Fish diversity and ecology, habitats and fisheries for the un-dammed riverine axis Paraguay-Parana-Rio de la Plata (Southern South America)

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The riverine complex Paraguay-middle Parana-Rio de la Plata extends more than 3700 km southwards from its sources in the western hills of the Brazilian Shield to its discharge into the Rio de la Plata River. The high variety of habitats is reflected in the large diversity of its fish communities, which are dominated by characiform and siluriform fish species. The potamic axis is evolutionarily and ecologically open to fish movements and there are more than 400 fish species listed for the whole system, but only 100 species are common to both upper and lower basins. However, data limitations in some portions of the system need to be addressed before creation of an ichthyogeographic classification. The river basins that make up the potamic axis are low to medium developed and environmental pressures are unevenly distributed. Chemical pollution is a concern throughout. In the Pantanal, small hydro-projects and sedimentation from agricultural activities have had adverse effects on fish habitat inducing a loss of fish diversity. Un-dammed but more regulated and developed lowland rivers, may be impacted by upstream dams that may create unsuitable habitats for fish adapted to normal main channel conditions because they increase river flows during periods that were formerly low waters or change flows at random. The fisheries are lightly to moderately exploited compared to other subtropical and tropical riverine fisheries, and retain several of their original characteristics in less developed river reaches, although changes are evident. Large potamodromous fish are usually present in the catch, but the abundance of large piscivores is lower and fish size at catch is smaller. The development of the riverine system is expected to continue throughout the basin. If it is implemented as it was executed in the past, a continual loss of fish habitats and a general decrease in ecosystem health can be predicted.

Keywords: large rivers, development effects, fish communities, habitat loss

Introduction

For large river-floodplain systems, fish biodiversity conservation and sustainable fisheries exploitation are issues of great concern at the present. However, large scale, long-term environmental changes in large river basins are subject to forces that are external to the river water and to biological issues. The main purpose of this paper is to overview some fish biodiversity and ecology characteristics for the riverine axis Paraguay-middle Parana-Rio de la Plata (PPLP) and to relate these subjects to its current

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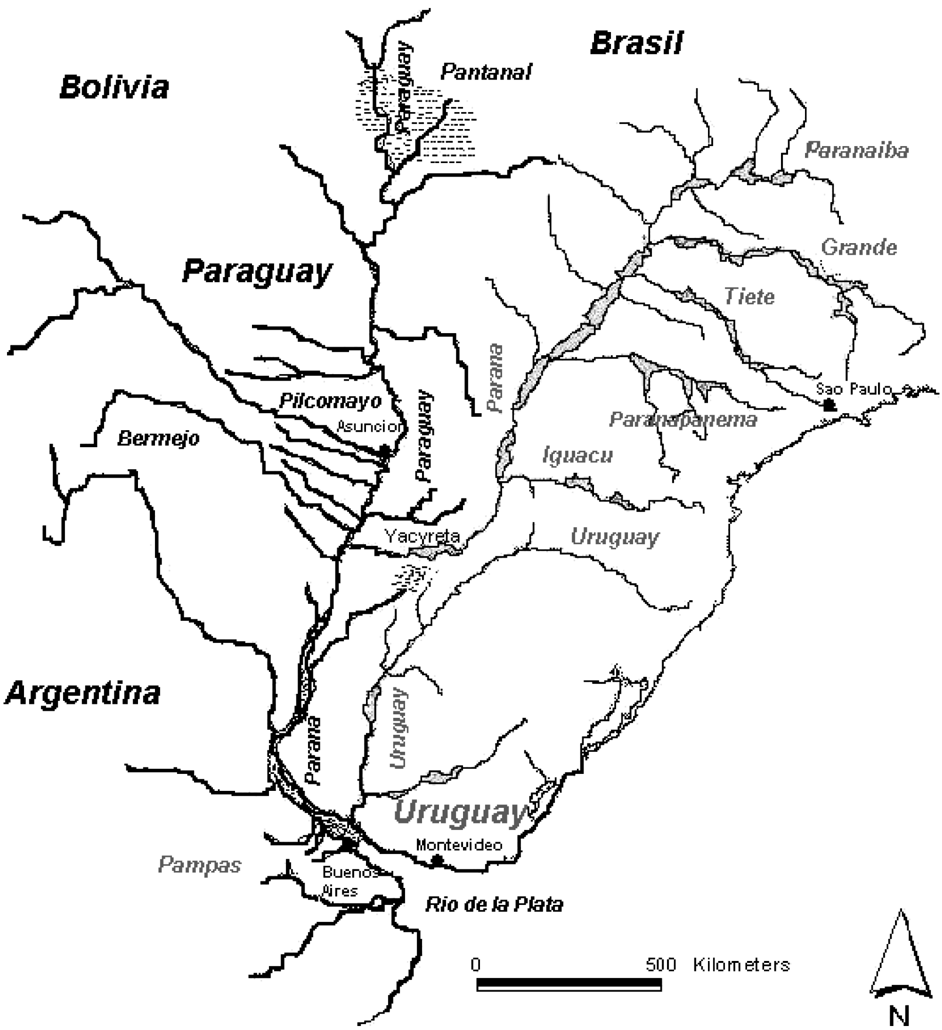

Figure 1. The Paraguay-Parana-Rio de la Plata riverine axis situated in the context of the La Plata river basin.

environmental and fisheries state. The riverine axis (complex regional channel system) is just part of the La Plata river basin (3.2×10^6 km^{-2}) (Figure 1). It drains, from north to south, large parts of Brazil, Bolivia, Paraguay, and Argentina. The Paraguay River extends 2,670 km southwards from its sources in the western hills of the Brazilian Shield at 300 m of altitude to its confluence with the Parana River. The "Pantanal" depression, situated 270 km south from the Paraguay sources, receives water from the Paraguay River itself and from many other tributaries. The Pantanal has a natural regulatory effect on the middle and lower Paraguay River discharge. After the confluence with the Paraguay, the Parana River changes its physiographic characteristics to develop a massive floodplain and flows one thousand kilometers southwards up to its discharge (20,000 m^3 s^{-1}) into the Rio de la Plata.

