

## 12 Fishes

LILIANA ROSSI<sup>1,2,3</sup>, ELLY CORDIVIOLA<sup>1</sup>, AND MARÍA JULIETA PARMA<sup>1,2</sup>

### 12.1 Introduction

The middle section of the Paraná River shows a great richness of habitats, constituting an environmental mosaic, due to its spatiotemporal dynamics, inhabited by several fish species with different life strategies. The important degree of connection among environments and the displacements of fish populations in the channel–floodplain complex favor the processes of colonization and the participation of these species in complex trophic webs that link different divisions of the system. As in other large floodplain rivers, the extension of periodically flooded areas and the duration of flood pulses influence productivity and diversity of species (Junk et al. 1989; Neiff 1990). High fish diversity and productivity are observed in this section of the Paraná River (Bonetto 1986). Although the study of ichthyofauna in this area began a long time ago, there are still many aspects of their biology and ecology that should be deeply investigated.

### 12.2 Richness, Distribution and Abundance of Species

From the ichthyogeographical point of view, this region is part of the Subtropical domain of the Guyanese-Brazilian subregion, “Parano-platense” (e.g., Paraná River and Río de la Plata) province (Ringuelet 1975). Most fish species inhabiting the Middle Paraná River have Brazilian origin. The Paraná River could have had an essential role in their penetration, acting as a faunistic corridor and facilitating the entrance of tropical and subtropical elements of the aquatic fauna (Lopez et al. 2005).

In the “Parano-platense” province, there are currently 422 native fish species, representing 92% of Argentine continental fish and approximately 10% of

---

<sup>1</sup>Instituto Nacional de Limnología (INALI). Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina (CONICET) y Universidad Nacional del Litoral (UNL). Santo Tomé, Argentina

<sup>2</sup>Facultad de Humanidades y Ciencias. Universidad Nacional del Litoral (UNL). Santa Fe, Argentina

<sup>3</sup>e-mail: loyrossi@arnet.com.ar

neotropical fish (Lopez 2001). Most represented orders are Characiformes (147 species) and Siluriformes (150 species). These groups also constitute the main fish component of other large Neotropical rivers (Lowe McConnel 1987). In the Middle Paraná River, there are 216 fish species (Drago et al. 2003), belonging to nine orders and 35 families (Table 12.1); this diversity is related to the important habitat richness of its great flooding area (Neiff 2001).

In these lotic systems, characterized by their great variability at different scales, the fish habitat becomes a continuous “trade-off” between that variability and life requirements (Leveque 1995). Considering life histories of the main species and their use of the habitat, Middle Paraná River populations can be grouped into three great categories, described by Welcomme (2000): species that mainly use the channel, those that mainly inhabit the lakes, and those whose life cycles involve the use of different types of habitats. Synthesis of the spatial distribution and relative abundance of species in the Middle Paraná River have been recently carried out by Drago et al. (2003) and Menni (2004). The first authors characterized different habitats and, considering different information sources, assigned values of relative abundance for each fish species. Therefore, they obtained the following information: a reduced number of species is frequent in only one habitat unit, whereas most fish use at least two out of three large units, e.g., the channel, the plain lotic environments and the lenitic area (Fig. 12.1). The most abundant species, frequently captured in the three macrohabitats, are the characid “sábalo”, *Prochilodus lineatus*, and small characid species, commonly called “mojarras” (*Astyanax* (A.)

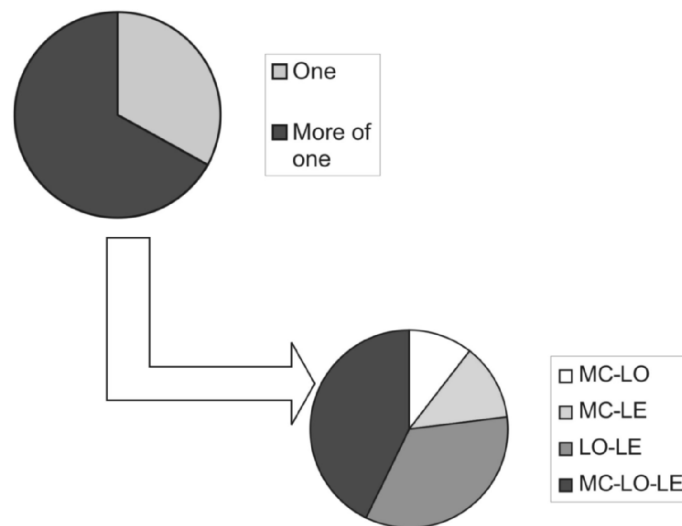


Fig. 12.1 Percentage representation of the registry of fish species per habitat of the Middle Paraná River (adapted from Drago et al. 2003). MC main channel; LO lotic environments of the flooding valley and LE lenitic environments

