Aquatic habitats, fish and invertebrate assemblages of the Middle Paraná River*

by

E.C. Drago, I.E. de Drago, O.B. Oliveros & A.R. Paira

Prof. Dr. Edmundo C. Drago, Prof. Dr. Inés Ezcurra de Drago, Dr. Olga B. Oliveros & Dr. Aldo R. Paira, Instituto Nacional de Limnología (CONICET - UNL), José Macia 1933, 3016 Santo Tomé, Santa Fe, Argentina; e-mail: inali@arnet.com.ar
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Abstract

The Paraná River hydrosystem harbors a large and diverse community of freshwater biota. The Middle Paraná River and its main tributary, the Paraguay River, are also an important inland artery for commerce and, up to day, their floodplain had suffered a moderate human impact, yet. The river-floodplain system maintains its aquatic habitat heterogeneity and the natural connectivity between lotic and lentic water bodies.The present review focuses on the description of the main lotic and lentic habitats of the Middle Paraná ecosystem as well as their hydrosedimentological relationships throughout the pulsing river regime. Aquatic habitats are classified according to their location at the main channel and within the floodplain. The hierarchical/functional classification of the floodplain channels is based on the mean annual discharge and its degree of intermittence. The relationships between river dynamics and the floodplain lakes evolution as well as the influence of the autogenic processes on the waterbodies are also described. The conservation of the ecological integrity and the management of aquatic ecosystem of the river requires a thorough understanding of its ecological habitats, the biotic communities, and their interrelationships. This paper examines the present state of our knowledge of the hydromorphological changes in the Middle Paraná aquatic habitats and describes the communities of fishes and benthic macroinvertebrates associated with them.
Keywords: **Paraná River, floodplain, connectivity, aquatic habitats, benthos, fishes.**

Resumo

A bacia fluvial do rio Paraná sustenta uma grande e variada comunidade de organismos de água doce. Embora o médio-Paraná e o seu maior tributário, o rio Paraguai, representem importantes rotas comerciais, até então, as suas áreas alagáveis sofreram poucos impactos antrópicos. O sistema rio-área alagável mantém a sua heterogenidade de habitats aquáticos e a sua conectividade natural entre corpos d'água, tanto lóticos quanto lênticos. A presente revisão concentra-se na descrição dos principais habitats lóticos e lênticos do ecossistema do médio-Paraná, bem como sobre as relações hidro-sedimentológicas que variam devido ao regime hidrológico deste. Os habitats aquáticos foram classificados de acordo com a sua posição dentro do leito principal e da área alagável. A classificação hierárquica e funcional dos canais na área alagável é baseada na descarga anual média e no seu grau de intermitência. São descritas as relações entre

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*Dedicated to Prof. Dr. Wolfgang J. Junk on the occasion of his 60th anniversary.

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a dinâmica do rio e a evolução dos lagos das planícies inundáveis, bem como a influência dos processos autogênicos nos corpos d'água. Além disso, é apresentada e uma lista das espécies de invertebrados bentônicos e peixes. Resumindo o atual conhecimento sobre os habitats e biota, bem como da sua interdependência com as variações hidro-sedimentológicas do médio-Paraná, esta publicação visa a providenciar uma ferramenta útil para a conservação da integridade ecológica e o manejo sustentável de um dos maiores ecossistemas fluviais do mundo.

Introduction

The Paraná is the second largest river in South America in terms of catchment area (1.51 million km^2), the second longest (4,400 km from the headwaters of Grande River in Brazil to the Río de la Plata estuary), and the third in terms of discharge (about 470 km^3 of freshwater carried to the sea annually). This hydrosystem drains nearly 32 % of Argentina, 100 % of Paraguay and 8 % of Bolivia. The 50 % of the catchment area is within southern Brazil. The basin contains the Paraguay-Paraná Hidrovía, a navigation waterway project of 3,440 km from the city of Cáceres to the Río de la Plata estuary (Fig. 1), which would produce severe impacts in the river and its wetlands (HAMILTON 1999). This continental river receives the contribution of mountain streams, semi-arid brooks, forest streams, vast grasslands and large swamps (DRAGO 1990).

The aim of this paper is to define the aquatic habitats of the Middle Paraná valley on a basis of features such as morphology, current velocity, suspended and dissolved solids, substrate, macrophytes, temperature and water chemistry. The most important river-floodplain relationships are described, and changes in the evolution of habitats through time are examined. Finally, the fish and benthos communities associated with the habitats are described.

The Middle Paraná River ecosystem

The Paraná catchment encompasses several geological and climatological regions, which influence to different degrees the fluvial dynamics and the geochemistry of the river ecosystem. The weak development of the Andean Cordillera and the Brazilian Shield in the catchment suggests that the influence of both geotectonic elements is probably not so important as formerly considered (IRIONDO 1988). However, the contribution of suspended sediments from the Andean Cordillera through the Bermejo River (Fig. 1) gives rise to strong changes in the lotic and lentic environments of the Middle and Lower Paraná River (DRAGO & VASSALLO 1980; DRAGO & AMSLER 1988). Furthermore, the Jurassic-Cretaceous area of the Upper Paraná and the Chaco-Pampa Plain in the west and south of the middle catchment also yield to the river important amounts of suspended and dissolved materials (DEPETRIS 1976; DRAGO & VASSALLO 1980; DRAGO & AMSLER 1988; IRIONDO 1988).

The Middle Paraná system may have formed in late Tertiary, about 3-4 million years B.P. (IRIONDO 1979). Since that period the Paraná River has flown from the Brazilian Shield to the Chaco-Pampa Plain in nearly the same course, where at present the Yac256retá dam is located (Fig. 1; IRIONDO 1979). During the upper Pleistocene, the river has flown to the west of its present position, in a depression that contains two palaeochannels where the present Saladillo River basin developed. By the end of the Pleistocene or beginning of the Holocene (10,000 years B.P.), the Middle Paraná River occupied its present position (IRIONDO 1979). According to IRIONDO (1979), the channel shifting occurred by avulsion due to the massive deposits of sediments carried by the river, which altered the slope of the valley floor. Subsequently, the river built an

extensive valley train that may have extended to the Río de la Plata estuary and caused the river to assume a braided pattern. During the late Pleistocene, the Middle Paraná River was subject to an arid climate, resulting in a desintegration of the river networks in the contiguous plains. The lower and middle Holocene was characterized by a humid climate that reactivated the fluvial systems; the present subtropical humid climate began about 1,000 years B.P. (IRIONDO 1984).

The middle and lower reaches of the Paraná River flow along a tectonic lineation, probably from the Pleistocene age (IRIONDO 1988). Most of the faulted blocks are tilted to the east; in consequence the main channel tends to flow along the eastern cliff of the valley. The complex lineation crosses minor blocks which undergo independent vertical movements (IRIONDO 1988), with the raised blocks narrowing the main channel and the sunken blocks widening the main channel. The former are nodal points, being the highest stable river habitats, some of them approximately one hundred years old (DRAGO 1990). These channel constrictions not exceed 1.5 km in width and range between 20 and 45 m in depth. On the other hand, the wide braided reaches are characterized by highest erosion and sedimentation rates, which are responsible for highly unstable river habitats (DRAGO 1977a). The cross-sections show maximum widths of 8 km and maximum depths of 20-25 m, including channel islands and sand bars (Fig. 2; DRAGO 1977a, 1990).

The aforementioned features suggest a very complex mosaic of riverine habitats, where the different physical structures are linked not only longitudinally (upriver-downriver linkage) but also transversally (main channel-floodplain linkage), reflecting also the sub-basin or tributary linkages.

Aquatic habitat description

The term "habitat" describes the physical and chemical structure within which an organism normally lives. Those interested in the aquatic environment may refer to the river as a system, or aquatic subsystem, with the term habitat referring to specific, smaller-scale features (BAKER et al. 1991). However, in large rivers there is often considerable variation in the recognized habitats. At the same time, COBB (1989), GORMAN (1987), ROSS et al. (1987), among others, have termed as "microhabitats" those units of the environment defined by a unique set of physical and chemical features. BAKER et al. (1991) recognized the composite nature of some riverine habitats and showed that physically and chemically unique areas supported distinctive fish communities. Thus, habitats are delineated largely on the basis of specific variables, including depth, current velocity, substrate type, instream structures (irregular bed, snags, macrophytes), position within the ecosystem (within the main channel or within the floodplain), and water quality (transparency, pH, dissolved oxygen, etc.). These variables were identified as important in structuring biological communities in a variety of running water ecosystems (GORMAN & KARR 1978; HAWKES 1975; HYNES 1970; PENNAK 1971).

In Table 1, the aquatic habitats of the Middle Paraná River are arranged according to their location in the alluvial valley. In spite of the increasing number of reservoirs in the Upper Paraná, the middle and lower reaches still maintain natural river dynamics. As a result, the relevant morphological and hydraulic variables have changed gradually, creating rather wide transition segments between adjacent habitats. Thus, the habitat descriptions are not always precise, mainly because we still have much to learn about large river-floodplain ecosystems.

Main Channel

Channel shape is a contributing factor in the distribution of depth and velocity of the water, and is a function of the overall basin hydrology and geology. The main channel of the Middle Paraná River has a braided pattern, showing a sequence of wide segments characterized by two or more anabranches and narrow and short reaches in which the river flows in a single channel (Table 1; Fig. 2). Clarification is needed regarding the terms "anabranches" and "secondary channels" used in this work. The channels divided by islands and bars **within the main channel** are termed anabranches, i.e., they flow parallell to one or both sides of the deepest channel (navigation channel). Floodplain channels (or secondary channels) conform the drainage system **within the floodplain**; thus, the channels branch and rejoin, but each is a distinct channel bounded by the surface of the alluvial plain ("anastomosing"; SCHUMM 1971) showing sometimes different planform patterns (Fig. 2).

The braided reaches or **wide-cross sections** of the main channel are the most unstable riverine habitats of the Paraná valley (DRAGO 1977a; Figs. 3, 4). Generally the islands and sand bars are unstable and change their location frequently (DRAGO 1977a). The channel division is associated with increased width of water surface, increased slope, and decreased depth. The ratio of depths in the divided reaches to depth in the undivided reaches ranges from 0.3 to 0.9 (mean = 0.6), similar to the data given by LEOPOLD & WOLMAN (1957) for natural rivers (0.6-0.9). The main channel and its anabranches carry the 80-85 % of the total discharge flowing throughout the valley. From an ecological perspective, major and minor anabranches within the main channel, were also characterized as channel habitat (Table 1). Measurements of the number of branches in the main channel of the Middle Paraná River, performed every 20 km along a reach of 700 km, showed a maximum division of six channels and a mean of two channels.

The **channel narrowings** are called **nodal points** or primary control points (COLE-MAN 1969). At these points, the Paraná main channel is narrow (700-1,500 m width) and quite deep, ranging the maximum depths between 30-45 m, in contrast to less than 30 m in the wide or non-restricted areas. At a nodal point, the bed water velocity measured during a 5-year period, ranged from 0.44 to 1.11 m s^{-1}. These cross-sections are the most stable river habitats, and generally remain rather fixed through long periods of time. An example is the Toma de Aguas Corrientes cross-section, located 3 km upriver of the Paraná city, which has showed only small variations since 1847 (Figs. 3, 4; DRAGO 1977a, 1990). The Tertiary sandstone deposits have not allowed the river to migrate as freely in this area as in others, where the main channel flows between alluvial banks. According to IRIONDO (1988), in most of the reach from the Paraguay River confluence to Paraná city, the main channel flows along the left cliff of the plain, indicating a west-east tilting of the tectonic blocks (Figs. 1, 2). Nodal points having some of the deeper points of the main channel could be also related to neotectonic processes, as fault systems and sunken blocks. Usually, the deep holes of tectonic origin are more than 30 m in depth (Fig. 2: points 1, 2 & 3), in contrast with the shallow scour holes originated by fluvial processes, which show depths lower than 20 m (Table 1; DRAGO, unpubl.). Ephemeral sand bars exist in the nodal points and channel cross-sections are either U-shaped or asymmetrically V-shaped (e.g., Toma de Aguas Corrientes and Punta Gorda cross-sections respectively (Figs. 2-4; DRAGO 1990). Some authors (OLDANI 1990) stressed the importance as areas to rest for migratory fishes of

the river bank areas of low depths (4-5 m) in the nodal points, as well as the border of the thalweg are used in orientation.

The narrow and wide cross sections of main channel shows also two clearly different mesohabitats, the **central strip** and the **bank strip** along the banklines. The former occupied 90-95 % of the wetted perimeter, being the more barren and homogeneous area of the river, with mobile sandy bed materials and where the river bottom is seldom flat. Physically, the central strip habitat changes little with season or river stage. Current speeds are always high, ranging from 0.5 to 2.6 m s^{-1} under low to moderate discharges and often exceeding 3 m s^{-1} during high flows. The bank strips are the habitats adjacent to the central strip, and the boundary between these habitats is not always easily determined. Slopes of natural banks are usually >25°-35° and are often nearly vertical in the upper portions of the banks. In the wide cross-sections, the steep banks as well as low ones sometimes are associated with sand bars, being habitats with different physical pattern in water depth, current speed and substrate. Furthermore, the bankline can be associated with high cliffs (>5 m to 80 m) or with low cliffs (<5 m) (Table 1). Large segments of the main channel left bank are faulted-raised cliffs (IRIONDO 1988), where sometimes very narrow beaches are developed but usually there are great depths immediately offshore of the bankline. DRAGO (1977a, 1990) measured maximum bankline extension and retreat averages of 139 m yr^{-1} and 78 m yr^{-1} respectively. Usually, the maximum bankline migrations are detected on the floodplain border and the minimum on the high fault-raised cliffs composed of Tertiary sandstone (Figs. 3, 4). As much as 20,000 m^3 of sediment may be involved in a single bank failure of 200 m length, changing drastically the onshore strip habitat (DRAGO, unpubl.). The complexity of the bank habitat is due to several factors, such as different high-low water level fluctuations, scalloping caused by block slumping, irregularities caused by the differential erodability of bank materials, fallen trees and brushes and mixing of allochthonous and autochthonous sediments (bad-sorting sediment). The accumulation of woody debris (mainly large snags) accelerated the sedimentation in the mouths of the anabranches, also fixing the bedforms and originating the joining of channel sand bars and islands on the banks. This process results in the loss of a portion of channel habitat and the formation of a floodplain lake (DRAGO 1976, 1989, 1990).

The bedforms of the Middle Paraná River were classified by DRAGO (1977b), in four groups: ripples, with wave height <0.30 m; megaripples, have a wave height ranging from 0.3 m to 1.5 m; dunes, the third category, range in wave height from 1.5 m to 7.5 m; and sand waves, that have a wave heights over 7.5 m. At high water stages the dunes move downriver at a mean velocity of 12 m d^{-1} and the average rate of movement of the superimposed ripples and megaripples reaches 37 m d^{-1}. During low stages the rate of movement decreases to 3.3 m d^{-1} for dunes, and 9.9 m d^{-1} for the superimposed ripples and megaripples (Fig. 5; LIMA et al. 1990).

Table 2 shows typical physical conditions in both banks and in the center of the main channel. Substrates at the channel center uniformly consist of sand (Table 3). In addition, the substrate is constantly shifting; bedload movement near Paraná city (Entre Ríos Province) ranged between 20 and 30 million metric tons per year (AMSLER & PRENDES, 2000). In the same area, based on data covering 66 years of surveying, DRAGO (1977a, 1990) calculated a mean annual deposition of 5.5 million m^3 of sediment (Fig. 4). The wash load transported by the river averages 100 million metric tons per year, with most of the transport occurring in the channel habitat (DRAGO &

AMSLER 1988).

The suspended sediment is composed largely of particles in the fine silt and clay ranges (<16 µm), and the percentages of wash load are never less than about 60 %. The maximum contributions of suspended sediments by the Bermejo River, an Andean tributary of the Paraguay River, increase the average suspended solid concentrations of Paraguay and Paraná rivers by 600 % and 130 %, respectively (DRAGO & AMSLER 1988). However, the intense reddish-brown water color of the Paraná River during the flood periods ("red wave") is due to the fine material coming from the Upper Paraná basin in Brazil, where the predominant latosols contain high concentrations of clay minerals with elevated amounts of kaolinite (DEPETRIS 1976). These materials together with the high sedimentary deliveries of the Bermejo River (April-May), drastically decreased the water transparency and limits the photic zone to <0.9 m (Fig. 6). The mean suspended sediment concentration of the Middle Paraná River is 250 mg l^{-1} (DRAGO & AMSLER 1988).

