12. The Uruguay River system

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Introduction

With its tributary the Cuareim, the Uruguay River forms the borders of the Oriental Republic of Uruguay (Fig. 1). The river system lies in temperate latitudes (28°10′S–37°08′S), in a region of tall prairie grasslands, with forests along the main water courses. Topographic relief generally is below 610 m AMSL. Pastoral regions in the NW are predominantly for sheep, but cattle are important S of the Río Negro. Cereal crop-growing areas extend some 100 km N of the capital, Montevideo, and N along the Uruguay River to Salto.

The Uruguay River extends over 1838 km, with a drainage area of about 365 000 km^2, and is third among the rivers of the La Plata Basin (3.1 million km^2; OEA 1969). Its main tributaries are the Ijuhy-Assu, Ibicuí, Cuareim and Negro rivers. These are all left bank streams, as the Paraná-Paraguay system drains the right bank region. The tributaries are often braided, with multiple branches that are distinctive among rivers of the Cuenca del Plata. In several other respects, the Uruguay provides interesting contrasts with the neighbouring Paraná system (cf. Bonetto 1986a).

Physical characteristics

Geographic and geologic features

The Río Uruguay rises in the Serra do Mar and Serra Geral, the coastal ranges of southern Brazil (Fig. 1). Its chief source, the Río Pelotas, rises only 64 km from the Atlantic coast and flows to meet the Río Canoas near Piratuba (1800 m AMSL), forming the mainstem river. The Uruguay flows W through southern Brazil, then SW as the border between Brazil and Argentina. At Monte Caseros (Argentina) it turns S, forming the border between Argentina and Uruguay. At Buenos Aires it combines with the Paraná River to form the great estuary of the Río de La Plata.

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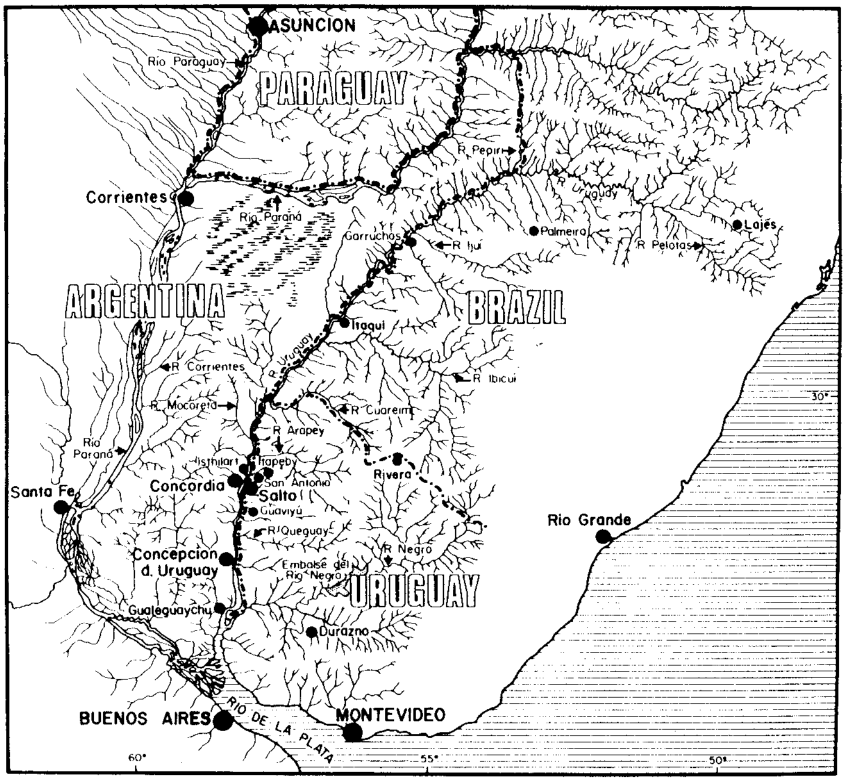

Figure 1. Geographic features of the Uruguay River system.

The Uruguay is the youngest of the La Plata rivers (Frenguelli in Soldano 1947). It probably originated in the Quaternary, as part of tectonic movements associated with the uplift of the Serra do Mar. The upper basin of the present system probably was formed at the time, impeding drainage to the Atlantic Ocean. There is evidence for this in the distinct convexity of some parts of the river profile (Fig. 2), the scarcity of islands in its valley, and the existence of numerous rapids. Prior to construction of a major dam at Salto Grande (see later), below the inflow of the Cuareim near Monte Caseros, the river fell 9 m in a 3-km reach. At Saltos del Moconá, above the junction with the Pepirí Miní, the river enters a 10-m basaltic gorge where it is constricted to a width of only 30 m. As a result of interruptions like these, the Uruguay is less important as a waterway than the rivers of the Paraná system. Large vessels (to 4.3-m draft) can reach Paysandú, about 200 km from the mouth, and smaller ships may reach Salto, another 100 km upstream.

In the upper reaches the river gradient is 0.15 to 0.30 m km^{-1} (Soldano 1947). The course is tortuous (sinuosity 2–3 in some reaches) as it passes through

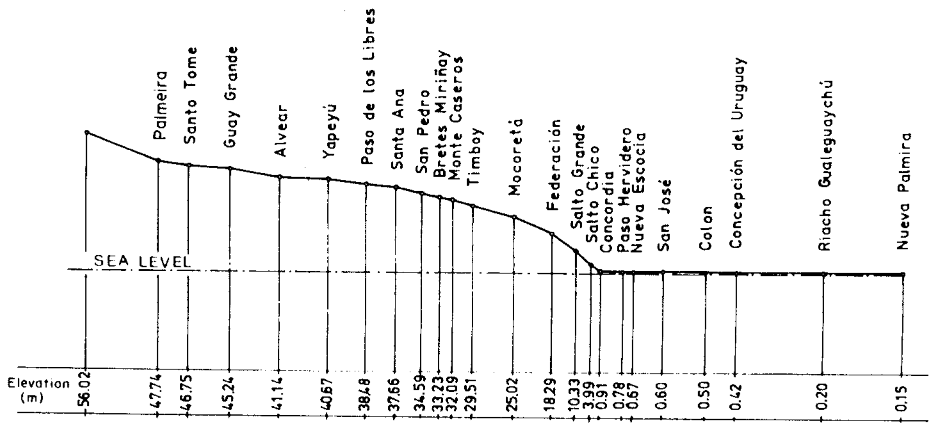

Figure 2. Vertical profile of the Uruguay River (Soldano 1947).

undulating hills, but gradually straightens in southern Misiones Province (Argentina). This section is less sinuous than corresponding parts of other rivers in the La Plata drainage, and the only significant falls are the aforementioned Saltos del Moconá. However, downstream of Garruchos (Uruguay) the river gradient is a mere 0.7 m over 300 km (Soldano 1947); the flow is correspondingly diminished, and the mainstem widens and branches.

