Acta Limnol. Brasil.	Vol. III	139-172	1990

THE PARANÁ RIVER IN THE FRAMEWORK OF MODERN PARADIGMS OF FLUVIAL SYSTEMS

BONETTO, A.A.* and WAIS, I.R.**

RESUMO -

Este trabalho se constitui num ensaio de aplicação de modernos paradigmas de ecossistemas lóticos em um rio de grande extensão, de grande volume de fluxo e de uma bacia bastante heterogênea morfológicamente, o Rio Paraná. O valor relativo destes paradigmas para os grandes rios em geral é também discutido. Em estudos que empregam a metodologia clássica, são consideradas as principais características limnológicas de diferentes trechos do Rio Paraná, incluindo alguns aspectos de seu maior afluente, o Rio Paraguai, e estes resultados são geralmente comparados com as previsões gerais formuladas nos paradigmas de maior difusão, como é o caso do Conceito do Contínuo Fluvial (RCC) e outros modelos relacionados (Espiral de Nutrientes, NSR e o Conceito de Descontinuidade Seriada). Os padrões de zonação também se incluem. Em geral os graus de ajuste são variáveis de acordo com o trecho considerado. Nos grandes rios, como é o caso do Rio Paraná, a presença de extensas e

* CONICET - Buenos Aires - Argentina

** CONICET - Museo Argentino de Ciencias Naturales - Buenos Aires - Argentina

complexas planícies de inundação, cria diferenças fundamentais na dinâmica de seu funcionamento. Com exceção do CDS, de particular aplicação nos trechos represados da bacia de drenagem, tais rios não apresentam uma clara assimilação destes paradigmas, precisando ser considerados separadamente, como "Rios com Planícies de Inundação".

ABSTRACT - THE PARANÁ RIVER IN THE FRAMEWORK OF MODERN PARADIGMS OF FLUVIAL SYSTEMS

An attempt is made to apply modern paradigms of lotic environments to a huge river basin with a large flow volume and extensive morphologically varied basin, the Paraná. The relative value of these paradigms for large rivers worldwide is discussed. In a general methodological framework, the main limnological features of the different reaches of the Paraná and some aspects of its most important affluent, the Paraguay, are considered in comparison to the general predictions formulated in the paradigms of the River Continuum Concept (RCC) and other related models (Nutrient Spiralling Resource, NSR and the Serial Discontinuity Concept, SDC). Zonation patterns are also included. In general, the degrees of adjustment are very varied according to the reach considered. Large basins such as the Paraná have extensive and complex floodplains which are temporarily connected with the river during the annual floods and play an important role in its functioning. Except in the case of the SDC, which is particularly applicable to dammed trends of the basin, such large rivers do not clearly fit in these paradigms. Thus, they should be considered in a separate category from those included in the models, as "Large Rivers with Floodplains".

INTRODUCTION

The Paraná River is the second largest in South America. It is not extremely complex and it is representative enough to permit a first analysis of the application of modern concepts to it, for a better limnological characterization and interpretation of large river ecosystems.

Even though literature on the Paraná River, including attempts at general limnological descriptions is constantly increasing (BONETTO & DRAGO, 1968; BONETTO, 1976; 1986a; di PERSIA, 1986; NEIFF, 1986) none discusses how the river adjusts to the so-called "modern paradigms of fluvial systems", and, to our knowledge, a similar analysis has not yet been carried out. Thus, this study reviews the applicability to the Paraná River of such stimulating concepts as "River Continuum", "Nutrient Spiralling", "Serial Discontinuity" and complementary ideas, for a better knowledge and understanding of such important ecosystems. Zonation patterns are also discussed.

Since the end of the last century European fishery biologists began developing a system of classifying "river zones" on the basis of the dominant fish species present. Early works on zonation were followed by others considering physical, chemical features and/or invertebrates of each zone. A whole review on river zonation may be consulted in HAWKES (1975).

Due to the many environmental influences on stream segments change with stream size, it would be expected that the balance between autochthonous and allochthonous resources will change with succesive stream segments. The idea that such longitudinal changes might show "predictable stretches" in the metabolism of stream ecosystems was developed in the River Continuum Concept (RCC) by VANNOTE et alii (1980) and MINSHALL et alii (1985). It was hypothesized that forested headwater streams are "heterotrophic"; as streams widen they become less shaded and "in situ" primary production is maximized; as streams become even larger, deeper and more turbid they return to an "heterotrophic condition". Organic matter budgets were an important component of the RCC studies and they were examined along the "stream continuum" (BENKE et alii, 1988). A central tenet of the RCC is that community structure and function are dominated by upstream processing. Indeed longitudinal linkages in the ecosystem are strong (VANNOTE et alii, 1980; MINSHALL et alii, 1985). RCC postulates that downstream communities "capitalize" the "inefficiencies" of the upstream communities in terms of organic matter and energy. However, MEYER et alii (1988) point out the relative importance of lateral influences (e.g. floodplain) has not been sufficiently well examined to provide a real test of the concept.

The Nutrient Spiralling Resource (NSR) represents an approach to measuring, reporting and conceptualizing of nutrient and carbon dynamics within a cycle combined with downstream transport. They result thus displaced while recycled in a stream, following an spiralling way (NEWBOLD et alii, 1981; ELWOOD et alii, 1983).

WARD & STANFORD (1983) proposed with the Serial Discontinuity Concept (SDC) a theoretical framework for conceptualizing the tendency of riverine response variables to reset or shift in predictable patterns a consequence of natural or anthropogenic regulation by on-channel impoundments, tested on many river basins, quite large ones as e.g. the Flathead system, at USA and Canada (STANFORD et alii, 1988), but even much smaller than the Paraná.

An analysis of the mentioned concepts above may contribute to a better development of such models particularly concerning large river basins having diverse hydrological characteristics, especially those of Tropical and Subtropical areas, important discharges and wide floodplains linked to the main stream bed.

