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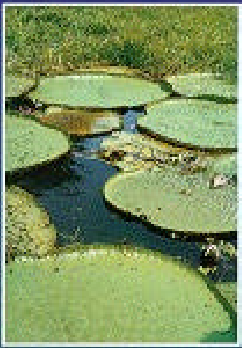

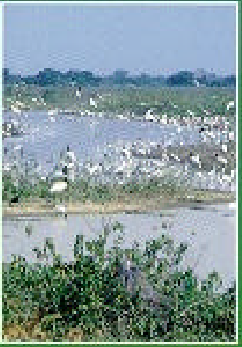

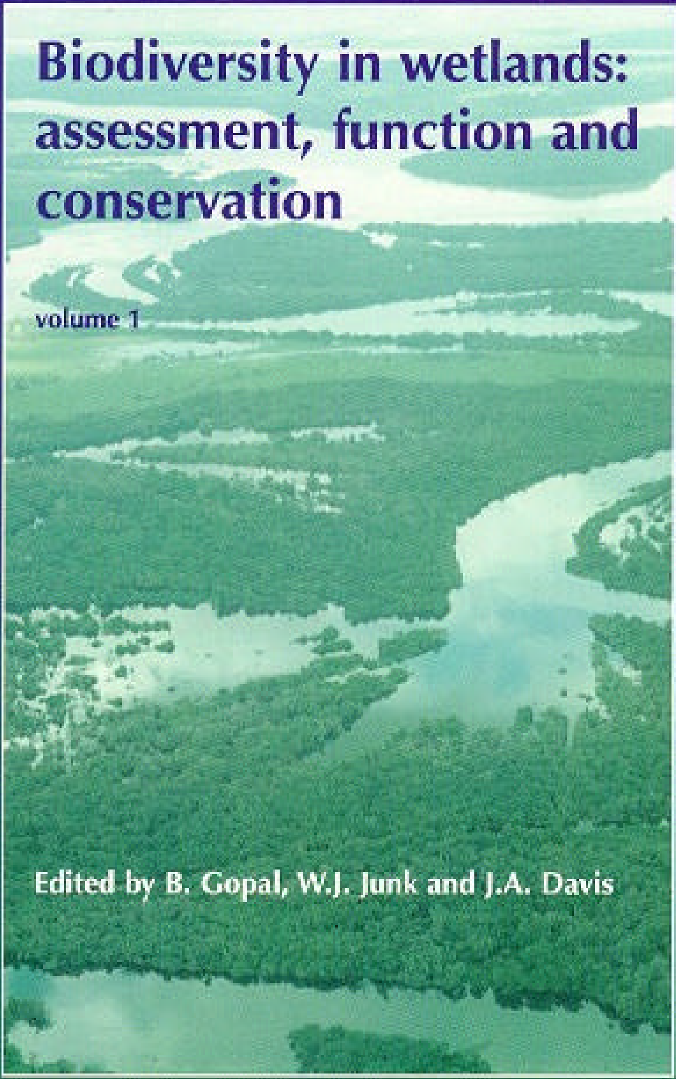

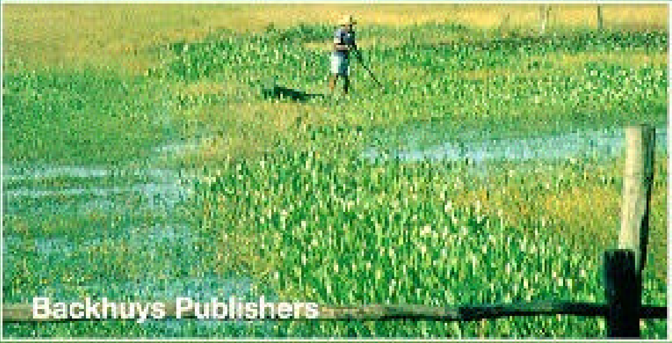

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BIODIVERSITY IN THE HIGH PARANÀ RIVER FLOODPLAIN

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Abstract

Despite being the most regulated river in the world, the high Paraná River in Brazil supports a great wealth of biological diversity. An extensive region of floodplain habitat remains within the high Paraná River between the Porto Primavera and Itaipu reservoirs, but it now experiences a modified flood regime due to the influence of the upstream reservoirs. Annual flooding and drying of the floodplain occurs, and this regime is greatly influenced by tributary rivers, especially the Ivinheima River which enters from the west. Most groups of aquatic organisms show high species diversity and strong patterns of ecological dynamics in response to habitat heterogeneity and water level fluctuations. Physicochemical attributes and primary production show high spatiotemporal variation in both river and floodplain habitats. In general, the floodpulse reduces phytoplankton densities, promotes periphyton and aquatic invertebrate production in the floodplain which supports juvenile fish feeding, growth, and development. Most fishes of the region are stimulated to spawn during the early stages of the annual flood pulse but some fishes reproduce over extended periods. The abundance of most species is positively associated with the timing and duration of the flood, and this is especially the case for migratory species with high fecundity. Several important iliophagous, herbivorous, and omnivorous fishes are among those showing evidence of enhanced recruitment during very high flood years. Some brood-guarding and piscivorous fishes show patterns of increased abundance in association with low flood years. We demonstrate how the integrity of the river-floodplain ecosystem of the high Paraná is dependent on the maintenance of some degree of annual flooding. Several conservation areas have been established to protect the biological diversity supported by the floodplain region that remains in a relatively natural condition.

Introduction

The Paraná basin has a drainage area of 28 x10^6 km^2, the second largest in South America, and drains the south-central region of the continent from the Andes to the Serra do Mar close to the Atlantic Ocean. From its source in the central plateau to its mouth in the La Plata estuary, this river runs 4,495 km. Its headwaters (the Paranaiba river, 1070 km long), its upper reaches (the confluence of the rivers Paranaiba and Grande up to the former Sete Quedas Falls, 619 km) and part of the middle section (from the former Sete Quedas falls to the mouth of the Iguaçu river,

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190 km) are within Brazil where the river drains 891,000 km^2 i.e., about 10.5% of the country's area. The falls that formerly separated the high and middle sections are now submerged beneath the Itaipu reservoir. The two rivers that form Paraná river (Grande and Paranaiba) are typical plateau rivers, with average gradients of about 0.8 m km^{-1}, decreasing towards their lower reaches (0.3 and 0.4 m km^{-1}, respectively) (Paiva 1982). With an average declivity of 0.18 m km^{-1}, the high Paraná river had an extensive floodplain between Tres Lagoas city, State of Mato Grosso do Sul, and Guaira, State of Paraná (a 480 km stretch, <20 km width). Until recently, this section was the only remaining stretch of the Paraná river in Brazilian territory free of dams, except 30 km downstream from the Itaipu reservoir (Agostinho and Zalewski 1996). In 1998, Porto Primavera dam, located in the middle part of this free stretch, was closed. At present the floodplain is restricted to 230 km between Itaipu and Porto Primavera reservoirs (Fig. 1). In this segment, where the Universidade Estadual de Maringá has developed a multidisciplinary research program, the river has a wide braided channel with a low gradient (0.09 m km^{-1} and great accumulation of sediments on its bed, giving rise to sandbanks and small islands. Complex anastomoses in this section of the river are formed by secondary channels, the Baía river, and the lower courses of rivers entering on the west bank (e.g., Ivinheima, Amambaí, Iguatemi). The east margin of the river is higher and tributaries have higher gradients (Paranapanema, 0.6 m km^{-1}; Ivaí, 1.30 m km^{-1}; Piquiri, 2.2 m km^{-1}) with smaller floodplains (Agostinho et al. 1995).

Above this stretch, the Paraná river basin has the greatest density of humans and concentration of industry within Brazil, intensive agriculture with heavy use of chemicals, and destruction of riparian vegetation, especially along the tributaries. Moreover, the river is regulated by 25 reservoirs larger than 100 km^2 affecting almost 70% of the rivers of the basin. Despite the influence of human activity upstream of the floodplain, including regulation of water discharge by hydroelectric plants, the high Paraná floodplain ecosystem still supports biotic diversity in this region of the continent, as we demonstrate in this chapter.

The annual flood pulse and limnological dynamics

In spite of several important tributaries that enter the floodplain, especially those from the north, the seasonality of the floodplain and associated habitats are dictated mainly by the Paraná river hydrology. In the Paraná, the high water period usually occurs from November/January to May/June. This phase is characterized by high water levels with some pulses of 2 to 3 m amplitudes (Fig. 2a). Two or three flood pulses are quite common during these phases, and they have been recorded even in the middle Paraná River in Argentina (Carignan and Neiff 1992). Smaller pulses (<0.5 m) occur weekly during the low water period (Fig. 2a), and they are caused by the operation of the upstream reservoirs (Thomaz et al. 1992a). This pattern of seasonal water level fluctuation is not continuously sinusoidal like those of other big rivers like the Amazon (Rai and Hill 1982), and uninterrupted periods of falling and rising water are rarely observed.

