). The number of species were similar in all habitats of the lake (average= 49; sd=13), but not the species composition. As one would expect piscivores were common in all habi-

tats, but open water had higher biomass of planktivorous species, and shore habitats has shown higher proportions of bottom feeders and herbivores species (Merona, 1988).

The same seems to occur in Lago do Prato, in the Arquipelago of Anavilhanas. The open water was dominated by insectivorous and planktivorous species (Garcia, 1995). These species were not found by Goulding et al. (1988) in the flooded forest surrounding the same lake. The largest fraction (60%) of the flooded forest fish community were eating terrestrial and aquatic plants and detritus (Goulding et al., 1988). Predators summed an important part of the biomass in both habitats. When the water level was low and the flooded forest was not available species typical of this habitat, such as *Semaprochilodus taeniurus*, *Curimatella meyeri* and *Hemiodus unimaculatus*, all detritivorous, become important part of the open water community (Garcia, 1995).

However, habitat use and activity period change within species daily and seasonally. The same species may exploit shore and open water, but at different periods of the day and for distinct activities. Stomach full characiforms and cichlids species, for example, migrate to the shore at dusk, where they rest at night (Barthem, 1987). At dawn they move to the open water to feed again (Barthem, 1987). Gymnotoids seems to have the opposite behaviour, migrating to the middle of the lake at night and returning to the shore during the day (Barthem, 1987). Zaret (1984) found that *Moenkhausia dichrourea* and *Ctenobrycon spilurus*, two small characids, migrate to the open water for a few hours a day, at dawn and dusk, to prey upon zooplankton, returning to the floating meadows later. Floodplain species migrate towards the ad-

jacent river to spawn or escape stressing environmental conditions caused by low water level (Fernandes, 1989). A good account of behavioural aspects of habitat use is given in Sazima (1986).

The availability of dissolved oxygen plays a key role in the species assemblages and habitat definition. Junk et al. (1983) found low species richness in areas of Lake Camaleão, Central Amazon, with lower dissolved oxygen concentrations. The assemblages in oxygen deficient areas of the lake were characterised by osteoglossids, erythrinids, loricariids, *Electrophorus electricus*, *Symbranchus* sp, *Lepidosiren paradoxa* and others species able to use atmospheric oxygen to some extent. The areas with better dissolved oxygen supply had some of these species, but also many others without air-breathing capabilities. Oxygen supply and habitat complexity also drive the diel distribution of juveniles in Amazonian and Paraná lagoons (Araujo Lima et al., 1986b; Soares, 1993; Verissimo, 1994).

Food chains and trophic aspects in rivers

The food of riverine fishes has been the focus of many studies in the Amazon (Goulding, 1980; Almeida, 1984; Santos, 1981, 1982; Aragão, 1981; Paixão, 1980; Goulding and Carvalho, 1982, 1984; Soares et al., 1986; Araujo-Lima et al., 1986b; Araujo-Lima and Hardy, 1987; Goulding and Ferreira, 1984; Carvalho and Goulding, 1985; Borges, 1986; Goulding et al., 1988; Braga, 1990; Leite and Jegú, 1990; and others) and Paraná basins (Basile-Martins et al., 1986; Fugi and Hahn, 1991; Catella, 1992; Meschiatti, 1992; Hahn et al., 1992; and others). The categories of food consumed, not in order of importance, are: fruits, seeds, flowers and leaves of flooded forest trees

and macrophytes, macrophytes roots, algae, detritus, zooplankton, terrestrial and aquatic insects (larval forms), aquatic invertebrates (crabs, shrimp, nematodes, mollusc, porifera, annelid, bryozoa), and fish (flesh, blood, scales and fins). Feeding specialisation is less common than feeding opportunism. Specialisation is probably not adaptive in communities exploiting ephemeral habitats, such as those of the floodplains. *Serrasalmus* spp, a piscivorous fish, for example, also forages on plants and fruits (Leão et al., 1991) and many species classified as herbivorous, occasionally prey on insects and invertebrates. Junk (1985b) suggested that to buffer the fluctuation in food availability many species build up fat reserves during the flood season which will provide them additional energy during low water period, when food supply is limited. High degree of diet overlap was found between species (Santos, 1981; Almeida, 1984). However, it does not necessarily translate to competition. In the Central Amazon floodplain, a community with a high degree of diet overlapping, had no significant density dependent effect on growth between potential competitors (Bayley, 1988), suggesting that there was enough resources to be shared.