Geomorphology determinates that the PPLP potamic axis is evolutionarily and ecologically open to fish movements. Moreover, its relatively low slope explains why the axis is presently mostly unregulated and thereby conserving most fundamental habitats and microhabitats for fish conservation. A striking characteristic of the system is that two large depositional sites are situated at both the headwaters (the Pantanal) and the discharge of the system (the lower middle Parana floodplain, the Parana delta, and the Rio de la Plata). The Paraguay basin is still functioning according to the main riverine forcing function, the flood pulse (Junk et al., 1989), but the river-floodplain system below the Paraguay-Parana confluence (middle-lower Parana and Rio de la Plata) is influenced by dam regulation of the upper Parana basin (Quirós, 1990, 2004). As for other large river systems, depositional zones are sites of higher fish food and fish productivity (Quirós and Baigún, 1985). However, for those kinds of sites the biota is usually most impacted by organic toxics and heavy metals pollution (Alho and Vieira, 1997; Colombo et al., 2000) products of development activities. When compared with other subtropical and tropical floodplain fisheries, the riverine axis is lightly to moderately exploited for fisheries in the upper and lower basins, respectively (Quiros, 2004). The Pantanal wetlands and the Parana-Paraguay confluence area are both bountiful recreational fishing resources. For the Parana-Paraguay confluence area, fishing effort has remained steady or trended lightly upward over the past 40 or more years. However, catch rate, harvest rate, and mean size of fish caught have been reported by sport anglers and commercial fishers as decreasing continuously during the last 20–30 years. Prevalent recreational species include fish of the genera *Piaractus*, *Salminus*, *Brycon*, *Paulicea*, *Pinirampus*, and two *Pseudoplatystoma* and several *Leporinus* species. In the lower basin, the large detritivorous fish *Prochilodus lineatus* is the prevailing fish species for commercial fisheries (Bonetto, 1986; Quiros and Cuch, 1989).

The PPLP riverine axis environment

Annual mean rainfall in the Plata Basin tends to decrease both from north to south and from east to west (Figure 1). The northern part of the basin has a well-defined annual cycle with maximum precipitation during summer (December–February). The central region (northeast Argentina/southern Brazil) has a more uniform seasonal distribution, with maxima during spring and autumn. Since the major rivers in the basin generally run from north to south, this rainfall regime contributes to the attenuation of the seasonal cycle downstream (Berbery and Mechoso, 2001). However, the Pantanal's slope is 0.25 m km^{-1} in the east-west direction but only 0.01 m km^{-1} in the north-south direction. This shallow slope produces a time lag of about five months in the flood peak for the Paraguay River at its confluence with the upper Parana (Figure 2). The mean annual temperature in the basin ranges from around 15°C in the south to more than 25°C in the northwest (Figure 1). In winter, monthly-mean temperatures have a clear north-south gradient. In July, for example, the mean temperature over the northwest part of the basin is more than 20°C, while that in the southern Pampa grasslands is around 10°C cooler. In summer the gradient is more zonal; the maximum mean temperatures are over 27.5°C in the western of Argentina in January, while they are less than 22.5°C in the coastal areas of southern Brazil, Uruguay and the Pampas (Berbery and Mechoso, 2001).

The middle Parana is formed by the confluence of two very different rivers, the upper Paraná which has a low conductivity (40–50 μS cm^{-1}), total suspended solids (40–180 mg l^{-1}) and pH (7.0–7.2), and the lower Paraguay which has higher conductivity (150–300 μS cm^{-1}), total suspended solids (600–800 mg l^{-1}) and pH (7.2–8.2) (Depetris,

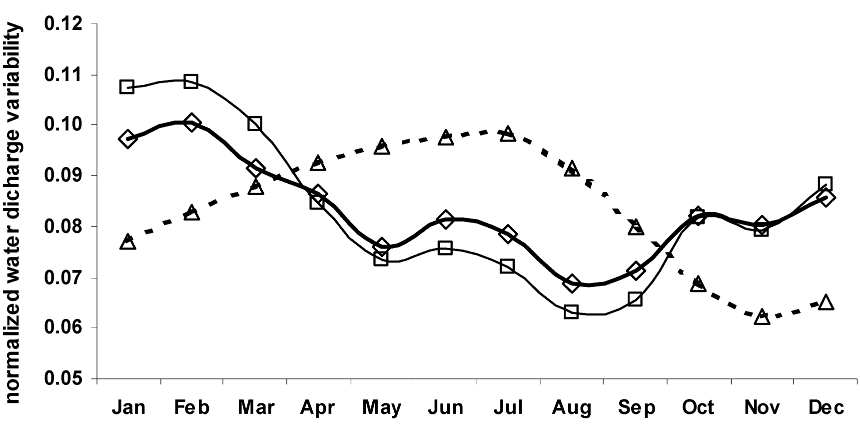

Figure 2. Round year normalized river discharges for the middle Paraguay River (Fecho dos Morros, 1966–1978), upper Parana River (Posadas, 1965–1979), and middle Parana River (Corrientes, 1969–1979).