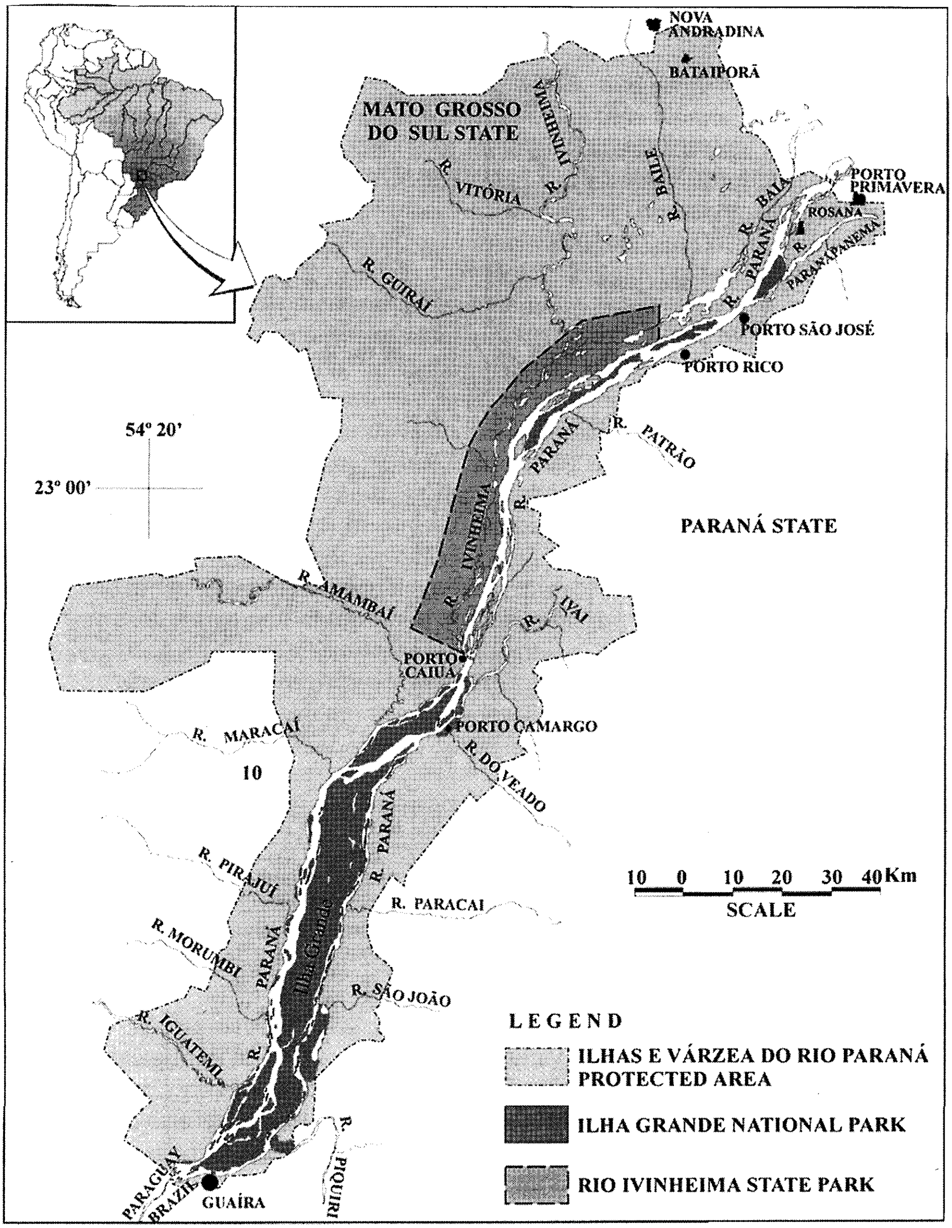

Fig. 1. High Paraná River and remaining floodplain. Conservation units are shown.

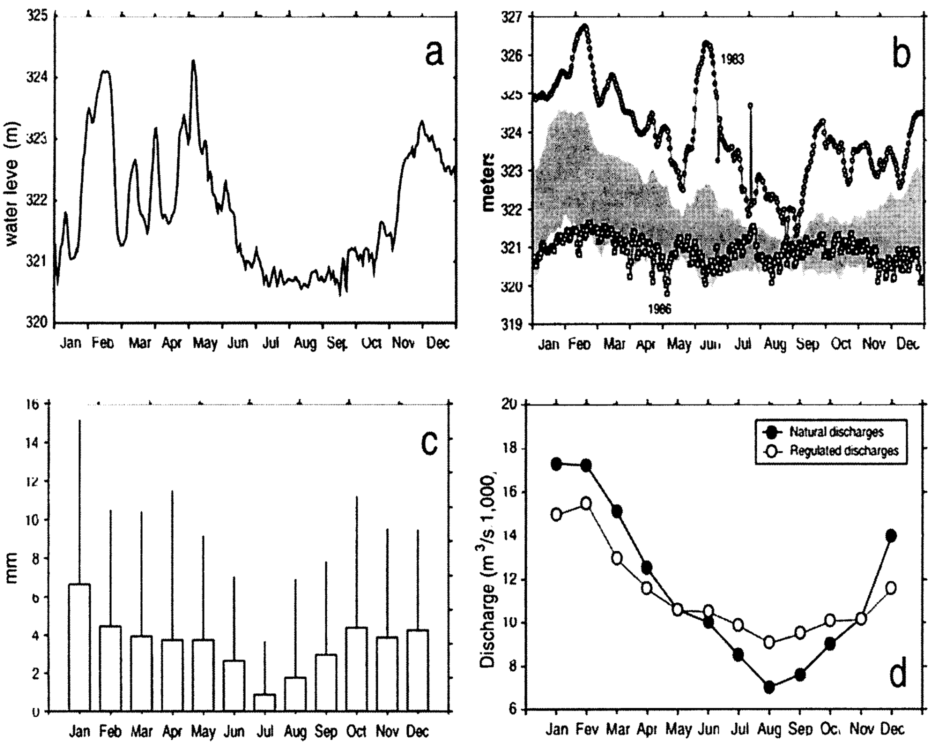

Fig. 2. (a) Water level variation of the Paraná River during 1992, showing several pulses between January and May, and smaller weekly pulses from June to October (modified from Thomaz et al. 1997); (b) Average water level (± s.d.) from 1978 to 1997. Extreme cycles with pronounced floods (1983) and absence of floods (1986) are also shown; (c) Average monthly precipitation from 1981 to 1995 (± s.d.); (d) Comparison of hydrologic regime of the high Paraná River before and after the existence of the cascade of reservoirs upstream (modified from Agostinho and Zalewsky 1996).

On average, the water level of the Paraná fluctuates about 2.5 m during each seasonal cycle, but considerable interannual variation can be observed (Fig. 2b). The flood amplitude may reach up to 7.5 m, but the near absence of floods has also been recorded (e.g., 1986-1987 in Fig. 2b). During years with no floods, the lagoons usually have higher chlorophyll-*a* concentrations and lower Secchi depth values than normal years (Thomaz 1991). The absence of floods also greatly influences the structure of aquatic community components like zooplankton and fishes. For example, the proportional abundance of cladocerans decreases and that of testate amoeba increases when flooding is greater (Lansac-Tôha et al. 1993). During the absence of flooding in 1986, predatory fishes were proportionally more abundant and juveniles of migratory species were less abundant (Agostinho and Zalewski 1996).

In fact, the natural hydrological regime of the high Paraná River has been severely altered by the cascade of reservoirs located upstream (Agostinho and Zalewski 1996). The control of the discharge by these reservoirs decreases the amplitude of seasonal water level fluctuations, decreasing the peaks and increasing the minimum water levels (Fig. 2d).

The period of low water occurs during winter, and so it coincides with lower temperatures and regional precipitation (Fig. 2c). These factors may also affect the biotic communities in the floodplain of the high Paraná, but their effect is difficult to assess since they covary with water level. The seasonal amplitude of the water temperature, for example, may reach up to 16°C (Thomaz et al. 1997), which appears to be important for periphyton dynamics (Rodrigues, L. 1998).

The limnological characteristics of the floodplain habitats are greatly affected by the hydrologic regime of the Paraná River, and high floods tend to homogenize river and floodplain habitats in terms of many physicochemical and biotic attributes (Fig. 3). During low water periods, floodplain habitats are less connected with the river and subjected to local processes like wind turbulence and inputs from small tributaries. For example, rotifer assemblages show higher between-site similarity during high water (Bonecker et al., in press). Also during the high water, chaoborid larvae are widespread in different habitats (Takeda et al. 1997).

Time lags in the response of physicochemical and biotic parameters to changes in water level of Paraná River have been noted in the floodplain habitats. The most predictive models have examined the relationship between limnological parameters, like nutrients, gases and chlorophyll-*a*, and variation in the average of the water level recorded six days before sampling (Thomaz et al. 1997). For phytoplankton, the best correlations were obtained when the average water level based on the preceding 14 days was considered (Rodrigues 1998).

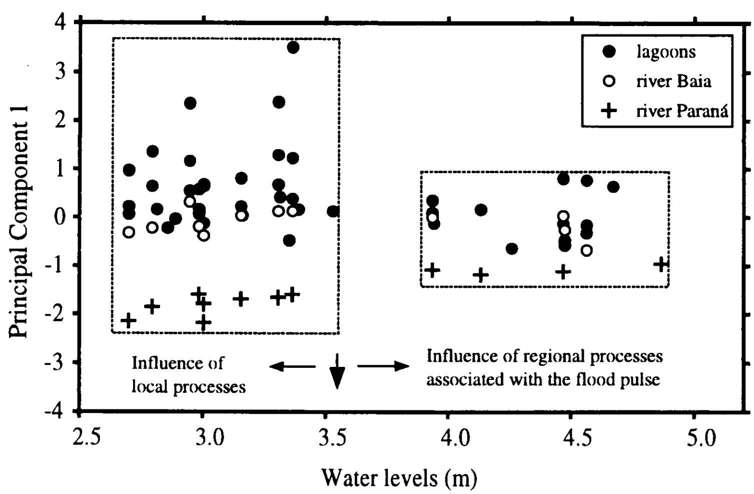

Fig. 3. Ordination of sites based on principal components analysis (PCA) using data for phosphorus, nitrogen, pH, conductivity, chlorophyll-*a* and dissolved oxygen. The first PCA axis is plotted against the average water level of the Paraná River during the 6 days preceding sampling. During high water, the different habitats tend to be more homogeneous in terms of these limnological characteristics (from Thomaz et al. 1997).