**Table 12.1** Taxonomic composition of the ichthyofauna of the Middle Paraná River (taken from Drago et al. 2003)

Order	Family	No. of species	
Myliobatiformes	Potamotrygonidae	6	
Clupeiformes	Clupeidae	3	
	Engraulidae	2	
Cypriniformes	Characidae	50	
	Serrasalminidae	8	
	Gasteropelecidae	1	
	Erythrinidae	2	
	Lebiasinidae	4	
	Anostomidae	8	
	Hemiodidae	3	
	Curimatidae	10	
	Characiidae	2	
	Gymnotidae	1	
	Apterontidae	3	
	Rhamphichthyidae	6	
	Siluriformes	Doradidae	8
		Auchenipteridae	4
Aspredinidae		4	
Pimelodidae		21	
Ageneiosidae		2	
Hypophthalmidae		2	
Cetopsidae		1	
Thychomycteridae		2	
Callichthyidae		5	
Loricariidae		30	
Atheriniformes	Belonidae	2	
	Cyprinodontidae	1	
	Jenynsidae	1	
	Poeciliidae	2	
	Atherinidae	2	
Synbranchiformes	Synbranchidae	1	
Perciformes	Sciaenidae	4	
	Cichlidae	12	
Pleuronectiformes	Achiridae	2	
Lepidosireniformes	Lepidosirenidae	1	

*fasciatus fasciatus* and *Odontostilbe pequirá*). Among the frequent but not very abundant species that also use the three mentioned units are: the jaw characin or “dorado”, *Salminus brasiliensis*, and medium-size Siluriformes, as the “moncholo” catfish, *Pimelodus albicans*, the “amarillo” catfish, *Pimelodus maculatus*, and another catfish, the “manduvé fino”, *Ageneiosus valenciennesi*. In lotic environments, large and medium-size Siluriformes are usually found and moderately abundant, such as the “surubí”, *Pseudoplatystoma coruscans*, the tiger shovelnose catfish or “surubí atigrado”, *P. fasciatum fasciatum*, the duckbill catfish or “manduvé cucharón”, *Sorubim lima*, the granulated catfish or “armado común”, *Pterodoras granulosus*, and the ocellated river stingray or “raya” *Potamotrygon motoro*. In lenitic environments, an ichthyophagous fish, the wolf fish or “tararira”, *Hoplias malabaricus malabaricus*, is frequently and abundantly found, whereas piranhas (genera *Serrasalmus* and *Pygocentrus*), cichlids, commonly known as “chanchitas” (*Gymnogeophagus australis* and *Cichlasoma facetum*), and the pike cichlid or “San Pedro”, *Crenicichla lepidota*, are also found, although they are less abundant.

The variability of local diversity patterns is related to the structural and functional complexity of the system, influencing the availability of microhabitats and resources. The composition of fish ensembles in lotic environments has been scarcely explored in this section of the basin, mainly due to the methodological difficulties for their study. Oldani and Oliveros (1984) analyzed the composition of commercial captures in the Paraná River (at sites near the city of Paraná, 31°42'34"S and 60°29'7"W) and certain periods of presence and frequency of captures for large species. Species represented in the channel during the hydrological cycle were the “sábalo”, *P. lineatus*, the “patí” catfish, *Luciopimelodus pati*, the “moncholo” catfish, *P. albicans*, and the “surubí” catfish, *P. coruscans*, being *P. lineatus* and *Pterodoras granulosus* the most abundant ones. The use of the channel has also been documented for large fish through the study of longitudinal migrations (Bonetto et al. 1971). In relation to lower flow lotic environments, Demonte and Arias (2005) surveyed all studies carried out in the Paraná River tributaries in the province of Entre Ríos, finding a total of 66 species. The information on the structure of lenitic communities is more abundant and diverse, since there are studies in temporary and permanent environments with different degree of connection to the channels, in different hydrological cycles and with different sampling efforts.

In temporary and semi-permanent lakes, periodically connected to the Salado River, a tributary environment of the Paraná River (31°40'37"S and 60°44'22"W), Bonetto et al. (1969, 1970) analyzed the specific composition and fish biomass during an isolation phase. The species richness was 60 for a total capture in a lake, whereas a total of 75 species were found in 18 lakes of the Los Sapos Island. In these temporary environments, investigated after their connection to the river, the community was mainly integrated by juveniles of *Prochilodus lineatus*, dominating in number and biomass. Mean biomass values were near 500 kg ha<sup>-1</sup> for the Los Sapos Island and 2,000 kg ha<sup>-1</sup>

for environments of the El Vado Island, being the latter probably influenced by the pronounced isolation period. The important variations in structure and biomass of fish communities in these environments have been mainly attributed to fluctuations at the hydrometric level (Cordiviola 1992).

