AMAZONIANA XVII (3/4): 291-341 Kiel, Dezember 2003

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
(Accepted for publication: August, 2003).

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

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

ISSN 0065-6755/2003/291/ © MPI für Limnologie, AG Tropenökologie, Plön; INPA, Manaus

a dinâmica do rio e a evolução dos lagos das planicies 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 Yaciretá 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 (COLEMAN 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 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 elephantipes, 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