During high-water periods when the lagoons are deeper, thermal stratification may persist for periods longer than 24 hours, which leads to vertical stratification of nutrients and gases (Thomaz et al. 1992c, Lansac-Tôha et al. 1995). During this phase, anoxic layers close to the sediment are frequently observed (Thomaz 1991). During the low-water phase, complete mixing of the water column occurs during the night or morning when the lagoons are usually shallower than 2 m (Thomaz 1991, Lansac-Tôha et al. 1995, Paes da Silva and Thomaz 1997).

A peak of phosphate and total Kjeldahl nitrogen in the floodplain lagoons usually occurs during the beginning of the floods, following the decomposition of the flooded biomass, but the concentrations decrease as soon as flooding ensues (Thomaz et al. 1992a,b). In other words, the water from Paraná River dilutes the water from the lagoons. This is especially true for total phosphate which averages 23 $\mu g\ L^{-1}$ and 64 $\mu g\ L^{-1}$ in the river and lagoons, respectively (Thomaz et al. 1997). The low phosphate concentration in the Paraná river was not expected given that this river and its main tributaries (e.g., Tietê River) drain areas with agriculture and industry. The low phosphate concentrations may be partially explained by the cascade of upstream reservoirs that function as phosphate traps (Esteves 1983, Tundisi et al. 1988, Agostinho et al. 1995). Thus the water of the Paraná River is very phosphorus limited (atomic ratio of inorganic nitrogen:inorganic phosphorus from 62 to 93), and this limitation endures during variable periods also in the lagoons (ratios from 17 to 93) (Paes da Silva and Thomaz 1997, Rodrigues L. 1998).

A second peak of nutrients in the lagoons is usually observed during low water (from July to October), and this peak is due mainly to sediment resuspension derived from the wind action (Thomaz et al. 1992b, Thomaz et al. 1997). During this phase, the autochthonous input of nutrients, together with the diel mixing of the water column, leads to greater phytoplankton production in lagoons (Paes da Silva and Thomaz 1997) and chlorophyll-*a* concentrations (Thomaz et al. 1997, Train 1998, Train and Rodrigues 1998).

In spite of being relatively phosphate-poor, the Paraná River has high concentrations of nitrate-N (25-232 $\mu g\ L^{-1}$) compared with floodplain aquatic habitats ($<25\ \mu g\ L^{-1}$), and the same is true for silicate (Thomaz et al. 1997, Paes da Silva and Thomaz 1997, Train 1998, Train and Rodrigues 1998, Rodrigues L. 1998). Nevertheless, nitrate is rapidly consumed and transformed into ammonium-N as soon as it enters into the floodplain (Pacs da Silva and Thomaz 1997, Pagioro and Thomaz, in press). Paraná River also has higher values for electrical conductivity, which increases in floodplain lagoons during the floods (Thomaz et al. 1992a, Agostinho et al. 1995).

Limnological differences associated with water level fluctuation are much greater for small ponds, some of them temporary and located on islands of the main river channel. In such habitats, total phosphorus may oscillate from 28 to 349 $\mu g\ L^{-1}$, total Kjeldahl nitrogen from 360 to 5360 $\mu g\ L^{-1}$ and conductivity from 24 to 131 $\mu S\ cm^{-1}$ during a single annual cycle (Pagioro et al. 1994, 1997, Okada 1995). Conversely, limnological parameters are much more constant over the course of a year in the Paraná River channel (Thomaz et al. 1997).

Species richness

Truly aquatic organisms are by far the most studied group of the high Paraná River floodplain. There are fewer data concerning the wetland fauna that inhabits the floodplain. Available data are summarised below. Since 1986, planktonic and periphytic algae, zooplankton, zoobenthos, aquatic macrophytes and fishes have been studied in different habitats of the floodplain.

Diversity of Aquatic Communities

Phytoplankton

A total of 300 taxa of phytoplankton have been recorded in the high Paraná River and associated floodplain habitats. One hundred and thirteen taxa were recorded from the main river channel (Oliveira et al. 1994), and 119 were identified from the Baía River, one of its principal tributaries (Train and Rodrigues 1998). Higher species richness seems to be found in the lagoons. At Patos lagoon close to the Ivinheima River, Rodrigues (1998) recorded 273 taxa, and in Guaraná lagoon, 220 taxa were identified (Train 1998). These lagoons have higher diversity than some floodplains studied in the Amazon and middle Paraná river basins (Train 1998).

In general, the Chlorophyceae are the group with highest diversity (Oliveira et al. 1994, Rodrigues 1998, Train 1998, Train and Rodrigues 1998). In the Paraná River, Bacillarophyceae also are important, being represented mainly by *Aulacoseira granulata* (Oliveira et al. 1994). In the floodplain lagoons, Cyanophyceae are important, especially during the low water period when blooms of some species like *Anabaena* species, *Microcystis aeruginosa* and *Anabaena spiroides* may occur (Train and Rodrigues 1997, Rodrigues 1998). Euglenophyceae ranks second in number of taxa (47), and they occur mainly in the temporary lagoons that are isolated for long periods from the river channel (Jati and Train 1994, Train and Rodrigues 1997).

No clear pattern of association between hydrology with algal diversity and richness has been identified. Greater species richness is observed during low water in the river channel (Train and Rodrigues 1997), temporary lagoons (Jati and Train 1994), and in the Patos lagoon (Rodrigues 1998). In the Guaraná lagoon and Baía river, the highest richness was observed during the high-water period (Train and Rodrigues 1997, Train 1998).

Phytoplankton density is usually higher during later stages of low-water period in both the main channel and lagoons (Train and Rodrigues 1997, Rodrigues 1998, Train 1998). The lower phytoplankton densities recorded during the high-water phase are caused mostly by a dilution effect (Thomaz et al. 1997, Rodrigues 1998). Considering the different aquatic habitats, higher phytoplankton densities (represented by chlorophyll-*a*) are obtained in lagoons and semi-lotic environments, and the lowest values in the rivers Paraná and Ivinheima (Thomaz et al. 1997, Train and Rodrigues 1997, Train 1998).

Although the hydrologic regime of the Paraná River has been considered the main factor driving seasonal patterns of biomass and composition of the phytoplankton community, the low nutrient concentrations, especially nitrate-N, also have been considered important in the reduction of phytoplankton biomass observed during the late falling-water phase (Train 1998). The heterocystous Cyanophyceae may have an important role for generation of inorganic nitrogen in lagoons during the low-water phase. In addition temperatures are lower during these periods, which probably also affects phytoplankton dynamics (Thomaz et al. 1997).

Zooplankton

The zooplankton community of the high Paraná floodplain is represented by 329 taxa, 55 of which are testate amoeba, 218 rotifers, 40 cladocerans, and 16 copepods (Lansac-Tôha et al. 1997, Bonecker et al., 1998). Most of these taxa are not exclusively planktonic; benthic, periphytic and littoral species are also represented.

Species richness of the various zooplankton groups varies with habitat. The greatest number of testate amoeba species is found in the rivers Paraná and Ivinheima (50 species), followed by the lagoons (46) and semi-lotic environments (39) (Lansac-Tôha et al. 1997). Lagoons support the highest number of rotifer species (133), followed by the rivers (106) and semi-lotic environments (105), whereas species richness of microcrustacea is similar in the different habitats researched in the high Paraná River floodplain (47-54) (Bonecker et al. 1994, Lansac-Tôha et al. 1997, Garcia et al. 1998). In general, higher species richness has been recorded from the littoral regions of all floodplain habitats, which tend to be associated with the greater habitat heterogeneity and resource availability (Bonecker et al. 1994, Lansac-Tôha et al. 1997).

Some zooplankton species are found exclusively in particular habitats. The rotifers *Brachionus urceolaris amazonicus, Lepadella rhomboides, Notommata tripus, Trocosphaera aequatorialis* and *Horäella thomasoni*, the cladoceran *Macrothrix triserialis*, and the copepod *Microcyclops* species are collected only from lagoons. The rotifers *Monommata mucronata, Notommata glyphura* and *Rotatoria tardigrada* are collected only from semi-lotic environments, and the rotifers *Lophocaris salpina* and *Pompholyx* species only from rivers (Lansac-Tôha et al. 1997).

The water level seems to affect the composition of several groups in a similar manner. Species richness of testate amoeba, rotifers, and microcrustacea is higher during high-water periods (Bonecker et al. 1994, Lansac-Tôha et al. 1997, Garcia et al. 1998). This pattern is caused primarily by the linkage of the floodplain habitats during the floods. Higher densities of testate amoeba, microcrustacea and rotifers usually are observed in the lagoons (Bonecker et al. 1994, Lima et al. 1996, Lansac-Tôha et al. 1997). This pattern may be associated with lower velocity, longer retention time, and higher food availability in lagoons (Bonecker and Lansac-Tôha 1996, Garcia et al. 1998), as indicated by higher chlorophyll-*a* concentrations and phytoplankton densities.

Water level fluctuations affect densities of different zooplankton differently in the various floodplain habitats. Higher densities of testate amoeba in rivers, rotifers in lagoons and semi-lotic environments, cladocerans in the lotic and semi-lotic environments, and copepods in all environments are observed during the high-water period (Lansac-Tôha et al. 1997, Garcia et al. 1998). During the low-water period, the lagoons and semi-lotic environments tend to have highest densities of testate amoeba, rivers have highest densities of rotifers, and lagoons have the highest densities of cladocerans (Lansac-Tôha et al. 1997).

Periphyton

The periphytic algal community has been studied in colonization experiments with artificial and natural (*Eichhornia azurea* petioles) substrates in three environments of the floodplain, during high water and low water periods (Rodrigues, L. 1998). Like most other taxonomic groups, periphytic algae are influenced by the hydrologic cycle of the Paraná river, as well as by habitat type. A total of 228 benthic algal species were identified, the classes with highest number of species were Bacillariophyceae (74), Zygnemaphyceac (62), and Chlorophyceae (34). The periphytic community is dominated by Bacillariophyceae, Chlorophyceae and Cyanophyceae, in terms of abundance. In terms of biovolume, Zygnemaphyceac are dominant in all environments and substrates, throughout the year.