THE PARANÁ RIVER

The Paraná is the result of the confluence of two important tributaries, the Paranahyba and the Grande Rivers (Fig. 1). Both run initially along an irregular stony bed, comformed upstream by the Precambrican "Brazilian Shield" and downstream by basaltic formations of the Upper Jurassic to Lower Cretaceous (OAS, 1969). It continues east to west on sandy and muddy plains (SOLDANO, 1947) as far as the confluence with the Paraguay River. Downstream, in Argentina, it runs from north to south as a typical plain river with movable bed (SOLDANO, 1947).

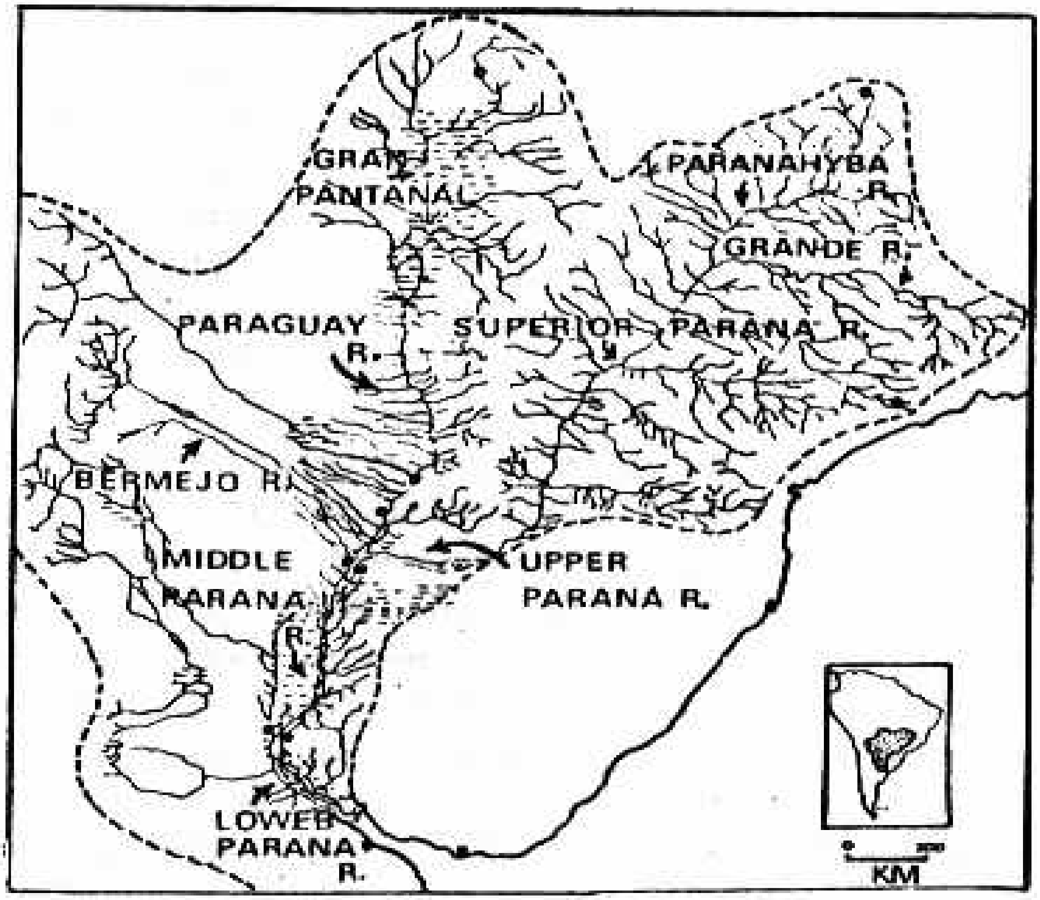

Figura 1 - The Paraná River Basin (modified from BONETTO, 1986a).

On the basis of geomorphological, hydrological and biological features, the Paraná River may be divided into four reaches: Superior, Upper, Middle and Lower (BONETTO & DRAGO, 1968; BONETTO et alii, 1987; BONETTO et alii, 1988).

The Superior Paraná

The first reach of the Paraná River was, before damming, originally winding; the predominantly rocky river bed was characterized by many rapids and falls. Its width varied between 800 to about 4000 m (as upstream Guayrá Falls before the construction of the huge Brazilian-Paraguayan Itaipú Dam and Reservoir). These falls, which defined the southern border of the Superior Paraná, constituted an impressive 100 m boundary at the head of a canyon of 60 m wide (SOLDANO, 1947). These falls clearly segregated diverse faunistic groups, particularly fishes, which contained in the Superior Paraná many endemic species. Since the man-made lake of Itaipú Dam flooded the falls, covering them completely, the first mixing of fish species of this reach with the next one, the Upper Paraná, is being allowed (BONETTO & WAIS, 1985/86).

According to zonation patterns, the Superior Paraná presents many characteristics of a *rhithron*, although differing in many aspects from the original definition of ILLIES (1961) and ILLIES & BOTOSANEANU (1963). We adopt WELCOME's (1985) use of the term *rhithron* to identify the streams covering the steeper, rocky, torrential upper reaches, with a secondary role for temperature values. STATZNER & HIGLER (1985, 1986) consider that flow characteristics (stream hydraulics) are the most important factor governing the zonation of stream benthos on a world-wide scale. This idea was suitable to interprete the Superior Paraná because the river widened when basaltic rocks protruded, the velocity of the water decreased and the temperature increased in the original conditions. Today human activities have substantially modified some characteristics of the Superior Paraná *rhithron*. Deforestation, water pollution, agriculture in the basin, and specially the installation of many large dams on the principal tributaries, affluents and on the Superior Paraná (OAS, 1985; BONETTO et alii, 1987) make that a real assimilation of a *rhithron* in the system seems somewhat arbitrary nowadays. Nevertheless, prospective localized surveys allow partial reconstruction of an initial and pristine image of the river and summary characterization of its features and properties from some modern theoretical paradigmatic points of view.