In other shallow environments of the Corrientes area (27°28'S and 58°59'W), Cordiviola de Yuan and Pignalberi (1985) also proved the dominance of *Prochilodus lineatus* in six out of 12 surveyed lakes, whereas in the others, *Plagioscion macdonaghi*, *Hypostomus robini*, *Potamotrygon* and *Apareiodon affinis* were dominant in the captures.

Several investigations have been carried out in permanent lakes of the alluvial valley, connected to the channels during a great part of the hydrological cycle. In the "La Cuarentena" Lake (31°42'S and 60°37'W), connected to the Paraná River, Tablado et al. (1988) analyzed the variations in species density and the specific composition of the community during an annual cycle. Twenty-eight species (belonging to 12 families, mainly Characidae and Pimelodidae) were registered in total in non-vegetated waters. The most abundant genus, and responsible for variations in total density, was *Prochilodus*, that generally constituted more than 50% of captures. Fish composition, despite the permanent connection of the lake, was similar to that of other valley lakes, with presence of sedentary species, as *Hoplias malabaricus*, and diverse Loricariidae. The mean density obtained was 24.8 fish/1000 m<sup>3</sup>, the annual mean abundance was 932 fish/ha, and the capture per unit effort reached an annual mean of 21.5 kg/day. The variables that influenced the changes in density were hydrometric level and temperature.

In another lake, directly connected to the waters of the San Javier River, a secondary channel of the Paraná River, del Barco and Panattieri (1986) also proved the influence of these environmental variables in density of large fish. In studies carried out during two hydrological cycles in the Tonelli Lake (Helvecia, province of Santa Fe), they found that 15 out of 16 of the studied species were associated to fluctuations in the hydrometric level and temperature, and 10 of them evidenced a significant seasonal use of the environment (e.g., *Luciopimelodus pati*; *Prochilodus lineatus*; *Sorubim lima*; *Pseudoplatystoma f. fasciatum*; *Pterodoras granulosus*; *Ageneiosus valenciennesi* and *Raphiodon vulpinus* were associated to spring-summer; whereas *Salminus brasiliensis* and *Schizodon fasciatum* were associated to winter). Density of *Pimelodus maculatus* increased with the decrease in temperature, whereas captures of other species, as *Prochilodus*, *Raphiodon vulpinus* and *Luciopimelodus pati*, were positively correlated with both variables.

In 17 alluvial valley lakes, located along 680 km (32°05'S and 60°40'W–27°20'S and 58°35'W), Cordiviola (1980) sampled free and vegetated waters during an isolation period. Captured fish, most of them of medium to small size, were mainly Characidae, being *Odontostilbe pequirá* the most abundant one. The maximum richness found in a lake was 27 species, with a record of 85 taxa for the total surveyed environments. Species

from these environments were grouped considering their habitat use into: open waters fish (e.g. *Apareiodon affinis*, *Astyanax* (P) *bimaculatus*, *Pimelodella gracilis*, *Parauchenipterus galeatus*); open waters species that live in vegetated habitats (*Odontostilbe pequira*; *Pyrrhulina australis*, *Cheirodon piaba*, *Hyphessobrycon callistus*; *Aequidens vittatus*, *Rhineloricaria parva*, *Astyanax* (A) *fasciatum*), and fish closely related to vegetation (*Aphyocharax rubropinnis*, *Corydoras hastatus*, *Gymnotus carapo*, *Eigenmania virescens*, *Hypoptopoma inexpectatum*, *Crenicichla lepidota*).

Different populations use the important macrophyte development in alluvial valley lakes, of high structural complexity and abundant associated fauna (Rossi and Parma 1992). Cordiviola de Yuan et al. (1984) analyzed fish ensembles associated to marginal vegetation in the “Los Matadores” Lake, near the city of Santa Fe, connected intermittently with the Correntoso River. Samplings were carried out during one and a half years and included a period of connection with the river. A total of 71 taxa were registered; the most abundant species were *Odontostilbe pequira*, *Apistogramma corumbae* and *Characidium fasciatum*. Specific diversity oscillated between 1.25 and 3.73 bits, whereas fish density in the vegetation was correlated with hydrometric level ( $r = -0.83$ ), showing maximum values of 232 ind.m<sup>2</sup> during isolation. Juveniles were frequently captured, corresponding to 59% of captured species. The use of vegetation for refuge and feeding by juvenile fish is very frequent. Agostinho et al. (2003) pointed out that 90% of High Paraná River juvenile fish were captured near the macrophytes.