Most studies in the Amazon and Paraná have dealt with adults of large size fishes, (<150 mm) and their juveniles. The feeding habits of small size and larval fishes remain largely unknown, except by the assemblages of Rio Negro (Goulding et al., 1988) and other less extensive studies (Zaret, 1984; Araujo-Lima et al., 1986b). The available information suggest that, like in the streams, they prey mostly on allochthonous and autochthonous invertebrates, but detritus and small fruits are also consumed. The food of larval fish has not been intensively studied, probably due to taxonomical

handicap. The current hypothesis is that larval fish prey upon the micro-crustacea living in the roots of the aquatic macrophytes (Goulding, 1980; Araujo-Lima et al., 1986b), but some exceptions suggest that it is not the rule. Aragão (1981) reported that larval *O. bicirrhosum* forages on micro-algae and Araujo-Lima and Hardy (1987) found larval *S. insignis* consuming detritus. Some evidences indicate that the ontogenetic shift towards the adult type of diet is fast and occurs early in the larval period (Araujo-Lima et al., 1986b; Araujo-Lima and Hardy, 1987).

Fruits and seeds are part of the diet of 10 to 30% of the species in the floodplain of the Amazon (Merona, 1988; Goulding et al., 1988) and few species of Paraná basin are also frugivorous (Basile-Martins et al., 1986; Hahn et al., 1992; Souza-Stevaux et al., in press). Most species consuming fruits and seeds also use other food items, certainly an adaptation to overcome the seasonal availability of forest foods. The forest is flooded for four to eight months (Goulding, 1980; Aires, 1993) and since the plants have different fructification periods the total offer lasts for the whole flood. Fish may forage on as much as 42 species of fruits and seeds (Paixão; 1980; Goulding, 1980; Borges, 1986; Rankin-De Merona, 1988; Zuanon, 1992). Floodplain seed production is still unknown for most species, but in one hectare there is at least 40 trees that produce edible seeds (Aires, 1993; Piedade, 1985; Rankin-de Merona, 1988). Deforestation of the flooded forest can threaten the supply of seeds to the fish fauna. Bayley (1983) estimated that only 53% of the original "varzea" forest (white water flooded forest) remains near Manaus.

Fruits and seeds consumed by fish have vari-

able nutrient contents. Some are rich in proteins and energy, such as Euphorbiaceae and *Pseudobombax munguba* seeds which have 16-21% (dry weight) of protein, 19-26 kJ·g⁻¹ and low water content (<50%). Other fruits and seeds have lower protein content, but are higher in carbohydrates, such as seeds of *Oriza* spp, palm trees and *Cecropia* (Piedade, 1985; Roubach, 1992; Waedoff, 1991; Aguiar pers. com). Some may not be readily digested by fish. Roubach (1992) reported that juveniles of *Colossoma macropomum*, an important frugivorous species, grew less when fed with diets composed of *Hevea* spp seeds, than with those of *P. munguba* and *Oriza* spp. His results could not be attributed to the nutrients contents of the food, since *Hevea* spp seeds were richer in protein than the two others seeds.