1996). An Andean tributary to the Paraguay, the Bermejo, has an average concentration of suspended solids of 4500 mg l^{-1} and is the main source of sediment to the middle Parana River (Drago and Amsler, 1988). On the other hand, the geochemical characteristics of the upper and middle Paraguay River are more similar to those of the upper Parana (Figure 1).

Riverine fish communities are naturally regulated by a continuum of abiotic-biotic factors, which change in pressure along the river continuum, whereas environmental pressures from development activities are usually unevenly distributed. Before most of the upper Parana reservoirs were formed, the middle Parana River showed a regular annual cycle, usually reaching its peak in early autumn and its minimum flow in late winter (Figure 2). However, the natural hydrological regime of the middle and lower Parana reaches has been lightly altered by the operation of upper basin dams (Quiros, 1990). These dams have resulted in an increase in minimum water levels in the middle reaches of the Parana and an extended period of floods. Although run-of-the-river dams do not have the possibility to control river flow at high waters, downstream control effects are important at low water states (Figure 3). The Paraguay river basin may be considered to be mostly unregulated. Sediment sources of Andean origin are still available for essential nutrient loading to the lower Paraguay and the middle Parana River.

The level of development among the countries of the La Plata Basin is not even. The Paraguay river basin is mainly agricultural, with mining being

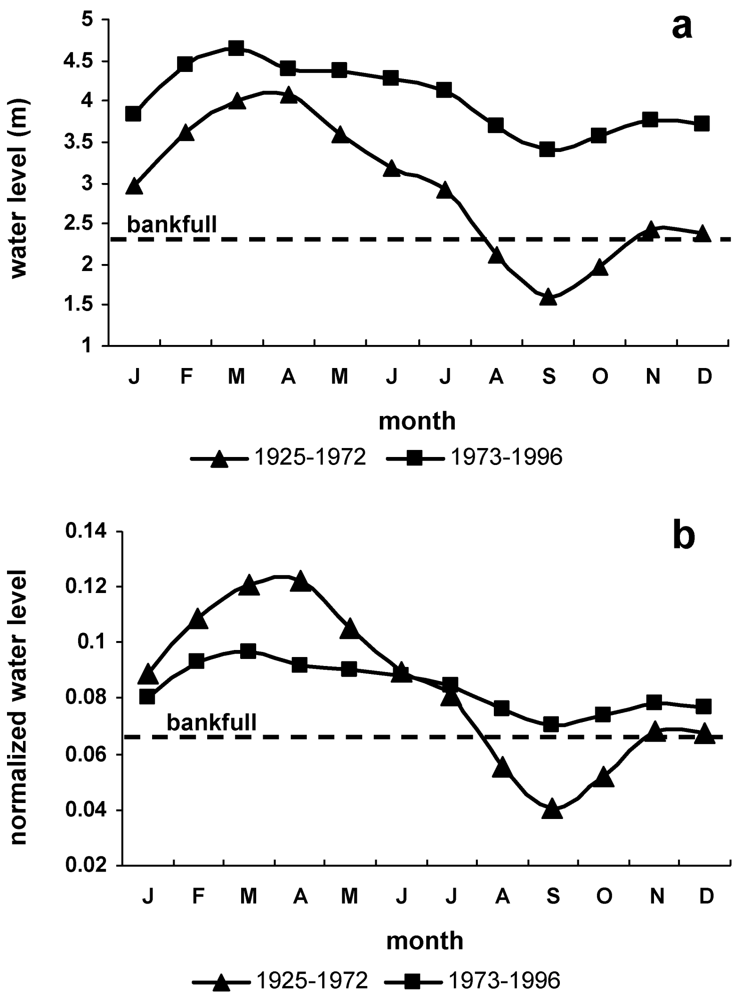

Figure 3. Water level variation in the middle Parana River (Santa Fe City) for the undeveloped and developed periods. a) actual data; b) round year normalized data (modified from Quiros, 2004).

relatively important there, as well as in the tributaries that drain the Andean ranges (Quiros, 1990). While human inhabitation and population density has always been low to moderate in the riverine axis, economic activities including cattle ranching, crop farming, logging, agri-industry, mining, fishing, and tourism are common. Industry and urban settlements are however important for both the upper and the lower Parana basin (Figure 1). Urban and industrial wastes are poorly to un-treated for most of the riverine axis. It is difficult to assess the water quality state for the riverine axis as a whole because water quality data, as well as water quality reports, are scarce, scattered and often contradictory. However, from the headwaters of the Paraguay river basin situated at the Planalto to the riverine axis discharge at the Rio de la Plata, passing by the Pantanal, the lower Paraguay, the middle Parana, and their main tributaries, water and fish pollution by persistent organic contaminants and heavy metals has been widely reported. As expected, in the upper basin, heavy metal levels were usually higher for top predators. Heavy metals are the main source of pollution for water, sediments and fish in rivers that drain the Andean ranges. *Prochilodus lineatus* is the species where higher metal concentrations were detected (Colombo et al., 2000).

Fish fauna and biodiversity at basin and floodplain-river reach levels

As with large river-floodplain systems, the PPLP potamic axis has a high variety of fish habitats, which is reflected in the large diversity of its fish communities. As with others large river basins in South America, the fish fauna of the riverine PPLP axis is dominated by characiform and siluriform fish species. Most species belong to the orders Characiforms (36–46%) and Siluriforms (37–43%), with some components of the orders Perciforms, Gymnotiforms, Myliobatiforms, Clupeiforms, Atheriniforms, Beloniforms, Synbranchiforms, Pleuronectiforms, Cyprinodontiforms and Lepidosireniforms. The number of identified fish species throughout the entire riverine axis is high, ranging from more than 260 in the Pantanal to almost 160 species at the riverine axis mouth at the Rio de la Plata. As expected, described endemic fish species are relatively few and usually inhabit lower order tributaries or small relatively isolated headwater basins (López et al., 2002).