Channel habitat is characterized by a vertically and laterally homogeneous distribution of water temperature (DRAGO 1984). The maximum differences detected between surface and near-bottom waters was 2.5 °C, with the maximum temperature recorded in summer at 30 °C (February) and the minimum in winter at 12.9 °C (June); the mean river water temperature is about 22 °C (DRAGO 1984). Chemical water quality along the channel center is similar to that of the bank habitat (VASSALLO & KIEFFER 1984). Predictable fluctuations occur seasonally and with river level, but compared to other riverine habitats, change in the main channel appear minor. However, there are differences in the hydrochemistry as well as other biotic and abiotic variables of the main channel compared with other habitats, such as secondary channels, lakes and tributaries (Tables 2, 3). Only large tributaries, such as the Paraguay River, strongly change the physical and chemical characteristics of the main channel, and can do so for more than 200 kilometers downriver of the confluence (DRAGO & VASSALLO 1980). However, the right-bank tributaries, some of which have high salt concentrations, sometimes increase the salinity of the secondary channels flowing along the right valley border by more than 100 %. This salinization effect increases strongly during low water stages of the main river, when the inputs of saline groundwaters are also important (MAGLIANESE 1969).

Benthos communities of the **main channel central strip** exhibit high density, low species richness and diversity (MARCHESE & EZCURRA DE DRAGO 1992; Tables 3, 4). However, the central strip of the river channels (main channel, anabranches and large secondary channels of the floodplain) are the zones of greatest descriptive and representative value for the characterization of the benthos (MARCHESE & EZCURRA DE DRAGO 1992; MARCHESE et al. 2002). The lowest values of biomass are detected in this habitat, where the organic matter content is also lowest (Table 3). Benthic macroinvertebrates are represented by one typical species assemblage: *Narapa bonettoi*, *Myoretronectes paranensis*, *Haplotaxis aedeochaeta*, *Tobrilus* sp. and *Parachironomus* sp. The **bank strip habitat** shows a remarkable change in the benthos structure in relation to the central strip habitat. Three of the dominant species of that association are lacking, being lower the density and higher the species richness and the species diversity (MARCHESE & EZCURRA DE DRAGO 1992; MARCHESE et al. 2002) (Table 4). According to these authors, both in the central and bank strip habitats, depth, current velocity, discharge, oxygen and sand, silt and clay percentages explain the variations in

density, species richnes and diversity of the bottom fauna (Tables 2, 3). In spite of the strong changes of the physical structure in these habitats during flood and drought phases, they show little changes in the benthos. Therefore, on a long-term basis, the benthic species assemblages remain relatively constant (EZCURRA DE DRAGO & MARCHESE, unpubl). The variations in the benthic associations in both instream mesohabitats was observed recently in the upper and lower segments of Paraguay River (MARCHESE et al., unpubl.; EZCURRA DE DRAGO et al., unpubl.).

The Middle Paraná River ecosystem may support as many as 207 species of freshwater fishes, or the 80 % of the total number of fish species registered for the Paraná River catchment. In relating fish species to habitats (Table 5), we have used several sources of information, from published and unpublished data to fishermen observations. The information on feeding habits of several species is still missing. Nevertheless, Table 5 is up to day, the most complete information on the habitat distribution and relative abundance of Middle Paraná River fish species. However, it is necessary to increase the information on several lotic and lentic habitats, which will be a huge task because the great size, depth and habitat heterogeneity of the Paraná River environments. Not surprisingly, habitats have been studied in inverse proportion to the difficulty in sampling them, so that a few have been relatively well sampled (e.g., floodplain lakes, shallow areas of the main and secondary channels) while others (e.g., deep scour holes, the center of the main channel and secondary channels, and associated micro-habitats in the largest floodplain lakes) are virtually unknown. Finally, many species are seasonal and it is probable that the collections in some habitats did not coincide with the presence or abundance of those species.

During high water stages (November-April) the main channel is used by migratory fishes for reproduction and spawning, especially by *Prochilodus lineatus* (BONETTO & PIGNALBERI 1964; BONETTO et al. 1971; QUIRÓS & CUCH 1989) which have a biomass of 500 kg ha^{-1} (OLDANI 1990). As was demonstrate by BONETTO and collaborators (BONETTO & PIGNALBERI 1964; BONETTO et al. 1981) fish species as *P. lineatus* and *Salminus maxillosus* among others, show large upriver and downriver migratory movements reaching distances of more than 1,000 km, with maximum daily movements of 18–22 km d^{-1}. The relative abundance of *P. lineatus* along the main channel appears to be inversely related to the proportion of lentic waterbodies in the floodplain (QUIRÓS & CUCH 1989). Also, as water stage increases, total fish abundance decreases in the main channel (OLDANI & OLIVEROS 1984; QUIRÓS & CUCH 1989). These relationships would be explained by the seasonal accessibility to floodplain lakes by fishes seeking to reach adequate feeding and spawning grounds, and underscore the importance of the lotic-lentic connectivity in alluvial rivers. The river bank areas of 4-5 m in depth in the nodal points are used by migratory fishes as sites to rest, whereas the border of the thalweg are used in orientation (OLDANI 1990).

Shoal habitats occur at both sides of the thalweg (middle bars), along the borders of islands, and in association with the floodplain margin or with banklines (lateral and alternate bars; Figs. 2-4). The sand bars and channel islands generally migrate, sometimes notably, downstream (COLEMAN 1969). Measurements in the Paraná main channel showed downstream and lateral migration rates of 60 m yr^{-1} and 36 m yr^{-1}, respectively (DRAGO 1977a, 1990). During the annual flood the islands are inundated, and, in some cases, the smaller islands are removed completely by erosion. The bar and islands give rise to channel instability as a result of the decrease in the cross-sectional

area. Because of that, in the widening of the main channel the habitats are more unstable than in the narrowing parts (Figs. 3, 4). Sediment analysis of several river bars (DRAGO, unpubl.) showed a predominance of sand (always over 90 %), mainly fine sand (over 50 %), and small amounts of silt and clay (less than 3 %).

Islands and sand bars can be separated from the river banklines by water even at low river stages. Although these two channel elements cannot be sharply separated, in general, islands have extensive woody forests, while mid-river bars have no or little vegetation and are often submerged at mid-water levels. Furthermore, a greater elevation of the islands permit sand bar habitat to exist along them over a greater range of river levels. However, at very low river stages many of these habitats decrease greatly in extent by drying. Ecologically, these habitats increase in importance during mean and low water levels, because their shallow depths, low current speeds, and finer sediments, are linked not only with activity of some fishes but also with macroinvertebrates and waterfowl. At higher river stages, the shifting sand substrate of shoal habitats is colonized by a diverse array of invertebrates similar to those in the channel habitat. Fish abundance in shoal habitats probably varies considerably more with season and river stage than any other habitat. *Prochilodus lineatus* is one the most abundant species in this habitat, which moves forming large schools, and *Potamotrygon motoro* usually occurs in great number. *Serrasalmus spilopleura*, *Pimelodus clarias maculatus* and *Hoplias malabaricus* are also common species.

On the whole, very low river levels can completely dewater these habitats; a small, rapid rise of level may introduce channel water changing some characteristics considerably (e.g., current speed, temperature, transparency); a large, rapid increase of level or uncommon floodwaters, may completely eliminate the shoal habitat.

Slack-water habitats (Table 1) are usually associated with large bankline irregularities (mainly originated by bank slumpings), downriver of islands and mid or lateral channel bars, downriver of channel junction bars, upriver or downriver of the tributary outlets, and on the mouth of directly connected lakes. Large eddies (up-river flows) are a very common feature of this habitat and may be over 150 m in length and extend up to 100 m into the river, showing relatively deep and slow-current areas. As is well established, slackwater habitats (velocity shelters) are recognized as very important for fish communities of large rivers (BAKER et al. 1991; STALNAKER et al. 1989). These habitats present fine bottom sediments, although coarse sediments and consolidated silt-clays occasionally occur. Eddies are characterized by slower current than the adjacent channel areas; however, their turbulence prevent any thermal or chemical difference between surface and bottom waters. The area and depth of individual eddies are closely linked to river level. Thus, following the water level fluctuations, eddies may display enlargements or reductions through the year. Although the eddies in the main channel of the Paraná may exist continuously for years, channel geometry changes may dissipate them completely.

Large migratory fishes as *Salminus maxillosus* ("dorado"), *Pseudoplatystoma coruscans* and *P. fasciatum* ("surubí") are commonly detected either resting or predating in these habitats. Furthermore, other fish species used the slack-water areas for resting or as shelters. The trap effect of shallowest eddies sometimes accumulates large quantities of snags and brushes, creating a transition area between channel and bank habitats. These areas are loci of strong deposition, therefore being ephemeral habitats.

Floodplain network: secondary channels

The anastomosing drainage network of the Paraná floodplain typically shows planform patterns ranging from sinuous to irregular meanders, with some straight reaches (Fig. 2). Large mid-sand bars and islands are uncommon elements of the floodplain streams, although in the larger secondary channels some bars and islands can be detected in the channel center or on the banks. Point bars are common habitats in the meandering reaches. The development of alternating shallows and deeps in the Paraná floodplain channels is associated not only with the meander channels but also with the stream junctions and in the bends of the low sinuosity channels.

We classified the floodplain channels of the Middle Paraná valley according to their mean annual discharges (Q_{SC}) in relation to the mean annual discharge of the main channel (Q_{MC}) and its degree of intermittence. The data of Table 6 are an example for the Santa Fe–Paraná cross-section (Fig. 2). Floodplain channels with mean discharges over 850 m^3 s^{-1} maintain a permanent flow during the year. On the other hand, channels with less than 100 m^3 s^{-1} show dry reaches and ponded water in the scour holes during the lowest stages of severe droughts. The permanent channels maintain the lotic connectivity between the parent river and its floodplain. On the contrary, during drought phases, the smaller intermittent channels stopped their flow, beginning short- or long-term "lenitification processes", according to the duration of the inundation phases (DRAGO, unpubl.).

Old floodplain areas (OFA) located far away of the main channel have a greater development of channel networks, showing channel geometries very different from the relatively new floodplain areas (NFA) (Fig. 2; Table 7). The data of Table 7 show a more complicated geometric structure of the channel network in the older floodplain areas, as a result of a complex array of hydrosedimentological, topographic and vegetation influences. Thus, the floodplain evolution gives raise to a greater lotic and lentic habitat heterogeneity and a more complicated connectivity processes between the aquatic environments (Fig. 2; DRAGO 1976, 1981, 1989, 1990; IRIONDO & DRAGO 1972). The ecological integrity of floodplain rivers depends on the diversity of water bodies with different degrees of connectivity, not only with the main river channel but also with the floodplain channels (DRAGO 1981, 1989; WARD & STANFORD 1995). The average channel width in the new areas of the floodplain is twofold that of channels on older parts of the floodplain (DRAGO 1976; IRIONDO & DRAGO 1972). The evolution of the channels from lotic to lentic water bodies is closely linked with biotic and abiotic factors. For example, the aquatic vegetation may begin to cover the narrower channels completely during spring and summer, thus accelerating the deposition process (DRAGO 1989; HOWARD-WILLIAMS & JUNK 1976; POI DE NEIFF et. al. 1994). In turn, the decreasing of channel depths allows the development of rooted macrophytes and consequently a strong diminution of the current velocity. Therefore, the accumulation of sediment and vegetation debris on the bed increases, changing the physical structure of the habitat. Therefore, the benthic fauna structure changes, beginning to be similar to that of older floodplain lakes completely covered by floating grasses and rooted vegetation (EZCURRA DE DRAGO et al., unpubl.). The floodplain areas with high density of narrow, shallow and high intermittence channels show higher terrestrialization processes, such as the former sets of scroll meanders.

Dunes and ripples are mainly associated with the largest floodplain channels, i.e., in channels with mean discharges over 800-1,000 m^3 s^{-1} (Table 6). The bed configuration

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is similar to the one detected in the main channel, but showing dunes with lower wave heights (less than 3 m). On the other hand, the lower hierarchy channels (mean discharges less than 200 m^3 s^{-1}) sometimes present ephemeral small ripples along the straight reaches. But the characteristic feature in the longitudinal profiles of these minor streams is the alternation of steps and scour holes (Fig. 7). The scour holes are deep, from 5 to 15 m, showing slow-water areas and up-river flows. During the lowest stages, the scour holes present still waters. On the other hand, the steps show maximum depths of 5-6 m and sometimes which of lesser depths are dry during the lowest water levels. On the whole, steps tend to support higher densities of benthic invertebrates (EZCURRA DE DRAGO et al., unpubl.), thus being important food-producing habitats for fishes. In terms of physical habitat, the scour hole-step sequence provides the major diversity of bedforms, bed sediments, local velocities and temperatures in the Paraná floodplain channels. Flat and loose muddy beds are common in the smallest and high-intermittency floodplain channels, as well as the development mainly along their banks of rooted-submerged macrophytes (e.g., *Ceratophyllum demersum* and *Cabomba australis*) and floating meadows (largely composed by *Echinochloa polystachya*, *Panicum elephanti-pes, Paspalum repens, Polygonum ferrugineum, Eichhornia azurea* and *E. crassipes*) which sometimes cover the entire stream surface area during high water periods (November-April). These species show strong biomass fluctuations according to the diverse hydroecological conditions of the floodplain channels. Furthermore, large drought phases as a consequence of climatic events as the long 1999 episode of El Niño/Southern Oscillation, which allowed the striking invasion of *Victoria cruziana* on the bank strip of a mean-intermitence channel (Table 6), near to the mouth of a lake which shows a large overgrowing of this species, usually covering 40 % of this waterbody. The low depth and the lack of current in the channel (coupled with this lake is the unique waterbody that contains this species in that floodplain area) allowed the grow of *V. cruziana* in a lotic habitat where never was see during more than 30 years (DRAGO, pers. observ.). It must be stressed that this species never grows in the floodplain channels during the normal low water levels. The next flood pulse carried away these plants.

During low waters, the smallest floodplain channels present a noteworthy diminution of current velocity, until in some of them the flow ceases, achieving temporary lentic characteristics that have been called "lentification process" (DRAGO, unpubl.). Thus, is usually to detect in drought phases strong gradients (physical bars) of suspended sediments, transparency and temperature at the junctions of permanent and intermittent channels (Table 8). The lentification process may be shorth or long in time, depending of the magnitude and duration of the drought phase and the location and morphological evolution of the channel in the floodplain drainage network. During mean and high water levels the chemical conditions of floodplain channels are similar to those of the main channel (Table 2). As in the main channel, water quality varies also slightly throughout the year. Some differences compared to the main channel are due to the salinization effect of the tributaries, mainly those flowing from the western margin (Chaco-Pampa Plain) (Table 2). Moreover, the changes in salinity along some reaches of the secondary channels are also caused by the inputs of high saline groundwaters (MAGLIANESI 1969). This author showed that those increments are over 100 % in average, mainly due to inputs of sodium chloride and sodium sulfate.

Studies on benthic macroinvertebrates have been demonstrated also the importance

of the floodplain channels hierarchies for hydroecological research in the floodplain streams. As was described for main channel, largest permanent secondary channels (Table 6) have also the same cross section mesohabitats: **central and bank strips**, showing the same benthic species assemblages (Table 4) (MARCHESE & EZCURRA DE DRAGO 1992; MARCHESE et al. 2002). Small floodplain channels (33 m^3 s^{-1} in low stage), show high species richness in mean and high water levels (Table 4), with remarkable temporal and spatial variations in the benthos structure during the maximum floods. The hydraulics conditions in steps and scour holes of smallest secondary channels during the flood phase show strong changes, mainly at the confluence scour holes. Thus, remarkable longitudinal variation in the benthos structure are found in the small channels, while in the main and large secondary channels high differences are detected at the cross section scale, as central and bank strip habitats (EZCURRA DE DRAGO et al., unpubl.).