### 12.3 Migratory Displacements

The habitat use and behavioral patterns of numerous populations are associated to the hydrological dynamics, and important longitudinal and lateral displacements have been detected in all the area from a long time ago. Extensive longitudinal migrations have been well documented in the Paraná River basin (Bonetto et al. 1971; Godoy 1975). Among the migrating species, large Siluriformes, such as two “surubí” species *Pseudoplatystoma coruscans* and *P. fasciatum fasciatum*, and Characiformes, as the “sábalo” *Prochilodus lineatus*, the “dorado” *Salminus brasiliensis*, and the “boga” *Leporinus obtusidens*, were observed. These species, that do extensive displacements upstream to reproduce, spawn in lotic environments and in high water phase, so eggs and larvae are dragged by the current downstream, colonizing the lakes connected to the alluvial valley, where their initial growth is produced (Bonetto 1976). Adult fish displacements downstream have been attributed to trophic purposes, due to the enormous richness and production of the alluvial plain. Similar migratory behavioral patterns have been registered in other Neotropical fish species (Godoy 1975; Agostinho et al. 1993).

Due to the increasing fragmentation of lotic systems and the important magnitude of their displacements, these migratory species are threatened in all large fluvial systems. Quiros and Vidal (2000) evaluated the conservation of distributional areas of migratory species in the lower section of the Paraná River, after the construction of several dams upstream, and found that these potamodromous fish maintain their position in the main channel, despite the regulation in the upper sections of the basin. Therefore, these species retain the migration patterns adjusted to the systems of pristine rivers, so that, in addition to the hydrometric level and temperature, other factors would act as triggers of the longitudinal displacements upstream.

Lateral displacements, that allow the use of lenitic environments and associated channels, have been scarcely documented in alluvial plains (Bonetto 1986; Cox Fernandez 1997). Cordiviola de Yuan (unpublished) registered lateral displacements of fish within the floodplain, through the use of a trap placed at the mouth of access to the so called "Don Felipe" watercourse (a lenitic environment associated to the Santa Fe River). The fishing art used in this study allowed to register the movement of fish (entrance to or exit from the watercourse), and abundance, sex, and gonadal developmental state were also recorded. The trap, placed in high water phase, was daily controlled for two months. The results obtained demonstrated that the highest percentage of displacing specimens corresponded to *Prochilodus*, followed by *Salminus*, *Leporinus*, and the yellow catfish, *Pimelodus maculatus*, together with different Loricariidae, and smaller fish. Captured specimens of *Prochilodus* ( $n = 78$ ), representing lengths of 34–58 cm, and ages between 1 and 4 years, mainly corresponded to females (70%). In relation to the direction of their displacements, most of them were going inside the watercourse (95%), and were mostly spawned, whereas those that were going outside the watercourse towards the river were all mature. In the case of males, from a total of 23 specimens, 96% were captured going inside the watercourse (77% of them were mature, 18% in the post-evacuation phase and only 5% were resting), and the only specimen that was going outside the watercourse was mature. These results coincide with those obtained by Tablado et al. (1988) in relation to the detection of recently spawned fish in lenitic environments connected to a channel.

Other lateral displacements that were not much documented are the movements of young fish among different environmental units. Observations carried out in the lower section of the Salado River recorded a massive migration of juvenile "sábalos" (Rossi unpublished). In March 1988, when the river level reached 3.40 m (Santo Tomé's hydrometer) and the Los Sapos Island lakes were connected to this channel, the displacement of shoals downstream was observed for two days. Fish concentrated in circles and moved near the surface. The capture of 113 specimens showed a structure of homogeneous lengths and an optimum condition state (Fig. 12.2).

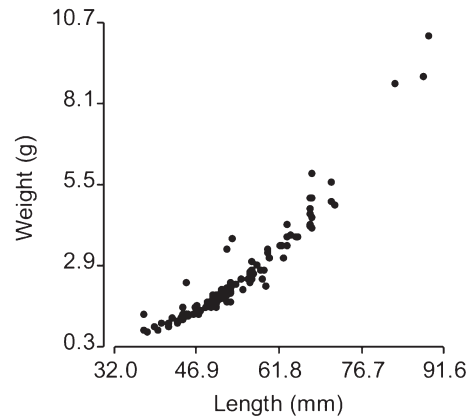


Fig. 12.2 Length–weight relationship of juveniles of *Prochilodus lineatus* captured in the Salado River during a summer migration at low waters

## 12.4 Reproductive Strategies and Life Histories

Floodplain rivers biota generally presents a high annual growth and high mortality rates, and develops life strategies to colonize large areas. In this way, the fauna can subsist in these systems, in which the great variability in the hydrological regime from one year to the other produces different accessible flooding areas, optimum for their growth and survival (Bayley 1995).