For the La Plata basin as a whole, there is no clear tendency for the number of fish species to increase from South to North among its larger component basins (Table 1), but with a decrease perhaps for the Rio de la Plata (López et al., 2002). In our analyses we have considered the fish species listed in published taxonomic lists and taxonomic fish name synonymies were checked using FishBase (2004) for all the fish lists used. For the middle Parana, Drago et al. (2003) listed 212 fish species whereas Britski et al. (1999) cited 250 species for the Pantanal and FishBase lists 150 species for the Paraguay River. The latter results restrict to 306 common fish species for the Paraguay basin. For the Parana River basin there were 201 species listed in FishBase (2004) while Agostinho et al. (1995, 1997) reported 203 species for the upper Parana basin. The total number of fish species included in our data base for the La Plata basin is 591. The number of fish species cited for the three large river basins is 47 whereas 380 species were cited just for only one of the compounding basins. However, the data should be interpreted with caution since new species are continually found and because fish taxonomy is constantly under revision; 64 fish species listed in FishBase (2004) for the Parana River are not cited in the other taxonomic lists used here. As expected for a large river basin,

Table 1. Fish species richness (N) of components of the PPLP riverine axis and a matrix of Jaccard similarity indices among them.

River	Source	N	2	3	4
1. Parana River	FishBase, 2004	201	20	22	27
2. Upper Parana basin	Agostinho et al., 1995, 1997	203		**18**	**17**
3. Middle Parana	Drago et al., 2003	212			**25**
4. Pantanal and Paraguay rivers	Britski et al., 1999 Fish Base, 2004	306			100

fish similarity for the La Plata basin is relatively low when main compounding basins are compared for common fish species richness (Table 1). Moreover, the similarity was lightly higher when connected basins in the Paraguay-Parana axis were compared (Table 1).

Fish community similarity among more connected large river reaches is, as expected, higher. For example, fish diversity in the high Paraná River from Yacyreta dam (Figure 1) has been described in COMIP (1994), Roa and Permingeat (1999) and Bechara et al. (J. Bechara, Universidad Nacional del Nordeste, 3400 Corrientes, Argentina, pers. comm.). For the lower Paraguay River, data from Ringuelet (1975) and Pignalberi de Hassan and Cordiviola de Yuan (1988) were employed in fish diversity comparisons. According to those authors, the number of species inhabiting both reaches would be of about 230, including those inhabiting permanent river channels and floodplain waterbodies. The number of species listed for the lower Paraguay River is 214; meanwhile 215 species are registered for the high Parana River below Yacyretá Dam. The Jaccard similitarity index for the Paraguay-Parana confluence is 63%.

Fish community similarity for nearby floodplain waterbodies and highly connected main channel sites is also high but, as expected, fish diversity is substantially lower than for the corresponding river basins (see above). For low water fish sampling in the Paraguay river system, Chernoff et al. (2004) reported a high fish similarity (Simpson's coefficient) between the coastal zone of the main river ("beaches") and diverse plain macrohabitats like backwaters (97%), floating vegetation (92%), flooded forests (88%), and lagoons (87%). Fish similarity was lower when river beaches were compared with clear backwaters (70%) and main channel (40%) macrohabitats. For the Miranda River (southern Pantanal), four near floodplain sites were compared for fish diversity using the Sorensen index (Resende, 2000; Resende and Palmeira (E.K. Resende, EMBRAPA Pantanal, Corumbá, Brasil, pers. comm.); fish similarity varied between 66 and 89% among sites during a monthly sampling for a complete hydrological year. The Shannon-Weiner weighted diversity index diminished with site depth for two permanently connected floodplain lakes. In contrast, for a synchronic floodplain lake comparison at the Negro river (southern Pantanal) floodplain just after lake isolation, the lakes that had the greatest diversity were the deepest ones and had only been isolated from the river recently (Suarez et al., 2001). For this study (# lakes = 19, # species = 51), simple matching coefficients varied between 38 and 82%, and more than 50% of sampled lakes had a fish similarity higher than 60% (Suarez et al., 2001). For the 200 km Parana reach below Yacyretá dam (Figure 1), main channel fish species similarity ranges between 60 and 64% when expressed as Jaccard index (4 sampling per year for the 1997–2003 period, # species = 115). On the other hand, when floodplain sites were compared (six sampling during two years, # species = 126) Jaccard index varied between 61 and 78% (J. Bechara, Universidad Nacional del Nordeste, 3400 Corrientes, Argentina, pers. comm.). Fish diversity in the main channel was higher for one El Niño year (1997–1998), and the lowest diversity was related to one La Niña period (2000–2001). This relationship can be explained by the increase in connectivity among different environments during high floods that allow fish dispersion, with the concomitant increase in number of species and equitability in the main channel.

Fisheries and fish harvest

For management purposes riverine fish have been classified as: a) the large and valued by humans or "whitefish" and b) the usually small and less valued or "blackfish." However, this management classification is based on ecological grounds. Most "whitefish" migrate hundreds or thousands of kilometers up and down rivers, while most "blackfish" may spend most of their lives in local waterbodies. There are 414 fish species listed for the Paraguay-Parana river axis; only 104 species are common to both river reaches. Most of the total fish species can be characterized as "blackfish." However, the most valuated by sport and recreational anglers and by both commercial and subsistence fishers (less than 15 species) are large migratory "whitefish" shared between both basins.