Other plant items such as leaves flowers and roots of trees and herbaceous plants, are foraged, but in relatively low amounts (Paixão, 1980; Goulding, 1980; Santos, 1981, 1982; Borges, 1986; Goulding et al., 1988). Most species that consume fruits, algae and insects, graze on leaves and flowers during low water season (Santos, 1982; Borges, 1986; Goulding et al., 1988; Leite and Jégu, 1990; Zuanon, 1992; Hahn et al., 1992). Grass leaves and roots are extremely abundant food sources in the floodplains and its is curious why very few species use these resources. Goulding et al., (1988) hypothesised that the low consumption is related to leaf toxicity and/or to their relative low nutritious value. The average protein content of leaves of C4 grass is 8.4%, but C3 macrophytes and flooded forest leaves have 13 to 18% of protein (Howard-Williams, 1974; Howard-Williams and Junk, 1977; Klinge et al., 1983; Furch et al., 1989), which is similar or higher than those re-

ported for seeds. Therefore, low digestibility or presence of toxins appears a more plausible hypothesis.

Filamentous and benthic algae is consumed by many species, but also in small amounts. This food has been reported in the diet analysis of notorious herbivorous (Santos, 1979, 1982; Sazima, 1986; Catella, 1992), and many other species (Paixão, 1980; Goulding and Carvalho, 1982; Santos, 1981; Araujo-Lima and Hardy, 1987). They are abundant in the roots of floating macrophytes, but not in the flooded forest (Alves, 1993). Goulding et al., (1988) and Fernandez (1993) reported that 75% of the filamentous algae consumed belonged to the green algae *Spirogyra* spp and the blue-green algae *Oscillatoria* spp.

Detritus (amorphous mass of organic matter and litter) associated with sediments and microflora (bacteria and fungi) are one of the most frequent items in the stomach content of riverine fish. Additionally to the specialised detritivorous, many omnivorous species consumed small amounts of detritus on a regular basis, together with fruits, insects or fish (Santos, 1982; Goulding et al., 1988; Meschiatti, 1992). Specialised detritivorous fish form a diverse and abundant group. They feed during the day (Barthem, 1987) and usually have complex stomach and very long intestines (Chaves and Vazzoler, 1984; Leite et al., 1988) to improve their digestion and assimilation process. These species ingest large quantities of detritus together with small fractions of algae and/or benthic invertebrates (Nomura and Hayashi, 1980; Carvalho, 1984; Soares et al., 1986; Araujo-Lima and Hardy, 1987; Braga, 1990; Sazima and Caramaschi, 1989; Almeida et al., 1993; Fugi and Hahn, 1991; Fernandez, 1993). Half of stomach content of the

detritivorous *Semaprochilodus insignis* is inorganic material, and only 10% of the remaining organic mass (dry weight basis) is algae and micro-invertebrates (Araujo-Lima and Hardy, 1987). Bowen et al (1984), Catella (1992) and Almeida et al., (1993) found smaller amounts of organic matter in the stomach of *Prochilodus lineatus* and curimatids and only 1.2% of algae and bacteria. The authors suggested that the detritus are also being assimilated by the fish.

The detritus pool in the floodplain originates from the vegetation. In the Central Amazonian floodplain flooded forest litter, macrophytes and phytoplankton produce 24, 70 and 5 % of the total organic carbon, respectively (Junk, 1985a; Piedade et al., 1992). Studies using stable isotope tracers showed that the detritivorous species do not use resources equally. In the Central Amazon, adults and large juveniles of prochilodontids and curimatids consume detritus originated from phytoplankton (Araujo-Lima et al., 1986a; Forsberg et al., 1993; Fernandez, 1993), with no contribution from aquatic grasses (C4 plants), whether the young detritivorous received up to 40% of their carbon from grasses. Loricariids are also assimilating a detritus relatively rich (11- 43%) in grass carbon. Phytoplankton has, indeed, a relatively small contribution to the total primary production of the Central Amazon floodplain (Junk, 1985a), however, considering Bayley's (1989) estimates, detritivorous production ($6.6 \cdot 10^3 \text{ t} \cdot \text{y}^{-1}$) would consume less than 3% of the $1.9 \cdot 10^5 \text{ t C} \cdot \text{y}^{-1}$ fixed by phytoplankton. A similar approach used in the Mogi-Guaçu floodplain were less conclusive, but again has shown that C4 grasses have a small contribution for the detritus pool assimilated by the main detritivorous fish (Vaz, 1992).