In large alluvial valley rivers, the synchronization between flood pulse and reproduction of migrating fish species has been recognized from a long time ago as an adaptive strategy that allows them to assure survival through the access to lenitic environments with a higher offer of refuge and food (Welcomme 1979). This interpretation, proposed by Bonetto (1976) for all migratory fish of the Paraná River, is assumed in the concept of “flood pulse”, when the main function of the river channel is being the migrating route and the dispersing system for populations to have access to resources and refuges (Junk et al. 1989). The mobile littoral provides excellent breeding areas during the flood, so that many fish species anticipate those conditions when reproducing before or during the increase in flow (Bayley 1995).

As in other large rivers, in the middle and lower section of the Paraná River, the ichthyoplanktonic drift, generated by spawning of migrating fish, is produced in high water phase, during spring-summer (Oldani and Oliveros 1984; Oldani 1990; Rossi 1989; Fuentes and Espinach 1998). The increase in flow constitutes a synchronizing trigger of spawning for these species, whereas temperature and photoperiod act as predictors that set off gonadal maturation (Vazzoler et al. 1997). This synchronization, that reveals the deep adjustment of these species to the dynamics of the hydrological cycle, coincides with the pattern observed in the drift of the main neotropical



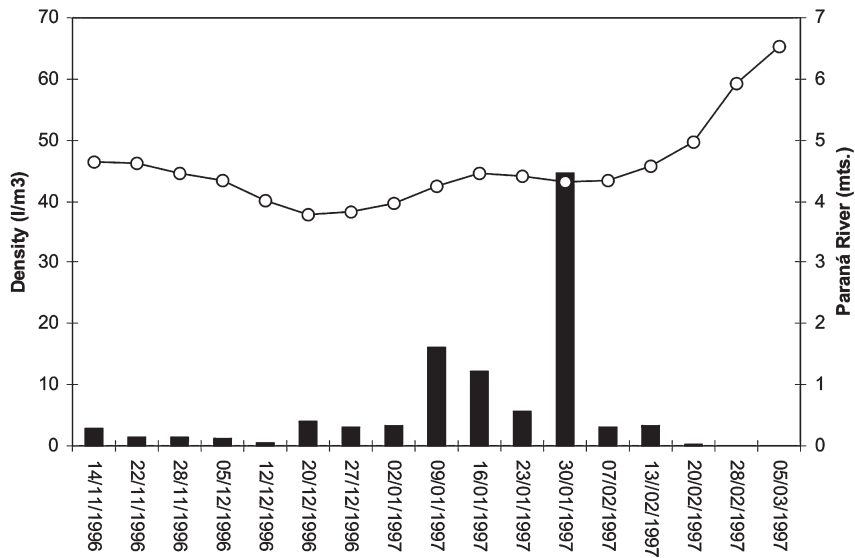


Fig. 12.3 Temporal distribution of ichthyoplankton in the Paraná River in relation to the hydrometric level (Paraná Port) during a high water phase

rheophilous species (Nakatani et al. 1997; Araujo Lima and Oliveira 1998; Merigoux and Ponton 1999; Mantero et al. 1999).

The temporal distribution of ichthyoplankton in surface waters is characterized by one or two drift pulses of higher intensity during the reproductive season, with maximum densities of 44.6 larvae/m<sup>3</sup> in the main channel (Fig. 12.3). The magnitude of these drifts reflects the importance of all the area for reproduction, especially if values obtained in other sections of the Paraná River are considered (Bialetzki et al. 1999; Fuentes et al. 1998). Therefore, this area has an extraordinary value for the maintenance and conservation of these populations.

In relation to ichthyoplankton composition, *Prochilodus lineatus* is the most abundant species, whereas the representation of *Leporinus obtusidens*, *Salminus brasiliensis*, *Pimelodus maculatus*, *Pseudoplatystoma coruscans* and *Sorubim lima* is generally lower and more variable from year to year. The size and age structure is heterogeneous: Characiformes *Prochilodus lineatus* and *Leporinus obtusidens* are always found at the first developmental stages, whereas *Salminus brasiliensis* and Pimelodidae are found in more advanced larval stages. This structure demonstrates the spatiotemporal variability of reproduction in the main species and the existence of spawning sites in different sections of the basin (Oldani 1990; Fuentes and Espinach 1998; Fuentes et al. 1998).

