

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 & VASSALLO 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 ($<15 \text{ ha}$) 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 $12\text{-}16 \text{ t ha}^{-1} \text{ yr}^{-1}$ (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 $31.6 \text{ g m}^{-2} \text{ d}^{-1}$ was measured, with maximum rates during isolation periods of $92 \text{ g m}^{-2} \text{ d}^{-1}$. The minimum sedimentation rates were measured during inundation phases, reaching $4.4 \text{ g m}^{-2} \text{ d}^{-1}$. 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 "lenticification" 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; MARCHESI et al. 2002; EZCURRA DE DRAGO & MARCHESI, 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 O₂ 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 diffuse 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 perirheic 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 overgrown 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 pioneer 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 typically 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 invador 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).

Conclusions

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 floodplain areas. However, the largest floodplain channels, i.e., which are permanent and with mean discharges ranging between $800 \text{ m}^3 \text{ s}^{-1}$ and $2,000 \text{ m}^3 \text{ s}^{-1}$, generated also strong hydrosedimentological 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 parallelly 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. Floodplain 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 environmental conditions of the neighbouring lakes. This change in the hydroecology of the minor floodplain channel have been termed "lenticification 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 characteristics of a "young connected lake", in the areas strongly influentiated by the connection with the river, from which typical 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 inhabit 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 *Prochilodus 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 an 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 outlet 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 MARCHESI & EZCURRA DE DRAGO 1992). Sample number for each station: 414.

	Paraná River		Main secondary		Minor secondary		Tributaries		Tributaries	
	main channel		channels		channels		(left bank)		(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
<i>Narapa bonettoi</i> *	<i>Oncosclera navicella</i>	<i>Cordylophora caspia</i>	Nematode sp. I	<i>Limnodrilus hoffmeisteri</i> *
<i>Myoretronectes paranensis</i>	<i>Uruguayella repens</i>	Nematode sp. I	Nematode sp. II	<i>Branchiura sowerbyi</i> *
<i>Haplotaxis aedeochaeta</i>	<i>Aulodrilus pigueti</i> *	<i>Aulodrilus pigueti</i> *	<i>Aulodrilus pigueti</i> *	<i>Dero (Dero)</i>
<i>Tobrilus</i> sp.	<i>Paranadrilus descolei</i> *	<i>Paranadrilus descolei</i> *	<i>Limnodrilus hoffmeisteri</i> *	<i>multibranchiata</i>
<i>Parachironomus</i> sp.	<i>Limnodrilus hoffmeisteri</i> *	<i>Limnodrilus hoffmeisteri</i> *	<i>Dero (Dero) obtusa</i> *	<i>Dero (Aulophorus)</i>
	<i>Dero (Aulophorus) lodeni</i>	<i>Limnodrilus udekemianus</i> *	<i>Dero (Dero) multibranchiata</i>	<i>furcatus</i>
	<i>Dero (Dero) nivea</i>	<i>Tubifex tubifex</i>	<i>Dero (Dero) lodeni</i> *	<i>Slavina evelinae</i>
	<i>Pristina americana</i> *	<i>Dero (Dero) obtusa</i>	<i>Dero (Aulophorus) borelli</i>	<i>Trieminentia corderoi</i>
	<i>Pristina osborni</i>	<i>Dero (Aulophorus) lodeni</i> *	<i>Dero (Aulophorus) furcatus</i>	<i>Eiseniella tetraedra</i> *
	<i>Eiseniella tetraedra</i>	<i>Pristina americana</i> *	<i>Dero (Aulophorus) lodeni</i> *	<i>Chironomus xanthus</i> *
	<i>Bohrioneurum americanus</i> *	<i>Pristina breviseta</i>	<i>Pristina americana</i> *	<i>Lopescladius</i> sp.
	<i>Parachironomus</i> sp.*	<i>Pristina osborni</i> *	<i>Pristina minuta</i>	<i>Chaoborus</i> sp.
	<i>Xenochironomus</i> sp.*	<i>Pristina jenkiniae</i> *	<i>Pristina proboscidea</i> *	
	<i>Cryptochironomus</i> sp.	<i>Pristina biserrata</i>	<i>Pristina jenkiniae</i> *	
	<i>Coelotanytus</i> sp.	<i>Pristina acuminata</i>	<i>Pristina biserrata</i>	
	<i>Ablasemia</i> sp.*	<i>Eiseniella tetraedra</i> *	<i>Pristina leidy</i>	
	<i>Ceratopogonidae</i> sp.1	<i>Bohrioneurum americanus</i> *	<i>Pristina acuminata</i>	
	<i>Pisidium</i> sp.	<i>Trieminentia corderoi</i>	<i>Slavina evelinae</i> *	
	<i>Limnoperna fortunei</i>	<i>Brinkhurstia americana</i>	<i>Bohrioneurum americanus</i>	
			<i>Branchiura sowerbyi</i>	