The larger fish species inhabiting the floodplain streams are *Salminus maxillosus, Potamotrigon motoro, Leporinus obtusidens, Pterodoras granulosus, Pimelodus albicans, P. clarias maculatus, Lucio pimelodus pati, Pseudoplatystoma coruscan, P. fasciatum fasciatum, Sorubim lima, Ageneiosus brevifilis, A. valencienne, Hypostomus commersoni* (Table 5). Juveniles of large species as well as small fishes use aquatic macrophytes as temporary or permanent habitats for shelter, feeding, reproduction and dispersion. When the flow ceased in the low intermittence channels during low river stages, the deep scour holes show a striking accumulation of large and small fishes, which have been detected during bathymetric surveys (DRAGO & PAIRA, unpubl.). It is common to observe species of *Salminus maxillosus* predating in these habitats.

Floodplain lakes

There is an heterogeneous terminology in the literature for the identification of the floodplain lakes, as oxbow lake, shallow lake, pond, slough, backsamp, backwater and lagoon. However, some terms as "lagoon" must be avoided because this type of water body is genetically associated with the marine coastal processes, and is properly also called coastal lake or albufera (STEVENSON 1968; TIMMS 1992). Floodplain lakes are defined here as permanent or temporary waterbodies which may present their surfaces free or covered by emergent vegetation. Usually, the largest lakes are free of macrophytes at the center of their surfaces, mainly due to their high fetch and depth. The temporary character of some of these water bodies depends on the frequency, magnitude and duration of the flood and drought pulses as well as their connection degree with lotic waters. Lentic waterbodies located within islands of the main channel are termed "levee lakes". They are formed by the following processes: 1) As water level fluctuated, mid-river bars can be transformed into levees which form downriver and ultimately meet to enclose a teardrop-shaped waterbody, being similar to the deltaic levee delta (TIMMS 1992). The new levee lakes show the form of a U with its open end directly connected with the river, and the subsequent evolution close this mouth and the waterbody is isolated from the river. They are shallow and show a temporary condition. 2) The annexation of channel islands and the isolation of an anabranche, created another type of levee lake. These waterbodies show a channel-shaped basin and are deeper than the preceding type. 3) The annexation of a sand bar to an island can be isolated a short river reach in between, forming another type of levee lake. In the Middle Paraná floodplain, more than 90 % of lakes are remnants of abandoned channel reaches, either

from the main river and their anabranches or from floodplain channels (DRAGO 1976, 1989, 1990). DRAGO (1989) distinguished seven main types of lakes, according to their origin and evolution. Swamps are terminal phases of the floodplain lakes previous to the terrestrialization. Since swamps developed in basins of senescent lakes, they are subject to expansion and contraction in area with changes of water level due to flooding or rainfall fluctuations. Usually, swamps formed from an isolated lake are temporary and those associated with connected lakes have a largest inundation phase. The swamp conditions are dominated by closely packed aquatic and subaquatic plants. The grow of emergent plants is often so dense that vast areas of water are enterily hidden from view. Thus, the constant fall of dead vegetation into the thin water layer below the emergent plants produces an accumulation of organic debris which, under swamp conditions, can lead to a strong reduction or the complete absence of oxygen in the water. The decomposition process also causes this water to be markedly more acidic than adyacent lake water, with values as low as pH 3. Dendritic and irregular lakes may contains swampy areas developed in the bays or associated with deltaic lake areas.

As a consequence of high discharges, the floodplain lakes are periodically inundated by the turbid floodwaters of the Paraná River. However, at low river levels, processes such as the growth and decay of primary producers (mainly macrophytes), and the mixing and resuspension of bottom sediments, govern lake metabolism. According to JUNK (1983), such water bodies are intermediate between closed lakes as accumulating systems and rivers as discharging systems; hence, they are not true lakes. During low and mid-river stages, the water regime of the lakes will be strongly dependent on the direct or indirect connection with the channels. Furthermore, the lengthening or shortening of the hydrological phases in the lakes will depend on their connectivity with the active channels (DRAGO 1980, 1981, 1989). A lake with a direct connection can be annually isolated 17 days and connected during 348 days. An isolated lake for the same period, showed a disconnection phase of 354 days and was only connected during 11 days. Both lakes are separate 7 km away (DRAGO, unpubl.).

Three levels of surficial hydrological connectivity between lotic and lentic waters can be distinguished according to the connection type: (1) direct or permanent connection through a mouth or an levee erosion ditch, (2) indirect or temporary connection through floodplain channels or a channel-lake systems, occurring from the rising phase up to the bankfull stage, i.e., the lotic water not overflows the levees yet, and (3) isolation o temporary connection occurring by overspill during highest floods. They are also two levels of lateral-vertical subsurficial connectivity: (a) groundwater from river infiltration, that may be important during the first time of flood pulse (rising phase), originating small elevations of the lake levels, when the river is still under the bankfull stage, and (b) the groundwater contribution from terrestrial aquifers, mainly those from the Chaco-Pampa Plain, which can largely increases the salinity of lotic and lentic floodplain waterbodies located on the westward border of the Paraná valley (MAGLIANESI 1969). This fact enhance the physical and chemical heterogeneity of the hydrosystem, besides originating fluvial ecotones of different magnitude.

This lotic-lentic connectivity allows an annual mix between flowing (regional) and standing (local) waters and an exchange of biotic and abiotic materials. This has a very strong influence on the lakes, on the river, and on the whole Paraná River ecosystem. Floodplains link main and secondary channels with the standing waters, because of that the lakes are flood-dependent ecological systems. These lotic-lentic floodplain systems

are intimately interrelated and linked by the annual cycle of high and low water river stages (DRAGO 1981, 1989; JUNK et al. 1989).

The river and floodplain dynamics have formed thousands of lakes in the Middle Paraná river. These water bodies range in shape from circular to irregular, with lengths from less than 100 m to more than 9 km and a mean length of 1.1 km (PAIRA, unpubl.). The shoreline development (D_L) is a measure of the degree of irregularity of the shoreline. Perfect circular lakes have a $D_L = 1.0$, while in dendritic lakes values between 3 and 5 or even higher can be expected. Floodplain lakes show D_L ranging from 1 to 9.3 and a mean value of 1.8, while the major number of lakes fall between D_L of 1.5-2.0. These values corresponding to the scroll lakes, which are the most numerous lake types in the Paraná floodplain. Figure 8 shows the number of lakes in relation to their D_L obtained from a geomorphological study of 1,500 waterbodies in the Paraná floodplain (PAIRA & DRAGO, unpubl.). Five typical lake basin shapes were detected: circular, subcircular, channel-shaped/lunate, dendritic and irregular. Channel-shape lakes originate from the abandonment or meander migration of floodplain channels. The later process created the oxbow and scroll lakes. The annexation to the floodplain of large islands and anabranches forms the dendritic lakes, which are large waterbodies with several long and deep bays (abandoned anabranches). Irregular lakes were originated by filling of minor sunken tectonic blocks with alluvial deposits of the river. These waterbodies are the largest lentic basins of the floodplain, showing very irregular shapes ($D_L = 9.3$) and some of them contains small uni- or multilobate deltas (DRAGO, unpubl.). Laguna Coronda and some of the lakes located to the south of Santa Fe city, are examples of these tectonic-alluvial lakes (Fig. 2: F). The oxbow lakes usually show a long-term evolution to swamps and terrestrialization in relation to the scroll lakes, because they have significantly higher depths. Dendritic and irregular lakes are also originate by the annexation of scroll lakes sets (DRAGO 1989, 1990). These irregular-dendritic lakes can be distinguished by the existence of small-elongated islands, that are the remnants of the old successive series of levees originated during the meander evolution. Floodplain lakes are shallow, rarely exceeding 4 m maximum depth at mid-water river level, with regular bottom topography, and with muddy substrates on the fluvial sands and an abundance of coarse organic particulate matter (COPM), usually leaves and sticks. The rejuvenation processes in the old as well as new areas of the floodplain depends of the distance between the lake and the active channel, shape of the lake basin, the transversal or parallel location in relation with the water course, and the type of riparian vegetation sorrounding the lake shoreline. An isolated channel-shaped lake located parallely to an active channel can be strongly rejuvenated during large floods. For example, a floating meadow (locally named "embalsado") which in some parts had 1.5 m thickness, covered completely a former channel-shape lake (790 m length), was carried away during a large flood. The 0.5 m layer of coarse particulate organic matter that covered the bottom was also wash out, emerging the original sand bed of the abandoned channel. During the inundation phase, the residence time of water was only twenty three minutes and the maximum surficial water velocity reached 0.95 m s^{-1}. Usually, this waterbody shows higher water residence times (one year or more), have being isolated 75 % of the time during three years (DRAGO, unpubl.). The new floodplain areas adjacent to the main channel are the most active of the valley, with highest rates of erosion and deposition, originating sometimes the fast annexation of channel islands and sand bars, the scour of abandoned channel or rejuvenation of lakes. Therefore, the change from flowing to still

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water condition or viceversa may occur in shorth-term periods. In the active border located downriver of Paraná city, it was measured a maximum rate of floodplain buildout of 222 m yr^{-1} and a maximum retreat of 90 m yr^{-1}. The maximum thalweg shiftings reached 350 m yr^{-1} and the sand bars and islands downriver migration showed a mean of 60 m yr^{-1} (DRAGO 1977a).

The floating and rooted vegetation, which is an important factor in the morphological and biological evolution of the lakes, show a high degree of variability in their percent coverage of the water bodies (Fig. 9; BAYO et al. 1981; DRAGO & VASSAL-LO 1980). According to DRAGO & VASSALLO (1980), 67 % of the variation in the transparency of the floodplain lakes is explained by the sediment trap effect of the aquatic plant cover. These authors found during a drought phase water transparencies ranging from 17 to 93 cm, within a range of 30 % to 70 % of vegetation cover. Usually, the highest percentages of emergent vegetation are detected in the smaller (<15 ha) and channel-shaped lakes located in the older areas of the floodplain, i.e., far away of the main channel (Figs. 2-9). The underwater matrix of stems and roots in the floating meadows is strongly associated also with the sedimentation processes (DRAGO & VASSALLO 1980). For example, the contribution of *Eichhornia crassipes* to the accumulation of organic and inorganic materials on the bottoms is very important. This floating plant has a production of 12-16 t ha^{-1} yr^{-1} (LALLANA 1980; NEIFF & POI DE NEIFF 1984). In the case of isolated lakes covered by aquatic macrophytes, an 80 % of the total particulate organic matter deposited on the bottoms is COPM, being mainly produced from *Eichhornia crassipes* (EZCURRA DE DRAGO & MARCHESE, unpubl.).

The intensity of resuspension-sedimentation processes is a function of several variables, including wind velocity, effective fetch, wind-driven currents, depth of water column, aquatic-terrestrial vegetation cover, and physical properties and distribution of the bottom sediments. Despite of the complexity of the phenomenon, some investigations demonstrate that sediment resuspension in a small lake is predictable from wind velocity (CARPER & BACHMANN 1984; HAMILTON & LEWIS 1990). In floodplain lakes, the deepwater wave exceeded the mean depth throughout the isolation phases, indicating that sediments could have been resuspended from much of the lake bottom. Thus, when a deepwater wave moves into water with a depth less than one-half its wavelength, the wave is said to "feel" the bottom. This means that there is an oscillatory horizontal motion of the water immediately over the bottom surface which may be sufficient to resuspended bottom sediments. During a study on sedimentation processes from July 1987 to August 1989 (DRAGO, unpubl.), an average sedimentation rate of 31.6 g m^{-2} d^{-1} was measured, with maximum rates during isolation periods of 92 g m^{-2} d^{-1}. The minimum sedimentation rates were measured during inundation phases, reaching 4.4 g m^{-2} d^{-1}. The sedimentated material presented a composition of 80-99 % of inorganic fraction, and the organic material ranged between 0.14 and 11.3 g C %. The gallery forests, brushes and aquatic and semiaquatic grasses surrounding the lakes and covering the aquatic-terrestrial transition zones (ATTZ, JUNK et al. 1989) affect some abiotic factors of the flood waters entering the lakes, as current velocity, suspended sediment concentration and transparency (DRAGO 1989). A decreasing of 29 % in the suspended sediment concentration of the main channel was detected when the water flowed no more than 30 m through a levee with gallery forest and brushes. The same value was reached after the flood water flowed 1.7 km into a neighbouring lake directly

connected with the river. In the first case, the current velocity fell to 92 % and in the second case, the same value was measured after the water flowed 3 km into the lake. At the same time, the transparency increased 300 % in the same distance (DRAGO, unpubl.).

During inundation, water chemistry is similar to that of the floodwater from the parent river in the majority of the lakes, but following isolation differences arise between the lentic waterbodies and their adjacent flowing waters. Furthermore, during mid-water stages, neighboring lakes can show different salinities, depending of the connectivity with the channels (Table 2). Thus, lentic waters directly connected with the channels show less salinity than those which are indirectly connected. Some waterbodies can be isolated one month a year, whereas another located very near, can be connected with the river only a month. This variability shows the hydroecological complexity of the system.

Highest open-water temperatures occur during summer, but dramatic increases in temperature have been measured in the upper 10 cm of the water within the floating meadows, reaching up to 46 °C (DRAGO & PAIRA 1987; DRAGO, unpubl.). At the same time, the colder waters are detected on the bottom under the meadows. However, these marked temperature stratifications are present during short time periods, being destroyed mainly by the winds and to a lesser degree, by nocturnal cooling. During floods the temperature of the lakes is similar to that of the floodwater from the parent river, but following isolation considerable differences develop between the lentic bodies and their adjacent flowing waters. As a result of its temperature and circulation patterns, the floodplain lakes can be classified as "continuous warm polymictic" (DRAGO & PAIRA 1987), according to LEWIS's classification based on mixing (LEWIS 1983).

Contrary to the central strip of the main channel and largest floodplain channels, the bottom fauna of the floodplain lakes is diverse. However, during particularly long drought periods, the floodplain streams of the lower hierarchy or those near to the isolation by erosion-deposition dynamics (e.g., the cutoff of meander loops), show a "lentification" process (DRAGO, unpubl.). This means that these waterbodies begin to show physical and chemical characteristics similar to the adjacent lakes. These lentic conditions are maintained until the next period of rising water, when the physical and chemical condition of these channels returns once again to resemble that of the permanent flowing waters.

The density, species richness and diversity of the benthos reach its maximum in the connected largest floodplain lakes of the NFA (Fig. 2), with dendritic basins ($D_L \geq 4$), and several deep and shallow bays. Furthermore, the benthos structure is different according to the connectivity between floodplain lakes and rivers (connected and isolated lakes), the diverse aquatic vegetation covering the lentic waterbodies and the quantity of CPOM deposited in the bottom (EZCURRA DE DRAGO 1980; MARCHESE et al. 2002; EZCURRA DE DRAGO & MARCHESE, unpubl.). The benthos community of the connected lakes has a higher density, species richness and species diversity compared these values with the bottom fauna of the isolated lakes. In these waterbodies, during the low water level, with anoxic conditions in the sediment-water interface, there are only tolerant species, as *Limnodrilus hoffmeisteri, Branchiura sowerbyi, Chironomus xanthus*, mainly (Table 4). It is remarkable that in these lakes is very common found the benthos represented by only one of the mentioned species. In circular and subcircular and irregular lakes the spatial distribution of the benthic structu-

re is rather homogeneous. On the contrary, in large dendritic connected lakes, there are a remarkable spatial heterogeneity in the benthos species assemblages between the main basin lake and the bays covered with vegetation and highest quantity of CPOM on the bottom. In low water phase, the benthos of the main basin lake has a higher species richness (Table 4: connected lakes), while the bay's bottom fauna is the same of isolated lakes due to the similar environmental conditions (Tables 4-9; EZCURRA DE DRAGO & MARCHESE, unpubl.). For example, *Chironomus xanthus* dominates in density as well as in biomass in these habitats where large amounts of CPOM are accumulated on the bottom (EZCURRA DE DRAGO 1980).

In the river systems of all sizes on all continents, a variety of fishes take advantage of seasonally inundated floodplains (BAKER et al. 1991; QUIRÓS & CUCH 1989; WELCOMME 1979). Large commercial species inhabiting of Paraná River, as *Prochilodus lineatus*, use the lentic areas for feeding and resting and the main and secondary channels for migrations. Thus, the heterogeneity and the degree of connectivity of the floodplain lakes are important factors for fishes, even for taxa typical of flowing waters (e.g., *Salminus maxillosus, Pseudoplatystoma fasciatum, P. coruscans*, etc.). According to BONETTO & PIGNALBERI (1964) and BONETTO et al. (1971), the floodplain lakes are essential environments for fish ecology, because of their richness in organic matter and their function as shelters for the larvae and juveniles of fishes.