On the riverine PPLP axis, fisheries before extensive human development were based on large potamodromous fishes, mainly siluriforms and some characins (see Quiros, (2004) for an overview). This is still the fishery state for the Paraguay basin (Catella, 2003) (Figures 4a and 4b). There was a higher proportion of large detritivores at depositional zones and at many river headwaters during seasonal fish migrations. Upper Parana regulation and basin development have led to some striking changes in fisheries in the lower basin.

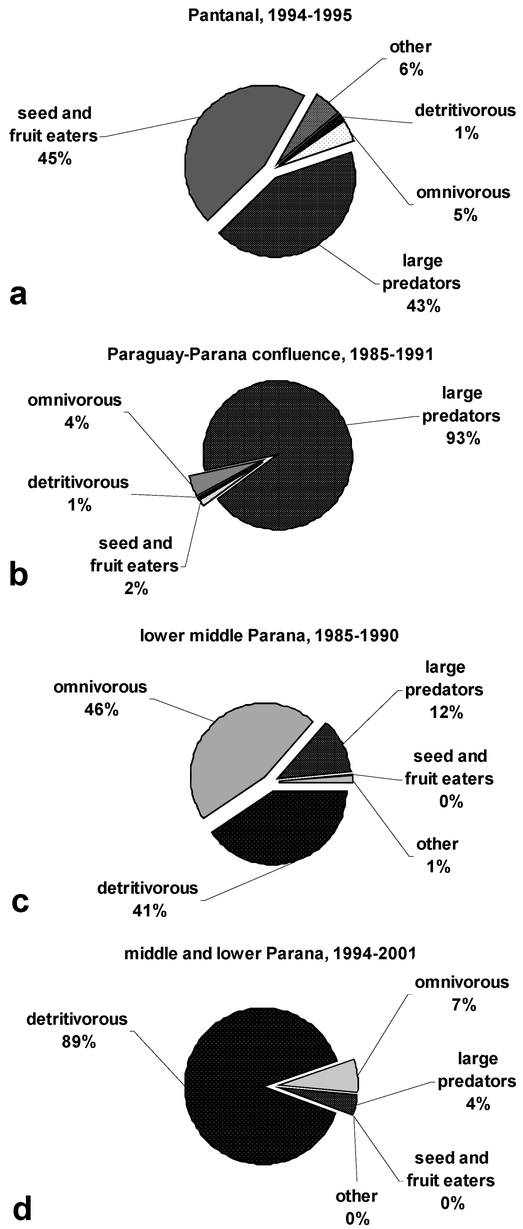

Figure 4. The community structure of fish captured from commercial and recreational fisheries on the riverine axis Paraguay-Parana. a) the Pantanal (Catella et al., 1996), b) the Paraguay-Parana confluence, c) lower middle Parana River (Rosario City), and d) fish exported from the middle and lower Parana (Quiros, 2004).

The abundance of obligatory migratory fish has decreased and the size of potamodromous fish decreased appreciably. In the middle and lower depositional reaches, the proportion of the detritivorous *Prochilodus* in fish catches gradually increased when compared with the large piscivorous fish (Figures 4c and 4d). Several fish species, mainly fruit and seedeaters, disappeared from zones where they were abundant during the predevelopment period. The exotic common carp (*Cyprinus carpio*) has become abundant in the lowland depositional rivers but not in fish catches. The time-lag between the year of flooding and the time when its effects are reflected in the catch are dependent on the time taken for fish to grow to the size range captured by the fishery (Quiros, 1990; Bechara and Ruiz Díaz, 2004).

The complex interplay between geomorphology and hydrology determines many of the biological characteristics of large river-floodplain systems (Quiros and Cuch, 1989). The catch per fisher per day now ranges from 10–15 kg for upper reaches to more than 110 kg in the lower middle Parana River and more than 300 kg at the Rio de la Plata River (Quiros, 2004). However, catch rate was 121 kg per fisher per day for Pantanal fisheries before regulations for recreational fisheries (Catella, 2003). Catch rates drop to 8–10 kg of high value fish at the Parana-Paraguay confluence and for the Pantanal fishery (see below). However, the fish and the fisheries characteristics for the present developing period differ according to the intensity of development and the position of each river reach in the basin. Striking differences in the fish species structure of the catch are noticeable among river reaches (Figure 4).

Fisheries retain several of their original characteristics in less developed river reaches, although many changes are still evident. For these reaches, large potamodromous fish are usually present in the catch and are highly preferred by fishers, but the abundance of large piscivores is lower (Quiros, 1990) and fish size at catch is noticeably smaller for most river reaches (Petrere et al., 2000; Quiros and Vidal, 2000). Small numbers of relatively large piscivorous fish are still captured in river reaches where fisheries are highly regulated for recreation. At the Parana-Paraguay confluence mesh size is usually regulated. Such management measures reserve the large piscivores for sport fishers, but they usually also lead to low fish catches with a minor proportion of the smaller omnivorous and detritivorous fishes. As in the Pantanal fisheries (Petrere et al., 2002), *Prochilodus* was the predominant species in these depositional river reaches. At present, these fisheries resemble the fishery in an undeveloped river, in spite of being controlled by very restrictive fishery regulations (Catella, 2003). Still, the trophy size and large piscivores abundance have been decreasing during the last two decades at the Parana-Paraguay confluence and at the rest of the Paraguay River reaches. Migratory whitefish are still the basis for fisheries. Fishing pressure on the detritivorous *Prochilodus* has increased heavily at the lower depositional reaches during the last decade, as shown by a large increase in fish catches (from 10,000 tn y^{-1} to 60,000 tn y^{-1}) and by the composition of freshwater fish exported to Brazil and other South American and African countries (Figure 4d). This type of fishery represents a fishery state corresponding to a developed river with floodplains still present.