Planktonic and benthic micro-crustaceans are complementary food of many floodplain species (Aragão, 1981; Ferreira, 1981; Santos, 1981, 1982; Zaret, 1984; Almeida, 1984; Soares et al., 1986; Araujo-Lima et al., 1986b; Araujo-Lima and Hardy, 1987; Meschiatti, 1992; Fernandez, 1993). Goulding et al. (1988) listed only six zooplanktivorous species in the floodplains of Rio Negro, and additional ones were reported in other systems (Ferreira, 1981; Merona, 1988; Bayley, 1983; Almeida, 1984; Soares et al., 1986; Catella, 1992; Agostinho et al., 1994; Garcia, 1994). Micro-crustaceans are also consumed by fish living in river channels (Vazzoler et al., 1982; Braga, 1990). Preliminary stomach content analysis of *Rhabdolichops eastwardii*, sampled in the Amazon river has shown that this species was consuming copepods and ostracods. Cladocerans seem to be the most preyed planktonic crustacean in the Amazonian floodplain, totalling over 47 %, of the total consumed, followed by Calanoida, which was preyed mostly during low water season (Honda, 1974; Carvalho, 1980; Carvalho, 1981; Carvalho and Goulding, 1985; Zaret, 1984). Detailed information about electivity is scarce. Available data has shown that juveniles (Carvalho, 1981) and adults of small sized fishes (Zaret, 1984) were selective and did not preyed upon the dominant zooplankter, contrasting with silurid *Hypophthalmus* spp, which has shown low electivity and is probably filter feeding (Carvalho and Goulding, 1985).

Other aquatic and terrestrial invertebrates are important for the fish diet in the floodplains, being one of the main links between of plant production and fish populations. There are accounts of fish preying upon insects, molluscs, Decapoda

(shrimps and crabs), Nematoda, Oligochaeta, spiders, millipedes and Porifera (Goulding et al., 1988; Goulding and Ferreira, 1984; Meschiatti, 1992). Among them insects, aquatic and terrestrial forms and shrimps, are abundant fish food. Goulding et al (1988) provided a comprehensive survey of insects preyed on by fish. They listed 15 and 30 fish species in the floodplain of the Rio Negro feeding (>25% of stomach content) on aquatic and terrestrial arthropods, respectively, but the number of occasional consumers was much higher. In general, Chironomids, Ephemeroptera, Diptera and Odonata larvae are the most consumed aquatic insects and Coleoptera, Formicidae, Orthoptera, Hemiptera and Homoptera are the terrestrial ones (Marlier, 1967; Aragão, 1981; Paixão, 1980; Borges, 1986; Goulding et al., 1988; Meschiatti, 1992; Verissimo, 1994). In the Amazon flooded forest terrestrial insects are more abundant in black than in white water floodplains (Adis, 1981), on the other hand, groups, such as, Orthoptera are linked to the macrophytes and therefore more available in white waters, where a single species may reach population densities of 43 ind·m² or 0.7 g·m² (Vieira and Adis, 1992). Preliminary stomach content analysis of *Rhabdophilops troschelli* and *R. caviceps* in the Rio Amazonas channel has shown only aquatic insects.