The permanent lakes of the Paraná River floodplain harbor up to 150 fish species, at least 50 of which are common to abundant (Table 5). Some species, as *Prochilodus lineatus* and *Hoplias malabaricus*, usually account for more than 80 % of the total fish density (CORDIVIOLA DE YUAN 1977). Some of them are unique to these habitats, such as *H. malabaricus* which shows strongly sedentary habits (BONETTO et al. 1971; CORDIVIOLA DE YUAN 1977). TABLADO et. al. (1988) detected an annual average density of 932 fish per hectare larger than 20 cm in length in a large floodplain lake.

When these habitats are isolated from the rivers, the fish community tends to remain stable, but during the lotic-lentic connection period (rising, flooding and falling phases; DRAGO 1989), changes in the fish community can be detected (CORDIVIOLA DE YUAN 1992). Usually, the fish community increases in diversity during the floods, when the floodwaters spread over the levees, flats and floodplain lakes. The mixing between running and standing waters reaches its maximum during the inundation phase (DRAGO 1989). Standing stock biomasses can reach high levels in the lakes, ranging from 130 kg ha^{-1} to 2,000 kg ha^{-1}, with a mean value of 600 kg ha^{-1} (CORDIVIOLA DE YUAN 1992). Furthermore, fish biomass in lentic waters appears to increase from those lakes most influenced by the main channel to those located in the distal border of the floodplain. There is evidence that at least some of these species can survive long periods of very low oxygen concentration (CORDIVIOLA DE YUAN et al. 1984; PARMA DE CROUX 1994). Moreover, species as *P.lineatus* and *Pimelodus clarias maculatus* can move horizontally and vertically toward loci with better oxygen-temperature conditions (PARMA DE CROUX 1994). However, these two species may be found in areas covered with dense mats of floating vegetation, where low oxygen levels can persist for several days with high water temperatures (CORDIVIOLA DE YUAN et al. 1984). *P. lineatus* and *H.malabaricus* have been observed inhabiting areas with very low oxygen concentrations, as low as 0.3-0.4 mg O_2 l^{-1} (DRAGO, unpubl.). The fish fauna in the vegetated lakes is rich in species; a total of 71 species have been observed, of which the most frequent were members of the Characidiidae and Cichlidae (CORDI-

VIOLA DE YUAN et al. 1984).

Differences and groupings of fish populations were found by CORDIVIOLA DE YUAN (1992) in lakes with different sizes, and especially within two typical microhabitats: open waters and vegetated areas. This author assumed that the water level fluctuations and the lake sizes are the main factors affecting fish populations within the floodplain. However, the differences in the physical structure of the microhabitats (i.e., depth, temperature, oxygen, and vegetation) would be also important. For example, a survey including several lakes along the middle reach of the Paraná River showed a negative correlation between the number of species and Secchi depth and percentage of macrophyte cover (CORDIVIOLA DE YUAN 1980). From the 85 taxa identified in the same study, 55 % were Cypriniformes, 27 % Siluriformes, 11 % Perciformes, 2 % Atheriniformes, 2 % Pleuronectiformes and 1 % Rajiformes (= Myliobatiformes). According to QUIRÓS & BAIGÚN (1985), aquatic plants could be a key factor in the spatial and temporal organization of biota in the floodplain. The structure of the Paraná River fisheries and their relationships with the geomorphology and temperature and water regime were largely described by QUIRÓS & CUCH (1989).

The aquatic-terrestrial transition zone (ATTZ)
The areas alternating terrestrial and aquatic phases were designated by JUNK et al. (1989) as the Aquatic-Terrestrial Transition Zone. During low waters the ATTZ is disconnected from lotic and lentic waterbodies. From the beginning of the rising phase up to the bankfull stage, the lotic waters begin to flow into the lakes with direct connection and then through which lakes with indirect connection. Thus, the lake levels increase a low and difusse inundation is produced, overflowing the low-lying areas of the ATTZ, i.e., the flooding begin from the "internal areas" of the floodplain. The littoral zone of the lakes changes position in direction to the high-lying areas of ATTZ (levees). At the same time, the "external areas" of the floodplain, as river banks and island perimeters, also begin to flooding. JUNK et al. (1989), called "moving littoral" to this change the position along the flood gradient throughout the entire alluvial valley according to the river stage. Thus, the first annual mixing between regional river water and local lentic water begins within the floodplain lakes, forming a mixing zone of the surface waters defined as "perirheic zone" (MERTES 1997). In largest floods, as occurred during El Niño events, the Paraná valley is completely inundated and the perhireic zone may shows several physical and chemical gradients in the lateral dimension. According to MERTES (1997), this zone performs the functions of an ecotone by serving as a boundary between source waters of differing chemistry and transparency. This zone is also a transition from still to flowing conditions in some lakes areas, even during the entire flood pulse. When the bankfull stage is overcome, the river water overflows the levees. Depending of the magnitude of the Paraná peak flood, the highest levees will be annually inundated and the lakes will loss partially their lentic identity.

In the ATTZ of the Paraná river-floodplain can be distinguished five main zones according to the frequency and duration of inundation: (1) old and high levees supporting gallery forests with major diversity, usually located at the inner parts of the floodplain; (2) high sandy areas or parkland savannas covered by grasses with sparse groups of *Acacia caven*; (3) young and low levees with gallery forests composed by mixed or monospecific stands of *Salix humboldtiana* and *Tessaria integrifolia*; (4) low areas overgrowed with a high density of *Panicum prionitis*; and (5) areas located on the lake

shorelines, covered by aquatic and semiaquatic grasses, as *Ludwigia peploides*, *Echinochloa polystachya*, *Polygonum ferrugineum*, *Alternanthera philoxeroides*, among others. The zone (3) is the less representative zone in the alluvial landscape. The frequency and duration of inundation increase from (1) to (5). *Tessaria integrifolia* and *Salix humboldtiana* are the piooner species of sand bars, river banks, alluvial plugs and sand splays. Herbaceous plants are representative in the aquatic and terrestrial phases. Perennial grasses as *Paspalum repens* and *Echinochloa polystachya* form extensive monospecific stands, being highly efficient sediment traps during the inundation phase. The zones (4) and (5) are sometimes under long aquatic phases, performing large marshy areas. Thus, it is common to detect the presence, mainly on the leaves of *Panicum prionitis* and on the stems of *Solanum glaucophyllum*, a high density and species richness of freshwater sponges, as *Corvoheteromeyenia australis*, *Eunapius fragilis*, *Heteromeyenia stepanowi*, *Radiospongilla crateriformis*, *Trochospongilla minuta*, *T. delicata*, *T. lanzamirandai*, *T. latouchiana*, *T. paulula*, *Drulia browni*, *Oncosclera navicella* and *Uruguayella repens* (EZCURRA de DRAGO 1993). These species are tipically periphitic, being only some of them of benthic habitat, such as *Uruguayella repens* and *Oncosclera navicella*, which are also registered on the bank strip habitats of the main and large floodplain channels (Table 4). From seven years ago, numerous populations of the invasor bivalve *Limnoperna fortunei* which last larvae stage (plantigrade) fixed in the same type of substrates occupied by the sponges in the ATTZ during the flood phase (EZCURRA de DRAGO et al., unpubl.). *L. fortunei* is also a benthic species, inhabiting the bank strip of main channel and large secondary channels, the clay substrate patches in small floodplain channels and in large connected lakes (Table 4). In these lakes, adults of this species is found only during the high water phases.

Tributaries
This habitat (a stream channel ecotone) includes the lowermost reaches of the tributaries, which are influenced by backwater flooding from the main channel or from secondary channels (Table 1). The upstream limit of this fluctuating habitat is sometimes difficult to delineate. However, the higher salinity (and in some cases the higher or lower turbidity) of the tributaries on the whole, make it possible to detect the reaches of mixing waters and the upper limits of this habitat. Furthermore, the fluctuations of the water level upriver in the tributaries show the influence of the hydraulic backwater effect on the channel habitats. Some indirect outlet tributaries flow parallel along the side of the floodplain more than 60 kilometers downriver, until they reach the parent river through a secondary channel ("deferred tributaries", LOBECK 1939). Tributary habitat is predominantly low-gradient, sand-silt or mud-bottomed, and relatively slow-flowing during most of the year. During high levels on the Paraná River, tributaries may be dammed and remain sluggish or even flow backwards. During extended low-water stage periods, the habitat shows the physical and chemical conditions of the tributary stream. During rising, high and falling levels of the parent river, the habitat shows a water mixing zone which extends upstream according to the peak flood magnitude. Even in the largest tributaries, as Paraguay and Salado del Norte rivers (Fig. 1), the Paraná floods can cause strong backwater effects which extend several kilometers upriver. For example, in the Paraguay River, this feature affects the lower 400 km (from its confluence with the Paraná River up to Asunción city, Paraguay), with velocities of

the hydrodynamical backwater up to 2.7 km h^{-1} and risings the river levels more than 1 m (SOLDANO 1947). As a consequence of the entrance of the Paraná River floodwater in the Salado del Norte River valley during high floods (e.g., El Niño 1998), the planktonic *Limnoperna fortunei* larvae can enter 10 km upriver and developing periphytic and benthic populations during high water phases. This *L. fortunei* invasion is possibly due to the strong decreasing of the water salinity of the Salado del Norte River (DARRIGRAN & EZCURRA DE DRAGO 2000). Some small tributaries may also change rapidly in response to localized, heavy rain, becoming swift and turbid.

The benthic structure of the tributaries shows differences between which flowing from the the eastern or western margins of the Middle Paraná valley. The tributaries of the eastern side present a greater macroinvertebrate specific richness and diversity than those of the western side (MARCHESE & EZCURRA DE DRAGO 1983, 1992). Furthermore, the eastern side tributaries show a benthic community similar to that of the floodplain channels. According to MARCHESE & EZCURRA DE DRAGO (1983, 1992), these differences in the zoobenthos between western tributaries and secondary channels are due to physical and chemical variables as depth, current velocity, discharge, transparency, type of substrate (sandy vs. muddy channel beds), pH and mainly, water salinity. Several tributaries, mainly which of the western margin, shows remarkable differences in benthic structure as a result of anthropogenic impacts (MARCHESE & EZCURRA DE DRAGO 1999). Furthermore, channel patterns together with channel bars distribution, produce several fluvial microhabitats in the most downstream portions of tributary streams, which are inhabited by different macroinvertebrate communities (Table 4).

In spite of the physical and chemical differences between tributaries and the parent river, the fish species found in the tributary habitats resemble those of the Paraná main channel (Table 5). Thus, small species as well as large ones use this habitat as migratory routes (BONETTO & PIGNALBERI 1964). The scarce data on fish migration in the tributaries, show that *Salminus maxillosus* and *Prochilodus lineatus* move 250 km and 100 km respectively upstream in the Salado del Norte River (BONETTO et al. 1971; Fig. 1).

Conclucions

The Middle Paraná main channel is typically braided, showing a sequence of wide segments characterized by one or more anabranches, with unstable sand bars and islands. Such stretches are separated by nodal points, i.e., well-defined single, deep and narrow channel reaches. The nodal points of the main channel are largely stable, long-lived habitats of the lotic environments, lasting more than 150 years. On the contrary, the braided segments are the most unstable areas of the river, showing highest aggradation and deposition rates. The hydrosedimentological dynamics of the river strongly drives the hydrographical articulation of the lotic and lentic waterbodies. On the border between the main channel and the floodplain, rapid shiftings from running to still waters environments or viceversa can be detected. Thus, floodplain lakes directly connected with the main channel as well as their anabranches may be connected or disconnected from the river during periods ranging between 10-20 years. These processes can be accelerated during macroclimatic influences such as El Niño/Southern Oscillations basin size. The annexation of sand bars and islands is the main process that increases the water bodies heterogeneity and decreases the hydrological connectivity

along the floodplain-main channel border. The intensity of these processes in the floodplain channels decreases with the increasing of the distance to the parent river. Moreover, the declining in connectivity resulting from geomorphological and ecological succession can no longer be compensated by river dynamics in the older flooplain areas. However, the largest floodplain channels, i.e., which are permanents and with mean discharges ranging between 800 m^3 s^{-1} and 2,000 m^3 s^{-1}, generated also strong hydrose-dimentological changes in the associated lentic waterbodies and can be rapidly reset their ageing processes.

Geomorphological studies in the Middle Paraná floodplain, demonstrate the existence of successional processes and the subsequent changes in connectivity. This lateral connectivity could be maintained or increased by the prevailing successional processes, which have been shown to be reversible by the rejuvenation events during large floods. Sometimes, these rejuvenation processes are remarkable even in the old areas of the floodplain, depending of the distance between the lake and the secondary channel, shape of the lake basin, their lateral or parallel location in relation with the active channel, and the type of vegetation surrounding the lake shoreline. Thus, a direct connected or isolated waterbody located parallely and near to an active channel with a channel-shaped basin can be deeply rejuvenated and a lower rate of succession is expected. In the older areas of the floodplain, where erosion is less effective, the prevailing process is the decreasing in connectivity. Meander scrolls developed in the largest floodplain channels, can be rapidly evolved to a scroll lake in no more than 10 years. The isolation of these types of lakes, i.e., from directly to indirectly connected or completely isolated will depend of the meander evolution and the developing of the channel sand bars. Flood-plain lakes directly connected with an active channel through a mouth can be also isolated by the formation of sand plugs during the annual flood phase. However, it must be stressed that every floodplain lakes located near the permanent active channels can suffer modifications during large hydrological events in their hydromorphological and ecological characteristics. At the waterbody scale, the lakes even the oldest, are unstable environments mainly because the continuous slow or swift changes in their hydrological, morphological and biological conditions. The autogenic processes are both direct and indirect factors for these changes. Large and permanent lentic waterbodies of the Paraná River floodplain are more productive than their lotic environments and even more than the main channel. When the floodplain lakes are highly connected to the running waters, a large part of their production drifts out into the main and secondaries channels, thus increasing the amount of food for riverine populations. These lentic waters also act as spawning and nursery areas for many migratory fishes and as shelters during highest floods.

Three levels of surficial hydrological connectivity between lotic and lentic waters may be distinguished according to the distance travelled by the river water through the floodplain: (1) direct or permanent connection, (2) indirect or temporary connection, and (3) temporary connection. During the largest droughts a large number the floodplain lakes remain isolated from the flowing waters, and the connectivity between the parent river and the floodplain is maintained by the permanent secondary channels. Intermittent channels temporally shift from lotic to lentic condition, developing similar environmen-tal conditions of the neighbouring lakes. This change in the hydroecology of the minor floodplain channel have been termed "lentification process". Two main factors are changing the connection times between lotic and lentic environments: the operational

management of dams located in the Upper Paraná River, which originated an increasing of 1.5 m of the minimum water levels during drought phases, and the hyperhumid period that began in the seventies, that has shown a noticeable increase of water discharges in the rivers of the catchment, a tendency that does not seem to revert. The higher minimum water levels means that thousands of lakes show an increasing in the frequency and duration of connection times and therefore a change in their hydrosedimentological regimes and ecological evolution.

Geomorphological, sedimentological, hydraulics and chemical characteristics of the aquatic environments are markedly reflected in the benthos structure of the river-floodplain system. The degree of connectivity and the alternation of flood and drought phases are also key factors, mainly at the floodplain waterbodies scale. The most stable spacial and temporal benthic species assemblages are detected in the main channel and in the largest floodplain secondary channels, where the first ones shows the highest rigorous life's conditions, being only colonized by very few taxa. Thus, in a channel cross section benthos species indicate two different habitats. The central strip contains the highest density values of very small organisms and the lowest values in species richness and species diversity. On the contrary, in the small floodplain channels there are not remarkable differences in the structure of the bottom fauna between the central and bank strips. Here, the most important changes are found in the longitudinal and temporal dimensions which are related with the channel morphology and hydraulics conditions, mainly at the confluences of the floodplain channels. These changes are enhanced during flood and low water phases. Some benthic species assemblages are characteristic inhabitants of regular bed morphology reaches with very low sediments mobility during flood phases, and other species assemblages are indicator of very different hydraulics conditions, as which found at the scour holes. Furthermore, the longitudinal heterogeneity in benthic structure is also maintained during low water stages, being the species assemblages of the scour holes more similar to which found in the connected lakes that the species inhabitants in the bed regular morphology reaches of the same river.