The greatest number of periphytic algal species has been recorded for lagoons (76-137, depending on the kind of substrate and period of the year), and lowest richness was obtained in a lateral channel of the Paraná River (56-76 species). Highest species richness was obtained during the high-water period in all substrates and environments. According to Rodrigues, L. (1998), this increase is caused by the increased nutrient concentrations, importation of propagules, and physical perturbation caused by the flood pulses.

The periphytic biomass, as determined by chlorophyll-*a* concentrations, also was greater during the high-water period. The greatest biomass values have been recorded from the lateral channel of the Paraná River. This pattern may be attributed to the continuous supply of nutrients (reduced boundary layer), rapid colonization, and frequent removal of the older parts of the community which stimulates the algae reproduction (Rodrigues, L. 1998).

Zoobenthos

Surveys of zoobenthos of the high Paraná river floodplain have identified up to 80 invertebrate taxa. There is considerable variation among lagoons, but, in general, microcrustacea, Chaoboridae, and especially Chironomidae are the most important benthic invertebrate groups (Takeda et al. 1991a,b,c, 1997). One lagoon (Guaraná) was dominated numerically by *Campsurus violaceus* (Ephemeroptera). Other lagoons were dominated by *Goeldichironumus, Polypedium, Branchiura sowerbyina, Cryptochironomus* and *Polypedilum* (all Chironomidae) in their littoral regions, and *Chironomus* and Chaoboridae dominated the pelagic regions (Takeda et al. 1997). Chironomidae dominated the margins of the Paraná river and the margins and center of Corutuba channel, which links the Paraná and Ivinheima rivers, however Oligochaeta (*Paranadrilus descolei*) were important in the Ipoitã channel and Ivinheima river. The main channel of the Paraná river is inhabited mostly by interstitial organisms, especially nematodes (high densities of *Narapa bonettoi*), Harpacticoida and Oligochaeta. In the Baía river (semi-lotic), *Glyptotendipes* (Chironomidae) and *Campsurus violaceus* (Ephemeroptera) dominate numerically, and the differences between this river and Paraná and Ivinheima river may be attributed to the texture of sediment and water velocity (Takeda et al. 1997). In the Baía river, higher densities of Chironomidae were associated with coarser substrates, especially the percentage of gravel (Higuti et al. 1993).

In lagoons, the rising flood waters have a greater influence on the benthic community than the gradual reduction of water level that follows the flood period (Takeda et al. 1991a). Cladocerans and Chironomidae dominate lagoons under low water conditions, but Chaoboridae dominate during high water (Takeda et al. 1991a, 1997). During the high water, the combination of low oxygen concentration in the deeper layers of the water column and predation on early larval stages of chironomids may favor the increase of the percentage of Chaoboridae, which are able to migrate vertically in the water column (Takeda et al. 1991, 1997). The high-water period also is associated with a decrease in the relative abundance of benthic cladocerans (Takeda et al. 1991a).

Aquatic Macrophytes

Specific studies of the aquatic and emergent macrophytes of the high Paraná floodplain have begun only recently. The only survey was published by Souza et al. (1997), but their work emphasized marginal and terrestrial vegetation. The total number of species of aquatic plants is estimated (including unpublished information) to be 48 of which 32 are emergent, 3 floating-leaved, 6 free-floating, 5 rooted submerged, and 2 free submerged.

An important species in the floodplain is *Panicum prionitis* (Poaceae), which is not a euhydrophyte but probably exhibits adaptations to survive underwater during floods. Due to its high biomass, this species probably affects the water quality of the environments of the floodplain and contributes with great inputs of detritus during inundation. *Eichhornia azurea* is another important species, which occurs in the littoral regions of the lagoons, secondary channels, lateral channels, river and backwaters of the Paraná and Ivinheima rivers. *Eichhornia crassipes, Salvinia auriculata, Pistia stratiotes* and *Utricularia* species are commonly encountered within the stands of *Eichhornia azurea.*

The biomass of some species of aquatic macrophytes is strongly associated with water level fluctuations of the Paraná River, but the seasonal sequence differs according to the species considered (Bini 1996). In a study carried out at Guaraná lagoon, a greater biomass of *Eichhornia azurea* was recorded during the low-water period, and the biomass of *Polygonum* species increased with water level, however no pattern of seasonal variation was obtained for *Salvinia auriculata* biomass (Bini 1996). Again, the data presented here are preliminary, and given the great importance of aquatic macrophytes for the Paraná floodplain ecosystem, additional ecological data are needed.

Some Considerations Regarding the Diversity of Invertebrate Aquatic Organisms

Results obtained from several habitats of the high Paraná River floodplain suggest that lagoons are the richest environments in terms of phytoplankton, peryphyton, rotifers, aquatic macrophytes and benthos species diversity. The highest abundance of phytoplankton, zooplankton and aquatic macrophytes is also observed in these habitats. This pattern of spatial distribution may be due to the greater stability of these lentic environments and their greater nutrient availability (especially phosphorus) derived from sediment re-suspension during low-water periods. In the absence of strong flow which is characteristic of channels, lagoons have greater food availability derived from the phytoplankton and periphyton primary production and detritus derived from abundant aquatic macrophytes.

Greater species richness of testate amoeba, rotifers, microcrustacea and periphytic algae usually are observed during high-water periods. This supports the view that the flood pulse, which increases the connectivity among different floodplain habitats, is important in the maintenance of high diversity in assemblages from diverse habitats of the floodplain.

In the lagoons, the low-water period is characterized by higher phytoplanktonic and aquatic macrophyte biomass and densities which, together with the favourable levels of dissolved oxygen, may promote higher densities of zoobenthos and planktonic cladocerans in these environments. On the other hand, the high densities of rotifers and testate amoeba during high-water periods may be associated with increases in food resources, such as detritus and bacteria originating from the inundated riparian vegetation.

Fishes

Surveys of the floodplain along the free stretch of the high Paraná River basin reveal an ichthyofauna composed of 170 species, six of which were introduced from other basins (see discussion below). In addition, at least 13 fish species gained access to the region after creation of the Itaipu impoundment, when the Sete Quedas Falls, a barrier to the upstream dispersal by fishes of the middle Paraná River were submerged (Agostinho et al. 1994). One hundred species have been recorded from the main channel of the high Paraná River. Among the most characteristic fishes are three stingrays of the genus *Potamotrygon,* which were absent from the high Paraná before the formation of Itaipu Reservoir, the canivete *(Parodon tortuosus),* pimelodids (e.g., the jail *Paulicea luetkeni* and jurupoca *Hemisorubim platyrhynchos)* and anostomids (e.g., the piapara *Leporinus elongatus* and piava *Schizodon altoparanae)* (Agostinho et al. 1997).

Among the main tributaries of the Paraná, the Ivinheima River has the highest number of species (91), most of which are recorded from its lower reaches. The Ivinheima has a low gradient over its last 70 km, which in some places runs parallel to and connects with the Paraná. The upper reaches of this river contain important spawning areas for migratory fishes of the basin (Nakatani et al. 1997, Vazzoler et al. 1997). Pacu (*Piaractus mesopotamicus*), the armado (*Rhinodoras d'orbignyi*), and pintado (*Pseudoplatystoma corruscans*), are the most easily recognized fish species – Table 1. The Iguatemi, a typical meandering river, harbors an intermediate species richness (77), with the armado (*Pterodoras granulosus*) and the cangati (*Parauchenipterus galeatus*) conspicuous. The Piquiri River, with a steep slope and turbulent waters, contains fewer species (57). It is notable for the absence of certain species that are otherwise widely distributed within the basin, such as the cangati (*Parauchenipterus galeatus*), the curvina (*Plagioscion squamosissimus*), the dourado-facilo (*Rhaphiodon vulpinus*), the genera *Loricaria, Loricariichthys* and

Roeboides, and the families Doradidae and Ageneiosidae. Yet, the Piquiri supports some species in abundance; for example, the piau (*Leporinus amblyrhynchus*), which occurs only sporadically in other localities, and the pimelodid (*Steindachneridion*) and the auchenipterid (*Tatia neivae*), which are otherwise recorded only in lower order rivers in other parts of the basin (FUEL 1991, Godinho et al. 1991). The streams and creeks of the region support a rich fish fauna (123 species) composed of small species mostly restricted to these habitats, such as lebiasinids, poeciliids, small tetragonopterine characids (e.g., *Astyanax eigenmanniorum, Astyanax scabripinnis, Holoshestes, Hyphessobrycon*), and small pimelodids (e.g., *Cetopsorhamdia, Nannorhamdia, Phenocorhamdia, Imparfinis, Chasmocranus*).

On the floodplain, which offers a high diversity of refuges and food resources, the number of species is relatively high, with 103 recorded in the lagoons and 101 in the channels that connect them to the river. The fishes of these environments, especially lagoons, are subject to more extreme fluctuations in physical and chemical characteristics of the water, in particular temperature and dissolved oxygen concentration. The fauna of the lagoons is composed of small species and the young

Table 1. The principal habitats and fishes of the high Paraná River floodplain.