The width of the basin increases gradually from about 200 km near its source to about 360 km near the confluence with the Río Negro (Tossini 1959). These progressive changes, and the regular distribution of the tributaries, prevent the formation of a major delta like that of the Paraná River.

Flow régime

The hydrologic régime of the Uruguay is quite different from that of the Paraná and Paraguay rivers. According to Ceppi (1937), the régime is of a "subtropical" type. There are two distinct zones:

(a) Upstream of Salto Grande. Floods in this zone occur 30–60 days after peak rainfall in autumn and winter (mean 1900 mm a^{-1} at Palmeira, Brazil).

(b) Downstream of Concordia. Rainfall is less and distributed more evenly through the year (1300 mm a^{-1} at Rivera, Uruguay), and flows are impeded by the low gradient and tides in the estuary of the La Plata.

Flow patterns in the upper zone are more predictable. At Salto Grande, Soldano (1947) recorded an annual mean flow of 124.740 million m^3, a peak flow of 391.658 million m^3, and current velocities up to 2.5 km h^{-1}. Minimum and maximum discharges were estimated as 92 and 36 000 $m^3 s^{-1}$, respectively. Water level fluctuations also are more pronounced in this region (Fig. 3). In

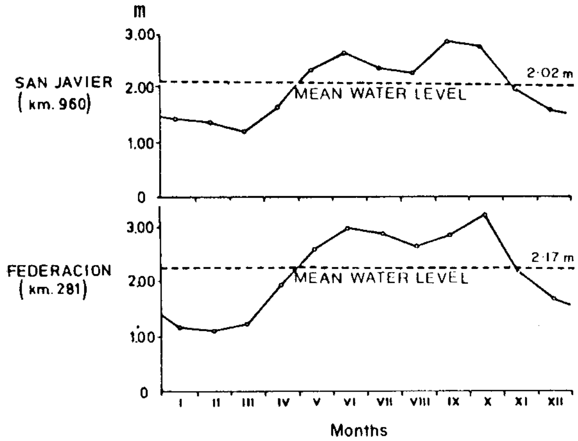

Figure 3. Water level fluctuations at localities on the Uruguay River.

1941, for example, levels at Puerto San Javier varied 11.5 m about a mean level of 2 m (Soldano 1947). In the lower zone salient hydrologic features are the relatively small difference between minimum and maximum water levels (mean level below 2 m) and the greater frequency of flash floods caused by the meeting of river and tidal flows.

Sediment régime

Above Salto Grande there are many basaltic outcrops and the river substratum typically is rocky. The lower river flows through sedimentary strata of variable thicknesses, mostly from the alluvial sandstone formations of Botucatú, along the Ibicuí and Santa María rivers. Erosion rates are low, and suspended solids loads are correspondingly small. Bonetto (1975) estimated the suspended load as 17 106 t a^{-1}, although it would be less in reaches above Puerto San Javier.

High transparencies are associated with the slow current and low suspended solids loads (INCYTH 1978). Secchi disk depths are 20–80 cm above the Pepirí-Guazú junction, on the border between Argentina and Brazil, and 10-45 cm near Colón (Argentina), 216 km from the river mouth. At low-water periods, transparencies are increased still further.

Other physical and chemical features

Salinities generally are low, although increased near the river mouth (OSE 1978), and conductivities are between 30–80 $\mu S\,cm^{-1}$. Quirós & Cuch (1981) recorded 49 mg l^{-1} dissolved solids in the middle reaches. Values of pH typically are 6.5 to 8. Seasonal temperatures are 18–28°C. Dissolved oxygen (DO) levels are high and, particularly in the turbulent waters of the upper river, may attain super-saturation. DO saturation values of 86–108% are reported from the region of the dam at Salto Grande (CTM Salto Grande 1977; Quirós & Cuch 1981). Phosphate levels reportedly are low (range < 0.002–$0.14\,mg\,l^{-1}$; Quirós 1981, 1982; Natale *et al.* 1982), and Sierra *et al.* (1977) recorded 0.8–$2.0\,mg\,l^{-1}$ nitrate in the region of Salto Grande. Lower nutrient levels may occur in downstream areas. Sierra *et al.* (1977) also reported Chemical Oxygen Demands (COD) of 7.6–$18.5\,mg\,l^{-1}$, and a calcium concentration of $5.4\,mg\,l^{-1}$.

There are some chemical similarities between the waters of the Uruguay and Paraná rivers, but the Uruguay's waters are distinguished by their low electrolyte content, and correspond to the calcium bicarbonate type. Low salinities are a common feature of the great South American rivers, and distinctive compared to large rivers elsewhere in the world (Livingstone 1963; Bonetto 1976, 1978).

Biological characteristics

Soils and vegetation

General information about the Uruguay environment is provided by Agudelo *et al.* (1978), STM Salto Grande (1977), FAO-UNESCO (1974), OEA (1969, 1971) and Plan Mapa de Suelos (1978). Here, an overview is provided.

For 600 km below its source, the Uruguay River passes through dense, pluristratified forests on red basaltic soils. The forests include *Balfourodendron riedelianum*, *Cedrela fissilis*, *Cabralea oblongifoliola*, *Apulia leiocarpa* and *Myrocarpus frondosus*. This association declines abruptly in southern Misiones Province, in the region of the 1600 mm annual isohyet, to be replaced by semideciduous forest dominated by piño Paraná (*Araucaria angustifolia*), with other species from the upstream region. The forests are heavily exploited for commercial purposes, exposing large areas to erosion.

Landsat imagery (1 : 500 000) and large-scale aerial photography show conspicuous differences between the left and right bank environments between 500 and 800 km from the river mouth. The left bank is elevated, often steep, and flanked by meadows interrupted only by the tributary forest-tracts; there is also extensive agricultural development (cattle production, cereal and citrus crops). The right bank is mainly low-lying reed and peat swamps where rice and cattle production are the principal agrarian activities.

Between river-km 200 and 560 forests occur on both river banks, although parts of the left bank lack well-developed herbaceous vegetation and soft gramineous and herbaceous legumes occur. The right bank supports a broad savanna ("espinillal" or "espinal") of spiny trees and bushes (e.g. *Acacia caven*, *Prosopis* *nigra, P. affinis*), among *Andropogon lateralis* and other grasses. The trees of this area have been largely displaced by agricultural development. Nearer the river mouth there are extensive humid grasslands ("Pampa Húmeda") on flat and slightly undulating country, with loessic soils suitable for intensive cattle and cereal production.