Floodplain lakes show the largest differences in the benthos structure of overall habitats of the Middle Paraná river-floodplain system. The key factors accounted for these differences are the origin, size and morphology of lake basins, the connectivity degree with lotic waters, percentage of aquatic vegetation cover, amount of CPOM deposited on the bottom and oxygen disponibility. There are remarkable differences in the benthos structure between different types of lakes as well as in different microhabitats within the same lake. Relevant examples are the largest dendritic-irregular lakes with direct connection, because several benthic species assemblages can be recognized around the same lake. Thus, it is possible to differentiate benthic species assemblages caracteristics of a "young connected lake", in the areas strongly influentiate by the connection with the river, from which tipical of "old small circular or subcircular isolated lake", in the vegetated lake bays far away of the site of lake-river connection. The first ones show higher density as well as higher species richness and species diversity, while the second ones can be represented only by one species showing a middle density.

In the tributary habitats, the main parameter in determining the benthic structure is the chemical water quality. In fact, the affluents can be splitted in eastern and western tributaries. The benthic species assemblages of the eastern tributaries are very similar to

which inhabite in the floodplain channels. On the other hand, the western tributaries have very different benthic species assemblages, having only some common species with floodplain channels.

In the Middle Paraná River are registered a 80 % of the total fish species harbor in the Paraná River catchment. These fish population inhabit in several types of lotic and lentic habitats. Migratory species use the main channel habitat (narrow and wide cross section) for reproduction and spawning during high water phase. In the banks and the others mesohabitats of the main channel these larger fishes rest or predate. Some no migratory large and small species are near the banks or in aquatic vegetation belts for feeding or shelter, being *Prochilous lineatus* the dominant species in the shoal habitats. Larger fish species inhabiting in the floodplain channels, as well as juveniles of these taxa or adults of small species, which found food and shelter in the floating macrophytes.

During the high water phase floodplain lakes play and important role. This waterbodies offers food for all the functional trophic groups, being the largest lakes which have the highest species richness and the standing stock biomass. In the low water phase, permanent lakes have a higher species richness of small fish species as well as some larger ones, being some of them tolerant to low oxygen concentration. Some sedentary species inhabit only in the floodplain lakes.

The water level fluctuations, lake basin size and direct connectivity are the main factors affecting fish populations within the floodplain.

Until recently, habitats have not been consistently viewed in terms of the variables important to the organisms. Furthermore, multidisciplinary information on the functioning of the lotic-lentic floodplain systems is relatively recent. The main aquatic habitats have been delineated and described on the basis of major variables, and the relationships among the habitats have been examined. The future increasing utilization of the Hidrovía Paraguay-Paraná will arise also several problems of pollution related with the navigation, industrial settlements, etc. One example of biological contamination effect from Hidrovía in this hydrosystem is the rapid and extensive colonization of the invasive bivalve *Limnoperna fortunei*, from the Río de la Plata estuary to Itaipú dam (Brazil) in the Upper Paraná and to Cáceres city (Brazil), in the Upper Paraguay. This species originate severe biofouling processes in dams, blockage in water pipelines, filter occlusions, etc.

The alliance of the above-mentioned features enhanced the complexity of the hydrosystem and the necessity of the implementation of research projects in order to the prevention and management of deleterious consequences in the river network. It must be stressed that South America is one of the largest river-fresh water reserve in a worldwide scale. Therefore, protection and management of the large South American river ecosystems requires an understanding of the interrelationships and functions of their lotic and lentic habitats. Thus, the recognition of the Paraná River habitats and their physical, chemical and biological relationships may provide a useful tool in order to prevent injurious and irreversible changes to the river integrity.

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Table 1: Main aquatic habitats of Middle Paraná River (the numbers between brackets correspond to the habitat cited in Table 5).

Main channel	Lotic components	Floodplain area ATTZ	Lentic components
Narrow cross-section (nodal point) (1)	Permanent channel (9)	High-lying area - young levee - old levee	Permanent lake - direct connection - indirect connection - isolated (13)
Wide cross-section (with sand bars and channel islands) (1)	Temporary channel (10)	Low-lying area - marsh permanent temporary	Temporary lake - indirect connection - isolated (14)
High steep bank (>5 m to 80 m) (2)	Sand bar - point bar -mid-channel (11)		Swamp
Low bank (< 5 m) (3)	Scour hole - in confluence - in meander (12)		
Channel sand bar - mid-channel - on banks - on islands (4)	Channel Island - levee lake		
Channel Island - levee lake permanent temporary (5)	Slack-water area - in bank - in bar - in island		
Scour/tectonic hole - Deep hole (6) -Shallow hole (7)	Tributary - indirect outlet permanent temporary		
Slack-water area - in bank - in bar - in island			
Tributary - direct oulet permanent temporary			

Table 2: Mean physical and chemical conditions of the main aquatic habitats of the Middle Paraná River. Sample number for each habitat: 100.

Parameter		Main channel	Secondary channels	Lakes	Left bank tributaries	Right bank tributaries
Current velocity (m/s)		1.17	0.57	-	0.28	0.21
Discharge (m^3/s)		17,000.00	700.00	-	35.00	15.00
Transparency (m)		0.24	0.27	0.58	0.45	0.18
Temperature (°C)		21.80	23.00	19.90	20.00	19.50
pH		7.50	7.10	7.20	7.70	7.90
Conductivity (μS/cm)		85.00	88.00	115.00	1,110.00	4,208.00
Salinity	(mg/L)	63.50	90.00	122.00	752.00	3,111.00
Oxygen	"	7.89	6.90	6.00	8.10	5.50
CO_3	"	0	0	0	0	9.60
$H CO_3$	"	36.00	35.00	38.00	160.00	246.00
Cl	"	4.80	14.30	13.10	288.00	1,192.00
SO_4	"	4.50	4.10	8.90	182.00	560.00
Ca	"	7.40	5.40	7.60	63.00	62.30
Mg	"	1.80	3.40	3.20	15.00	49.80
Na	"	5.0	10.40	9.90	232.00	961.00
K	"	2.10	2.50	2.60	4.00	29.60
NO_3	"	0.95	1.30	0.91	0.15	1.84
NO_2	"	0.02	0.02	0.07	0.01	64.00
NH_4	"	0.09	0.25	0.28	0.97	0.63
SiO_2	"	14.40	23.00	19.00	25.02	26.00
PO_4	"	0.06	0.21	0.22	0.05	1.88
Fe	"	0.55	0.71	0.66		0.47
Alkalinity	"	0.60	0.57	0.76		4.20

Table 3: Mean (x) and standard deviation (s) of the abiotic and biotic variables in the channel centre (A) and channel banks (B) (modified from MARCHESE & EZCURRA DE DRAGO 1992). Sample number for each station: 414.

	Paraná River main channel		Main secondary channels		Minor secondary channels		Tributaries (left bank)		Tributaries (right bank)	
	x	s	x	s	x	s	x	s	x	s
A										
Sand (%)	98.97	1.671	97.50	2.646	81.56	32.109	84.75	12.892	72.60	35.330
Silt (%)	0.70	1.922	1.50	1.290	13.05	22.567	9.87	9.372	14.70	21.060
Clay (%)	0.19	0.431	1.00	1.414	5.38	10.043	5.37	6.277	12.70	20.450
Organic matter (g C %)	0.02	0.099	0.03	0.024	0.38	0.218	0.23	0.240	0.39	0.562
Density (ind/m^2)	5394.03	12565.215	2468.00	1606.298	1036.38	1268.563	698.62	681.063	293.60	311.300
Diversity (H)	0.60	0.565	0.65	0.472	1.59	0.976	0.49	2.067	1.11	0.690
Species richness	4.00	2.867	5.75	3.403	7.94	5.045	2.16	6.125	4.00	2.250
B										
Sand (%)	19.72	18.812	52.25	43.965	19.74	23.093	76.50	14.803	39.40	32.346
Silt (%)	59.60	23.798	40.00	38.996	48.01	30.486	16.50	11.973	43.90	28.462
Clay (%)	18.37	15.552	7.75	5.619	33.13	27.390	7.00	4.408	16.70	15.040
Organic matter (g C %)	0.49	0.207	0.19	0.196	0.42	0.245	0.14	0.092	0.75	0.581
Density (ind/m^2)	529.33	684.464	934.50	1670.335	745.36	818.070	503.12	382.784	531.30	373.911
Diversity (H)	1.50	0.867	1.49	0.640	2.20	0.858	1.32	0.470	1.08	1.014
Species richness	4.85	3.124	4.75	4.991	4.90	9.808	4.25	1.982	3.90	3.239

Table 4: Common benthic species in lotic and lentic habitats of the Middle Paraná River. (* - Dominant species)

Main and large flood-plain channel - central strip	Main and large flood-plain channel - bank strip	Small floodplain channel	Connected lake	Isolated lake and bay of dendritic lake
*Narapa bonettoi** *Myoretronectes*	*Oncosclera navicella*	*Cordylophora caspia*	Nematode sp. I	*Limnodrilus hoffmeisteri**
paranensis	*Uruguayella repens*	Nematode sp. I	Nematode sp. II	*Branchiura sowerbyi**
Haplotaxis aedeochaeta	*Aulodrilus pigueti**	*Aulodrilus pigueti**	*Aulodrilus pigueti**	*Dero (Dero) multibranchiata*
Tobrilus sp.	*Paranadrilus descolei**	*Paranadrilus descolei**	*Limnodrilus hoffmeisteri**	*Dero (Aulophorus) furcatus*
Parachironomus sp.	*Limnodrilus hoffmeisteri**	*Limnodrilus hoffmeisteri**	*Dero (Dero) obtusa**	*Slavina evelinae*
	Dero (Aulophorus) lodeni	*Limnodrilus udekemianus**	*Dero (Dero) multibranchiata*	*Trieminentia corderoi*
	Dero (Dero) nivea	*Tubifex tubifex*	*Dero (Aulophorus) lodeni**	*Eiseniella tetraedra**
	Pristina americana *	*Dero (Dero) obtusa*	*Dero (Aulophorus) borelli*	*Chironomus xanthus**
	Pristina osborni	*Dero (Aulophorus) lodeni**	*Dero (Aulophorus) furcartus*	*Lopescladius* sp.
	Eiseniella tetraedra	*Pristina americana**	*Pristina americana**	*Chaoborus* sp.
	*Bothrioneurum americanus**	*Pristina breviseta*	*Pristina minuta*	
	Parachironomus sp.*	*Pristina osborni**	*Pristina proboscidea**	
	Xenochironomus sp.*	*Pristina jenkinae**	*Pristina jenkinae**	
	Cryptochironomus sp.	*Pristina biserrata*	*Pristina biserrata*	
	Coelotanypus sp.	*Pristina acuminata*	*Pristina leidyi*	
	Ablasbemia sp.*	*Eiseniella tetraedra**	*Pristina acuminata*	
	Ceratopogonidae sp.I	*Bothrioneurum americanus**	*Slavina evelinae**	
	Pisidium sp.	*Trieminentia corderoi*	*Bothrioneurum americanus*	
	Limnoperna fortunei	*Brinkhurstia americanus*	*Branchiura sowerbyi*	

Diplodon spp.
Castalia spp.
Pisidium sp.
Eupera sp.
*Limnoperna fortunei**

Nimbocera paulensis
*Helobdella adiastola**
Helobdella sp.
Parachironomus sp.*
Cryptochironomus sp.*
Endochironomus sp.
Xenochironomus sp.*
Polypedilum sp.*
Corynoneura sp.
Djalmabatista sp.
Ablabesmya sp.*
Coelotanypus sp.
Ceratopogonidae sp.I
Ceratopogonidae sp.II
Campsurus notatus
Tricoptera sp.I
Diplodon spp.
Castalia spp.
Pisidium sp.
*Limnoperna fortunei**

*Eiseniella tetraedra**
Trieminentia corderoi
Brinkhurstia americanus
Chironomus xanthus
Parachironomus sp.*
Xenochironomus sp.*
Cryptochironomus sp.
Polypedilum sp.*
Endochironomus sp.
Lopescladius sp.
Corynoneura sp.
Djalmabatista sp.
Cricotopus sp.
Ablabesmya sp.*
Coelotanypus sp.*
*Helobdella adiastola**
Helobdella sp.I*
Hirudinea sp.II
Ceratopogonidae sp.I
Ceratopogonidae sp.II
Ostracoda sp.I
*Campsurus notatus**
Diplodon spp.
Castalia spp.
Anodontites spp.
Monocondylaea sp.
Pisidium sp.*
Eupera sp.
Limnoperna fortunei

Table 5: Habitat distribution and relative abundance of Middle Paraná River fish species.

| Species** | Floodplain | | | | | | | | | | | | | | |
| | Main channel | lotic area | | | | | | Lotic area | | | | Lentic area | | | |
	A	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Myliobatiformes															
Potamotrygonidae "rayas"	car														
Potamotrygon brachyurus (GUNTHER, 1880)	-	-	-	-	-	-	-	-	-	U	-	-	-	-	-
P. brumi DEVINCENZI, 1942	T	T	-	-	-	-	-	-	-	-	-	-	-	-	R
P. castexi CASTELLO & YAGOLKOWSKY, 1969	U	-	-	-	-	-	-	-	-	U	-	-	-	-	-
P. falkneri CASTEX, 1963	-	-	-	-	-	-	-	-	-	R	-	-	-	-	-
P. motoro (MÜLLER & HENLE, 1841)	C	C	C	C	C	U	-	U	T	C	-	-	-	R	-
P. paukei CASTEX, 1963	-	-	-	-	-	-	-	-	-	U	-	-	-	-	-
Clupeiformes															
Clupeidae															
Ilisha flavipinnis (VAL., 1849) "*lacha*"	car	-	-	-	-	-	-	-	R	-	-	-	-	U	-	
Ramnogaster melanostoma limnoica															
(A. DE ARÁMBURU, 1961) "*mandufia*"	car	-	-	-	-	-	-	-	U	-	-	-	-	R	-	
R. m. melanostoma (EIG., 1907) "*sardina*"	car	-	-	-	-	-	-	-	-	-	-	-	-	R	-	
Engraulidae															
Lycengraulis olidus GÜNTHER, 1868 "*anchoa*"	car	T	-	-	-	-	-	-	-	T	-	-	-	-	C	U
L. simulator FUSTER DE PLAZA, 1962 "*anchoa de rio*"	car	T	-	-	-	-	-	-	-	T	-	-	-	-	U	U
Cypriniformes															
Characidae															
Raphiodontinae															
Raphiodon vulpinus AGASSIZ, 1829 "*machete*"	car*	-	-	-	-	-	-	-	R	R	-	-	-	-	U	R
Characinae															

Taxon	diet	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Acestrorhynchus pantaneiro MENEZES, 1992 "*dientudo paraguayo*"	car*	-	-	-	-	R	-	-	U	U	-	-	-	R	C
Charax gibbosus (LINNÉ, 1758) "*dentudo jorobado*"	car*	-	-	-	-	U	-	-	R	R	-	-	-	R	R
C. stenopterus (COPE, 1894) "*dentudo transparente*"	car	-	-	-	-	C	-	-	C	-	-	-	-	C	C
Oligosarcus hepsetus (CUVIER, 1829)		-	-	-	-	-	-	-	R	R	-	-	-	-	-
O. jenynsi (GUNTHER, 1864) "*dentudo*")	car	-	-	-	-	R	-	-	U	-	-	-	-	U	U
Roeboides bonariensis (STEINDACHNER, 1879) "*dientudo*"	car*	-	-	-	-	-	-	-	U	R	-	-	-	U	U
R. paranensis PIGNALBERI, 1975	car	-	-	-	-	-	-	-	-	R	-	-	-	R	U
R. prognathus (BOULENGER, 1895) "*dientudo*"	car	-	-	-	-	-	-	-	R	R	-	-	-	R	-

Cynopotaminae

Taxon	diet	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cynopotamus argenteus (VAL., 1847) "*dientudo*"	car	-	-	-	-	-	-	-	R	R	-	-	-	R	U
Galeocharax humeralis (VAL., 1847) "*dientudo*"	car	-	-	-	-	-	-	-	R	R	-	-	-	R	-

Bryconinae

Taxon	diet	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Brycon orbygnianus (VAL., 1849) "*pirapitá*"	car	U	-	-	-	-	-	-	-	R	-	-	-	R	-
Salminus maxillosus (VAL., 1840) "*dorado*"	car*	C	C	C	-	R	-	C	U	C	-	-	C	C	U
Triportheus paranensis (GÜNTHER, 1874) "*golondrina*"	car	-	-	-	-	-	-	-	R	R	-	-	-	U	C

Paragoniatinae

Taxon	diet	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Prionobrama paraguayensis (EIG., 1914)	car	-	-	-	-	U	-	-	-	-	-	-	-	U	-

Aphyocharacinae

Taxon	diet	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Aphyocharax alburnus GÜNTHER, 1969	car	-	-	-	-	U	-	-	-	-	-	-	-	U	-
A. anisitsi EIG. & KEN., 1903	car	-	-	-	-	C	-	-	-	-	-	-	-	C	-
A. dentatus EIG. & KEN., 1903	car	-	-	-	-	-	-	-	-	C	-	-	-	R	-
A. nasutus AHL., 1936		-	-	-	-	-	-	-	-	-	-	-	-	R	-
A. rubropinnis PAPPENHEIM, 1923	car	-	-	-	-	U	-	-	-	-	-	-	-	A	R

Glandulocaudinae

Taxon	diet	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Diapoma terofali (GERY, 1964)	car	-	-	-	-	-	-	-	-	-	-	-	-	R	-
Pseudocorynopoma doriai PERUGIA, 1891 "*mojarra de velo*"		-	-	-	-	P	-	-	-	-	-	-	-	P	-

Tetragonopterinae "mojarras"

Taxon	diet	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Astyanax (*Astyanax*) *fasciatus fasciatus* (CUV., 1819)	om	C	-	-	-	C	-	-	A	C	C	-	-	A	A

Table 5: Continuation.