Applying the RCC and SDC, a consideration should be mentioned. Although the riverbed of the Superior Paraná is very irregular and its width and bottom materials vary (on the wide reaches the rocky bottom alternates with sand and even finer materials, consequently having different benthic communities), this does not seem to affect substantially the picture of the river as a continuum in the sense of the RCC ("sensu" VANNOTE et alii, 1980; CUSHING et alii, 1983; BRUNS et alii, 1984; CUMMINS et alii, 1984). Such natural discontinuities, even though remarkable, would not invalidate the concept of the gradient of general limnological conditions of the basin. The Superior Paraná was an extense reach of the system that might be seen as "a whole river" presenting the complete sequence of lotic stretches shown on the RCC, from the headwaters up to Itaipú Dam.

The Guayrá Falls distincly divided the river into the Superior and Upper reaches, creating conditions upstream which biologically differed in many aspects from those downstream. Fish communities which were not able to traverse the falls remained restricted above Guayrá, generating a typical endemicity in conditions of isolation (BONETTO & DRAGO, 1968; BONETTO, 1986b). Some fishes of the Superior Paraná were recently reported downstream Itaipú

Dam. Furthermore, there are introduced species brought to the area to enhance fish production in the reservoirs. As these man-made lakes have no fish-ladders, reduction of migratory fish production has resulted.

This segregation may be seen in other faunistic groups, such as the Pelecipoda (BONETTO, 1965), with parasitic larvae on fishes, *glochidium* and *lasidium*, and perhaps to other zoological groups. Thus, the significant manmade discontinuity represented by the many dams established on this reach, led in the Superior Paraná the schemes outlined in the SDC are specially suitable. At present the Superior Paraná and its catchment area is cut by many large dams (OAS, 1985). In some cases, e.g. the Grande River, dams are located immediately upstream from the tailwaters of the next reservoir downstream. We consider that the better, perhaps the only, possibility to study these dammed reaches is under the lens of the SDC, although the remnant lotic reaches in many areas are nowadays very reduced and they practically will dissapear when the damming program will be finished (OAS, 1985; BONETTO et alii, 1987).

According to the NSR, the river did not present substantial problems of adjustment on the Superior and the first reaches of the Upper Paraná. However, the strong flow turbulence and the frequent changes of velocity with variations of bed width result in a difficult reconciliation to the original model in some localized areas, e.g. in lotic stretches between reservoirs.

The Upper Paraná

The Upper Paraná extended formerly from Guayrá, but today downstream from Itaipú. The river runs through a narrow bed, gradually increasing its width and characterized by important differences of depth, up to Corpus, where a large dam is planned. Downstream Itaipú the

Paranã receives an important affluent, the Iguassu River, which contains the famous 80 m falls. These falls exert the same influence as the Guayrã on the Paranã, determining a clear biotic endemism above the falls.

At Corpus the Paranã is 1500 m wide, still possessing a fundamentally stony bottom. Downstream from this point, the riverbed widens rapidly and changes its direction to the west, and the bottom turns progressively sandy with a remarkable irregularity of depth. This tendency is interrupted by the elevation of the bottoms through the Yacyretã-Apipé Rapids, where a new large dam is being built. There the river is divided into several branches including extensive islands and many other smaller ones. The bed reaches 30 km wide, because of the elevation of the basaltic bottoms, and bavigation is hindered. The basalt outcrops disappear downstream and the sandy riverbed gradually increasses its wodth, with variations of 500 to 5000 m, to the confluence with the Paraguay River.

The paradigms adjustments on the Upper Paranã have diverse degrees of significance. The differences between the rocky sectors at the beginning of the Upper Paranã and the sandy sectors downstream, from Corpus and especially downstream at Yacyretã-Apipê, are rather steep and define a remarkable differentiation into patches of the benthonic fauna as well. On the stones and on the parts less exposed to the current, abundant encrustating sponge colonies establish. They are very similar to those described by BONETTO & EZCURRA (1967) in the affluent rivers and creeks. Thick covers of epiphytic algae and formations of Podostemacese also occur on the stones. The riparian forest, originally very dense, is nowadays variably modified by anthropic activities.

Downstream from Yacyretã Apipé, the conditions change because the sandy substrata become more extensive. The benthos presents a peculiar composition, where psammic harpacticoid copepods, oligochetes clearly dominated by

Narapa bonettoi, nematodes, chironomids, mollusks (*Sphaericea*), flatworms (Turbellaria), etc. are the main components (VARELA et alii, 1983). Though this disruption is very marked, it is present over a short reach, and does not seem to depart from the general theoretical foundation of the RCC and the NSR, especially since these animals are predominantly detritivores, feeding on the finely particulate organic matter of the Superior Paraná. The organic matter comes mainly from the riparian vegetation and, in limited quantities, from the Podostemaceae and the algae. What departs from RCC in this reach would be the presence of large concentrations of ultrafine particulate inorganic matter. The primary production is strongly limited by these fine suspended solids (BONETTO, 1983). Though they are not gravimetrically important, they give the water a high and persistent turbidity and a remarkable reddish colour (BONETTO, 1976).

Zonation patterns seem not to be clear in this "transitional" reach, characterized by succesive rather abrupt changes between the rocky and sandy beds and associated biota. As an extension of the classic zonation definitions we may consider also the Upper Paraná as a *rhithron sensu* WELCOMME (1985), within a system where the Middle and Lower Paraná would constitue the *potamon*. The last stretch of the Upper Paraná, nevertheless, might be considered as a transition between the Superior reach (*rhithron*) and the Middle and Lower Paraná (*potamon*), according to what is observed next to the Confluence area.

It is also difficult to reconcile much of this stretch to the NSR because of the width of the riverbed (up to 500 m) and the moderate and variable depth. The river is divided into several shallow arms, separated by islands and sandy banks, with a very complex flux. This fact suggest a very irregular pattern of nutrient and carbon transport. SDC ideas, on the other hand, can be applied to the Upper Paraná when Yacyretá-Apipé and Corpus dams introduce enough changes as to permit its analysis, especially because the remaining lotic reaches will become sufficiently larger to test the ecological theories proposed by WARD & STANFORD (1983).