In Landsat images the Uruguay River appears as a strip of vegetation becoming wider downstream. Cabrera (1951) termed this the "gallery forest", and ascribed its presence to the microclimate established by the river. The green belt begins in the Brazilian semideciduous forests, dominated by *Peltophorum vogelianum, Tabebuia impetiginosa, Anadenanthera macrocarpa, Albizia hassleri* and other species. In the south some species progressively are replaced by others, including *Terminalia australis, Salix humboldtiana, Sapium haematospermum* and *Eithrina crista-galli.*

Development of the gallery forest in the Uruguay Basin, as in other parts of the Plata drainage, is strongly influenced by flow and sediment régimes and by adjacent environments. Generally, species richness and structural complexity decrease with increasing latitude. The main determinants of this latitudinal gradient are progressive changes in river bank elevation, edaphic changes (e.g. soil depth), increasing river width, decreasing rainfall and changes in the annual régimes of temperature and photoperiod.

In the upper basin the gallery forest is little affected by seasonal and short-term changes in water level. Downstream, however, the forests and islands of the valley are subject to variable levels, imposing complex patterns on the distribution and abundance of the vegetation. This is most evident near the river mouth, where the effects of the river microclimate, its flow and sediment régimes and the tidal influence of the Río de La Plata are superimposed.

The maturity of the gallery forest along the Uruguay resembles that of the Paraná at similar latitudes, and may reflect a comparatively low rate of erosion. The lower Uruguay has fewer islands, and their shape is less changeable because the river has a stony substratum and carries smaller loads of fine suspensoids.

Aquatic and riparian vegetation

Various complex interactions of geomorphic, hydrologic and edaphic features suggest that the plant habitats recognised for floodplain rivers by Adams (1964) and Welcomme (1979) should be redefined for the special case of the Uruguay River. A more effective classification may be as follows (cf. Neiff 1978):
(a) Waterfalls,
(b) Mainstem river and large tributaries,
(c) Small streams,
(d) Oxbows,
(e) Wetlands,

(f) Seasonally flooded areas, and
(g) Areas inundated only by exceptional floods.
This scheme is employed in Figs. 4 & 5, illustrating various features of the aquatic plant communities of the Uruguay Basin.

Waterfall habitats are dominated exclusively by the Podostemaceae ("tachyrheophyton" of Dugand 1944). Communities of *Podostemum* occur on rocky substrata, just below the surface of waterfalls and rapids. The plants adhere to the rocks by means of root-hairs (hapters) which secrete a glue-like subtance. Vegetation growth occurs during intermediate water levels, and flowering occurs at low water. During the flowering period, which may last only 24 h (Went in Van Royen 1951), the plants are covered by a thin layer of clear water and desiccation is offset by lignification of the stem tissues. Clearly, these communities depend intimately upon the river's flow behaviour.

The river mainstem has no permanent aquatic vegetation, reflecting variable water levels, steep banks and coarse substrata. The tributary rivers typically have two distinct tracts. In the uppermost reaches the channel section is U-shaped and the tachyrheophyton is little developed. The lower reaches are bordered by extensive wetlands where water is present for variable periods of time. Wetlands near Salto Grande are described by Marchesi (1978), CTM Salto Grande (1977) and Sierra *et al.* (1977). During low-water periods in the tributaries, *Cabomba australis*, *Ceratophyllum demersum* and *Potamogeton striatus* may become established in sheltered marginal areas. Neiff (1978) provides a comparative analysis of the vegetation of different environments in relation to flow patterns. Figs. 4 & 5 illustrate the nature of plant communities in these environments.

In permanent wetlands *Scirpus californicus* ("juncales") is common and provides a habitat for floating rooted species (*Ludwigia peploides*, *Myriophyllum brasiliense*, *Leersia hexandra*) and free-floating species (*Azolla caroliniana*, *Salvinia* spp.). Generally, free-floating plants are of little significance in the Uruguay River. They occur in association with juncales or other rooted species, in areas with stable water levels. Thus, *Eichhornia* species (*E. crassipes*, *E. azurea*) and *Pistia stratiotes* rarely occur. This is a significant difference between the Uruguay and Paraná systems (cf. Neiff 1986).

Seasonal wetlands ("bañados") often are populated by euryoecious plants like *Panicum prionitis* ("pajonales"), *Paspalum rufum* and *Rhynchospora corimbosa*. Floating rooted plants (*Ludwigia*, *Myriophyllum*, *Eleocharis* and *Sagittaria*) are common, as might be expected in habitats subject to changeable water levels. A particular type of wetland, the "bañados-bosque", is exposed to alternate wet and dry periods, and the vegetation is of herbaceous species with sparse trees and shrubs (e.g. *Acacia caven*, *Phyllanthus sellowianus*, *Cephalanthus glabratus*). The aperiodic wetlands are transitional with terrestrial habitats, and are dominated by euryoecious grasses like *Andropogon lateralis* and *Sorghastrum agrostoides*.