Concurrent development activities can also impact negatively on fish. The Pantanal fisheries management in Brazil has been directed principally to recreational and sport fisheries during the last 20–25 years (Catella, 2003). Up to 1985, when diverse fishing gears were permitted for commercial and subsistence fishers, total catch was 2800 tn y^{-1} and the detritivorous *Prochilodus* was an important component in catches. For the year 1984, recreational/sport and commercial fisheries contributed 25% and 75%, respectively, to the total catch of fish. Between 1979 and 1983, when fishers were permitted to use gillnets and cast nets, commercial fishers caught a mean of 121 kg day^{-1}. In contrast, for the period 1994–1995, recreational/sport and commercial fisheries contributed 72% and 28%, respectively, to the total catch of fish (1,450 tn y^{-1}) (Catella et al., 1996). The main species harvested were *Piaractus mesopotamicus*, *Pseudoplatystoma corruscans*, *Pseudoplatystoma fasciatum*, "*piranhas*" (*Serrasalmus* sp., *Pygocentrus nattereri*), *Leporinus* spp., *Pinirampus pinirampu*, *Luciopimelodus pati*, *Salminus brasiliensis*, *Paulicea luetkeni*, and *Prochilodus lineatus* (Figure 4a). At least 89% of the harvest is composed by potamodromous "whitefish", and commercial fishers caught a mean of 11.5 kg day^{-1}. The recreational fisheries sector at the Pantanal has suffered an economic crisis since 2000, and many commercially important fish species are underexploited (Catella, 2003).

Subsistence fishing for some areas of the Pantanal has been described by Oliveira and Nogueira (2000). In the Pantanal of Mato Grosso, this fishing activity is practiced by a considerable human contingent, mainly composed of indigenous people, riverside populations and urban inhabitants (Oliveira and Nogueira, 2000). Among them, most fish to get their daily food supply; fish is a source of protein. The main species caught by subsistence fishers are "blackfish" species (*Hoplias malabaricus*) and the "piranhas" (*Serrasalmus* spp., and *Pygocentrus nattereri*), and they are thoroughly used as food by the fishers and their families. The "piranhas" (38.5%) and Hoplias (59.4%) are captured continuously with varying frequency, depending on the season.

Fisheries management issues for the riverine axis

The fisheries of the riverine axis are based on a relatively large number of species and a wide range of fishing gears. Such multi-species, multi-gear, fisheries are not generally amenable to the more classical methods of stock evaluation. It is often not a useful approach for river fisheries (Coates et al., 2004), except possibly for those in undeveloped river reaches which concentrate on a few large species or where recreational and sport fisheries are considered valuable (e.g.: fisheries at the Pantanal and the Paraguay-Parana confluence) (Table 2). For most of middle Parana fisheries management time-series catch data were used and for some of them fishing effort data are also included, though the continuity of data is not ideal. For this river reach, the application of classical stock-assessment is highly controversial.

Fishery resources in large rivers are also affected greatly by environmental factors (both natural and human induced). Environmental degradation and habitat loss, not excessive fishing effort, is reported as the major cause of declining fisheries in most rivers under stress (Coates et al., 2004). Multi-species models (see Welcomme, 1999) predict better the behavior of multi-gear riverine fisheries under both environmental pressure and increasing fishing effort. Fishing and environmental decline modify the structure, species composition and reproduction rates of both targeted and non-targeted fish stocks. The use of multi-species models for the most impacted river reaches in the La Plata basin has been suggested (Quiros, 2004). However, riverine fisheries science is not explicit on how to separate the effects of overfishing and environmental change in complex systems where both effects are at play. A more environmentally friendly management of terrestrial ecosystems will certainly contribute to sustaining and even improving riverine ecosystems health and their fisheries. To monitor fishing pressure, total fishing effort and catches, together with time-series data for water quality, for most important landing sites are agreed to be essential information

Table 2. The range of states of the riverine axis fisheries and the potential applicability of stock assessment based management approaches (adapted from Coates et al. (2004) and Quiros (2004)).

Management objective	Relevant fish size/habits	Maximization	State of river reach	Biodiversity concerns explicit in management	Stock assessment	Basin examples
Few and valuable large species	Large/ potamodromous	Conservation (?) recreation	Undeveloped or low developed	No	Yes	Upper Paraguay and Pantanal, Paraguay-Parana confluence
Few and less valuable large species	Large and medium/ potamodromous	Economic yield	Developing	No	No?	Lower Paraguay, middle Parana
Any fish larger than minimum size for first reproduction	Medium and small/ many	Fish yield	Developing	Not prevailing	No?	Lower middle Parana
Limited management, fished-down fisheries, low value fish	Medium and small/ many	Employment	Developing developed	Not prevailing	No?	Parana delta, Río de la Plata

(Coates et al., 2004). Such data can also contribute to assessing important links between catches and hydrology. As for other large river floodplain fisheries, the riverine axis fisheries exhibit a high degree of variation both between and within years (Quiros and Cuch, 1989; Quiros and Vidal, 2000). Long time series for data are therefore highly desirable, but often lacking due to the inability to sustain monitoring programs. This is at least partly because knowledge/information systems are often external to users and stakeholders. Aquaculture of native species is not an important activity for the riverine axis. There is still abundant large fish in the wild. The culture technology to produce *Piaractus mesopotamicus* and *Pseudoplatystoma* spp. has been developed. These species have been proposed to be produced by aquaculture techniques (Catella, 2003). The culture of *Prochilodus lineatus* has been proposed at the middle Parana.