The Paraná widens progressively on a bottom of predominantly middle to coarse sand up to the Paraguay River mouth.

The Paraguay River and its distinctive features

The Paraguay river is distinguished from the Paraná and the other South American rivers by several peculiar characteristics. In the upper basin, a very large floodplain develops. This complex system of lentic and lotic environments called the "Gran Pantanal" is completely atypical, because floodplains of large rivers are usually on the middle and/or lower reaches. This situation removes the system even more from limnological schemes of general acceptance among modern paradigma. The watershed divided into the Paraguay River and the Southern Amazon Basin is not a typical *divortium aquarum* either. On the upper basin of the Paraguay, effective contacts with the Amazonian headstreams may take place, allowing an active biotic interchange. Thus, as far as we know, the Upper Paraguay has the largest biotic diversity of the whole "Del Plata" Basin, which comprehends the Paraná plus the Uruguay basins.

The "Gran Pantanal", besides playing an important role in the limnological characteristics of the Paraguay River, stores in the rainy season large volumes of water, which are slowly released, regulating the flow volume of the river at a rather constant value of about 4500 m^3/s. The consequent concentration and retention of suspended solids also has an interesting atypical pattern and regime. They tend to decrease during high water periods (BONETTO et alii, 1981). Similar variations may occur in conductivity values as a function of the hydrometric levels. In those flooding periods the "Gran Pantanal" contributes enormous masses of floating aquatic plants (as *Eichhornia azurea*) and affects the dissolved oxygen regimes of the river as well. At the first flood stages, dissolved oxygen values become reduced, and the phosphates low (BONETTO et alii, 1981). Some relatively frequent fish mortalities are attributed to this strong reduction of DO at the "Gran Pantanal" (PAIVA, 1984) reaching the Paraguay River.

Other distinctive features are related to very high concentrations of suspended solids on the Lower Paraguay, due to contribution of the Bermejo River (Fig. 1). The presence of this suspended inorganic matter strongly influences the limnological characteristics of the Middle Paraná, a reach extending southward below the Paraguay-Paraná confluence. These enormous quantities of suspended solids (more than 62000000 m^3/year, SOLDANO, 1947) affect the Paraguay and Paraná Rivers not only in theyr hydrological aspects and properties, but also in their limnological features, particularly those regarding the biotic communities. Phyto, zooplankton and benthos are altered and a marked decreasing of the primary productivity is characteristic.

Finally, it is important to point out that in the confluence of the Paraná and Paraguay Rivers, both streams originate large hydrodynamic backwaters, producing important limnological consequences. At high water periods these backwaters may extend through the Paraguay River even up to Asunción City. The Paraguay River should be considered together with the Middle Paraná for analysis of lotic paradigms, because of their close relationship. The Upper Paraná, with its width of 1500 to 5000 m, is chacracterized by a current following a rather anarchic direction, with turbulence and instability in flux areas (BONETTO, 1976). Downstream from the confluence, the conditions change. The NSR is difficult to analize because of the backwaters phenomena from the confluence.

The Middle and Lower Paraná

Downstream from the joining of the Paraguay and the Paraná Rivers, the stream changes again its east-west direction to a north-south one at the Middle Paraná (Fig. 1). Its unique riverbed appears divided at the bottom into a right side, corresponding to the Paraguay, and a left side, where the Paraná waters "sensu stricto" run. This "parallel way" of both rivers introduces a strong heterogeneity into the initial sections of the Paraná, affecting suspended and dissolved solids as well as the biotic communities.

The waters of both rivers attain complete mixing about 400 km downstream from the confluence. The Paraguay substantially increases the dissolved solids of the Paraná. The conductivity of this river increases from about 50 µS/cm to 100 µS/cm, with a slightly modified ionic composition. The suspended solids increase greatly according to the floods from the main Lower Paraguay affluent, the Bermejo, approximately 10 to 15 times at the right margin, on the beginning of the Middle Paraná, in the section Corrientes-Resistencia (BONETTO & ORFEO, 1984). Nevertheless, this difference tends to decrease over a short distance because of the larger size of particles characteristic of the Bermejo suspended solids and the effect of the hydrodynamic backwaters of the confluence of both rivers. The suspended solids determine serious but variable reductions in the plankton, including marked variations in specific composition and population densities.

Important quantities of absorbed phosphorous are added to the system with the suspended solids (PEDROZO, 1988). The main nutrients have an atypical behaviour. Average orthophosphate contents are twice greater in the

Paraguay than in the Paraná. Concentrations of nitrates are almost four times higher in the Paraná. The oxidability (QOD) results are about double as well.

From the lens of the paradigms, the upper reaches of the Middle Paraná may be seen as a transitional zone between the Paraguay, on one hand, and the Upper Paraná, on the other, and the remaining reach of the Middle Paraná downstream from about 400 km mixing zone (BONETTO, 1986a) in the sense of transition for middle reaches expressed by ILLIES (1953), SCHMITZ (1957) and MAINTLAND (1966) for lotic communities in European rivers. However, a comparison is difficult because the Paraná and the Paraguay are wide and large rivers with a major faunistic complexity than those considered by these European authors.

This transitional stretch of changes, product of the confluence of two rivers of very distinctive features which join in one unique system at the Middle Paraná, logically affects the idea of the "continuum" as stated in the RCC as a process of progressive development and without major perturbations. Nevertheless, the esence of the concept would not be modified in a general view of the basin as a whole, considering the lotic system "per se" if the floodplains could be excluded. The transitional zone, on the other hand, change the physical and chemical caracteristics of the waters but does not modify greatly the benthos, where these changes are much less evident (VARELA et alii, 1983; BONETO et alii, 1985/86).