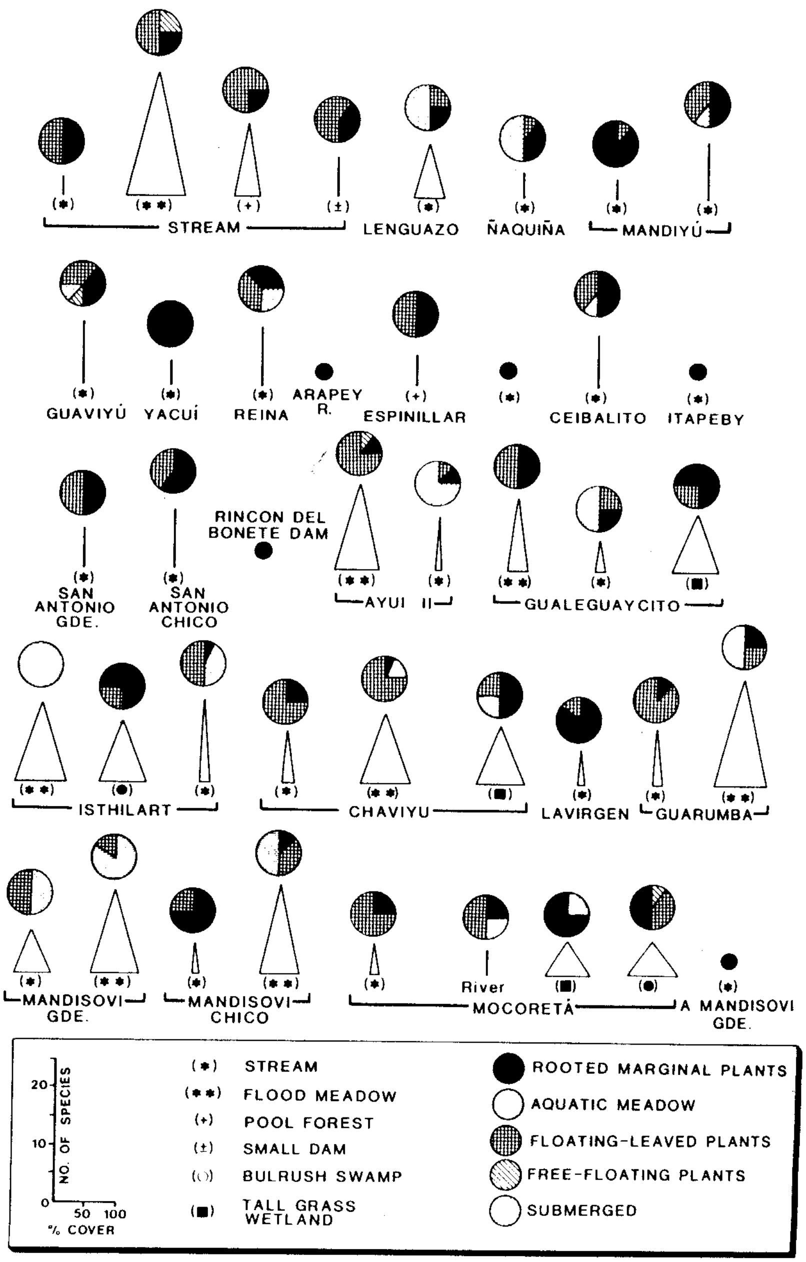

Figure 4. Features of the aquatic vegetation at places in the Uruguay Basin. Various habitat types are indicated. The proportional representation of different vegetation types is indicated by pie diagrams, and the numbers of species (vertical axis) and percentage cover (horizontal axis) are shown as triangles.

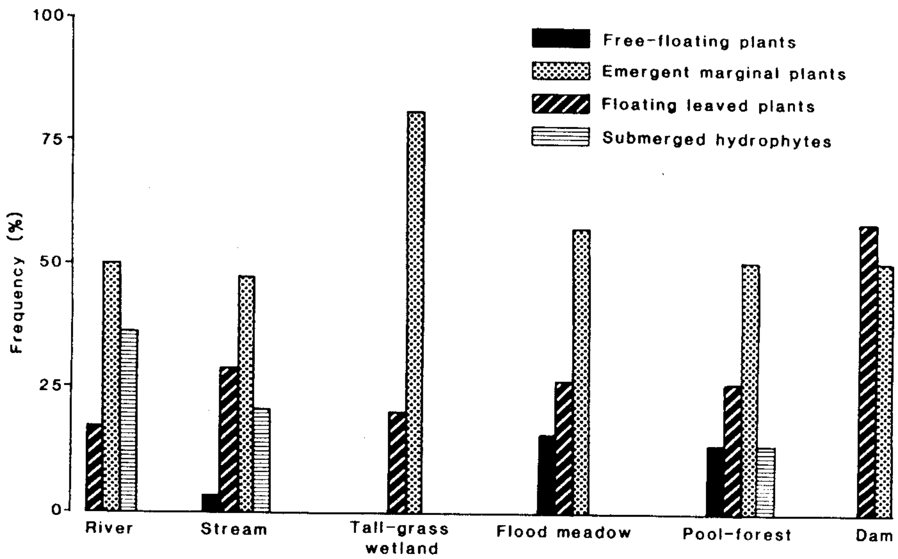

Figure 5. Relative frequencies of aquatic plant types in habitats of the Uruguay system.

Lentic waterbodies, including oxbows ("madrejones"), are comparatively few. They occur on some islands and along the river margins, and are seasonally connected with the river. Their vegetation includes *Scirpus californicus*, *Pontederia lanceolata* and other species adapted to variable water levels.

The floristic richness of the Uruguay Basin reflects the variety of environments represented. In the 150-km segment now inundated by Salto Grande Reservoir, Bacigalupo & Burkhart (1977) recorded 831 species, comprising 800 native species and 31 exotics, although these numbers would be considerably less if only plants within the zone of the river's influence were considered (Neiff 1978). Near Salto Grande, in a 10–15 km wide belt, 300 species would be included from the total recorded by Bacigalupo & Burkhart. Of these 65 are aquatic and semi-aquatic species, and 37 are tree species represented in the riparian forests. These numbers refer to total recorded species and, given the variability of the river régime, they would be significantly less if one year's occurrences only were considered.

Neiff (1978) made quantitative comparisons of the vegetation in environments exposed to different flooding régimes. Near Salto Grande, prior to dam construction, similarity coefficients (Kulczynski–Sørensen Index) of 0.22–0.57 were obtained for various wetland, river and pond communities (Fig. 5). The maximum value, however, was recorded in comparisons between seasonal and annual wetlands, and a more typical range would be 0.20–0.40.

The significance of flooding régimes (hence current velocity, water residence time etc.) is reflected in the presence of two reasonably discrete plant groups:

(a) Euryoecious plants, able to persist through changing conditions. These dominate where there are wide fluctuations in water level; examples are *Rhynchospora corimbosa*, *Polygonum acuminatum*, *Ludwigia peploides*, *Paspalum rufum*, *Panicum prionitis*, *Andropogon lateralis*, *Salix humboldtiana*, *Sapium haematospermum*, *Inga uruguensis* and *Acacia caven*.

(b) Stenotypic plants, limited to a narrow range of conditions. In the Uruguay system these are plants capable of rapid vegetative growth, including species of *Hydrocotyle*. Some trees (e.g. *Luehea divaricata*, *Tabebuia impetiginosa*) dependent on the river are a special case, confined to stable areas which allow them to persist despite variable flows.

Each group is represented by many species, if records accumulated over long periods are considered, but species richness may be low at any one stage of the seasonal cycle. Natural communities generally consist of relatively few euryoecious species and a variable complement of transient, stenotypic species dependent on particular conditions.

Another feature of the relationship between the plant communities and patterns of flow is seen in the periodicity of occurrence of particular species. This is most evident in herbaceous communities, particularly the wetlands, where there are sharp distinctions between stages in the flooding cycle. Periodicity is reflected also in the reduced herbaceous understory of the gallery forests subject to annual flooding. These species are scarce also in the island communities because most of these are subject to annual floods. Tree species in these insular communities are dependent on floods for dispersal and germination, as with similar communities elsewhere in the Plata drainage system (Neiff 1981).