Species**		Main channel lotic area						Floodplain Lotic area				Lentic area			
	A	1	2	3	4	5	6	7	8	9	10	11	12	13	14
A. (A.) eigenmanniorum (COPE, 1894)	om	-	-	-	-	-	-	-	-	-	-	-	-	R	-
A. (A.) lineatus (PERUGIA, 1891)	-	-	-	-	-	A	-	-	C	R	-	-	-	A	-
A. (A.) paranahybae EIG., 1911	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-
Astyanax (Poecilurichthys) abramis (JENYNS, 1842) "*mojarra pacusa*"	om	-	-	-	-	U	-	-	U	-	-	-	-	C	U
A. (P.) alleni (EIG. & Mc ATEE, 1907)	car	-	-	-	-	-	-	-	U	-	-	-	-	U	U
A. (P.) bimaculatus bimaculatus EIG., 1921	om	-	-	-	-	-	-	-	-	U	-	-	-	C	-
A. (P.) b. paraguayensis EIG., 1921	om	-	-	-	-	U	-	-	U	-	-	-	-	A	U
A. (P.) correntinus (HOLMBERG, 1891)		R	-	-	-	-	-	-	-	-	-	-	-	-	-
A. (P.) erythropterus (HOLMBERG, 1891)	-	-	-	-	-	-	-	-	U	-	-	-	-	R	-
A. (P.) pellegrini EIG., 1907	om	-	-	-	-	R	-	-	-	R	-	-	-	R	-
Ctenobrycon multiradiatus (STEINDACHNER, 1878)	det+	-	-	-	-	R	-	-	-	R	-	-	-	-	-
Hemigrammus caudovittatus AHL, 1924	-	-	-	-	-	U	-	R	-	-	-	-	-	R	R
H. mattei EIG., 1910		R	-	-	-	-	-	-	-	-	-	-	-	-	-
Hyphessobrycon anisitsi (EIG., 1907)	om	-	-	-	-	U	-	-	U	-	-	-	-	U	R
H. bifasciatus ELLIS, 1911	om	-	-	-	-	-	-	-	-	-	-	-	-	R	-
H. callistus (BOULENGER, 1900) "*serpe*"(car)	-	-	-	-	-	R	-	-	-	-	-	-	-	U	-
H. reticulatus ELLIS, 1911	-	-	-	-	-	-	-	-	-	-	-	-	-	R	-
H. luetkeni (BOULENGER, 1887)	-	-	-	-	-	-	-	-	-	-	-	-	-	U	U
Moenkhausia dichroura (KNER, 1858) "*piki*"	car	-	-	-	-	R	-	-	-	-	-	-	-	R	U
M. sanctae-filomenae (STEINDACHNER, 1907)	om	-	-	-	-	R	-	-	-	-	-	-	-	R	-

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Taxon	Diet														
Psellogrammus kennedyi (EIG., 1903)	om	-	-	-	-	-	-	-	-	-	-	-	-	R	-
Tetragonopterus argenteus CUVIER, 1817 "*mojarrita*"		-	-	-	-	-	-	-	-	-	R	-	-	R	R
Cheirodontinae															
Cheirodon interruptus interruptus (JENYNS, 1842) "*mojarrita*"		-	-	-	R	-	-	U	-	-	-	-	-	R	U
C. leuciscus Ahl., 1936	R	-	P	-	-	-	-	-	-	-	-	-	-	-
Holoshestes pequira STEINDACHNER, 1882	om-car	-	-	-	-	-	A	-	-	A	-	-	-	A	A
Odontostilbe paraguayensis EIG. & KEN., 1903	det	-	-	-	-	A	-	-	A	-	-	-	-	C	-
O. piaba LÜETKEN, 1874	om-car	-	-	-	-	C	-	-	-	-	-	-	-	C	-
Serrasalmidae															
Serrasalminae "palometas"	car*														
Serrasalmus (Pristobrycon) serrulatus (VAL., 1850)		R	-	P	-	-	-	-	-	-	-	-	-	-	-
S. (Serrasalmus) rhombeus marginatus VAL., 1847		-	C	-	-	C	-	-	U	-	-	-	-	R	U
S. (S.) spilopleura KNER, 1860		C	C	C	C	R	-	-	U	U	-	-	-	C	C
S. (Taddyella) nattereri (KNER, 1860)		-	-	-	-	-	-	-	U	U	-	-	-	C	U
S. (T.) ternetzi (STEINDACHNER, 1908)		-	-	-	-	-	-	-	-	-	-	-	-	R	-
Myleinae															
Metynnis maculatus (KNER, 1860) "*pacú*"		-	-	-	-	-	-	-	-	-	-	-	-	R	-
Mylossoma duriventris orbignanum (VAL., 1848) "*pacucito*"	her	-	-	-	-	-	-	-	R	-	-	-	-	U	R
Piaractus mesopotamicus (HOLMBERG, 1887) "*pacú*"	om	U	U	U	-	-	-	-	-	-	-	-	-	-	-
Gasteropelecidae															
Thoracocharacinae															
Thoracocharax stellatus (KNER, 1860) "*pechito*"	car	-	-	-	-	-	-	U	-	U	-	-	-	R	U
Erythrinidae															
Hoplerythrinus unitaeniatus (SPIX, 1829)		-	-	-	-	P	-	-	P	-	-	-	-	-	-
Hoplias malabaricus malabaricus (BLOCH, 1794) "*tararira*"	car*	R	C	-	-	U	-	-	C	C	-	-	-	A	C
Lebiasinidae															
Pyrrhulininae															

Table 5: Continuation.

Species**		Main channel	Floodplain												
	A	Lotic area 1	2	3	4	5	6	7	8	9	10	Lentic area 11	12	13	14
Pyrrhulina australis EIG. & KEN., 1903	car	-	-	-	-	U	-	-	R	-	-	-	-	U	U
P. brevis STEINDACHNER, 1875		U	-	-	-	-	-	-	-	U	-	-	-	U	-
P. melanostoma (COPE, 1870)		U	-	-	-	-	-	-	-	U	-	-	-	U	-
P. rachoviana MYERS, 1926		U	-	-	-	-	-	-	-	U	-	-	-	U	-
Anostomidae															
Anostominae															
Abramites hypselonotus (GUNTHER, 1868) "*jikii*"		-	-	-	-	R	-	-	-	-	-	-	-	-	-
Leporinus acutidens (VAL., 1847) "*boga*"		U	-	-	-	-	-	-	-	-	-	-	-	-	-
L. obtusidens (VAL., 1847) "*boga*"	om	C	C	C	-	-	-	-	C	C	-	-	-	C	U
Leporinus sp.		C	-	-	-	-	-	-	-	C	-	-	-	-	-
L. striatus KNER, 1859 "*trompa roja*"		-	-	-	-	-	-	-	-	-	-	-	-	R	U
Schizodon borelli (BOULENGER, 1900) "*boga lisa*"	her	-	-	-	-	-	-	-	U	U	-	-	-	U	U
S. platae (GARMAN, 1890) "*boga*"		-	-	-	-	-	-	-	R	-	-	-	-	R	-
S. vittatum (VAL.,1849) "*boga*"		-	-	-	-	-	-	-	R	-	-	-	-	-	-
Hemiodidae															
Parodontinae															
Apareiodon affinis (STEIND., 1879) "*virolito*"	det+	U	-	-	-	R	-	-	U	R	-	-	-	U	C
Parodon carrikeri FOWLER, 1940		-	-	-	-	-	-	-	-	-	-	-	-	R	-
Hemiodinae															
Hemiodus orthonops (EIG. & KEN., 1903)	R	-	-	-	-	-	-	-	-	R	-	-	-	R	R
Curimatidae															

Prochilodinae

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Prochilodus lineatus (VAL., 1847) *"sábalo"*	det	A	A	A	A	C	-	-	A	A	-	-	-	A	C

Curimatinae

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cyphocharax voga (HENSEL, 1870) *"sabalito"*		-	-	-	-	C	-	-	C	R	-	-	-	C	C
C. platanus (GUNTHER,1880) *"sabalito plateado"*	det	-	-	-	-	A	-	-	C	U	-	-	-	A	A
C. saladensis (MEINKEN, 1933)	det	-	-	-	-	-	-	-	U	-	-	-	-	R	-
Curimatella australe EIG.& KEN., 1903		R	-	-	-	-	-	-	-	R	-	-	-	-	-
Steindachnerina conspersa (HOLMBERG, 1891)	det	-	-	-	-	U	-	-	-	-	-	-	-	R	C
S. biornata (BRAGA & AZPELICUETA, 1987)		-	-	-	-	-	-	-	-	R	-	-	-	-	-
S. brevipinna (EIG. & EIG., 1889) *"huevada"*		-	-	-	-	R	-	-	U	-	-	-	-	U	C
Potamorhina squamoralevis (BRAGA & AZPELICUETA, 1983) *"blanquillo"*		-	-	-	-	-	-	-	U	R	-	-	-	U	U
Psectrogaster curviventris EIG. & KEN., 1903		-	-	-	-	-	-	-	R	-	-	-	-	R	R

Characiidae

Characidiinae

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Characidium fasciatum fasciatum REINHARDT, 1866 *"tritolo"*	car	-	-	-	-	C	-	-	C	-	-	-	-	R	R
Jobertina rachowi REGAN, 1913	car	-	-	-	-	R	-	-	U	-	-	-	-	U	C

Gymnotidae

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Gymnotus carapo LINNÉ, 1758 *"morena"*	car	-	-	-	-	R	-	-	R	R	-	-	-	R	R

Apteronotidae

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Apteronotus albifrons LINNÉ, 1766 *"morena negra"*		-	-	-	-	-	-	-	-	R	-	-	-	R	-
Porotergus ellisi ALONSO DE ARÁMBURU, 1958 *"morena"*		-	-	-	-	-	-	-	-	R	-	-	-	-	-
Sternacorhamphus hahni MEINKEN, 1937		R	-	-	-	-	-	-	-	-	-	-	-	-	-

Rhamphichthydae

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Eigenmania virescens (VAL., 1847) *"ratona"*	car	-	-	-	-	R	-	-	R	U	-	-	-	R	R
Gymnorhamphichthys hypostomus ELLIS,1912		R	-	-	-	-	-	-	R	R	-	-	-	-	-
Hypopomus artedii (KAUP, 1856) *"morenita"*		-	-	-	-	-	-	-	U	-	-	-	-	U	-
H. brevirostris (STEINDACHNER, 1868) *"morenita"*	car	-	-	-	-	R	-	-	-	-	-	-	-	U	-
Rhamphichthys rostratus (LINNÉ, 1766) *"anguila picuda"*		-	-	-	-	-	-	-	-	R	-	-	-	R	-

Table 5: Continuation.

Species**		Floodplain													
	Main channel	lotic area						Lotic area				Lentic area			
	A	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Sternopygus macrurus (BLOCH & SCHNEIDER, 1801) *"cuchilla"*	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Siluriformes															
Doradidae "armados"															
Anadoras wedelli (CASTELMAN, 1855)		-	-	-	-	R	-	-	-	-	-	-	-	-	-
Doras eigenmanni (BOULENGER, 1895)		-	-	-	-	-	-	-	-	R	-	-	-	-	-
Megalodoras laevigatulus (BERG., 1901)		-	-	-	-	-	-	-	-	R	-	-	-	-	-
Oxydoras kneri BLEEKER, 1862 *"armado chancho"*	car	U	C	-	-	-	-	-	-	R	-	-	-	U	-
Platydoras costatus (LINNÉ, 1776)		U	-	-	-	R	-	-	-	U	-	-	-	-	-
Pterodoras granulosus (VAL., 1833) *"armado común"*	her	A	C	-	-	-	-	-	-	C	-	-	-	R	-
Rhinodoras dorbignyi (KROYER,1855) *"armado amarillo"*		U	-	-	-	-	-	-	U	R	-	-	-	R	-
Trachydoras paraguayensis (EIG. & WARD, 1907)		R	-	-	-	-	-	-	-	-	-	-	-	-	-
Auchenipteridae															
Auchenipterus nigripinnis (BOULENGER, 1895) *"hocicón"*		-	-	-	-	-	-	-	-	-	-	-	-	U	-
A. nuchalis (SPIX, 1829) *"hocicón"*		U	-	-	-	-	-	-	-	U	-	-	-	R	-
Parauchenipterus ceratophysus (KNER, 1857)		-	-	-	-	-	-	-	-	R	-	-	-	-	-
P. galeatus (LINNÉ, 1766) *"bagre rojizo"*	car	-	U	-	U	-	-	-	R	R	-	-	-	R	R
Aspredinidae															
Amaralia hypsiura (KNER, 1855)		-	-	-	-	-	-	-	-	R	-	-	-	-	-
Dycichthys coracoideus COPE, 1874 *"guitarrita"*		-	-	-	-	R	-	-	R	R	-	-	-	R	-
D. iheringi BOULENGER, 1891 *"guitarrita"*		-	-	-	-	U	-	-	-	-	-	-	-	R	-
D. rugosus EIG. & KEN., 1903		-	-	-	-	-	-	-	-	R	-	-	-	R	-

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Pimelodidae

Pimelodinae

Taxon	car														
Bergiaria westermanni REINHARDT, 1874 "*bagre trompudo*"		R	-	-	-	-	-	-	R	R	-	-	-	R	-
Microglanis parahybae (STEINDACHNER, 1880)		-	-	-	-	-	-	-	-	-	-	-	-	R	-
Parapimelodus valenciennesi (KRÖYER, 1874) "*bagarito*"	car	-	-	-	-	-	-	-	C	-	-	-	-	U	R
Pimelodella gracilis (VAL., 1840) "*bagre cantor*"	car	U	-	-	-	C	-	-	C	R	-	-	-	U	U
P. howesi FOWLER, 1940		-	-	-	-	-	-	-	-	-	-	-	-	R	-
P. laticeps EIG., 1917 "*bagre cantor*"		-	-	-	-	R	-	-	R	-	-	-	-	R	R
Pimelodus albicans (VAL., 1840) "*moncholo*"	car*	C	C	-	-	R	-	-	C	C	C	U	C	U	R
P. argenteus PERUGIA, 1891 "*bagre*"		U	-	-	-	-	-	-	-	-	-	-	-	-	R
P. clarias maculatus (LACÉPÈDE, 1803) "*bagre amarillo*"	car*	C	C	C	C	R	-	-	C	C	C	C	C	C	U
P. ornatus KNER, 1857 "*bagre fajado*"		-	-	-	-	-	-	-	R	-	-	-	-	-	-
Pseudopimelodus zungaro zungaro (VAL., 1840) "*manguruyú amarillo*"		R	-	-	-	-	-	-	U	-	-	-	-	-	-
R. quelem (QUOY & GAIRMARD, 1924) "*bagre sapo*"		R	-	-	-	R	-	-	R	-	-	-	-	-	-
R. sapo (VAL., 1840) "*bagre sapo*"		-	-	-	-	-	-	-	R	-	-	-	-	-	-