By analyzing the behavior of the nutrients and organic matter, evidence of important alterations which take place in relation to the original paradigm of NSR seem to be clear. Thus, the Paraguay, which substantially changes its limnological characteristics downstream from the Bermejo, would present during the high water periods of the Paraná, a "shortening of the nutrient spirals" at its mouth ("sensu" NEWBOLD et alii, 1982; ELWOOD et alii, 1983). The backwaters formed at the confluence with the

Paraná would actively conduct to this "shortening". After the confluence the spiralling of the Paraguay nutrient tends to widen and distend towards the right margin. That of the Paraná, on the other hand, though may distend to the left bank, does not present important variations from that of the Upper Paraná. For this reason the mixing processes may be seen as two "spirallings" practically separated at the beginning, slowly interlacing downstream. The complete unification occurs about 400 km downstream, depending from the relative influence of the flow volume carried by both rivers. Both "spirallings" would practically "disappear" as soon as the waters invade the extensive alluvial valley linked to the Middle and Lower Paraná river during the annual floods, when the process turns mainly laminar and rather erratic the nutrient flux. Furthermore the riverbed at Middle Paraná is divided into several arms among islands, which conforms to a braided system of a *potamon*, complicating even more the nutrient and carbon fluxes. The real limits of the "spirals" are not identified when "dissolved" in the alluvial valley during floods through the yearly coupling. The floodplain developed downstream from the confluence with the Paraguay River is located on the right margin, changing to the left one along the Lower Paraná. At its beginings it has an average width of 15 km, but it widens downstream to about 60 km continuing into the delta.

The alluvial valley has a complex and varied structure, where lentic and semilentic environments link temporarily with the main stream of the river, rather differentiated between them, forming a tight compact system of islands and lowlands, plenty of ponds, oxbow-lakes and other lentic water bodies, connected by a net of secondary creeks and rivers. Every year during the ordinary floods, and even more during the extraordinary ones, the Paraná establishes a close relationship with the alluvial valley, flooding the lowlands and the lentic water bodies. Ponds and oxbow lakes reduce their water levels during the remainder of the year and, during floods, they regain the "maximum" level. During extraordinary floods, all the valley is covered by a mantle of water in which only the higher parts of the trees, located on the levées, can be distinguished. In those conditions, the water runs initially through creeks and then in a predominantly laminar way with a general direction similar to that of the river, through large changes in velocity and ways of propagation. The lentic environments, although shallow and differentiated, have many basic properties in common. In any case, these waters conduce a general uniformity to the alluvial valley.

Currently the flooding processes are not fast and build very slowly the fluvial-lake physionomy and the changes of the alluvial valley. Thus, the progressive invasion of the waters overpasses the marginal natural levée, locating different ways of penetration as the water level of the river rises. The run and distribution of the floodwaters are easily perceived due to their remarkable strong reddish colour, which contrast with the muddy waters of the alluvial valley. The velocity and direction of occupation of the valley vary longitudinally and locally. Transformations and interchanges between the mainstream of the river and the floodplain were extensively described in detail by BONETTO (1976). BONETTO & WAIS (1987) described the changes of suspended and dissolved solids and those of plankton, fishes, etc., and emphasized as well as the complexity of the processes involved (Fig. 2), theis theoretical and applied interest and the need of more profound limnological research.