Other biological features

Phytoplankton

The little information that exists for the phytoplankton of the Uruguay system is summarised by Onna (1978) and Quirós & Luchini (1982). Onna was concerned with the Argentine section of the river, from the junction with the Pepirí Guazú (in Misiones Province, near the Brazilian border) to the Río de La Plata. Peak densities occurred in spring and summer, with 37 000 ind. l^{-1} near river-km 583 (Paso de los Libres, Corrientes Province). In the lower river, at km 178 (Concepción del Uruguay, Entre Ríos Province) the summer maximum density was 40 000 ind. l^{-1}. Otherwise, low densities are typical of the system, and may reflect the paucity of lentic water bodies in the floodplain (cf. Onna 1978), relative to the Paraná system (Bonetto 1978).

Onna recorded 71 genera of algae, including 31 genera of Chlorophyta, 2 Chrysophyta, 28 Bacillariophyta, 6 Cyanophyta, 2 Euglenophyta, 1 Pyrrophyta and the remainder Dinoflagellata. Many genera were distributed uniformly along the river throughout the seasonal cycle. Bacillariophytes were represented by *Melosira* (*M. granulata*, *M. varians* and *M. italica*, with few *M. roeseana* and *M. undulata*), *Pinnularia*, *Navicula*, *Synedra*, *Gomphonema*, *Cymbella*, *Surirella*, *Eunotia*, *Gyrosygma* and *Amphipleura*. Among the chlorophytes *Scenedesmus*, *Pediastrum*, *Closterium* and *Cosmarium* were most common, although *Staurastrum*, *Coelastrum* and others were also present in the lower reaches. Among other taxa only euglenophytes (*Trachelomonas*) were consistently abundant.

Some of these genera were present, although less abundant, in the region of Salto Grande prior to dam construction (Sierra *et al.* 1977). Among 31 recorded genera, diatoms sometimes accounted for more than 80% of the biomass. Chlorophytes were consistently present, but comprised only 2–15% of the total. Other taxa did not exceed 1–2%, except in some tributary streams in various seasons. The phytoplankton of tributaries may have a quite distinct composition, and their influence on the mainstem phytoplankton may be considerable. In the Pepirí Guazú, pyrrophytes, euglenophytes, cyanophytes and chrysophytes made up more than 25% of phytoplankton densities in spring, and euglenophytes, cyanophytes and chrysophytes comprised 20% of the biomass in summer. In the Arapey River in summer Euglenophyta accounted for 70% of the total biomass, Bacillariophyta for 28%, and Chlorophyta were scarce.

Onna (1978) recognised two patterns of phytoplankton abundance. The first, involving spring and autumn maxima, is typical of reaches upstream of about river-km 624 (near Yapeyú). The second, characterised by a summer peak, is typical of the section from the river mouth to km 489 (near Monte Caseros).

Onna also noted seasonal differences in the relative proportions of centric and pennate diatoms. In spring, centric diatoms represented 30–50% of the total diatoms at km 1170 (El Soberbio), and 60–80% near km 768 (Santo Tomé). In summer, pennate diatoms assumed dominance at km 379 (Federación). In autumn, centric diatoms were most abundant in the upper river and in the 200 km before the river mouth, but the two types occurred in similar proportions between km 203 and km 489 (Colón and Monte Caseros, respectively). In winter the two types were equally represented, although centric diatoms had a slight ascendancy up to about km 309, and pennate diatoms were slightly more common upstream of that region.

Quirós & Luchini (1982) investigated the phytoplankton in the section of river now occupied by Salto Grande Reservoir. They analysed phytoplankton community structure in regard to various environmental characteristics, and concluded that algal biomass was strongly influenced by the flow and sediment régimes. Chlorophyll *a* levels were higher in tributaries (205 mg m^{-3}) than in the mainstem (1.2–18.4 mg m^{-3}). Diatoms were most abundant, although cyanophytes were significant during periods of high turbidity.

Diatoms often dominate in the phytoplankton of the large South American rivers (e.g. Bonetto 1978, 1986a). This is associated with high concentrations of reactive silica and low concentrations of calcium relative to large rivers in other parts of the world (Livingstone 1963).

Zooplankton

Information about zooplankton is limited to scattered samples from the lower reaches (Brian 1925; Paggi 1976; Pezzani 1980). About 40 species have been recorded, including rotifers, copepods, cladocerans and protozoans. Most are from lentic habitats.

Copepods reported from the river include the calanoids *Notodiaptomus incompositus* and *N. anisitsi* (= *inflexus*) and the cyclopoid *Eucyclops neumanni neumanni* (Brian 1925). José de Paggi (1978) has recorded – from samples near the river mouth – six rotifer species (*Trichocerca rattus*, *Polyarthra trigla*, *Keratella tropica*, *K. cochlearis*, *Euchlanis dilatata*, *Notholca* sp.), the cladoceran *Bosmina longirostris* and the calanoid *Pseudodiaptomus richardi*.

Although there are few quantitative data, it appears that zooplankton abundances are remarkably low. Isolated samples have indicated densities of 1–10 ind. l^{-1} (José de Paggi 1978). This may reflect the irregular river profile and shorter water residence times.

Fish

The fish fauna of the Uruguay Basin has been neglected in comparison to studies of the Paraná and Paraguay rivers. According to Ringuelet (1975), most of the Uruguay's fauna is typical of the Guiano-Brasilic zoogeographic subregion (Río de La Plata Basin within the Domain Paranense, and parts of the Alto Paraná and Parano-Platense ichthyogeographic provinces). Characiforms and siluroids are dominant elements. Most of the Gymnotoidei (gymnotiforms) and Cichlidae (perciforms) are of Brazilian origin.

Fowler (1954) recorded 28 species for the Uruguay and some tributaries in Brazil. Other investigations have yielded a list of more than 140 species for the Argentine section of the river (e.g. Devicenzi & Teague 1942; López *et al.* 1980; Miquelarena *et al.* 1981; Prensky & Baigun 1982; Ringuelet *et al.* 1967; Ringuelet 1975). In comparison, Ringuelet (1975) listed 230 species for the Paraná River in Argentina, and more than 360 species for the Paraguay River (cf. Bonetto 1986b).

Table 1 lists the fish species known from the Uruguay system, but excludes those of doubtful occurrence and anadromous and estuarine species. Important anadromous species include Engraulidae (*Lycengraulis olidus* and *L. simulator*, "anchoas de río" and Clupeidae (*Ramnogaster melanostoma melanostoma*, "sardina o mandufia"), *Brevoortia pectinata*, *B. aurea* and *Pellona flavipinnis* ("lachas"). Estuarine species which make short excursions into the lower river include the muraenid *Prionodophis ocellatus* ("morena") and the zoarcid *Iluocoetes fimbriatus* ("viuda").