Habitat	**Characteristics**	**Conspicuous species**
Paraná river channel	sandy or arenitic substrate, lotic	*Paulicea luetheni, Loricaria*, and adults of big fishes *Potamotrygon species, Parodon tortuosus, Hemisorubim platyrhynchos, Leporinus elongatus, Schizodon altoparanae*
Larger tributaries of Paraná river	meandering streams with sandy bottom (Ivinheima e Iguatemi), greater diversity; or rapid water and rocky bottom (Piquiri), lower diversity	Meandering streams: Doradidae, Ageneiosidae, *Schizodon, Hoplias, Rhaphiodon*, Auchenipteridae, *Pimelodus, Roeboides, Piaractus mesopotamicus, Pseudoplatystoma corruscans*. Rapid water: *Leporinus amblirhynchus, Schizodon nasutus, Galeocharax knerii, Apareiodon, Myloplus*
Creeks	variation in gradient, substrate, size, size, proportion riffles/pools, cover, and conservation of riparian vegetation	Small fishes: Cheirodontidae, Tetragonopterínae, small Pimelodidae, Loricarídae, Trichomycteridae
Marginal lagoons (floodplain)	shallow, sand or mud bottom, abundant macrophytes, with diel stratification, low fish diversity	*Loricariichthys, Hoplosternum, Leporinus lacustris*, young of *Prochilodus* and others rheophilic species
Secondary channels (floodplain)	semi-lenitic, drain the floodplain	Lagoon species plus *Trachydoras, Iheringichthys, Serrasalmus* species
Ephemeral pools	form during water recession, drying up during different periods of the year, mud bottom, stressful environment	End of drying period: *Astyanax bimaculatus, Cheirodon notomelas, Steindachnerina insculpta, Hoplias malabaricus and Roeboides paranensis*

of larger species that utilize these habitats during their early development. The cascudo chinelo (*Loricariichthys platymetopon*), the caboja (*Hoplosternum littorale*), the traíra (*Hoplias malabaricus*), the corró (*Leporinus lacustris*), and young of the curimba (*Prochilodus lineatus*) are the most common species in catches from experimental fishing performed in lagoons. Young of other species, such as the pintado (*Pseudoplatystoma corruscans*), the jurupoca (*Hemisorubin platyrhynchos*), the piava (*Schizodon altoparanae*), and the piavuçu (*Leporinus obtusidens*) also are frequently captured.

In the ephemeral lagoons, characiforms dominate numerically (55%) over the siluriforms (22%). Of the total number of individuals caught by Veríssimo (1994) in three ephemeral floodplain lagoons, 90.5% were characiforms. Okada (1995) made similar observations in six other locations on the floodplain, reporting the dominance of *Astyanax bimaculatus, Steindachnerina insculpta* and *Roeboides paranensis* which comprised more than 50% of the catches. In a drying pool (area 3.7 m^2; depth 10 cm), Okada et al. (in press) identified 30 of the 64 fish species recorded in lagoon habitats of the floodplain. Fish density in this pool peaked at about 300 individuals m^{-2}. These ephemeral habitats are scattered throughout the floodplain, and during the drying period (May to September) massive fish mortality occurs. This fish mortality is increased by delays in the natural flooding period or short-term pulses in the drainage of the main river imposed by operation of the dam turbines upstream.

The relative proportions of the different taxonomic orders in the ichthyofauna of the region reflect the general situation in neotropical rivers (Lowe-McConnell 1987). That is, more than 85% of the fauna belongs to the orders Characiformes and Siluriformes, with characiforms predominating slightly. Even in the Piquiri River, characiforms make up 57% of species and siluriforms 24%. This is despite the previously mentioned absence of some siluriform species, genera, and even families that are otherwise widely distributed in the high Paraná basin. Perciformes, the third-ranked order in number of species in the region, are represented by a similar number of species in nearly all the bodies of water, however there is considerable variation in composition among locations.

Diversity of Wetland Communities

Vertebrates

Relative to the truly aquatic flora and fauna, other biota in the high Paraná River is poorly studied. Most of the available information for amphibians, reptiles and mammals is from environmental impact studies made with regard to the construction of Porto Primavera dam (THEMAG, ENGEA and UMAH 1994). Nevertheless, for birds the high Paraná River area is one of the best known in south Brazil (Straube et al. 1996).

During the impact assessment, 22 species of amphibians were collected, with the most speciose families being the Hylidae (8 species) and Leptodactilidae (8 species) (Table 2). Eight amphibian species were recorded for the first time in this area during the assessment. Most of the species have large biogreographical distribuition (60%). Others as *Physalaemus fuscomaculatus* have restricted distribution.

Thirty-seven reptile species from 13 families have been recorded, the most speciose families being the Colubridae (16 species) and Teiidae (6 species). Nine of these species were collected for the first time during the impact assessment and 40% of the species have wide biogeographical distribution. Three crocodile species occur in the region, the most conspicuous of which is the yellow-pouch alligator (*Caiman latirostris*). There are a small number of poisonous snakes (e.g., *Bothrops* species) and a large number of non-poisonous species recorded as *Helicops infrataeniatus, Hydrodinastes gigas, Mastigodryas bifossatus*, that inhabit marshes. The most abundant among the non-poisonous snakes are *Chironius* and *Philodryas* species.

In the area, there are 58 bird families, 18 from the Passerine order (Straube et al. 1996). This region is one of the richest in Paraná State due to the influence of several biogeographical events. Since 1950, the alterations in the natural vegetation have promoted a large change in species composition. Of the 351 species cited for the area, 253 composed the original fauna, 256 compose the actual fauna. Out of the original avifauna, 83 have become locally extinct and 96 other species are local colonizations (Straube, in preparation).

Approximately 14% of the bird species are truly aquatic, as the big-sized Ciconiidae (e.g., *Mycteria americana, Ciconia maguari, Jabiru mycteria*), the biguatinga (*Anhinga anhinga*), the Ardeidae (*Ardea cocoi, Egretta alba, Egretta*

Table 2. Species richness within terrestrial/wetland vertebrates families in the high Paraná River.

Amphibians	S	Reptiles	S	Birds	S	Birds	S	Mammals	S
Bufonidade	2	Gekkonidae	1	Tinamidae	7	Nyctibiidae	2	Didelphidae	3
Hylidae	8	Haplocercidae	1	Podicipedidae	3	Caprimulgidae	7	Dasypodidae	3
Leptodactylidae	8	Tropiduridae	1	Phalacrocoracidae	1	Apodidae	5	Myrmecophagidae	2
Microhylidae	3	Scincidae	1	Anhingidae	1	Trochilidae	10	Phyllostomidae	1
Pseudidae	1	Teiidae	6	Ardeidae	11	Trogonidae	2	Vespertilionidae	1
		Anguidae	1	Ciconiidae	3	Alcedinidae	4	Noctilionidae	1
		Amphisbaenidae	1	Threskiornithidae	5	Momotidae	2	Molossidae	2
		Colubridae	16	Anhimidae	2	Galbulidae	2	Cebidae	2
		Typhlopidae	1	Anatidae	6	Bucconidae	4	Canidae	2
		Boidae	2	Cathartidae	5	Ramphastidae	6	Procyonidae	2
		Viperidae	1	Pandionidae	1	Picidae	12	Mustelidae	4
		Chelidae	2	Accipitridae	16	Dendrocolaptidae	7	Felidae	6
		Alligatoridae	3	Falconidae	10	Furnariidae	19	Tapiridae	1
				Cracidae	3	Formicariidae	15	Cervidae	4
				Phasianidae	1	Tyrannidae	68	Tayassuidae	2
				Aramidae	1	Pipridae	7	Suidae	1
				Rallidae	8	Cotingidae	3	Cricetidae	4
				Heliornithidae	1	Oxyruncidae	1	Muridae	2
				Jacanidae	1	Hirundinidae	14	Sciuridae	1
				Recurvirostridae	1	Motacillidae	1	Erethizontidae	1
				Charadriidae	5	Troglodytidae	3	Caviidae	1
				Scolopacidae	4	Mimidae	2	Dasyproctidae	1
				Sternidae	2	Turdidae	4	Agoutidae	1
				Rhynchopidae	1	Emberezidae	42	Hydrochaeridae	1
				Columbidae	11	Parulidae	7	Leporidae	1
				Psittacidade	12	Vireonidae	3		
				Cuculidae	9	Icteridae	15		
				Tytonidae	1	Ploceidae	1		
				Strigidae	8	Corvidae	2		

Source: THEMAG, ENGEA and UMAH (1994) for amphibians, reptiles and mammals; Straube et al. (1996) for birds.

thula, Nycticorax nicticorax, Tigrisoma lineatum) and Threskiomithidae (*Theristicus caudatus, Ajaia ajaia*). The Anatidae (*Dendrocyagna vidauta, Dendrocyagna autumnalis, Cairina moschata*) are conspicuous. Some North American migrants such as *Tringa solitaria* and *Tringa flavipes* also occur in the area. Forty-three species considered threatened in Paraná State (Straube 1995) and 10 species considered threatened in Brazil (Brazilian Institute for the Environment, decree n. 1522) occur in the area. Some of these as the macuco (*Tinamus solitarius*) are common in the area (Brazilian Institute for the Environment, decree n. 1522).

At least sixty mammal species from 25 families have been documented from the floodplain in the region. The families containing the most species are the Phyllostomidae (11 species), Felidae (6 species), Cervidae and Cricetidae (4 species each). Forty-four mammal species were recorded for the first time during the Porto Primavera assessment. Among the most notable mammals in the area are the Felidae predators (*Felis concolor* and *Panthera onca*) which are now listed as endangered species. The floodplain supports large populations of the capybara (*Hydrochaeris hydrochaeris*), a semi-aquatic rodent. Common in the area are populations of wild pig (*Tayassu tajacu*), wild dog (*Dusicyon thous*), tapir (*Tapirus terrestris*), marsh deer (*Blastocerus dichotomus*), deer (*Mazama* species), arinadillos (*Dasypus* species, *Euphractus* species, *Priodontes* species), anteaters (*Tamandua tetradactyla, Myrmecophaga tridactyla*), bugio (*Alouatta caraya*), monkeys (*Cebus* species), coati (*Nasua nasua*), racoon (*Procyon cancrivorus*) and the irara (*Eira barbara*). Twenty percent of the mammals of the region are listed as threatened with danger of extinction (Brazilian Institute for the Environment, decree n. 1522).