In the Amazon floodplains 42 species prey upon shrimp (Bayley, 1983; Goulding and Ferreira, 1984; Annibal, 1985; Merona, 1988; Garcia, 1994). Shrimps are more abundant under the aquatic macrophytes (Odinetz-Collart, 1988), but they seem to receive little energetic input from this vegetation (Padovani, 1992). Their production in the Amazon floodplain reach 0.3 g C·m⁻²·y⁻¹ (Bayley, 1989). Its availability and high nutritional

value explains its high electivity by fish. Fish flesh scales, fin rays and blood are important food items in rivers (Vazzoler et al., 1982; Bayley, 1983; Goulding et al., 1988; Merona, 1988; Santos, 1991; Zuanon, 1990; Agostinho et al., 1994). Flesh predators, may swallow the whole prey or bite off pieces of flesh (Goulding, 1980; Goulding et al., 1988; Leão et al., 1991; Zuanon, 1992; Bittencourt, 1994). Swallowed preys were identified in a few studies and the data has not indicated any preference for trophic or taxonomic group (Goulding, 1980; Barthem, 1981; Aragão, 1981; Goulding et al., 1988). Piscine predators, however, elect a certain prey size range. In the Rio Solimões floodplain, 95% of the preys measured less than 40% of the length of their predators (mean= 22%) (Barthem, 1981). Goulding (1980) and Goulding et al. (1988), found similar prey/predator ratio in the Rio Negro and Rio Madeira floodplains (data for Rio Negro included samples of river shore, as well). Piscivorous seem to specialise in habitats and activity time rather than preys, what is probably related to their pursuit and catch strategies. Exceptions to this hypothesis are the large catfish predators which show preferences for specific prey groups, i.e. *Brachyplatystoma filamentosum*, *Pseudoplatystoma tigrinum* and *B. flavicans*, prey upon siluroids, gymnotoids and characiforms, respectively (Zuanon, 1990). However, it is not clear if the electivity reflects distribution patterns or prey specialisation.

Scale and fin eating are considered by Goulding et al. (1988) as a form of parasitism. Scales appear in the stomach content of few specialised scale eaters (Vieira and Gery, 1979; Sazima, 1986; Leite and Jegú, 1990) and many opportunistic species, including those considered

detritivorous and herbivorous (Goulding, 1980), which may be consuming them accidentally. Omnivorous and carnivorous species also ingest scales, on a regular basis, though in smaller quantities than other items (Barthem, 1981; Goulding, 1980; Goulding et al., 1988; Leão et al., 1991; Meschiatti, 1992). Sazima (1984) summarised the feeding adaptations and strategies of these species.

RESERVOIRS

The biotope

It is estimated that the 70 major dams and artificial lakes constructed for the production of electricity are responsible for a flooded area of over 28000 km² or nearly 0.35% of the Brazilian land mass (Eletrobrás, 1990, 1993). Approximately 90% of this area is a consequence of the hydric installations established in the last 40 years in the South Western, Center-Western and Southern regions. In the Rio Paraná basin a chain of dams and artificial lakes has been built along the principal tributaries (Rios Grande, Tiete, Paranapanema, Iguacu and Paranaíba) and the main channel (Rio Paraná). These dams spread over 70% of the 810 km of the Brazilian part of the basin (Agostinho et al., 1994).

Reservoirs are ecologically heterogeneous and complex environments. They are hybrids between rivers and lakes and may be classified at different positions in the gradient of these two ecological systems. The hybrid character, however, manifests itself in the limits of each reservoir (Thornton, 1990). Such environments may be structured in three interactive longitudinal compartments with a variable extension. The first one, called the river

compartment comprehends the source of the reservoirs, where the body of water is relatively narrow, shallow and turbid, with low primary production and where transport is the predominant process. The transitional compartment with a predominance of depositional process shows higher productivity. The lacustrine compartment, relatively wide, deep and closer to the dam, has low amounts of material in suspension, but low productivity.

Vertical structuralization, more pronounced in the lacustrine zone and followed by the transitional one, has a temporary and irregular character. It is influenced by the renovation of water in the dam. It presents marked spatial and temporal variations, chiefly dependent on the operational procedures of the dam, position of water outlet, morphology of reservoir and flood regimen of tributary rivers. The gradient in physical, chemical and biological attributes of the reservoirs determine, to a large extent, the distribution and abundance of the species of fish along these environments (Benedito-Cecilio, 1994), the populational stratification (Okada, 1990) and consequently the fishery (Okada et al., in press; Agostinho et al., in press a; Agostinho et al., in press b).