Among bottom-living species, the Loricariidae ("viejas del agua") is the largest family of South American catfish. The Potamotrygonidae and some Pimelodidae (Pimelodinae are called "bagres"), Auchenipteridae, Aspredinidae, Ageneiosidae and several other families include bottom-living species. The Callichthyidae ("cascarudos"), Achiridae ("lenguados de río") and Doradidae ("armados") show similar preferences, but are more widely distributed. Some inhabit stony areas in fast-flowing water, and others prefer the muddy substrata of small streams and still waters. In general these are omnivorous, sedentary species. The diet of some species includes sponges (Porifera), which are widespread in the Uruguay system.

Predatory characiforms like *Salminus* and *Brycon* are typical of open-water environments. These are schooling species that undertake extensive migrations for reasons not clearly understood. Some move upstream to spawning grounds and others make feeding migrations downriver, but schools often are encountered moving in opposite directions. Tagged specimens of *Salminus maxillosus* in the Uruguay River have been recaptured up to 327 km from the release site N of Concordia (Bonetto 1976). Some cichlid species (*Crenicichla*, *Batrachops*) are sedentary but aggressive predators resembling the pikes (Esocidae) of the Northern Hemisphere.

In a survey of areas with rocky substrata during flood conditions, Sierra *et al.* (1977) recorded about 39 species, including abundant Callichthyidae, Cichlidae, Loricariidae and others. The pimelodid *Heptapterus mustelinus* also was recorded.

The "pechito" (*Thoracocharax stellatus*), a member of the Gasteropelecidae (hatchetfish, or flying characins), is a small and picturesque fish that frequents the water surface, and may "fly" above the surface by means of rapid movements of the pectoral spines. Another curiosity is the pygidiid *Homodiaetus maculatus*, whose dispersal is enhanced as a temporary ectoparasite of *Luciopimelodus pati* and *Parabranquioica taequei*. Other host species are *Salminus maxillosus*, *Prochilodus platensis*, *Pimelodus clarias maculatus* and *Serrasalmus nattereri*.

In temporary waters, cyprinodontids of the genus *Cynolebias* are common. These are referred to as "annual fish", because their life cycle lasts one year. The eggs are deposited in the sediment at *c.* 15-cm depth, and require a period in the substratum before hatching.

Among carnivorous species, the Serrasalmidae is widespread in South America and represented by several species of the renowned *Serrasalmus* ("pirañas" or "palometas"). These are aggressive and prone to attack other animals, including large vertebrates. They are most frequently encountered in quiet waters. Other quiet-water fish, including iliophagous and herbivorous

Table 1. Fish reported from the Uruguay system, including species of doubtful occurrence and anadromous and estuarine species. Asterisks indicate species significant in the fishery. For references see text.

ORDER, Family	Species	Common name
CHARACIFORMES		
Anostomidae	*Abramites solarii*	jikii
	**Leporinus obtusidens*	boga
	Leporinus striatus	trompa roja
	Leporinus fasciatus	boga lisa
	Leporinus friderici	boga
	Leporinus trifasciatus	
	**Schizodon fasciatus*	boga lisa
	Schizodon nasutus	
	Schizodon platae	
Characidae	*Acestrorhynchus falcatus*	dientudo
	Acestrorhamphus altus	dientudo
	Acestrorhamphus jenynsi	dientudo
	Aphyocharax anisitsi	
	Aphyocharax rubropinnis	
	Asiphonichthys stenopterus	dentudo transparente
	Astyanax abramis	mojarra pacusa
	Astyanax bimaculatus	mojarra
	Astyanax fasciatus	mojarra
	**Brycon orbygnianus*	salmón criollo
	Bryconamericus iheringi	
	Bryconamericus stramineus	
	Charax gibbosus	dentudo, dentudo jorobado
	Cheirodon interruptus	mojarrita
	Cheirodon piaba	mojarrita
	Cynopotamus argenteus	dientudo jorobado
	Glandulocauda terofali	
	Holoshethes pequira	pequira
	Hyphessobrycon anisitsi	
	Hyphessobrycon meridionalis	
	Macropsobrycon uruguayanae	
	Oligosarcus hepsetus	dientudo
	Oligosarcus oligolepis	dientudo
	Prionobrama paraguayensis	
	Pseudocorynopoma doriai	mojarra de velo
	Rhaphiodon vulpinus	chafalote
	**Salminus maxillosus*	dorado
	Triportheus paranensis	machete, golondrina
Characidiidae	*Characidium ayuiensis*	
	Characidium fasciatus	tritolo
	Characidium teaguei	tritolo
Curimatidae	*Curimatorbis platanus*	sabalito plateado
	**Prochilodus platensis*	sábalo
	Pseudocurimata gilberti	sabalito
	Pseudocurimata nitens	

Table 1. (continued)

ORDER, Family	Species	Common name
Cyprinidae	*Cyprinus carpio*	carpa
Erythrinidae	**Hoplias malabaricus*	tararira, tarango
Gasteropelecidae	*Thoracocharax stellatus*	pechito, chirola
Hemiodidae	*Apareiodon affinis*	virolito
	Parodon suborbitale	
Potamotrygonidae	*Potamotrygon brumi*	raya
	Potamotrygon hystrix	raya
	Potamotrygon motoro	raya
Serrasalmidae	**Colossoma mitrei*	pacú
	Serrasalmus nattereri	palometa, piraña
	Serrasalmus spilopleura	palometa, piraña
CYPRINODONTIFORMES		
Cyprinodontidae	*Cynolebias bellottii*	
	Cynolebias spp.	
Jenynsiidae	*Jenynsia lineata*	madre de agua
Poeciliidae	*Phalloceros caudimaculatus*	madrecita de una mancha
	Cnesterodon decemmaculatus	madrecita de agua, pechito
	Phalloptychus januarius	
GYMNOTIFORMES		
Apteronotidae	*Apteronotus brasiliensis*	morena negra
Gymnotidae	*Gymnotus carapo*	anguiya flecuda
Rhampichthyidae	*Eigenmannia virescens*	ratona
	Hypopomus artedii	morenita
	Rhampichthys rostratus	anguiya picuda
	Poecilia vivipara	
MUGILIFORMES		
Atherinidae	**Basilichthys argentinensis bonariensis*	pejerrey
	Basilichthys guazu	
Synbranchidae	**Synbranchus marmoratus*	anguila criolla
PERCIFORMES		
Cichlidae	*Aequidens portalegrensis*	
	Aequidens tetramerus	acará
	Batrachops scotti	
	Batrachops semifasciatus	
	Cichlaurus facetus	chanchito
	Crenicichla acutirostris	cabeza amarga
	Crenicichla lacustris	cabeza amarga
	Crenicichla lepidota	cabeza amarga
	Crenicichla saxatilis	san pedro, cabeza amarga
	Crenicichla vittata	cabeza amarga
	Geophagus australis	chanchita
	Geophagus balzani	
	Geophagus brachyurus	
	Geophagus brasiliensis	san pedro, castañeta
	Geophagus gymnogenys	