Flora

For the flora of the high Paraná River floodplain, the main sources of information are a floristic inventory performed by the NUPELIA/Universidade Estadual de Maringá research group (Souza et al. 1997) and the environmental impact assessment performed for the Porto Primavera dam (Mantovani and Catharino 1994). These surveys were performed at most 200 km apart, and the Souza et al. (1997) inventory provides most of the information supporting the design of conservation units of the floodplain. The NUPELIA inventory is not yet concluded, and some plants have yet not been identified at the genus or species level.

The number of species found in each family is shown in Table 3. Souza et al (1997) mentioned 97 families, 295 genera, and 450 species of phanerogams for the region. In terms of species richness, the most important families are the Fabaceae (38), Myrtaceae (23), Euphorbiaceae (22), Rubiaceae (22), Solanaceae (20), and Mimosaceae (18). There are 22 families and 357 species that were collected in the Porto Primavera region and not in the Porto Rico region at least 40 km to the south. Because the vegetation surveys have not been completed, this difference may be due partly to sampling effort, but nonetheless provides an idea about the regional biodiversity.

In a comparison between six localities near Porto Rico in the southern part of the floodplain (data from Assis 1991, Souza-Stevaux and Cilinski 1996, Souza and Monteiro 1996, Souza-Stevaux et al. 1995, Cislinski and Souza 1996, Previdello et al. 1996), Souza et al. (1997) found that most of the species occurred only at one

Table 3. Plant families of the high Paraná River. Families written in bold were found exclusively in Porto Primavera region. PR = Number of species found in Porto Rico region (Souza et al. 1997), and PP = Number of species found at Porto Primavera region (Mantovani and Catharino 1994). X indicates the presence of the family.

Phanerogames	**PR**	**PP**		**PR**	**PP**		**PR**	**PP**
Acanthaceae	2	1	Dilleniacea	3	1	Nyctaginaceae	2	1
Alismatacea*	3	6	**Droseraceae***		1	Nympheaceae*	1	1
Amaranthaceae*	4	3	**Ebenaceae**		1	Ochnaceae		4
Anacardiaceae	4	5	Elaeocarpaceae	2	1	Onagraceae*	2	5
Annonaceae	6	9	**Ericaulaceae**		2	Opiliaceae		1
Apiaceae*	3	3	Erythroxylaceae	2	3	**Orchidaceae**		7
Apocynaceae	5	3	Euphorbiaceae	22	15	Oxalidaceae	1	
Araceae*		6	Fabaceae	38	10	Passifloraceae	2	1
Araliaceae		1	Flacourtiaceae	10	2	Piperaceae	4	3
Arecaceae	3	8	Gesneriaceae	X	1	Phytolaccaceae	6	1
Aristolochiaceae	4	2	**Heliconaceae**		1	Poaceae*	14	7
Asclepiadaceae	4		Hydrophyllaceae	1	1	Polygalaceae	1	1
Asteraceae	14	11	Hippocrateaceae	2	1	Polygonaceae*	9	2
Bambusaceae	2		Iridaceae	1		Pontederiaceae*	4	
Begoniaceae	1		Lamiaceae	6		Portulacaceae	1	
Bignoniaceae	7	10	Lauraceae	9	8	**Proteaceae**		2
Bombacaceae		2	Lecythidaceae	1		Rhamnaceae	3	2
Boraginaceae	9	3	Lentibulariaceae	1	2	**Rosaceae**		1
Bromeliaceae	4	3	Limnocharitaceae*	1	1	Rubiaceae	22	23
Burmmaneaceae		1	Liliaceae	1		Rutaceae	11	2
Burseraceae	1	1	Loganiaceae	X	1	Sapindaceae	14	5
Cabombaceae*		1	Loranthaceae	1		Sapotaceae	5	6
Cactaceae	2	4	Lythraceae	2	1	Schrophulariaceae	4	3
Caesalpiniacea	9	5	Malpighiaceae	4	11	Simaroubaceae	2	2
Campanulaceae	X		Malvaceae	4	5	Smilacaceae	1	1
Cappaparaceae	2		**Magnoliaceae**		1	Solanaceae	20	1
Caprifoliaceae	X		Maranthaceae	1		Sterculiaceae	7	2
Caryocaraceae		1	Mayacaceae*		1	Theophrastaceae	1	
Cecropiaceae	1	1	Melastomataceae	5	10	Tiliaceae	4	
Chrysobalanaceae	2	1	Meliaceae	8	4	Trigoniaceae	1	
Clorospermaceae		1	Menispermaceae	2	1	Turneraceae	1	
Clusiaceae	2	4	Mimosaceae	18	11	**Typhaceae***		1
Combretaceae	2	1	Molluginaceae	1		Ulmaceae	2	3
Commelinaceae*	3		Monimiaceae	X	1	Urticaceae	2	1
Compositae		11	Moraceae	4	6	Verbenaceae	6	2
Connaraceae		1	Musaceae	1		Violaceae	1	1
Convolvulaceae*	6	2	**Myristicaceae**		1	Vitaceae	3	
Costaceae	1	2	Myrsinaceae	1	2	Vochysiaceae	1	2
Cucurbitaceae	1		Myrtaceae	23	21	Xyridaceae	1	3
Cyperaceae*	7	18	Najadaceae*	1				

Pteridophyta	**PR**		**PR**		**PR**
Aspleniaceae	2	Lycopodiaceae	1	Salviniaceae*	2
Blechnaceae	3	Polypodiaceae	4	Schizaeaceae	3
Cyatheaceae	1	Psilotaceae	1	Thelypteridaceae	3
Denstaedtiaceae	1	Pteridaceae	10		

* These families have at least one species with adaptation to aquatic/wet environment.

locality (62%), and only 3% of the species occurred at all the localities. Among the locations sampled, the highest between-site similarity was 54% and the lowest was 13%. The similarity between the Porto Rico and the Porto Pimavera regions was very low. This analysis indicates that beta diversity is high in this region. Alpha diversity, or local diversity, is low due, in part, to the stressful conditions imposed by the annual floods, and also to direct human impacts on the forests (Souza et al. 1997).

Fish fauna

Diversity Patterns

The alpha diversity of fishes of the region was evaluated using species-abundance curves (Whittaker plots), rarefaction curves, and diversity indices (Magurran 1988). Diversity is highest in the rivers, intermediate in the secondary channels, and smallest in the lagoons. The number of individuals caught per unit effort is lower in the rivers than the lagoons, but species richness and the equitability values are higher (Agostinho et al. 1997) (Table 4).

Species relative abundances were more evenly distributed for rivers relative to lagoons (data for 1986-87 when there were no floods, and 1987-88 when there was moderate flooding) (Agostinho et al. 1997). Using the whole database for fish in the high Paraná river floodplain (420 point samples with gillnets in channels, lakes, rivers and ephemeral lagoons, data for 1986-88 and 1992-94) we estimated species richness at 95 by extrapolation with the Incidence-based Coverage Estimator (ICE, Colwell 1997, Chazdon et al. 1998). This estimate is close to the number of species actually captured from these habitats using gillnets during the surveys (90).

Beta, or regional, diversity can be evaluated using similarity coefficients (Magurran 1988). For different aquatic habitats of the floodplain, similarity ranges from 0.31 to 0.77 (Jaccard coefficient of similarity). The most dissimilar environments are ephemeral lagoons, streams, and one of the main rivers in the region, Piquiri (Agostinho et al. 1997) (Table 5).

In floodplain rivers, species diversity and the density of each species are strongly controlled by the flood regime. Variation in the duration, time of year, and magnitude of floods affect species in different ways, since their ecological requirements and the timing of vital processes such as reproduction, feeding, growth, and maturity differ. Since flood events affect the various floodplain habitats to different

Table 4. Simpson species diversity index (H), evenness (E), and richness (S) in three habitats during the study period.

Habitat	**1986-87**			**1987-88**			**1992-93**			**1993-94**		
	S	**H**	**E**	**S**	**H**	**E**	**S**	**H**	**E**	**S**	**H**	**E**
Lagoons	53	0,840	0,856	52	0,862	0,878	51	0,916	0,934	48	0,907	0,926
Secondary Channels	54	0,895	0,912	58	0,919	0,935	48	0,930	0,949	49	0,884	0,902
Rivers	63	0,954	0,968	62	0,936	0,951	72	0,932	0,945	62	0,900	0,915

Source: Agostinho et al. (1997).

Table 5. Similarity matrix (Jaccard similarity coefficient) comparing sites among high Paraná floodplain habitats lying between the Paranapanema river and Itaipu reservoir.

Habitat	Paraná river	Ivinheima river	Piquiri river	Iguatemi river	Streams	Lagoons	Channels
Ivinheima river	0.69	1.00					
Piquiri river	0.38	0.38	1.00				
Iguatemi river	0.62	0.65	0.46	1.00			
Streams	0.42	0.40	0.36	0.36	1.00		
Lakes	0.61	0.67	0.33	0.56	0.47	1.00	
Channels	0.72	0.68	0.37	0.59	0.46	0.77	1.00
Ephemeral lagoons	0.47	0.45	0.31	0.38	0.34	0.50	0.48

Source: Agostinho et al. (1997).

degrees, annual variation in the hydrological regime must produce different responses in the species assemblages of aquatic organisms, affecting the relative proportions of species and consequently diversity (Agostinho et al. 1997).

In the high Paraná floodplain, pronounced floods occurred during the last two periods of field study (1992-93, 1993-94). In contrast, the period 1986-87 had virtually no flood, and the total discharge was only 45% of that recorded in 1987-88 (Thomaz 1991). The differences in diversity and evenness (Table 4) among study periods may be explained by this difference in flood intensity. To some degree, the low water level of the first two periods appears to have been caused by control of the Paraná River discharge by the dams located upstream from the basin (Agostinho et al. 1997).