Community structure in reservoirs

Surveys on the composition of fish communities in the main body of reservoirs were undertaken by Junk (1981), Vieira (1982), Ferreira (1984a, b), Merona et al. (1987) and Leite (1993) in the Amazon basin, Britski et al. (1988) in the São Francisco basin, CETESB (1976), Castro and Arcifa (1987), Romanini (1989), Romanini et al. (1994), Cruz et al. (1990), Gehal (1991), Agostinho (1992), Agostinho et al. (1994), Amaral (1993),

Benedito-Cecilio (1994), Santos (1994), FUEM-NUPELIA/Itaipu Binacional (1987, 1990a,b), FUEM-NUPELIA/COPEL (1994a) in the River Paraná basin and by Castro and Arcifa (1987) in the rivers of the Eastern basin. Although the majority of these inventories sampled with gill nets (what are size selective) and did not have sufficient spatial and/or temporal scope, they indicate that the reservoir's ichthyofauna have a predominance of sedentary species.

Species richness in 19 reservoirs analysed ranged from 4 to 116 (Fig. 1). The highest diversity occurred in Tucuruí reservoir. A covariance analysis of these results suggest that 61 % of the variation in species number between reservoirs are positively related the sampling frequency during the inventory ($p=0.0006$) and to the reservoir area ($p=0.04$). The effect of reservoir depth, latitude and basin were not significant. Among the seven orders of Osteichthyes recorded, Characiformes were the most diverse in 17 reservoirs, except in the Itaipu and Segredo Reservoirs, which are deepest and where the proportions of Siluriformes species were greatest.

Fish communities of the reservoirs are the result of a restructuring process of those communities that previously occupied the dammed fluvial segments. They are marked by local extinction of some components and by drastic alterations in the abundance of the majority (Agostinho, 1992). Full knowledge of the process is still not available, but some indications about it have been provided for the Itaipu Reservoir by Agostinho et al. (1994) and Benedito-Cecilio (1994) and by Romanini et al. (1994) for the Rosana Reservoir and Leite (1993) for Tucuruí Reservoir. In the Itaipu Reservoir, changes imposed by the damming

were: a) the local extinction of species dependent on allochthonous food (*i.e.* *Brycon orbignyanus* and *Piaractus mesopotamicus*; b) the reduction in the catch of big migratory fish, such as *Salminus maxillosus*, *Pseudoplatystoma corruscans* and *Paulicea luetkeni* in the adjacent fluvial areas, and; c) the proliferation of opportunistic species, such as *Auchenipterus nuchalis* with a short life cycle and internal fecundation; *Hypophthalmus edentatus*, a planktophagous species with a high reproductive plasticity; and *Plagioscion squamosissimus*, originating from the Amazon basin, with a generalist diet and multiple spawning. Surveys undertaken at Rosana and Tucuruí dams reveal similar trends (Leite, 1993; Romanini et al., 1994). However, the small but significant effect of reservoir area on species richness suggest a residual effect of richness of the original river, since large rivers have more species, or an extinction rate inversely related to habitat size as suggested by MacArthur and Wilson (1967)

Trophic guilds were variable between reservoirs, except the by herbivores species, that were rare in the seven communities analysed (Fig. 2). Again, two or three species were responsible for more than half the ichthyomass caught. Piscivorous were among the dominant species in most reservoirs and detritivorous and planktivorous in some (Tab. 1).