Table 1. (continued)

ORDER, Family	Species	Common name
Sciaenidae	*Pachyurus bonariensis*	corvina de río
	Pachyurus paranensis	corvina de río
PLEURONECTIFORMES		
Achiridae	*Achirus jenynsi*	
	Achirus lineatus	lenguado de río
SILURIFORMES		
Ageneiosidae	**Ageneiosus brevifilis*	mandubé, manduvé
	**Ageneiosus valenciennesi*	manduví, manduvé
Auchenipteridae	*Auchenipterus nuchalis*	
	Auchenipterus paysanduanus	mandubí bastardo
	Trachycorystes galeatus	bagre rojizo
	Trachycorystes striatulus	torito
	Trachycorystès teaguei	torito con guampas
Ariidae	*Netuma barbus*	bagre de mar
Aspredinidae	*Bunocephalus coracoideus*	guitarrita
	Bunocephalus iheringi	guitarrita
	Bunocephalus retropinnis	
Callichthyidae	*Callichthys callichthys*	cascarudo
	Cascadura maculocephala	
	Corydoras paleatus	tachulea
	Hoplosternum littorale	cascarudo
Doradidae	*Megalodoras laevigatulus*	
	Oxydoras kneri	armado chancho
	**Pterodoras granulosus*	armado común
	**Rhinodoras d'orbignyi*	armado amarillo
Loricariidae	*Ancistrus cirrhosus*	vieja
	Ancistrus hoplogenys	vieja
	Loricaria anus	vieja, vieja de agua
	Loricaria commersonoides	vieja
	Loricaria devincenzi	
	Loricaria felipponei	vieja
	Loricaria labialis	vieja de agua
	Loricaria maculata	vieja de agua
	Loricaria nudiventris	vieja
	Loricaria thrissoceps	vieja
	Loricaria vetula	vieja de látigo
	Otocinclus flexilis	
	Plecostomus latus	vieja de agua
	Plecostomus borellii	vieja de agua
	Plecostomus commersoni	vieja de agua
	Plecostomus luteomaculatus	vieja de agua
	Plecostomus pleostomus	vieja de agua
Pimelodidae	*Heptapterus mustelinus*	bagre anguilla
	Iheringichthys westermanni	bagre trompudo
	**Luciopimelodus pati*	patí
	**Megalonema platanum*	bagra blanco

Table 1. (continued)

ORDER, Family	Species	Common name
	Parapimelodus valenciennesi	bagarito
	**Paulicea lütkeni*	manguruyú
	Pimelodella gracilis	bagre cantor
	Pimelodella laticeps	bagre gris
	**Pimelodus albicans*	bagre blanco, moncholo
	**Pimelodus clarias*	bagre amarillo
	**Pseudoplatystoma coruscans*	surubí manchado
	**Pseudoplatystoma fasciatum*	surubí atigrado
	Rhamdia hilari	mandi bagre
	Rhamdia microps	
	Rhamdia sapo	bagre sapo
	**Sorubim lima*	manduví cucharón
	Steindachneridion inscripta	
	**Zungaro zungaro*	manguruyú
Pygidiidae	*Homodiaetus anisitsi*	
	Homodiaetus maculatus	camarón
	Homodiaetus vaz-ferreirai	
	Parabranchioca teaguei	sanguijuela
	Pygidium eichorniarum	
	Scleronema angustirostris	
	Scleronema operculatum	

species, are *Prochilodus*, *Leporinus* and *Schizodon*, some species of *Characidium*, *Apareiodon* and other characiforms. Otherwise, piscivorous pimelodids like *Zungaro*, *Paulicea* and *Pseudoplatystoma* generally occur in deep, open-water habitats.

Fisheries are of great importance to the human populations of the Cuenca del Plata (the region bordering the Río de La Plata). The major exploited species are indicated in Table 1. Despite the importance of the fishery, few statistics are available other than those issued by the Dirección Nacional de Pesca Continental de la Argentina. Most of the catch is marketed as fresh fish, but large portions are used in production of oil, fertiliser, fish flour and other products.

The yield in 1979 was the highest recorded aggregate for the period 1950–1981. In that year the records for Argentina indicate a national freshwater production of 16 339.2 t, or 2.8% of the total (marine and inland) production. Of this, 93.3% came from the rivers of Cuenca del Plata, and 37.5% of this was represented by ichthyomass (the remainder being crustaceans and molluscs). In contrast, the river fisheries in 1920 represented 30–40% of total production and in 1942 the proportion was 45.6%. The obvious decline since has been due mainly to expansion of the marine fishery.

Local catches may be very patchy. In 1981 near Santo Tomé (Corrientes Province) the catch was a mere 0.26 t, and 0.62 t upstream near San Javier (Misiones Province). Virtually the entire yield came from the lower reaches; the maximum catch was 1208.2 t at Gualeguaychú (Entre Ríos Province). Most of the total yield in that year was sábalo (*Prochilodus platensis*, 1205.5 t), with a variety of less significant species [*Parapimelodus valenciennesi* (10.6 t), *Luciopimelodus pati* (5.7 t), *Salminus maxillosus* (4.8 t), *Pseudoplatystoma* spp. (3.4 t) and *Basilichthys argentiniensis bonariensis* (1.5 t)]. The remainder consisted of small contributions from other asterisked species in Table 1.

Other vertebrates

Information about the frog fauna of the Uruguay system is provided by Cei & Roig (1961) and Sierra *et al.* (1977). The fauna includes Bufonidae (*Bufo paracnemis*, *B. granulosus*), Hylidae (*Hyla faver*, *H. raddiana*, *H. semiguttata*, *H. trachytorax*, *H. minuta*, *H. squalirostris*, *H. evelinae*, *H. pulchella*, *Aplastodiscus perviridis*, *Phyllomedusa iheringi*) and numerous Leptodactylidae (e.g. *Leptodactylus mystacinus*, *L. ocellatus*, *L. riograndensis*, *L. prognathus*, *L. pentadactylus*, *Physalaemus gracilis*, *Crossodactylus dispar*).