Current status of fish habitats and threatened fish

The entire riverine PPLP axis faces vast environmental threats. This region is on the verge of major developmental changes. An expanding infrastructure, growth in population, and expansion of agriculture and industry are all part of the changing reality of the river-floodplain systems and the surrounding highlands. One increasingly serious concern is water contamination, including mining byproducts, agrochemicals, sewage and garbage. Another serious challenge for the riverine axis is the evident increase in erosion and sedimentation. Human activities accelerate these natural processes. A lot of these problems are present in the watershed and naturally affect the floodplains.

Another challenge in the Pantanal region is modification of the natural hydrology through construction of local dams and dikes. In addition, there are other significant megaprojects of potential concern to the integrity of the riverine axis. Some examples are the proposed Paraguay-Parana waterway or "Hidrovia" and the damming of the middle Parana that would affect seriously the huge floodplains at the Pantanal and at the middle Parana (Figure 1), respectively.

Regional plans to identify critical areas for fish biodiversity conservation that capture representative macro and microhabitats as well as rare and endangered species, usually captured for bait and pet fish, need to be developed for practically all the riverine axis. For the Pantanal, 262 fish species have been recorded until now (Britski et al., 1999), but knowledge of their natural history, behavior and ecology is relatively limited. For the Pantanal ecosystems, relevant aspects of fish biology, ecology and production were related to river hydrology by Ferraz de Lima (1981). Nine trophic guilds have been identified for the Pantanal (Resende, 2000). There exists an initial classification for fish ecoregions in the lower parts of the riverine axis (López et al., 2002). Further biological data and inventory are necessary in order to improve the species characterization of fish ecoregions. For the middle Parana River, more than 200 fish species are classified according to the location of their habitats in the main channel and the floodplain lakes (Drago et al., 2003). Data limitations in some portions need to be addressed to create a fish zoogeographical classification for the connected basins in the riverine axis. Some authors consider the upper basin of the Paraguay river a unique fish zoogeographic unit (Olson et al., 1998; Higgins et al., 2005) but also a region poor in data that only are useful to provide a pragmatic way to account for representative freshwater biodiversity at scales appropriate to regional assessments (Higgins et al., 2005). In conclusion, extensive areas of the riverine axis fish biology and ecology are still poorly known. Macrohabitats can be used to represent the diversity of environmental settings within each watershed.

Un-dammed but more regulated and developed lowland rivers (Figure 1), may be impacted by upstream hydroelectric dams that may create unsuitable habitats for fish that are adapted to normal main channel conditions because they increase river flows during periods that were formerly low waters (Quiros, 2004) or change flows at random (Quiros and Vidal, 2000; Bechara et al., 2000; Bechara and Ruiz Díaz, 2004). In the middle and lower Parana Basin the river has lost several of its main characteristics, water cycles are less intense among and within years and water is on the floodplain most of the year (Quiros, 2004). Several signs of environmental stress on fish assemblages have been reported for the lower basin (Quiros, 1990). Changes in fish species composition in commercial landings in the lower basin have been reported (Quiros, 1990). There was also a noticeable decrease in the frequency and size of the top predators in landings from the lower middle Parana southwards to the Rio de La Plata (Quiros, 1990). Moreover, massive fish kills have been regularly reported for depositional regions on the riverine axis (Bonetto, 1986; Colombo et al., 2000; Catella, 2003) and in the high Parana River due to gas supersaturation (Bechara et al., 1996). These kills could be further exacerbated with future basin development.

Some river reaches, mainly depositional, usually have heavy metal and persistent organic toxics concentrations in water and sediments exceeding guidelines for freshwater aquatic life (Alho and Vieira, 1997). Bioaccumulated persistent organic pollutants had been detected in potamodromous "whitefish" as well as in more floodplain related "blackfish." At the Rio de la Plata, metal concentrations in sediments, suspended particulate matter and bivalves are comparable to those reported for other moderately to highly polluted world rivers. Persistent organic pollutants concentrate in river sediments and biota. They are highly concentrated in detritivorous fish such as *P. lineatus* exceeding guidelines for human consumption at certain coastal areas (Colombo et al., 2000).

Fish knowledge, legislation and policy

The fishing activity in the riverine axis exploits a fish community that is poorly known in scientific terms. Lack of fish research and fish susceptibility in the face of development activities are widespread in the lower reaches of the riverine axis. There are no reported individual fish migrations from the lower to the upper extreme of the riverine axis. Therefore, is highly probable that fish stocks for both extremes of the riverine axis are different (Catella, 2003). More research would be necessary in order to execute a responsible fisheries management for the entire international riverine axis (Catella, 2003). However, in the basin there are others species with no or very little commercial value, but that are consumed by subsistence fishermen and that provide protein for numerous poor families in the area.

For most of the PPLP riverine axis, little explicit information is available about the impact of introduced fishes on the native fauna. However, it remains important to ensure that any further moves to deliberately widen the range of the non-native species are made only after careful considerations of the likely ecological risks and the potential gains.