The alluvial valley of the Paraná and its limnological significance

A short time after floods, ponds and oxbow lakes

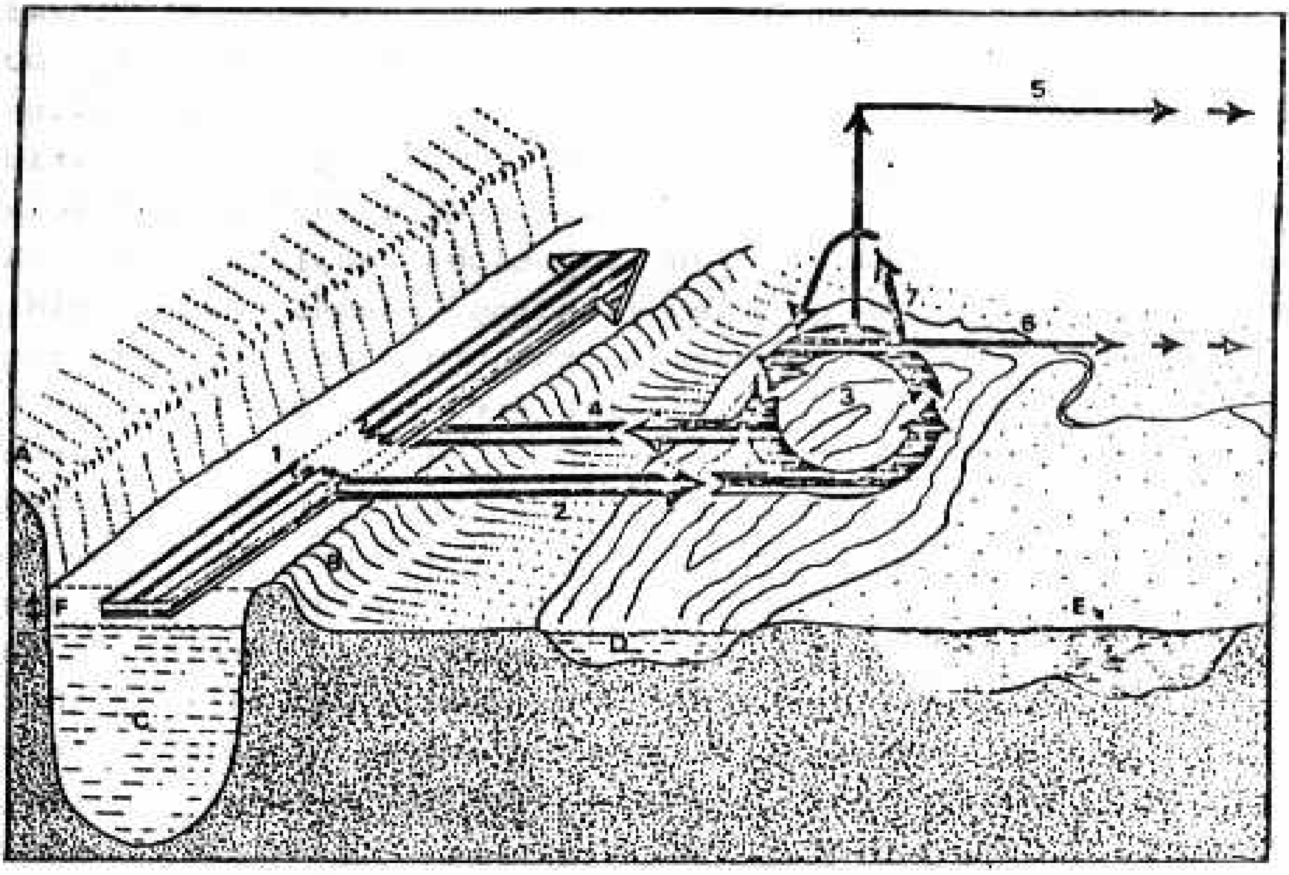

Figure 2 - Schematic section of the Paraná River and its alluvial valley. Bioproductive mechanisms and energy transfer. 1- Energy flux in the main stream of the Paraná River; 2- input of floods in which the waters of the river reach a pond of the alluvial valley; 3- metabolization of the contributions of the river with the bioproductive components of the pond; 4- output of the low water phase, contributing to the river important quantities of organic matter, macrophytes (especially the floating ones), phyto and zooplankton, fishes, etc; 5- export of energy to the "aerial environment" (particularly adult insects and components of the diet of ichthyophagous birds); 6- export to terrestrial areas and to interphase fauna, including possible feeding of the cattle through this source (cattle of "invernada", reared during the low waters, on autumn-winter) and 7- bioproductivity which does not export, accumulates *in situ* (rooted vegetation, floating plants, etc.), concurrent to the infilling of the water body. A- High bank of the river; B- marginal levés of the alluvial valley; C- main stream of the Paraná River; D- pond of the alluvial valley; E- silted pond; F- fluctuations of the water level in the year (After BONETTO & WAIS, 1987).

substantially reduce the concentration of dissolved solids in the water. Transparency increases. Changes of dissolved oxygen contents are varied. The flooding waters may invade the ponds and oxbow lakes with low concentrations of DO, due to washout and runoff of organic matter on its laminar displacement. During the low water periods large vegetation masses may also cover whole lentic environments, producing strong reductions in DO even to total depletion at the bottom. Nevertheless, the floating plants are rapidly dispersed during the floods. On the other hand, large parts of the emergent rooted vegetation die, not being able to adjust to the increasing level of the waters. Submerged macrophytes, though not very common in these environments, may be affected by the high turbidity and DO reduction.

The plankton, usually very rich, suffers important and interesting changes in the community structure and density. At first, quantities decrease; then, after a short time, the number of organisms may surpass former levels. Species richness increases as well (BONETTO et alii, 1972; BONETTO, 1975; 1976). The floating vegetation, mainly represented by *Eichhornia*, is eliminated by several processes when the water levels decrease. It is washed out, trapped by trees or forms clogs which are eliminated during reduction of water levels combined with rainy periods (BONETTO, 1975). The aquatic vegetation accumulates at the outlets of depression oxbow lakes, clogging normal drainage until released into the main channel of the river as complex masses called "embalsados" (WELCOMME, 1985). When the lentic environments recover their individuality after these processes, they are practically bare of aquatic floating vegetation (Fig. 3).

The suspended solids tend to precipitate, contributing nutrient such as adsorbed phosphorus, particularly at the beginning of the alluvial valley, where Bermejo solids predominate. Consequently the waters are much more clear and productive (BONETTO & WAIS, 1987;