When analyzing the composition of larval drift and the gonadal developmental state, Oldani and Oliveros (1984) considered the middle section of the

Paraná River as the spawning and breeding site for *P. lineatus*, *L. obtusidens*; *P. albicans* and *Sorubim lima*, and only a breeding area for *S. brasiliensis* and *P. coruscans*. On the other hand, numerous species whose life cycles are mainly found associated to lenitic environments of the alluvial valley and that can do short displacements show complex reproductive behaviors. Some of these species have partial spawnings and external fecundity, as numerous members of the family Characidae, whereas others, as *Hoplosternum littorale* and *Hoplias malabaricus*, build nests and show parental care.

## 12.5 Feeding Habits

The great productivity and diversity of the alluvial plain constitutes an important source of trophic resources for fish and, since a long time ago, its importance in relation to the channels, with a lower offer of resources, has been emphasized. Among mesohabitats of lotic environments, those that show a lower current flow, as the bank areas, generally constitute more favorable feeding sites.

Fish show a great diversity of feeding habits that allow them to develop different behaviors and use a wide variety of aquatic (and even terrestrial) resources (Gerking 1994). The flexibility in the feeding behavior is another characteristic of fish species, revealed by spatial, temporal and ontogenetic changes in the diet, frequently related to changes in accessibility and availability of resources.

Spatial changes in the diet have been proven in species of lenitic environments, showing an important flexibility in relation to the availability of vegetated areas. Thus, *Astyanax abramis* behaviors as omnivorous, consuming a great amount of plants in macrophyte-abundant lakes, and as carnivorous in non-vegetated lakes; *Corydoras paleatus* presents a carnivorous diet in vegetated lakes and an omnivorous diet in non-vegetated lakes due to its high algae consumption, whereas *Odontostilbe piaba* consumes different proportions of algae and invertebrates in those environments (Oliveros 1980). Some species also show changes in their diets when they feed in the channel or in the lakes, as *Pimelodus maculatus* (Montalto et al. 1999).

Seasonal changes in the diet are observed in numerous species that, in some cases, as the *Pimelodus* catfish, can adjust rapidly to changes in availability of resources produced by flooding. Such plasticity in the feeding habits, as well as the abundance of generalist species in these lotic systems, constitutes another evidence of the adjustment of species to variations in the hydrological regime (Junk 2000). The use of terrestrial organisms is also an interesting component of fish feeding strategies in these systems. Among these organisms, frequently dragged by washout of marginal areas, we find the Formicidae, consumed by small and large species (as the characid “mojarras”, *Astyanax*, *Pyrrulina australis* and “monedita”, *Toracocharax stellatus*, and the catfish, *Ageneiosus valenciennesi* (Oliveros 1980, Oliveros and del Barco 1991, Arias and

Rossi 2005). Their capture is frequently carried out in surface waters and has been proven at connection sites during the flood phase (Gogniat and Rossi 2007).

The accidental introduction of the exotic mollusk *Limnoperna fortunei* (registered for the first time in the Paraná River in 1996), enriched the offer of resources and began to be used by numerous fish populations, modifying the trophic webs of the system. Montalto et al. (1999) registered their consumption in 9 out of 39 studied species, being very frequent in the diet of *Pterodoras granulosus* (with records of up to 150 mollusks in only one specimen), the characid *Leporinus obtusidens*, the catfish *Pimelodus maculatus*, *Pimelodus albicans*, *Pimelodus* sp. and *Hypostomus* cfr. *Laplatae*. Bechara et al. (1999) also registered their consumption in several omnivorous fish species downstream of Yacyretá Reservoir. The habits of this invasive species are epifaunal, in contrast with those of native mollusks, so it can colonize benthos and periphyton. This fact favors its availability for fish with different feeding habits. The great floodplain extension offers *L. fortunei* a great availability of substrates, and prolonged floods would favor its expansion and colonization (Montalto et al. 1999). The consumption of planktonic larval stages of *L. fortunei* by fish larvae of different species (mainly Pimelodidae) has been proven in different lotic environments of the Middle Paraná River (Rossi and Ezcurra de Drago unpublished).

The ontogenetic changes in the diet of several species reveal interesting behaviors related to changes in habitat and associated to the dynamics of the hydrological cycle. Thus, the early life history of *P. lineatus* appears as a good example of Bonetto's model (1976), which emphasizes the importance of the access to lakes for their first feeding. This species, during its lotic drift in the main channel and in the secondary channels, is found in early developmental stages and with a high intestinal emptiness, so it is highly probable that it would not begin its external feeding under these conditions (Oldani 1990; Fuentes et al. 1998; Rossi 2001). On the contrary, in protected and vegetated lotic habitats, as the banks of tributary rivers, characid "sábalos" exploit the littoral communities and continue their growth (Rossi 1992). In these habitats, an important ontogenetic change is produced in their diet, beginning as planktivorous fish and becoming early detritivorous fish, obtaining detritus from the roots of floating plants through profound changes in their trophic morphology. Therefore, the diversity of habitats, related to the lateral dimension of the river-floodplain system, used by this species during all its early ontogeny, constitutes a valuable gradient of conditions and resources for its survival and recruitment. The tolerance to starvation during these first life stages, that has been experimentally demonstrated (Libertelli and Espinach Ros 1994), should contribute to its survival in the channel until colonizing more favorable areas, abundant in refuge and food.