The use of space and reservoir habitats

The reduction in water velocity in the dammed area, associated to the passage from the process of sediment transportation to the depository process, leads to marked limnological gradients which manifest themselves in the principal body of the reservoirs and in the reservoir arms that advance

on the lateral tributaries (Agostinho et al., 1994). The superior stretches, where fluvial conditions prevail, are occupied by species characteristic of lotic environments, especially by piscivorous species, which are attracted by the high availability of small-sized species, in general opportunistic, that proliferate in dammed waters. The fluvial zone of the reservoirs is generally explored by a greater number of species than the innermost ones (Vieira, 1982; Benedito-Cecilio, 1994). In the Itaipu Reservoir, the fluvial zone extends to about 1/3 of total extension and contains all the species recorded in the other zones (Agostinho et al. in press a). The great migratory pimelodids (*P. corruscans*, *P. luetkeni*, *P. pirinampu*) have their occurrence restricted to this segment, where as other migratory species, such as *P. lineatus* and *P. granulosus*, were more abundant in the fluvial zone, advance a bit further in the internal zone. The fish biomass captured in this region is intermediary between the transitional zone (depository) and the lacustrine zone (Okada et al. in press). The latter has greater productivity than the others (Thornton, 1990), as suggested by the high landing of *H. edentatus*, a planktophagous filter-feeder. Ferreira (1984a, b) also found high biomass of planktivorous species in the transitional zone of an Amazonian reservoir.

Few species explore the top layers of the open areas and deep habitats of large reservoirs. In the Itaipu Reservoir only *H. edentatus* and its predators, *P. squamosissimus* exploit these habitats (Okada, pers. com.). The open water niche, however, is not occupied in other reservoirs (Cruz et al., 1990; Torloni et al., 1993; Santos, 1994), except the Rosana reservoir, which was closed after the dispersion of *H. edentatus* (Romanini et al., 1994). Even in small and shallow reservoirs, such

as Americana (12 km² and 9 m deep), the less inhabited area are the open and deep ones. Arcifa et al. (1988) attribute this fact to the origin of riverine fauna that occupies the reservoir, to the low diversity of habitat and to the scarcity of shelter and alimentary resources for preys. In the Curua-Una reservoir the lentic habitats had high abundance of *Serrasalmus rhombeus* and *Hemiodopsis* sp, both foraging on algae and aquatic invertebrates (Ferreira, 1984a, b).

The littoral zone (< 30 m deep), seems to contain almost all the fauna of a given reservoir (Agostinho et al., in press c). Studies conducted by FUEM-NUPELIA/Itaipu Binacional (1990a) revealed a markedly vertical zonation, where surface waters are preferentially inhabited by *A. nuchalis*, *P. galeatus*, *Serrasalmus marginatus* and *A. bimaculatus*; the subsurface waters (5 meters) are preferred by *H. edentatus* and *Ageneiosus ucayalensis*; and the bottom (20 meters) by *P. luetkeni*, *Pimelodus maculatus*, *P. granulosus*, *Cathatiridium jenynsii* and *Potamotrygon motoro*. A transversal zonation, in the direction of open waters also occurs. Small *Aphyocharax* sp, cheirodontids and juveniles of the majority of the species concentrate inshore, followed by parodontids, cichlids, *Moenkhausia* sp, *Astyanax* spp, *Roeboides* sp, *Leporellus vittatus* and *S. insculpta* offshore. Large-sized species are grouped further offshore. Variations in these distribution patterns can, however, be imposed by the physiography of the area (aquatic and bank vegetation, declivity, bottom type) and by nyctemeral movements of the species. Agostinho et al., (in press c) reported that *H. edentatus* spends the day in deeper areas and concentrates at night at shore surface. Its movements are attributed to food

searching and predator avoidance. Arcifa et al (1988) and Arcifa and Meschiatti (1993) showed similar variations in density for *A. bimaculatus* and other species in small reservoirs. Arcifa et al. (1991) suggested that vertical stratification is adaptation evolved by *A. bimaculatus* and *A. fasciatus* to reduce the competition imposed by their high degree of diet overlapping in the limited space of reservoirs. The conditions of shore habitats may be stressed by the operational procedures of the dam and the action of waves, difficulting the establishment of a stable benthic and vegetation community, important as shelter and as food for fish (Agostinho, 1992).