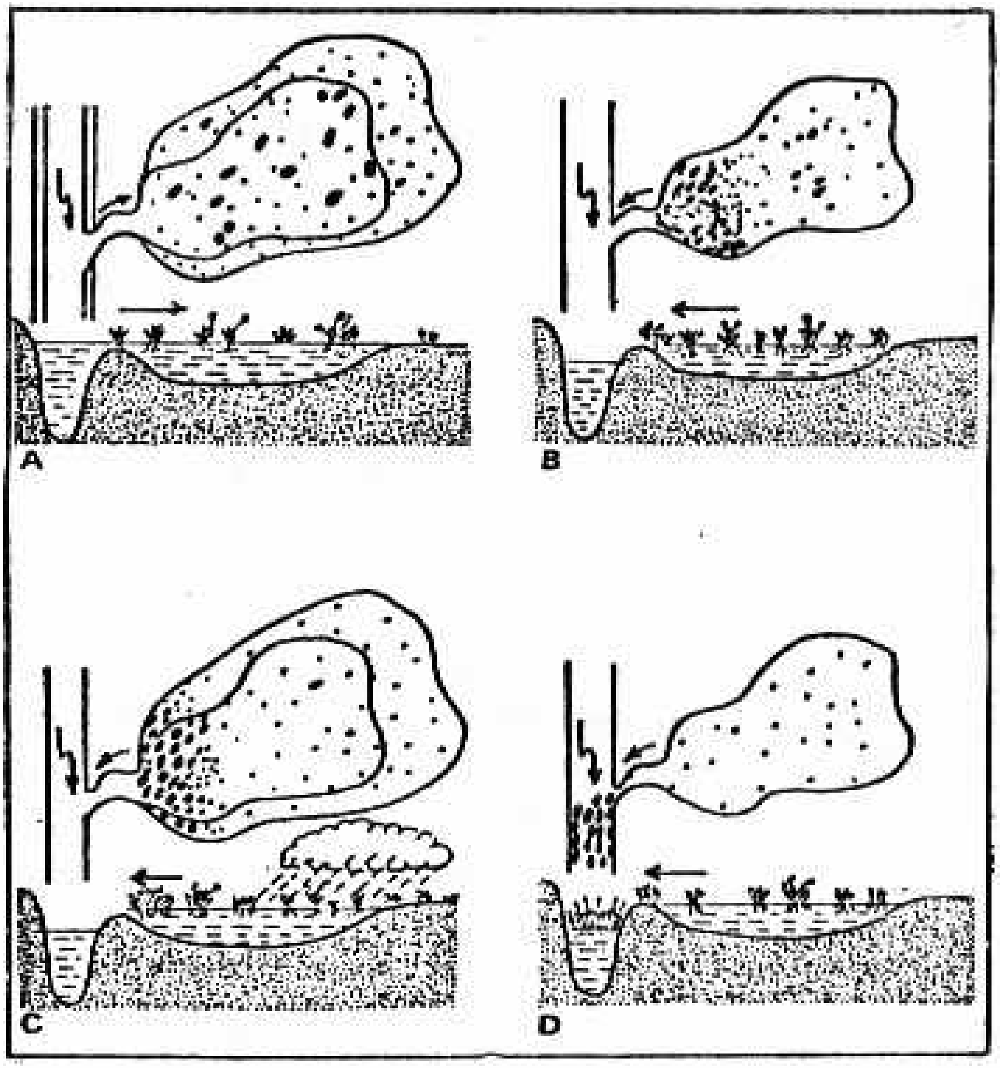

Figure 3 - Mechanism of release of floating vegetation masses, "embalsados", during the flood cycle. A- ponds with "embalsados" in flood condition; B- drainage clogged by vegetation after flooding; C- the same situation during the rains; D- release of the "embalsados" into the river (After BONETTO, 1975; WELCOMME, 1985).

PEDROZO & BONETTO, in press). The fishes have important exchanges between the river and the lentic environments of the alluvial valley. The larvae, alevines or young fishes products of reproduction of species migrating upstream during floods enter the ponds and oxbow lakes from the river. They remain in the lentic environments one ore more years in better conditions for them than those of the river (BONETTO, 1976). Then, they return to the main stream of the Paraná during new floods and participate as adults in new migratory processes.

When waters return to the river, the vegetal and animal biomass apported to the river from the alluvial valley is very important. Sometimes the excess of detritic organic matter causes a decrease in dissolved oxygen in the river (BONETTO, 1986a). Most of the biotic content of ponds and oxbow lakes is washed out to the river. Once separated from the main channel, the lentic water bodies of the alluvial valley develop diverse phytoplankton and usually zooplankton communities as well, with large population densities. However, the benthos is less affected by these hydrologic processes and may mantain a biomass over 1000 kg/ha of fresh weight (especially contributed by pelecypods of the genus *Diplodon* (BONETTO et alii, 1970b; 1973). Fish biomass usually surpasses 1000 kg/ha of fresh weight in permanent water bodies, by presenting a clear dominance of mudd-eater detritivorous fishes (60% *Prochilodus platensis*, BONETTO et alii, 1969; 1970a).

Diplodon clams do not occur in the main channel of the Paraná except very occasionally in pools, in areas protected from the current where the bottom is richer in clay and silt. The mouth of the Lower Paraná at the Del Plata estuary presents these characteristics, but a large part of this area is now affected by coastal pollution. Production of large and middle-sized gastropods of the genera *Pomacea* and *Asolene* is high, and to a lesser extent that of shrimps and crabs.

The alluvial valley-river system does not present a model of a gradual process of fragmentation of organic matter by shredders and progressive use of it downstream, as postulated by the RCC. In the Paraná, processes of degradation result much more from participation of fungi and bacteria attacking fallen parts of plants (DIONI, 1967). Insect activity affects the plants rather as a whole. Even though they directly utilize only a small part of the vegetation, they play an important role in its deterioration and death (POI de NEIFF et alii, 1977), with subsequent active degradation by microorganisms. Most of the rooted plants die and are utilized "in situ". The floating vegetation, once in the river (Fig. 2), may dry at the margins and be attacked locally by microorganisms or even reach the ocean during exceptional floods. These floating masses often transport animals, including occasionally some large reptiles and mammals.

Though the lentic environments of the floodplain mantain a freatic relationship with the river, the alluvial valley of the Middle and Lower Paraná is only temporarily related to the main stream because of the yearly hydrological cycle. The period of low waters is one of "decoupling" of the two subsystems, "floodplain" and "river" "sensu stricto", and that of flooding, of "coupling". Both periods vary, but typically are six months each, usually with only one periodic yearly articulation during high waters of spring-summer.

The analysis of the river may respond to the RCC, considering only some reaches. Changes of direction, velocity, suspended and dissolved solids load through the oscillations of the waters due to the hydrological cycle, are common with important differences affecting the quantitative biotic contents, bioproductive mechanisms, their development downstream, metabolism and energetic transfers. In most of the areas of the Middle and Lower Paraná it is very difficult or even impossible to assimilate the river to RCC and NSR paradugms.

The alluvial valley does not constitue an ephemeral episode in the life of the Parná. This valley do not silt up to be extinguished and to "return" to a simple stream in conformity with the RCC. The Paraná, on the contrary, seems to maintain a close relationship with its alluvial valley, not only in space but also in time. The suspended solids and organic detritus may cover ponds and oxbow lakes, and locally and circumstantially engender a more difficult relationship between the alluvial valley and the river. But even so, the waters both during floods and while their return to the river at low water periods, especially during rapid returns, permanently carve the alluvial valley, forming new creeks, small rivers and islands with ponds and oxbow lakes in a constant evolution.

At its Middle reach, the Paraná erodes the high left bank, and deposits the sediments on the right one. The situation is the opposite at the Lower Paraná, where the high bank is the right one. This system of equilibrium between erosion and sedimentation phenomena is dynamic and is characterized by a narrowness of the main channel and a widening of the alluvial valley (SOLDANO, 1947).