Reptilia are represented by two families of tortoises, the Testudinidae (*Chrysemys dorbignyi*) and Chelidae (*Hydromedusa tectifera*, *Phrynops geoffroanus* and *P. hilarii*) (Freiberg 1977a; Sierra *et al.* 1977). One crocodilian species ("yacaré", *Caiman latirostris latirostris*) occurs (Achaval 1977; Freiberg 1977b), although it is near extinction as a result of hunting for leather. Snakes found in aquatic environments include numerous Colubridae ("culebras") (e.g. *Helicops carinicaudus infrataeniatus*, *Liophis jeageri*, *L. miliaris*, *L. anomalus*, *Lystrophis dorbignyi*, *Oxyrhopus rhombifer rhombifer*, *Philodryas patagoniensis*, *Thamnodynastes strigilis*). Two other colubrids, *Sibynomorphus turgidus* and the tree-living *Chironius bicarinatus* commonly occur in the gallery forests. The largest aquatic snakes ("curiyú", *Eunectes notaetus*, and "ñacaniná", *Cyclagras gigas*) belong to the Boidae; numbers of both have been drastically reduced by hunting. Poisonous species occur among the Viperidae (Crotalinae), notably *Crotalus durissus* ("cascabel") and species of *Bothrops* ("yarará"), including the widespread *B. alternatus*, the more restricted *B. neuwiedi*, and *B. jararaca*, *B. jararacussu*, *B. atrox* and *B. cotiara*, all found in the upper basin as far upstream as Misiones Province, Argentina. In addition, *Micrurus frontalis* and *M. corallinus* are recorded. Further information is given by Achaval (1977) and Di Tada & Abalos (1976).

Birds are represented by many families and species. Indeed, the name "Uruguay" comes from the Guaraní Indian word for "river of birds". Among the common aquatic species are Ciconiidae (*Mycteria americana* ["doroteo"], *Ciconia maguari* ["cigueña"], *Jabiru mycteria* ["jabirú"]) and Ardeidae ("garzas", "mirasoles"; e.g. *Ardea cocoi*, *Egretta thula*, *Syrigma sibilatrix*, *Nycticorax nycticorax*, *Butorides striatus*, *Tigrisoma lineatum*). According to De la Peña (1978) and Sierra *et al.* (1977), the Anatidae ("patos") is represented mainly by

Dendrocygna viudata, *Anas georgica*, *A. flavirostris*, *A. versicolor* and *Cairina moschata*. Other common birds are Podicipedidae ("macáes"), Phalacrocoracidae ("viguáes"), Anhingidae ("bigúa víboras"), Threskiornithidae ("bandurrias"), Jacanidae ("gallitos de agua"), Rinchopidae ("rayadores") and Alcedinidae ("martín pescador").

Aquatic mammals include the didelphid *Chironectes minimus minimus* ("comadreja acuática"), now much less abundant than formerly (Massoia 1976). Two mutelids (Lutrinae) occur, both capable swimmers even in fast-flowing water. These are *Lontra longicaudis longicaudis* ("lobita de río") and *Pteronura brasiliensis paranensis* ("lobo grande de río"). Both are hunted for their valuable pelts.

Rodents include three principal families. The Cricetidae include species of the very common *Holochilus*, namely *H. brasiliensis vulpinus* ("rata de agua chica"), which causes damage to fruit trees and willows, and *H. magnus* ("rata de agua grande"). The Myocastoridae are represented by the well-known *Myocastor coypus bonariensis* ("guiyá", "coypu" or "nutria"), another commercial fur species. The Hydrochaeridae are represented by *Hydrochaeris hydrochaeris* ("carpincho" or "capybara"), the largest of all extant rodents, attaining 50-kg weight. This species too is hunted for its pelt and meat.

Features of Salto Grande Reservoir

The man-made lake at Salto Grande is the largest impoundment on the Uruguay River system. It commenced operation in 1979, and generates *c.* 1890 MW hydro-electric power through 14 turbines. The costs of construction and maintenance are shared by Argentina and Uruguay.

Salto Grande Dam (31°S, 58°E) is approximately 370 km N of Buenos Aires, between Concordia (Argentina) and Salto Grande (Uruguay). Some morphometric features are shown in Table 2. In particular, the reservoir has a length of 144 km, a surface area of 780 km^2 and a maximum depth of 35 m. The basin generally is narrow and shallow, and hence the water renewal rate is rapid (29.4 a^{-1}).

Table 2. Morphometry of Salto Grande Reservoir, Uruguay River

Surface area	780 km^2
Volume	$5 \times 10^9 m^3$
Maximum depth	35 m
Mean depth	6.4 m
Mean width	5.4 km
Length of shoreline	1190 km
Shoreline development	11.2
Mean annual inflow	4640 $m^3 s^{-1}$
Water renewal rate (approx.)	29.4 a^{-1}

The reservoir has five principal arms, corresponding to the flooded valleys of tributary systems. On the right bank (Argentina), these are the Mocoretá, Mandisoví and Gualeguaycito rivers, and on the left bank (Uruguay) they are the Arapey and Itapebí rivers (see Fig. 1). Quirós & Cuch (1981) discuss the chemical features of the reservoir with regard for the various effects of these tributary inflows. As mentioned earlier, the reservoir has flooded the rapids which gave Salto Grande its name. Another 12 dams are planned for construction on the Uruguay system.

Conclusion

In several respects, the Uruguay system differs fundamentally from the neighbouring Paraná and Paraguay rivers. These differences mainly reflect the geomorphic immaturity of the Uruguay Basin, indicated by the river's profile (Fig. 2) and the prevalence of rocky substrata and strong currents, especially upstream of Salto Grande Reservoir.

The reservoir separates two tracts. The "High Uruguay", from the headwaters to the dam site, has a pronounced slope and a flow régime determined mainly by rainfall in the upper catchments. The "Lower Uruguay", downstream of the dam, has a lesser gradient, higher suspended load and a flow régime subject to the tidal influences of the Río de La Plata. Each tract is distinguished by other physical, chemical and biological differences.

The tributary rivers have a profound influence on the mainstem, but they have similar ecological characteristics and their individual contributions are not easily discerned. This is illustrated, for example, by the work of Onna (1978) on phytoplankton. It is an unusual situation among large rivers.

Scarce nutrient supplies, high turbidities and rapid flow rates undoubtedly contribute to the generally low phytoplankton productivity (cf. Quirós & Luchini 1982). Further, the productivity of hydrophyte communities is low, reflecting the flow régime and the lack of extensive wetlands compared to the Paraná system (Neiff 1986; Bonetto 1975, 1976, 1986a). Hence in the Uruguay system there may be an increased dependence on allochthonous detritus, as in woodland rivers and streams elsewhere (e.g. Cummins *et al.* 1966; Minshall *et al.* 1983). This is merely one interesting sideline in a river where biological information, especially, is lacking. In many respects, the Uruguay may lay claim to being among the least-known of the great South American rivers. The prospects for future research, therefore, are exciting indeed.

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