Abundance

During 1986-88 and 1992-94, experimental fishing was carried out monthly in the high Paraná River floodplain using stationary nets of various mesh sizes (3 to 16 cm between alternate knots). Results expressed as individuals or biomass (kilograms per 1,000 m^2 of net during a 24 hour period) reveals that the average catch per unit effort varied from 208 to 687 individuals, and from 40.9 to 76.2 kg for the different habitats (Table 6).

Table 6. Annual mean values for catch per unit effort ($CPUE_N$ = number of individuals per 1000 m^2 net/24 h; $CPUE_B$ = kg per 1000 m^2/24 h) in different environments of the Paraná River floodplain.

Locality	Lagoons		Channels		Rivers		All	
Period	$CPUE_N$	$CPUE_B$	$CPUE_N$	$CPUE_B$	$CPUE_N$	$CPUE_B$	$CPUE_N$	$CPUE_B$
1986-87	525	61.3	413	43.5	208	52.1	416	53.2
1987-88	452	40.9	442	46.9	305	59.4	421	46.4
1992-93	526	47.5	691	63.3	407	67.8	494	60.8
1993-94	685	76.2	687	70.6	341	62.6	514	68.4

Source: Agostinho et al. (1997).

Fish were considerably more abundant in the lagoons than in the other habitats, especially the lotic ones, during low-water years (1986-87). During the high (1992-93) or moderate flooding years (1987-88; 1993-94), catch per unit effort, in numbers as well as biomass, increased in rivers and channels. The values (Table 6) were lower and less variable than in the Amazon basin (21.6 to 119.3 kg; Ferreira 1984, Ferreira et al. 1988) and higher than in other parts of the basin with more regulated hydrology (12.0 to 22.0 kg in Segredo reservoir- Bini et al. 1997; 28.7 to 58.5 in Itaipu reservoir- Agostinho et al. 1994), as was expected (Lowe-McConnell 1975, Welcomme 1979, Agostinho and Zalewski 1996).

The facts, that the number of specimens caught per unit effort was much higher in the lagoons than in the river channels, and that the difference in biomass between these environments did not show the same level of contrast, show clearly that the individuals in the main channel of the basin are larger than those in lakes. Floodplain waterbodies usually support a rich fauna of small fishes, with short life cycles and high reproductive effort (r-strategists or opportunists, *sensu* Winemiller 1989, 1992). These fish share the environment with juveniles of large species that find favorable conditions for feeding and shelter from predators (Bonetto et al. 1969, Lowe-McConnell 1987, Goulding et al. 1988, Agostinho and Zalewski 1996). Gomes and Agostinho (1997) found that recruitment success of *Prochilodus scrota* (= *lineatus*) in this region was related to the occurrence of floods during summer and autumn, indicating that the flooding pattern is important to the availability of food and refuges, and hence, growth and survival of the young of this species.

Life History Strategies and the Flood Pulse

Reproduction Dynamics

In the high Paraná River floodplain, like in other tropical floodplains, the flood regime is the primary factor influencing fish populations and communities. The synchrony between the hydrological cycle and biological events like gonad maturation, migration, spawning and larval development, growth and feeding corroborate this importance (Agostinho et al. 1993, Agostinho et al. 1995, Vazzoler 1996, Gomes and Agostinho 1997). The relationship between the time, duration, and intensity of the floods and recruitment success (Gomes and Agostinho 1997) provides additional evidence. However, information on Paraná River fishes, accumulated during the last decade, demonstrates distinct ecological responses to the annual pattern of flooding (Agostinho et al., in press).

On the basis of previous reviews (Miyamoto 1990, Vazzoler 1996, Agostinho et al. 1995, Vazzoler et al. 1997), the main reproductive strategies exhibited by fishes of the high Paraná River can be classified into five groups (Table 7):

(i) *Species with external fertilization, long distance migration, and no parental care*: In general, this group includes large fishes (maximum standard length >40 cm) with seasonal and total spawning, small eggs, and high fecundity (periodic strategy, Suzuki 1992). This group constitutes about 19% of the regional species richness and 21% of the total catch numerically (Table 7). Three of these fishes (*Prochilodus lineatus, Rhaphiodon vulpinus, Leporinus obtusidens*) are among the most abundant. These fishes show a pattern of seasonal occurrence of adults in floodplain habitats. Some of these species (e.g., *Brycon, Salminus*) reproduce in the upper reaches of major tributaries, whereas others (e.g., *Pseudoplatystoma, Pterodoras*) spawn in rivers along the margins of the floodplain, and all of them use the floodplain as nursery habitat (Agostinho et al. 1993). Migratory fishes depend on large stretches of free-flowing river and are the most affected by the series of impoundments constructed on the high Paraná River.

(ii) *Species with external fertilization, short distance migration, and no parental care*: This group of fishes contains species with high fecundity and restricted spawning periods. In general they are intermediate-sized fishes (maximum standard length 20-40 cm), and spawning may be total or partial depending on the species. About 14% of the total floodplain species from experimental gillnet samples belong to this group, which also represents 13% of the total regional catch. Four species of this group are among the most abundant. The migration distance is usually shorter than 100 km, and the spawning may occur in smaller tributaries than those used by group i. This characteristic permits these species to maintain populations within reservoirs located in upper stretches of the basin.

(iii) *Species with external fertilization, no migration, and with parental care*: This group contains the equilibrium strategists (Winemiller 1992) characterized by well-developed parental care, large eggs, and low fecundity. This group is the most important in terms of species number and abundance in catches (34% and 42%, respectively). This group includes mostly small and intermediate-sized species with partial spawning over a period lasting several months. In general, spawning by members of this group is less dependent on the hydrological regime. Five of the most abundant species of the floodplain belong to this group. Males of *Loricariichthys platymetopon* transport their eggs and larvae on the ventral surface of the head and chest. *Hoplias malabaricus* and two *Serrasalmus* species guard the eggs and larvae. *Hoplosternum littorale* constructs a floating nest which it guards against potential egg and larval predators.

(iv) *Species with external fertilization, no migration, and no parental care*: In general, these are small species, with small egg diameter, partial spawning, and long reproductive periods (opportunistic and periodic strategies *sensu* Winemiller 1992). Twenty-seven percent of the total number of species and 18% of the total floodplain catch belong to this group. Species of this group are seasonally abundant in temporary lagoons (e.g., *Aphyocharax, Bryconamericus, Cheirodon, Moenkhausia, Roeboides*). Some of these species are successful colonisers of the reservoirs of the high Paraná basin (e.g., *Astyanax, Moenkhausia, Steindachnerina*) (Agostinho et al., 1999).

(v) *Species with internal fertilization, no migration, and no parental care*: In general these species have sexual dimorphism associated with mating behavior. Only 7% of the regional species belong to this group, and it comprised 5.5% of the total catch by number of individuals. Two auchenipterid catfishes (*Auchenipterus nuchalis, Parauchenipterus galeatus*) are among the 20 principal species of the floodplain, and they dispersed upstream from the middle Paraná river after Itaipu impoundment. However, this strategy was successful in Itaipu reservoir, where three of the six species in this group were among the most important during the first years after the dam had been closed.

Table 7. Reproductive strategies of fishes captured in experimental gillnets in the high Paraná River floodplain. Strategies in parentheses follow the scheme of Winemiller (1992).

Reproductive Strategies	**Species Number**	**Abundance (%)**
External fertilization, non-migratory, with parental care (equilibrium)	29	41.73
Internal fertilization, non-migratory, no parental care (periodic)	6	5.54
External fertilization, non-migratory, no parental care (equilibrium and opportunistic)	23	18.34
External fertilization, short distance migrants, no parental care (periodic)	12	13.42
External fertilization, long distance migrants, and no parental care (periodic)	16	20.98

In summary, there is a prevalence of fishes with a reproductive period ranging from November to February, with some that spawn from September until April (Agostinho et al. 1995). Relatively few species reproduce from May to September. It is important to emphasize that the reproductive period for most fishes coincides with increasing water level, lengthening photoperiod and increasing temperature in such a way that puts larvae in favorable habitats with high availability of food and cover during flooding. Gomes and Agostinho (1997) found that the timing and duration of the annual flood were more correlated with the recruitment of *Prochilodus lineatus* than the flood amplitude. Reproduction by species that have parental care can be favored during drier years, although Agostinho et al. (in press a) showed that, even among these species, the absence of flooding is adverse due to increased predation.

Trophic Dynamics

Although some tropical fishes specialize on certain types of food resources, most show great plasticity in their diets (Lowe-McConnell 1987). In tropical floodplains, the food spectrum as well as the feeding rhythm of fish are influenced by the hydrological fluctuations. Welcomme (1979) reported that the diet of fishes in such regions is highly seasonal in response to the flood regime. Junk (1980) added that changes in hydrological conditions in floodplain environments affect not only the quantity but also the quality of food available to fish. These environmental fluctuations broaden trophic niches, making food webs very complex (Winemiller 1990). Araujo Lima et al. (1995) reported that trophic specialization is probably not adaptive in communities exploiting ephemeral habitats, such as river floodplains. Most fishes of the high Paraná floodplain show considerable diet plasticity. Yet, there are species that show morphological and behavioral traits associated with feeding specialization, for example the iliophages (mud eaters) (*sensu* Fugi et al. 1996), filter-feeding planktivores, and fin nipping piranhas (Agostinho et al. 1995).

Piscivorous and iliophagous fishes predominate in the region, although the proportions of these and other categories vary according to the type of environment and year considered. The abundance of piscivorous fishes in and around the floodplain is logical in view of the fact that the area is an important nursery for many species.