*Salminus brasiliensis*, one of the main piscivorous fish in the system, initially consumes zooplankton and then begins to consume fish, preying on fish larvae (mainly *Prochilodus*) from 14 mm of total length (Rossi 1989) during its lotic drift by the Middle Paraná River main and associated channels. Therefore, the channel conditions seem to be unfavorable for *Prochilodus*, not only because

of its high starvation, but also because of the risk of predation by sympatric ichthyophagous fish as *Salminus*. The early ingestion of fish observed in larvae of this species allows them to acquire a rapid specialization in its feeding habits, using an abundant resource available during the summer. The early piscivory and the use of detritus and substrate during ontogeny have also been proven in fish of other Neotropical systems (Merigoux and Ponton 1998).

Other fish species of the Paraná River also use the channel as the first breeding area. Thus, larvae of Pimelodidae exploit the zooplanktonic component and accidental-drifting organisms (as insects and oligochaetes) that enrich the channel conditions during the flood (Rossi 2001). The availability of these organisms during the drift has been scarcely studied in this section of the Paraná River, although being frequently retained in ichthyoplankton nets. In other fluvial systems, Amoros and Roux (1988) have also recognized the importance of the channel enrichment with zooplankton and benthos from the alluvial plain.

The obtained information reveals that external feeding of *Sorubim lima* and other Pimelodidae, as *Pimelodus maculatus* and *Pseudoplatystoma coruscans*, can begin in the channel, and that larval development can be completed in the lotic compartment of the river-floodplain system. The time of access to the valley lakes seems to be very variable for the different species; Siluridae grow using the channel resources while they disperse along them. Thus, the river constitutes the first breeding area for numerous species, in addition to a route of migration and dispersion for fish, so its role is essential in the early history of these populations (Fig. 12.4). Other authors have also

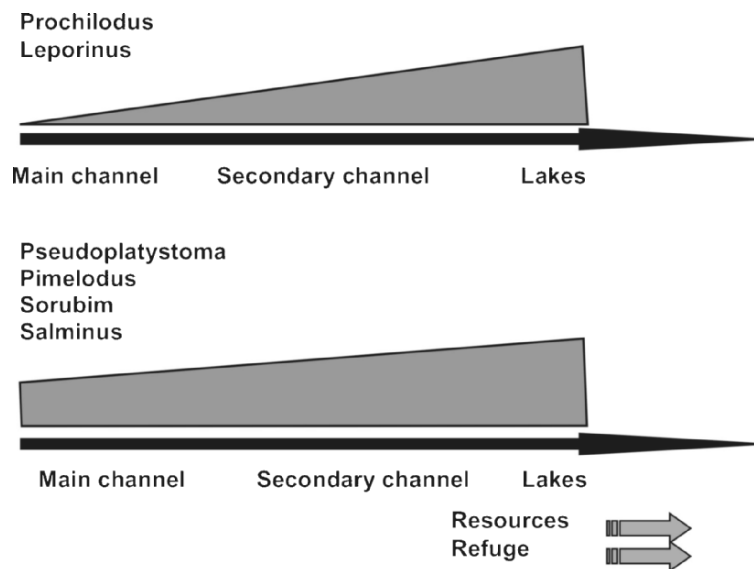


Fig. 12.4 Changes in the trophic use of lateral dimension habitats by fish larvae of different species of Paraná River

recognized the importance of the channels for fish growth and recruitment in large rivers (Schiemer and Zalewski 1992; Roux and Copp 1996).

*Hoplias malabaricus*, a sedentary species frequent in alluvial valley lakes, presents a sequence of ontogenetic changes in its diet similar to that of other piscivorous species of the area, with an initial ingestion of microcrustaceans, replaced by the consumption of insects and fish. Ichthyophagy is also present early in its life cycle and its importance increases rapidly with growth, so that juveniles already have a piscivorous diet (Oliveros and Rossi 1991). Adults, frequently captured with their empty intestines, have a notable capacity to bear periods of starvation that increases gradually with age. This characteristic would be related to an increasingly sedentary behavior, the development of “waiting and watching”- prey capture strategies, and a low metabolic rate (Parma de Croux 1983b). Among the available resources in the Middle Paraná River, detritus and littoral-community organisms represent important feeding sources.