Luciopimelodinae

Taxon	car														
Luciopimelodus pati (VAL., 1840) "*pati*"	car*	C	-	-	-	-	-	-	C	-	-	-	-	U	-
Megalonema platanum GÜNTHER, 1880 "*bagre blanco*"		R	-	-	-	-	-	-	U	-	-	-	-	-	-
Pinirampus argentinus (MAC DONAGH, 1938) "*pati de aletas negras*"		U													

Sorubiminae

Taxon	car														
Hemisorubin platyrhynchos (VAL., 1840) (*jiripoca*)		R	-	-	-	-	-	-	R	R	-	-	-	R	-
Paulicea luetkeni STEINDACHNER, 1876 "*manguruyú*"		R	R	-	-	-	-	-	-	-	-	-	-	-	-
Pseudoplatystoma coruscans (AGASSIZ, 1829) "*surubi pintado*"	car*	C	C	-	-	-	C	U	U	C	-	-	-	U	-
P. fasciatum fasciatum (LINNÉ, 1766) "*surubi atigrado*"	car*	C	C	-	-	-	C	-	U	C	-	-	-	U	-
Sorubim lima (SCHNEIDER, 1801) "*manduvi cucharón*"	car	U	C	C	-	-	-	-	U	C	-	-	-	U	-

Ageneiosidae

Taxon	car														
Ageneiosus brevifilis VAL., 1840 "*manduvi cabezón*"	car*	C	C	-	-	-	-	-	R	C	-	-	-	U	-
A. valenciennesi BLEEKER, 1864 "*manduvi fino*"	car*	U	C	-	-	-	-	-	U	C	-	C	-	-	-

Hypophthalmidae

Table 5: Continuation:

| Species** | Floodplain | | | | | | | | | | | | | | |
| | Main channel lotic area | | | | | | | Lotic area | | | | Lentic area | | | |
	A	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Hypophthalmus edentatus SPIX, 1829 "*bagre rosado*"		-	-	-	-	-	-	-	-	-	-	-	-	C	-
H. oremaculatus NANI & FUSTER DE PLAZA, 1947 "*bagre rosado*"	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cetopsidae															
Pseudocetopsis gobioides (KNER, 1857)	U	-	-	-	-	-	-	-	-	R	-	-	-	-	-
Trichomycteridae															
Stegophilinae															
Homodiaetus maculatus (STEINDACHNER, 1879) "*camarón*"	hem	-	-	-	-	-	-	-	-	U	-	-	-	-	-
Vandellinae															
Branchioica bertonii EIGENMANN, 1918 "*chupa sangre*"	hem	C	-	-	-	-	-	-	-	C	-	-	-	-	-
Callichthyidae															
Callichthys callichthys (LINNÉ, 1758) "*cascarudo*"		-	-	-	-	-	-	R	-	-	-	-	-	R	-
Corydoras hastatus EIG. & EIG., 1888 "*tachuela*"	car	-	-	-	-	U	-	-	U	U	-	-	-	U	-
C. paleatus (JENYNS, 1842) "*tachuela*" (*om*)	om	-	-	-	-	U	-	-	U	-	-	-	-	R	R
Hoplosternum littorale (HANCOCK, 1828) "*cascarudo*"		-	-	-	-	-	-	-	-	U	-	-	-	U	R
H. thoracatum thoracatum (VAL., 1840) "*cascarudo*"	car	-	-	-	-	R	-	-	R	-	-	-	-	R	-
Loricariidae															
Hypoptopomatinae															
Hypoptopoma inexpectata (HOLMBERG, 1893)	det+	-	-	U	-	U	-	-	-	U	-	-	-	-	-
Microlepidogaster maculipinnis (REGAN, 1912)		-	-	-	-	-	-	-	-	U	-	-	-	R	-
Otocinclus flexilis COPE, 1898		-	-	-	-	-	-	-	-	U	-	-	-	-	-
O. vittatus REGAN, 1912 "*limpiavidrios*"	det	U	-	-	-	C	-	-	U	-	-	-	-	U	C
Loricariinae "viejas del agua"															

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Farlowella knerii (STEINDACHNER, 1883)		R	-	-	-	-	-	-	-	-	-	-	-	-	-
F. paranaense MEINKEN, 1937		R	-	-	-	-	-	-	-	-	-	-	-	-	-
Lamontichthys filamentosa (LA MONTE, 1935)		R	-	-	-	-	-	-	R	-	-	-	-	-	-
Loricaria apeltogaster BOULENGER, 1895		R	-	-	-	-	-	-	-	-	-	-	-	-	-
L. simillina REGAN, 1904		R	-	-	-	-	-	-	-	-	-	-	-	-	-
Loricariichthys anus (VAL., 1840)		-	-	-	-	-	-	-	R	-	-	-	-	A	-
L. labialis (BOULENGER, 1895)	car	-	-	-	-	R	-	-	R	-	-	-	-	R	-
L. platymetopon ISBRUCKER & NIJSSEN, 1979		-	-	-	-	-	-	-	R	R	-	-	-	-	-
L. maculata (BLOCH, 1794)	car	-	-	-	-	U	-	-	C	-	-	-	-	U	U
Paraloricaria vetula (VAL., 1840)		-	-	-	-	-	-	-	T	-	-	-	-	-	-
Pseudohemiodon laticeps (REGAN, 1904)		-	-	-	-	-	-	-	-	-	-	-	-	R	-
Rhineloricaria catamarcensis (BERG, 1895)		-	-	-	-	-	-	-	-	-	-	-	-	R	-
R. lima KNER, 1854		-	-	-	-	-	-	-	-	-	-	-	-	R	-
R. parva (BOULENGER, 1895)	det	-	-	-	-	C	-	-	-	-	-	-	-	U	-
R. phoxocephala (EIG. & EIG., 1889)		-	-	-	-	-	-	-	-	-	-	-	-	R	-
Spatuloricaria evansii (BOULENGER, 1892)		-	-	-	-	-	-	-	-	-	-	-	-	R	-
Sturisoma robustum (REGAN, 1904)		R	-	-	-	-	-	-	-	-	-	-	-	-	-

Neoplecostomatinae

Rhinelepis aspera SPIX, 1829		R	-	-	-	-	-	-	-	-	-	-	-	-	-

Plecostomatinae

Hypostomus alatus CASTELNAU, 1855		-	-	-	-	-	-	-	-	-	-	-	-	R	-
H. commersoni VAL., 1840		-	-	-	-	-	-	-	C	C	-	-	-	C	-
H. laplatae (EIG., 1907)		R	-	-	-	-	-	-	R	-	-	-	-	-	-
H. robini VAL., 1840		-	-	-	-	-	-	-	-	-	-	-	-	C	-
Cochliodon cochliodon (KNER, 1854)		-	-	-	-	-	-	-	-	R	-	-	-	-	-
Pterygoplichthys anisitsi EIG. & KEN., 1903 "*vieja del agua*"		-	-	-	-	-	-	-	U	-	-	-	-	C	U
Pekoltia vittata (STEINDACHNER, 1882)		R	-	-	-	-	-	-	-	-	-	-	-	-	-

Ancistrinae

Megalancistrus aculeatus (PERUGIA, 1891)		R	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 5: Continuation.

| Species** | | Main channel lotic area | | | | | | | Floodplain Lotic area | | | | Lentic area | | | |
	A	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Atheriniformes																
Belonidae																
Pseudotylosurus angusticeps GÜNTHER, 1866 *"pez aguja"*		-	-	-	-	R	-	-	-	R	-	-	-	-	-	-
Potamorrhaphis eigenmanni A. DE MIRANDA RIBEIRO, 1915	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	R
Cyprinodontidae																
Pterolebias longipinnis GARMAN, 1895	car	-	-	-	-	-	-	-	R	R	-	-	-	R	-	
Jenynsidae																
Jenynsia lineata lineata (JENYNS, 1842) *"madre del agua"*		-	-	-	-	-	-	-	R	-	-	-	-	-	-	
Poecilidae																
Cnesterodon decemmaculatus (JENYNS, 1842)																
"madrecita del agua"	det	-	-	-	-	R	-	-	-	-	-	-	-	R	-	
Phallotorynus victoriae OLIVEROS, 1983	car	-	-	-	-	-	-	-	R	R	-	-	-	R	R	
Atherinidae																
Odontesthes bonariensis (CUV. & VAL., 1835) *"pejerrey"*	car	U	-	-	-	-	-	-	R	U	-	-	-	-	-	
O. perugiai (EVERMANN & KEMDALL, 1906) *"juncalero"*		-	-	-	-	-	-	-	R	-	-	-	-	R	R	
Synbranchiformes																
Synbranchidae																
Synbranchus marmoratus Bloch, 1795 *"anguila criolla"*	car*	-	-	-	-	-	-	-	U	-	-	-	-	U	U	
Perciformes																
Sciaenidae "corvinas de río"																
Pachyurus bonariensis STEINDACHNER, 1879	car	-	-	-	-	U	-	-	-	-	-	-	-	R	-	
P. paranensis DANERI, 1956		-	-	-	-	-	-	-	R	-	-	-	-	-	-	

Species		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Plagioscion macdonaghi DANERI, 1954		-	-	-	-	-	-	-	-	R	-	-	-	C	R
P. ternetzi BOULENGER, 1891		-	-	-	-	-	-	-	-	R	-	-	-	U	-
Cichlidae "chanchitas"															
Aequidens portalegrensis (HENSEL, 1870)	car	-	-	-	-	R	-	-	U	-	-	-	-	R	U
A. vittatus (HECKEL, 1840) *"acará"*	car	-	-	-	-	U	-	-	-	-	-	-	-	U	-
Apistogramma combrae (REGAN, 1906)	car	-	-	-	-	C	-	-	-	-	-	-	-	C	-
A. borelli (REGAN, 1906)	car	-	-	-	-	R	-	-	-	-	-	-	-	U	-
Batrachops semifasciatus HECKEL		-	-	-	-	R	-	-	-	-	-	-	-	-	-
Cichlasoma facetum (JENYNS, 1842)		-	-	-	-	-	-	-	-	-	-	-	-	U	U
Crenicichla lacustris (CASTELNAU, 1855) *"San Pedro"*		-	-	-	-	-	-	-	-	R	-	-	-	R	-
C. lepidota HECKEL, 1840 *"cabeza amarga"*	car	-	-	-	-	-	-	-	-	R	-	-	-	U	R
C. vittata HECKEL, 1840 *"cabeza amarga"*		-	-	-	-	-	-	-	-	-	-	-	-	R	-
Gymnogeophagus australis (EIG., 1907)		-	-	-	-	-	-	-	-	-	-	-	-	U	U
G. rhabdotus (HENSEL, 1870)		-	-	-	-	-	-	-	-	R	-	-	-	-	-
G. balzani (PERUGIA, 1891)	car	-	-	-	-	-	-	-	-	R	-	-	-	U	-
Pleuronectiformes															
Achiridae "lenguados de río)															
Achirus jenynsi (GÜNTHER, 1862)	car*	-	-	-	-	-	-	-	-	R	-	-	-	C	-
A. lineatus (LINNÉ, 1758)	car	-	-	-	-	-	-	-	-	P	-	-	-	R	-
Lepidosireniformes															
Lepidosirenidae															
Lepidosiren paradoxa FITZINGER, 1837		-	-	-	-	-	-	-	-	R	-	-	-	-	-

** Derived from references cited in the text and from unpublished data of the authors. **1**: narrow and wide cross-section; **2**: high steep bank; **3**: low bank; **4**: sand bar; **5**: levee lake; **6**: deep hole; **7**: shallow hole; **8**: tributary; **9**: permanent channel; **10**: temporary channel; **11**: sand bar; **12**: scour hole; **13**: permanent lake; **14**: temporary laguna. **(A)** abundant: usually found in high numbers; **(C)** common: usually found in moderate numbers; **(T)** typical: occurs regularly, but in low numbers;**(U)** uncommon: irregularly found, usually, but not always, in low numbers; **(R)** rare, seldom encountered, almost always in low numbers; **(P)** probable; likely to occur, but records lacking or inconclusive.

(car): carnivorous; (car*): parcially or totally piscivore; (om): omnivore; (det):detritivore; (her): herbivore; (det+): algae feeder; (hem): hematofagous. A: Feeding habits are incomplete due to the lack of information.

Table 6: Hierarchical/functional classification of the floodplain channels according to their mean annual discharge (Q_{SC}) in relation to the mean annual discharge of the Main channel ($Q_{MC} = 17{,}000$ m^3 s^{-1}) and its degree intermittency (see Fig. 2).

Channel classification	% of Q_{MC}	Example	Q_{SC} (m^3 s^{-1})	Months without flow
		Colastiné River	2,200	
Permanent channel	>5			0
		Coronda River	1,125	
Low-intermittency channel	>1-<5	Tiradero Viejo River	500	1-2
Middle-intermittency channel	<1	Correntoso River	94	2-4
High-intermittency	<0.5	Yacaré River	35	>4

Table 7: Different floodplain drainage structure according their location in old floodplain area (OFA) and in new floodplain area (NFA). The data were obtained from an area of 4,000 km^2 (see Fig. 2).

Parameter	OFA	NFA
Channel number per km^2	2.5	1.0
Drainage density (km/km^2)	2.3	1.0
Mean channel width (km)	0.03	0.06
Number of channel junctions per km^2	30	12
Angles of channel junctions (˚)	85	45
Radius of curvature (km)	0.32	2.5
Amplitude range of channel bearings (˚)	160	77
Main vector bearing (˚)	240	247

Table 8: Typical physical/chemical bar at the confluence of a permanent channel (Correntoso River) and an intermittent channel (Yacaré River) during low water stage. V: water velocity; SD: Secchi disk; SSC: suspended sediment concentration; T_w: water temperature; K: conductivity. (1): water condition during high level (see Fig. 2 and Table 6).