Moreover, the floodplains provide abundant food resources for small forage fishes of other trophic groups, especially detritivores (*sensu* Fugi et al. 1996) and benthophages (Agostinho et al. 1997).

The great abundance of iliophages stems from the fact that the region is subject to seasonal oscillations in the water level. Seasonal inundation of terrestrial vegetation provides substrate for development of periphyton, increases the organic content of the bottom sediments, and favors development of the microflora through liberation of nutrients. Bowen (1983) likewise reported a high biomass of iliophages, mainly prochilodontids and curimatids, in the largest river systems in South America, and attributed this pattern to the great abundance and high quality of detritus. Studying fish communities of the lower Rio Negro, Goulding et al. (1988) reported a high proportion of iliophages, mainly two species of the family Prochilodontidae. The great abundance of iliophagous and piscivorous fishes is a general characteristic of fish communities in tropical and temperate waters. Welcomme (1979) and Lowe-McConnell (1987) reported that piscivores in tropical waters also show high species diversity.

In the high Paraná floodplain, piscivore biomass tended to increase during years without flooding (1986-87), especially in the lagoons. The proportion of piscivores within the total biomass caught in lagoons exceeded their proportions in the other habitats only during these drought years. However, during the following year, the proportion of piscivores fell sharply (38.0-12.3 kg per 1000 m^2 of net/24 hour) (Agostinho et al. 1997). Agostinho and Zalewski (1995) attributed that decline to higher fishing efficiency by large predators near the confluences of the lagoons and channels in drought years. Welcomme (1979) commented that the relative abundance of piscivorous predators tends to increase during the dry season, because of the wide availability of forage. Lowe-McConnell (1964) and Bonetto et al. (1969) also noted the abundance of piscivores and the absence of small fishes in floodplains of the Rupununi River in British Guiana, and in the Paraná, respectively. On the other hand, Kushlan (1976) reported that prolonged stable floods in the Everglades produced an increase in piscivorous species, mostly because of migration of large predators that do not tolerate extreme flooding conditions. The greater proportional biomass of predators in lagoons during the years without flooding was largely due to dominance of piranhas *Serrasalmus* species.

Iliophagous fishes reached higher biomass during years of intense flooding (rivers) or very intense flooding (all environments). During floods, the previously mentioned enrichment of the bottom deposits and the greater total surface area for periphyton production must favor these fishes. The curimba, *Prochilodus lineatus*, and three species of curimatids were the dominant iliophages. Without floods, the catches of juvenile *Prochilodus lineatus* decline markedly, and recruitment essentially fails (Gomes and Agostinho 1997). This decline is, however, largely compensated by increases of the curimatids *Steindachnerina insculpta* and *Cyphocharax nagelli* in the lagoons, and *Steindachnerina insculpta* in the rivers (Agostinho et al. 1997).

In contrast to the detritivores, benthivorous and omnivorous fishes showed an increase in biomass during years with larger floods. For benthophages this tendency was more accentuated within lentic habitats (lagoons), and for omnivores in lotic habitats (Agostinho et al. 1997). The increases recorded for the benthivorous caboja (*Hoplosternum littorale*), mandi (*I. labrosus*), piaus (*Leporinus friderici,* *Leporinus obtusidens*), and the omnivorous cangati (*Parauchenipterus galeatus*) follow this pattern. Increases in biomass also were reported for herbivores in both lentic and lotic habitats (e.g., the piava, *S. borelli*). This species appeared to compensate for a reduction in catches of the corró (*Leporinus lacustris*), which was reduced in biomass during years of intense floods. Although the total biomass of insectivores fluctuated only slightly, there were large variations within the group. Species that feed primarily on chironomids and terrestrial insects increased in biomass during flood years, while species with diets composed of nymphs of ephemeropterans decreased.

Agostinho et al. (1997) used a bifactorial multivariate analysis of variance (MANOVA) to examine the influence of the hydrological regime (absence, moderate, intense, and very intense floods) and of the type of habitat (lagoons, secondary channels, rivers) on biomass values of different trophic categories. According to their analysis, the hydrological regime exercises a strong influence on the temporal variability of the biomass of the different trophic categories. The trophic categories that contributed most to the differentiation of the flood regime centroids were the omnivores and the herbivores. In general, both categories showed higher biomass values during years of extraordinary floods. These results corroborate Goulding's (1980) contention that the Amazonian fishes most influenced by the drought and flooding regime are the herbivores and omnivores. The results of the MANOVA also provided evidence of the influence of habitat type on the trophic structure of the ichthyofauna. The main categories differentiating the habitat centroids were the benthophages and detritivores. The lagoons and channels showed higher biomass values for these trophic categories independently of the flood regime considered.

Given of the high degree of trophic adaptability shown by most fishes, species assignments in these trophic categories may change in the response to changing environmental conditions and ontogeny. Considering that a specialist may become a generalist if a specific food source declines, fish feeding behavior should be examined under varying conditions of food supply (Gerking 1994). Yet, in some cases, morphological/ physiological specializations may limit dietary shifts (e.g., iliophages).

Introduced Species

More then 20 fish species have been introduced into the Brazilian section of the Paraná River basin, usually with the purpose of improving the fisheries yield. In addition, an unknown number of species escaped from fish culture tanks. Orsi and Agostinho (1999) report the entrance of more than 1.2 million adult fishes (11 exotic species) during the catastrophic flooding (January 1997) in the Tibagi, a medium-sized river in the basin. They attributed this accidental introduction to the illegal occupation of the riparian zone by the aquaculture facility, and its failure to observe accepted measures designed to avoid escape.

Despite the existence of several programs for exotic fish stocking and frequent escapement, the representation of exotic species in the fish fauna of the Paraná River floodplain is estimated to be less then 2% of the total catch, with *Plagioscion squamosissimus* as the principal contributor (1.5%). This species has successfully colonized virtually all habitats of the basin, especially reservoirs. Other species captured during experimental fishing were *Cichla monoculus, Astronotus ocellatus, Colossoma macropomum* and *Clarias gariepinus*. Except for *Clarias*, these species are native to the Amazon basin.

Excluding the exotics already mentioned, at least 13 species dispersed upstream from the middle stretch of the Paraná River and reached the floodplain when Itaipu reservoir submerged the Sete Quedas waterfalls, which, according to Bonetto (1986), divided two ichthyofaunal provinces. Four of these species – a serrasalmid (*Serrasalmus marginatus*), a doradid (*Trachydoras paraguayensis*), and two auchenipterids (*Parauchenipterus galeatus* and *Auchenipterus nuchalis*) – rank among the 20 most abundant. The others include three species of stingrays (*Potamotrygon* species) and the filter-feeding zooplanktivore *Hypophthalmus edentatus* (Júlio Jr and Dei Tós 1995). The great reduction of *Serrasalmus spilopleura* concomitant with the explosion of *Serrasalmus marginatus* in the floodplain over the last 15 years suggests competition between these congeners.

Impacts and conservation status

The remaining stretch of the Paraná River floodplain is the last unimpounded section of this river within Brazilian territory. In spite of the state of degradation in the upper parts of the basin, plus regulation of the river discharge in this wild stretch by the reservoirs upstream, this area contains a good representation of the original fauna and continues to play a critical role in maintaining regional biological diversity. This conclusion is supported by the region's high species richness of aquatic and terrestrial organisms, which includes species threatened with extinction.

The entry of water from several unregulated tributary rivers, such as the Ivinheima, Ivaí, Amambaí and Piquiri, minimizes the effects of the discharge control imposed by the upstream impoundments. In addition, the vegetation has a great capacity for regeneration, neutralizing the most obvious effects of burns within a few months.

Using the criteria employed by Welcomme (1979) to determine the stages of human modification of floodplain rivers, we can classify the High Paraná River floodplain as "slightly modified", with more limited areas that are "unmodified". However, the conservation status of the region is spatially uneven. The areas of the plain near the cities are considerably changed, whereas the more distant areas retain environmental conditions close to their natural state.

The arboreal vegetation, naturally confined to the higher parts of the islands, the natural levees of secondary channels, and the left bank of the Paraná, which is higher than the right, has undergone intensive deforestation. These areas are now used for cattle ranching or subsistence farming (corn, beans, rice), and a few families or nomadic fishermen are established there.

The area near the mouth of the Ivinheima River remains closest to the original conditions. Inventories of eggs and larvae of fishes in the five main rivers of the wild stretch of the Paraná show their highest densities in the Ivinheima, which indicates the major importance of the upper reaches of this sub-basin river as a spawning ground of important species such as *Salminus maxillosus, Pseudoplatystoma corruscans, Brycon orbignyanus* and *Piaractus mesopotamicus*.

In view of the fact that most human activities in the area are in conflict with current environmental legislation, many local environmental activists are putting pressure on ranchers to remove their cattle from the várzeas (flood-prone riparian zones) and islands, and seeking prohibition of the removal of *Pfaffia*, a root used in the cosmetic industry. Likewise, government resource agencies of the affected states have consulted with government and private research agencies in search of solutions that will promote sustainable regional development.

An important step for the conservation of the high Paraná River floodplain was the creation of three conservation units:

(i) The Area of Environmental Protection (APA) of the Islands and Várzeas of the Paraná River (10,031 km^2) extends from the mouth of Paranapanema River to Itaipu reservoir;

(ii) The Ilha Grande National Park (788 km^2), including the lower stretch of the former Area of Environmental Protection; and

(iii) The State Park of Ivinheima River (700 km^2), which includes the floodplain of the lower stretch of the Ivinheima River.

Nevertheless, the effective conservation of the high Paraná River floodplain and its biological diversity will depend on the prompt and effective management of these conservation areas, and maintenance of the hydrological regime of the Paraná River (now affected by the operation of upstream reservoirs) as close as possible to its natural state.

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