Food chains and trophic aspects in reservoirs

Fish communities of reservoirs seem to be sustained mostly by resources originating in the aquatic environment itself. Agostinho and Zalewski (in press) estimate that, for the community of fish of Itaipu Reservoir, over 70% of the biomass is composed of species that feed on autochthonous elements (plankton, benthic organisms and fish), 25% utilise detritus of mixed origin and only 5% are supported by ecotone sources (leaves, fruit, insects from the adjacent terrestrial areas). Contribution of allochthonous resources increases in the upper reaches of the reservoirs. Five years after the closure of the Itaipu Reservoir more than 75% of the biomass caught was composed of insectivorous, planktophagous and piscivorous species, in this order of importance (Hahn, 1991). Similar results were recorded for Curua-Una reservoir (Ferreira, 1984a, b). Among the species common to both reservoirs, *A. nuchalis*, an opportunistic

species, benefited from the abundance of chironomids and ephemeropterans as an alimentary resource. *Hemiodopsis* sp, an algivorous species, with a tendency to planktivory, predominant in the inner areas of the Curua-Una reservoir, had the planktophagous *H. edentatus* as the corresponding species in the Itaipu reservoir. Variations in proportion of the trophic categories along the longitudinal axis of the Itaipu reservoir were analysed by Hahn (1991) who discusses the dominance of insectivorous species (*Moenkhausia intermedia* and *A. nuchalis*), followed by piscivorous and omnivorous ones in the fluvial zone (upper third part) and the dominance of planktophagous, insectivorous and piscivorous species in the rest. The community of the Upper Rio Paraná and its tributaries are composed of omnivorous species (Romanini, 1989; Romanini et al., 1994; Carvalho, in press; Gehal, 1991).

In shallow reservoirs detritus is one of the main item in the diet of the species, second only to aquatic insects (Arcifa et al., 1988; Arcifa and Meschiatti, 1993). The detritus origin is not clear, but Mozeto et al. (1988) suggested that in southern part of the Lobo reservoir it is composed mostly of carbon from macrophytes and input from tributaries. The authors, also, suggested that algae carbon has minor importance in that reservoir.

The piscivores species are variable in reservoirs of River Paraná basin, where *P. squamosissimus*, a wide-range carnivorous species, is the main predator (Hahn, 1991; Romanini et al., 1994; Agostinho et al., 1990; Santos, 1994), except in those reservoirs where it was not introduced. In the later cases, *H. malabaricus*, *S. spilopleura* or *Galeocharax kneri* were dominant

piscivores (Caramaschi, 1979; FUEM-NUPELIA/COPEL, 1994b; Gehal, 1991; Arcifa et al., 1988; Carvalho et al. in press). *Serrasalmus spilopleura* is a specialised fin-feeder (Northcote et al., 1991).

The number and type of predators in a reservoir effects community productivity and structure. In a comparison of 17 reservoirs in the Northeast, Paiva et al. (1994) have shown that those with two predators presented highest yields. The authors explained the effect by the competition for resources by the prey and between predators for the prey in reservoirs with less than and more than two predators. Santos et al. (1994) compared to reservoirs, one of which has been colonized by the piscivorous *Ciclha ocellaris* and *P. squamosissimus*. The reservoir with the two predators had a higher species richness and lower diversity index than the one without them.

However, the available information is still insufficient for the establishment of variation patterns in the trophic structure of reservoirs. The results obtained in different studies suggest that among the factors that determine the trends of trophic structuralization of fish assemblage in a reservoir during the process of colonisation is the specific composition of the river ichthyofauna that originated it, besides the characteristics related to the state and to the general trophic succession (site of basin, morphology, time of residence of water, level of physical structuralization of community and dam operation).

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