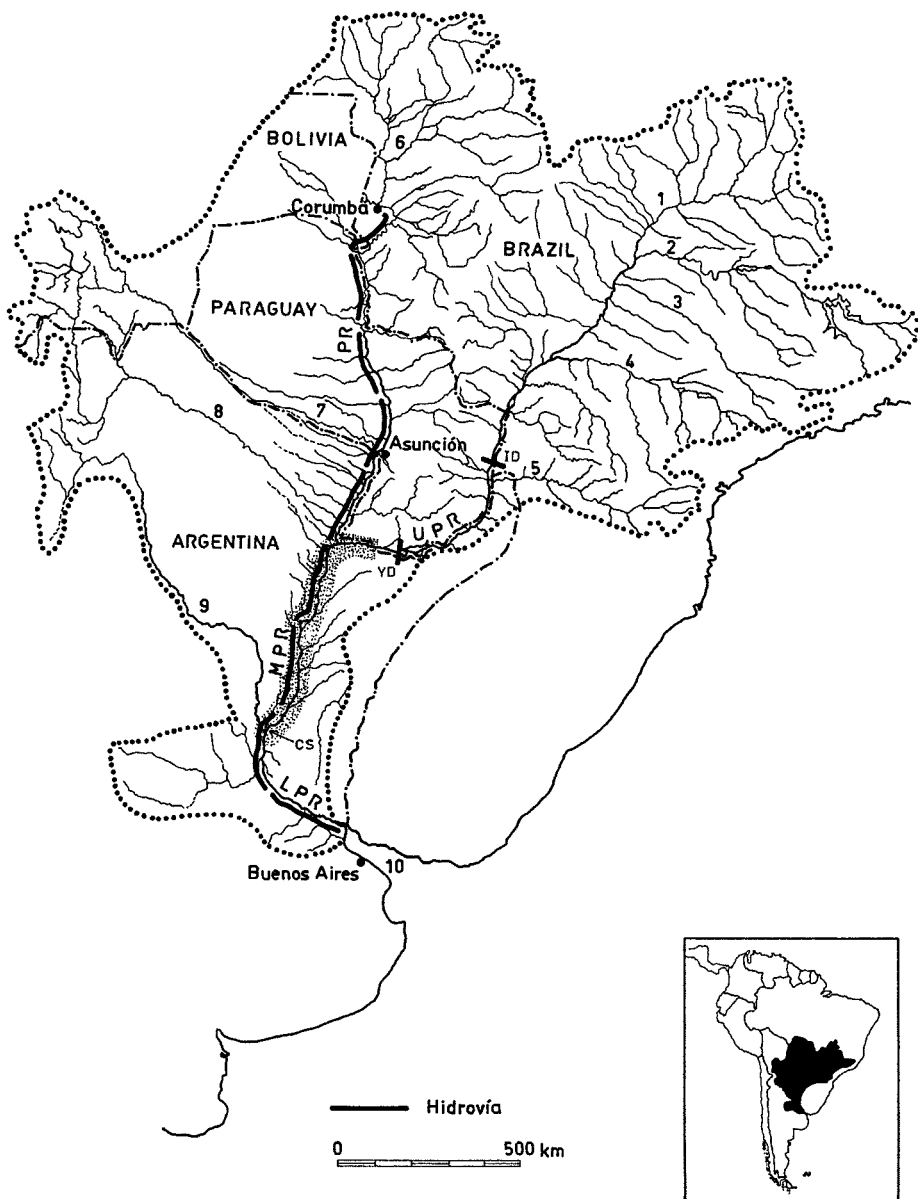| River	V (cm/s)	SD (m)	SSC (mg/L)	T_w (˚C)	K (µS/cm)
Correntoso	<2	0.22	81	29.0	487
Yacaré	0	0.90	17	23.0	344
Correntoso (1)	34	0.17	130	27.7	90
Yacaré (1)	20	0.15	100	27.6	90

Fig. 1:
The Paraná River drainage basin. **UPR**: Upper Paraná River; **PR**: Paraguay River; **MPR**: Middle Paraná River; **ID**: Itaipú Dam; **YD**: Yaciretá Dam; **CS**: Aguas Corrientes cross-section; **1**: Paranaiba River; **2**: Grande River; **3**: Tieté River; **4**: Paranapanema River; **5**: Iguazú River; **6**: Cuiabá River; **7**: Pilcomayo River; **8**: Bermejo River; **9**: Salado del Norte River; **10**: Río de la Plata Estuary. Shaded area indicate the studied fluvial segment.
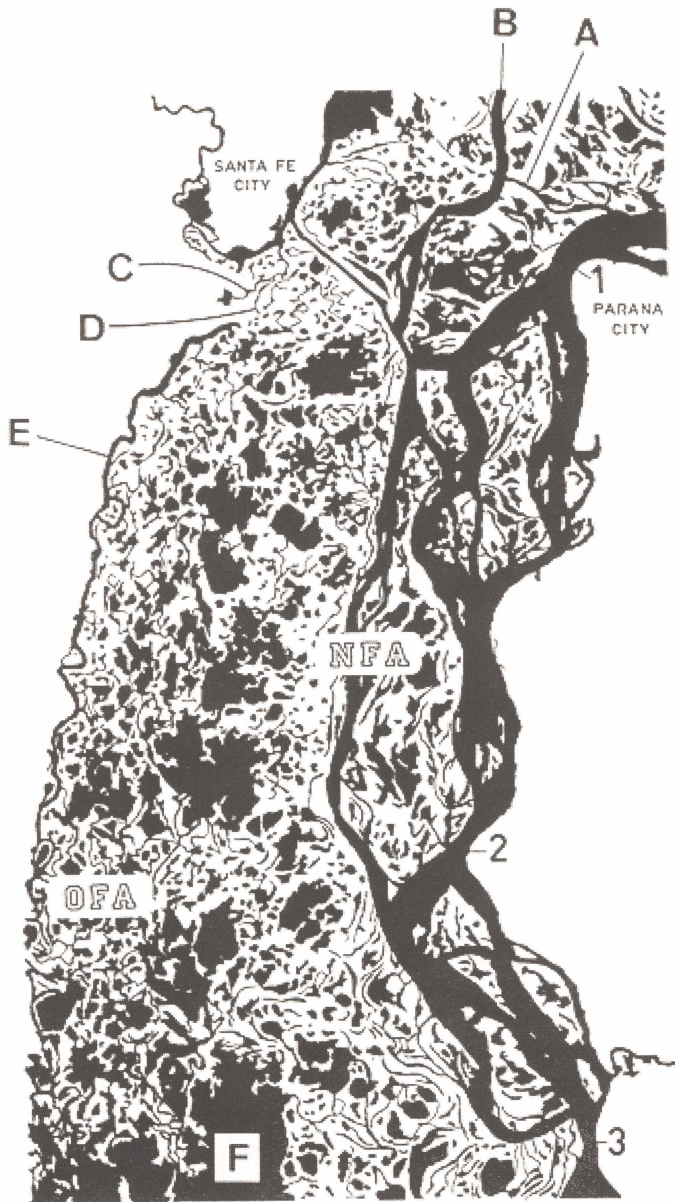
Fig. 2:
Middle Paraná River valley. Note the braided main channel on the right and the fringing floodplain on the left; **1, 2** and **3**: nodal points; **3**: Punta Gorda cross-section; **OFA**: old floodplain areas; **NFA**: new floodplain areas. **A**: Tiradero Viejo River; **B**: Colastiné R.; **C**: Correntoso R.; **D**: Yacaré R.; **E**: Coronda R.; **F**: Laguna Coronda. The area covers about 53 x 25 km (drawn from a Landsat satellite image).
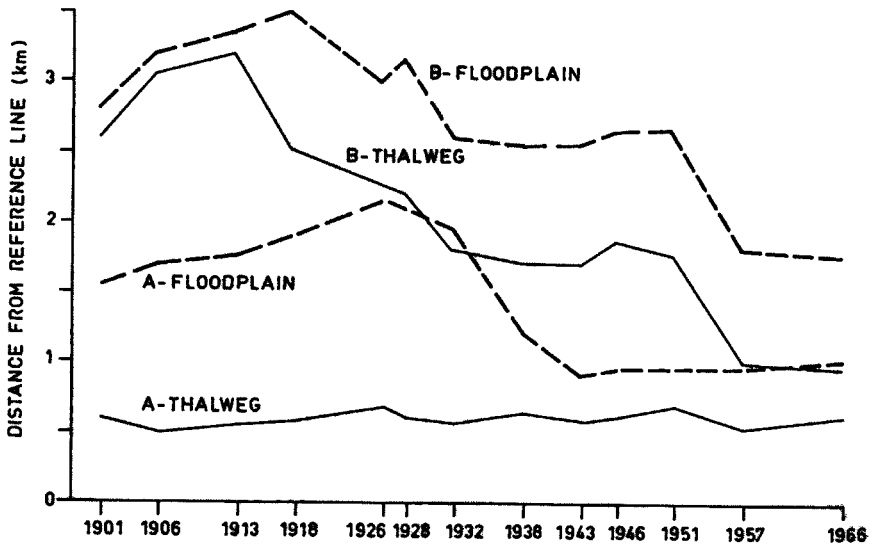
Fig. 3:
Shiftings of the thalweg and floodplain bankline in two cross-sections: **A**: narrow section or nodal point, Toma de Aguas Corrientes; **B**: wide section (see Fig. 4).
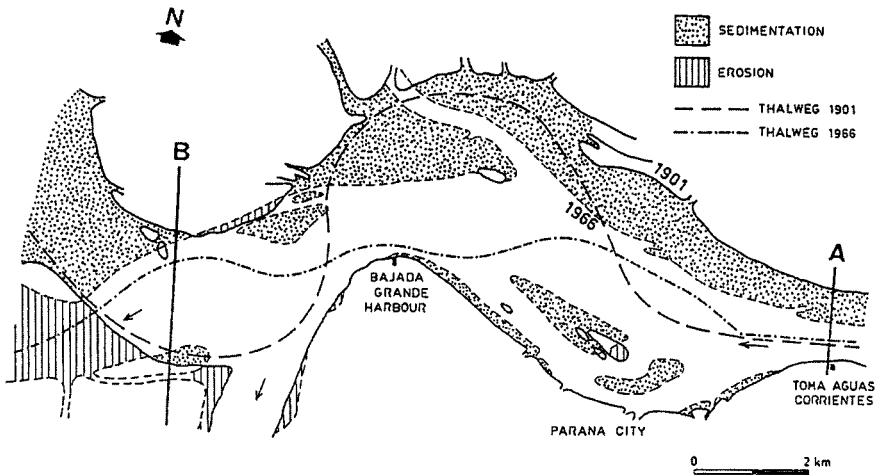
Fig. 4:
Bankline migration, shifting of the thalweg and main sites of erosion and deposition during 1901-1966 period. **A**: narrow cross-section or nodal point, Toma de Aguas Corrientes cross-section; **B**: wide cross-section. The reach is just located downriver of the Aguas Corrientes nodal point (see Fig. 3).
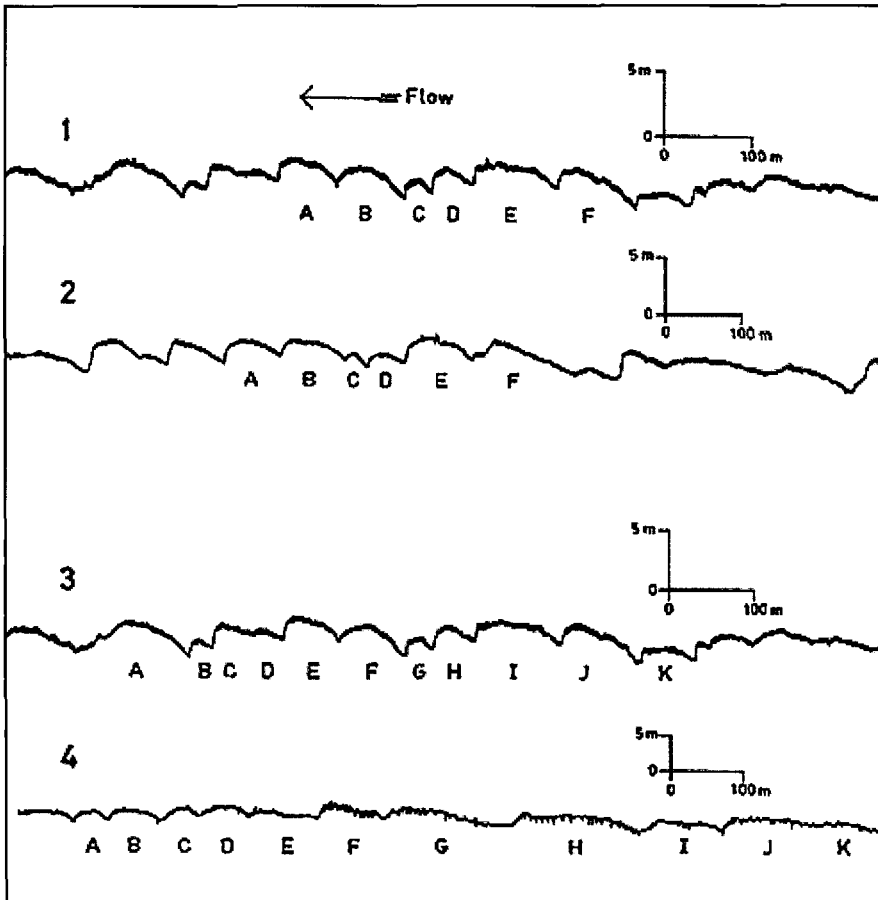
Fig. 5:
Reproduction of hydrograph tracings from the center of the main channel showing well-developed dunes and their migration in a 30-day period (1-2), and during a rising river stage, showing the strong change in the bedforms in a 73-day period (3-4) (redrawn from LIMA et al. 1990).
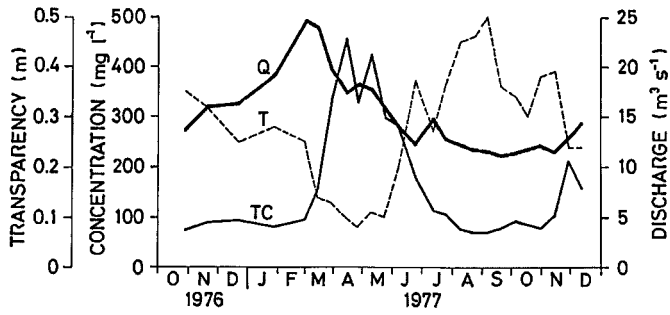
Fig. 6:
Temporal variation of the discharge (Q), SECCHI disk (T), and total suspended sediment concentration (TC), in the surficial water at the center of the Middle Paraná River main channel.
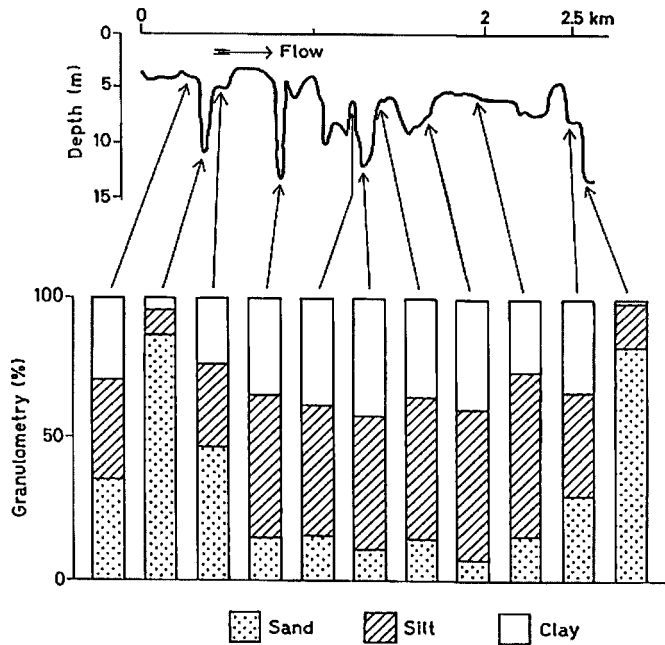

Fig. 7:
Longitudinal echogram of a secondary channel (Corentoso River) showing the hole-step sequences, and their depth and bed granulometry variation in a mid-water stage (see Fig. 2).
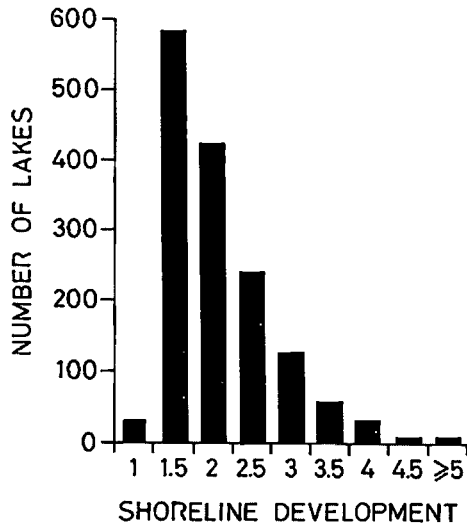
Fig. 8:
Distribution of lakes according to their shoreline development. Total number of lagunas: 1,500.
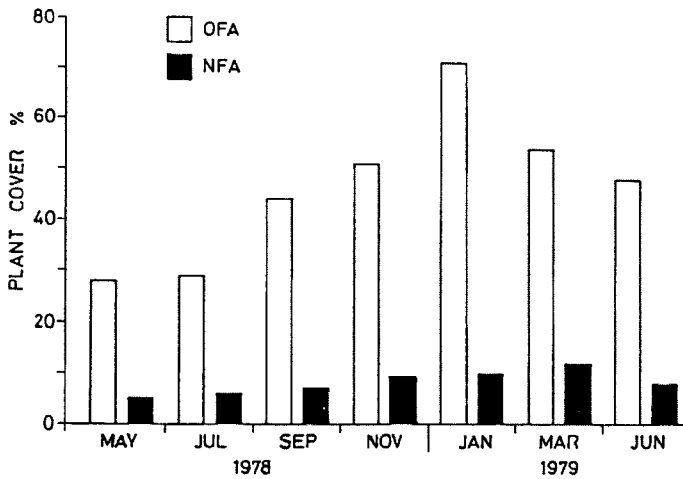

Fig. 9:
Percentages of plant cover in 187 ha of lenitic waters in a old floodplain area (OFA), and in the 741 ha of lenitic waters in a new flooplain area (NFA). Total number of lagunas sampled: 107 (data from BAYO et al. 1981).