As well as for other environmental and natural resource themes, freshwater fisheries management is usually not recognized as an important issue, for most of the riverine axis. For the lower Paraguay basin and the middle Parana, just a few and sporadic fisheries programs directed mainly to control conflicts among river resource stakeholders were in place. Among them, many programs have failed to eliminate conflicts because of little or no funding provided to local governments, lack of adequate water and fisheries legislation, fragmented authority and responsibility, overlapping boundaries and jurisdictional disputes, inadequacy of technical expertise, poor problem solving skills, and a lack of adequate public participation in fisheries planning process. Moreover, the current approach fails to recognize the interrelated processes and important linkages in the ecological, social and economic systems of watersheds. Participatory research methods incorporating local knowledge to improve the performance of the limnological and fish research have been proposed (Calheiros et al., 2000).

The international treaty among the nations that share the PPLP axis provides for joint action of the member states, but without interfering with "those projects and enterprises that they decide to carry out in their respective territories". Moreover, it does not give attention to environmental or fisheries issues (Quiros, 2004). The water law of Brazil (1997) emphasized watershed-level management of its water resources. Priority environmental concerns are mainly due to economic activities currently being operated using unsustainable methods within a relatively weak institutional framework. In the Brazilian Pantanal, fisheries regulations and laws of fishing gradually banned the use of certain gears, and prohibited the commercialization of fish derived from subsistence fishing. However, a fraction of these catches is usually sold informally in nearby markets. At present, the only methods allowed by fisheries legislation are hook hand line and long-line, and rod fishing. For the lower basin, only isolated legislative regulations are in act in reference to fisheries management. They are difficult to apply to widely distributed fishers and fisheries. For the lower basin, fisheries management measures are highly discussed among the multiple stakeholders. Mesh size limits and closed seasons are internationally accorded for the lower Paraguay basin and legislatively imposed in the middle and lower Parana River. Nevertheless, poaching, fishing below legal size limits, and the use of banned fish gear are common practices.

The productivity of most riverine fisheries is affected by three major factors: natural and human induced environmental variation, human use through increasing external pressures with usually negative impacts, and exploitation of fish stocks. However, those factors are hierarchically ordered; economical and social issues impact the environment (fish habitat quantity and quality, water quality) and usually have negative effects on riverine fish and their fisheries. For the potamic PPLP axis, fisheries vary widely between regions. Relevant factors include management objectives, the state of the resources and environment, population pressures, levels of economic development and socio-political settings. Some of these factors were illustrated in Table 2 for the PPLP riverine axis. Policy development for large river fisheries needs to bear in mind this wide range of operating circumstances as well as the flood pulse concept (Junk et al., 1989) that determines the basic structure and functioning of river-floodplain systems.

Conclusions

In spite of changes, the Paraguay-Parana-Rio de la Plata riverine axis and its floodplains continues to support a wealth of distinctive natural diversity; we have listed more than 400 fish species for the riverine axis. Riverine fish communities are naturally regulated by a continuum of abiotic-biotic factors, which pressure changes along the river continuum. However, environmental pressures from development activities are unevenly distributed over the riverine axis. Although the riverine axis is under accelerated development and indications of river degradation are evident, there is no evidence of a reduction in the number of fish species and fish community diversity is still high. However, sub-lethal effects of river pollution are apparent for most of the riverine axis. Most intense pollution effects, as at the Rio de la Plata, tend to be very broad affecting many different species. The response at the community level is a reduction in diversity and a shift in species composition towards relatively smaller, shorter-lived forms. At the population level, they tend to mimic the changes expected from heavy fishing and are therefore apt to reduce the amount of fish available to the fisheries (Welcomme, 1985). It is highly probable that depositional riverine water bodies are receiving a significant proportion of polluting chemicals from upstream so that effects far distant from the source can be expected. Nutrient-rich wastes may be enhancing fishery resources, although they usually tend to favor the production of small fish of low economic value.

Biodiversity of fish, expressed as total number of fish species, looks, at the present, little impacted for the complete riverine axis. However, some of the few endemic fish species for the riverine axis have been noted to be at risk of extinction. Some of the major migratory fish species have been reported to be missing as adults for the middle lower Parana and the Rio de la Plata (Quiros, 1990). Weighted fish biodiversity, expressed as the relative species abundance, appears as highly reduced mainly for those river reaches more negatively impacted by human activities. Furthermore, it is highly probable that both current commercial and sport fisheries contribute to diminishing still more an apparently reduced fish biodiversity. However, fish diversity is a topic usually not properly considered for the riverine axis. That biodiversity losses are, at the present, generally due to anthropogenic actions, is a fact. Most of the Paraguay-Parana axis is a low to medium threatened region. However, there exists a lack of accord about which actions are more detrimental to fish biodiversity. Some authors considered overfishing as the main factor, at the same hierarchical level as habitat loss due to dam construction and operation, generally omitting habitat quality losses because of water and sediment pollution. Moreover, most fisheries management recommendations usually ignore conflicts between land and water uses in floodplains and urgent social and economical issues. To maintain fish diversity, realistic recommendations to improve fish habitat protection and implementation of environmentally sustainable agricultural and industry activities should be proposed.

The fisheries of the Paraguay-Parana-Rio de la Plata axis are lightly to moderately exploited compared to other subtropical and tropical floodplain fisheries (Quiros, 2004). However, the development of the riverine axis is expected to continue throughout the basin; if it is implemented as was executed in the past, a continual loss of fish habitats and a general decreasing in ecosystem health can be predicted. Fisheries are, in fact, generally not the culprit for reduction of fish diversity, but rather the victim of environmental degradation. Controlling development and protecting habitats, however, will often involve painful social and political choices.

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