The floodplain of the Paraná represents indeed a very important subsystem, from an structural and functional point of view, mainly characterized by the very high organic productivity transmitted to the river, as well as to the terrestrial and interphase areas related to it. These latter, perhaps, are even more important than the former, even more the interphase areas provide a suitable source for feeding the cattle during low waters.

DISCUSSION

As MARGALEF pointed out (1983), a fluvial system is a "functional continuum", though its organization and functioning may be extremely varied. This conceptualization of a lotic continuum, is appropriate even for the mighty rivers of the world. Many researchers have recently worked to develop models stimulating and formulating those theories which could allow consideration of the fluvial systems from a more holistic and deterministic sense. These view points intend a transition from a descriptive limnology of rivers to a more predictive one (MINSHALL et alii, 1985). Among the most elaborated of these concepts are the RCC, the NSR and the SDC. First steps have included the recognition of river zonation in most parts of the world (BOTOSANEANU, 1979).

Even when a concept seems to be applicable world-wide, current theories of classification may not fit the features of some systems. For example, the original ideas of RCC and NSR and their possible areas of applicability were born in Northern America and would be useful in many river systems, especially those of small to moderate extension. Larger rivers present a different situation because of the many related net processes, particularly if they have large floodplains. On the other hand, zonation ideas have been developed significantly (BOTOSANEANU, 1979), and they are useful in rheobiological research in many parts of the world, even e.g. in South Africa (HARRISON, 1965).

However, Northern Hemisphere-based schemes of longitudinal river zonation do not apply in Australia (LAKE et alii, 1986; WILLIAMS, 1980; 1981) and even the relative value of the RCC is critically discussed in that continent (BARMUTA & LAKE, 1982). The situation in New Zealand seems to be more like the originally described RCC (WINTERBOURN et alii, 1981; WINTERBOURN, 1982). STATZNER & HIGLER (1986) advocate modifications of the theoretical background of the RCC based on European experience. An attempt to reconcile the river zonation with RCC statements was made for some Patagonian basins (WAIS, 1984).

It is not our purpose to discuss these paradigms, but we intend testing their applicability to the large rivers, especially those with extensive floodplains, characteristic of South America and Africa, from the viewpoint of the degree of adjustment of the Paraná River. The large rivers with alluvial valleys are very peculiar fluvial systems distinctive from typical streams, with their own functional model (BAYLEY, 1979). The wide floodplain on the upper reaches of the Paraguay River, the "Gran Pantanal" is even much more spread-out and extended, and perhaps is more complex than the Paraná floodplain, according to preliminary studies (FROEHLICH, pers. communic.). This wide floodplain is atypical and unusual, even more because during the rainy season the Paraguay headwaters may contact Amazon affluents allowing biotic exchanges between both basins (BONETTO, 1986a), transforming the Paraguay into the most intricate and diverse of all the components of the Paraná system.

Pursuant to the general concept of the "continuum" in a generic sense as expressed by MARGALEF (1983), floodplain rivers should be kept separate from the cited speculations because of the extraordinary tangle of their features, which are far removed from those of the remaining rivers. The floodplain systems have special bioproductive mechanisms due to the intermittent periodic articulation between their lentic and lotic environments. The temporary mixture of their waters and the high degree of export of the organic matter from both aquatic and terrestrial habitats make it convenient to segregate them in a different category: that of the "Large Rivers with Floodplains", which should be considered separately from the current fluvial systems.

On the other hand, the SDC seems to be suitable world-wide, even for floodplain rivers, although WARD & STANFORD (1983) point out that more data are needed for the analysis of the SDC in some continents (e.g. South America). The ideas proposed by the SDC would indeed represent a very useful tool applicable to the Paraná because of the increasing damming of the rivers in this basin, including the Middle reach where most of the alluvial valley is located (OAS, 1985; BONETTO et alii, 1987; 1988), especially because dams seem to be generating serious limnological problems (BONETTO & WAIS, 1985/86; 1987).

The data are not yet sufficient to permit analysis from the viewpoint of linearity of processes. It is very difficult, for example, to conceptualize the nature of the movement of nutrient and carbon in the anarchic flux regime of water (Plury-de-flux) in the alluvial valley during floods, and its relationship to the main stream of the river; thus an agreement with NSR is not possible. NSR model is not able to be applicable for the circulation of nutrients and carbon in lentic water bodies of the floodplain. Studies in this direction should be intensified (QUIRÓS, 1988).

Paradigms as RCC or NSR were conceived for river systems of lower order despite the aims of the original papers (VANNOTE et alii, 1980 (RCC) and ELWOOD et alii (1983) (NSR)) of intending a general concept. As a consequence, we completely coincide with WELCOMME (1988) in the sense "we are not in a position to address the problems of the lower 2000 or 3000 km of a river to the same extent that we address to the lower-order streams in the first few hundred kilometers of drainage network. This is partly because the effort that has been devoted to studying large systems is much less than that for studying small ones. As a result, a lot of the theory on zonation and the RCC is based on small lower-order rivers. We do not yet have such detailed theories to describe the functioning of large rivers at any latitude" (WELCOMME, 1988). For this reason we agree with McCONNELL (1988) in the sense the study or large rivers with extensive floodplains should be estimulated at multidisciplinary levels with international participation.

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ACKNOWLEDGMENTS

To Drs. R.L. Welcomme and P.B. Bayley for their encouragement and advice regarding the problem of modern paradigms in the Paranã; to Dr. B. Higler for his valuable suggestions, and to the Organizing Committee of the II CBL and the actions of Drs. R. Henry and J. Reid for their support to attend the Congress through the Coordenadoria de Aperfeiçoamento de Pessoal de Nível Superior do Ministério da Educação do Brasil.

ENDEREÇO DOS AUTORES

BONETTO, A.A.
CONICET, Av. Independencia 2047, 5C
(1225) Buenos Aires, Argentina

WAISS, I.R.
CONICET, Sec. Limnología, Museo Argentino de Ciencias Naturales, Av. A. Gallardo 470
(1405) Buenos Aires, Argentina