In a study of the diet in 71 small and medium-size species captured in 17 lakes isolated from the alluvial valley, Oliveros (1980) found that most species showed a carnivorous diet, predominating copepods in some species (*Aequidens portalegrensis*, *Apistogramma corumbae*, *Pyrrulina australis*, *Aphyocharax alburnus* and *Roeboides paranensis*) and insect larvae in others (*Potamotrygon motoro* and *Geophagus brasiliensis*). Although the diet composition of some species revealed the exploitation of different communities (as in *Moenkhausia dichroua*, *Aphyocharax dentatus*, *Trachycorystes galeatus*, *Pachyurus bonariensis*, *Pimelodella gracilis*, and *Odontostilbe pequirá*), littoral macrophyte-associated organisms constituted the main source of feeding (Fig. 12.5). This important degree of trophic participation in littoral fish has also been registered in communities of other sections of the Paraná River (Segatti Hahn et al. 1997).

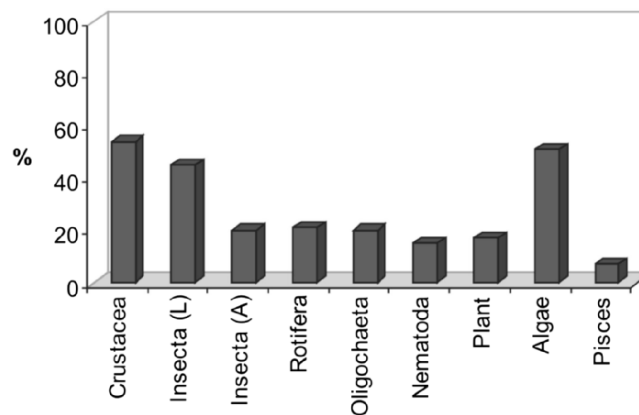


Fig. 12.5 Frequency of fish species that use different feeding resources in the lenitic environments of the floodplain valley of the Middle Paraná River L: larvae, A: adults (adapted from Oliveros 1980)

The use of resources allows grouping the species into trophic categories. In alluvial valley lakes, detritivorous, omnivorous and carnivorous (mainly insectivorous and piscivorous) species are the most represented. The importance of detritivorous species, mainly represented by *Prochilodus*, has been emphasized by Winemiller and Jepsen (1998), who pointed out that these fish increase the ecological efficiency of trophic webs by transferring biomass from the lower levels directly to species of higher levels, increasing the production of piscivorous fish through these short chains.

Among the piscivorous fish, that constitute another specialized group, we can mostly find *Salminus brasiliensis*, which mainly preys on *Raphiodon vulpinus*, *Serrasalmus* sp., *Prochilodus*, and several Siluriformes in open waters of the Paraná River (del Barco 1990). The representation of these categories in the trophic structure of the different habitats can change with the different hydrological phases. In the High Paraná River, Agostinho et al. (1997) proved that changes in the hydrological cycle strongly influence the variability of biomass in the different categories, increasing the representation of omnivorous species in flooding periods. The gradual isolation of temporary environments can also generate changes in the availability of oxygen and resources that have repercussions on the species richness and the trophic structure of these communities.

## 12.6 Respiratory Metabolism

### 12.6.1 Oxygen Consumption

There are different (physical, chemical, and biological) processes interacting in a complex way to determine the amount of dissolved oxygen in freshwater bodies. Such processes include photosynthesis and respiration, light diffusion, organic decomposition, oxygen diffusion, among others. Different oxygen requirements lead to a distinctive distribution of fish in accordance with oxygen concentration in the respective habitats (Junk et al. 1997).

Knowledge of respiratory requirements in fish is very important to evaluate natural fish production systems. Food requirements of fishes are related to their energy expenditure because the energy contained in the food consumed is expended on metabolism and growth.

The rate of oxygen consumption has been taken as a general measure of metabolic rate (Fry 1957) and the quantitative dependence on body weight was well expressed by an exponential equation. Generally, the high correlation coefficients reflect a close correlation between both variables. It is commonly expressed in milligrams of oxygen per unit of weight per hour, usually decreases as body size increases, and varies with time of day, season, temperature, activity and feeding (Doudoroff and Shumway 1979; Brett and Zala 1975).

Laboratory measurements of metabolic parameters provide information on energy requirements and uses in fish, but little information has been reported in relation to middle Paraná River ichthyofauna. It is well known that the metabolic level of fishes is related to their different degrees of activity (Lipskaya 1974), their way of life, and behavior (Newmann et al. 1981).

By comparing the metabolic rates of some Paraná River fish with different types of respiratory patterns, we can acquire a good indication of the animal needs and the way it uses O<sub>2</sub>. Although the different metabolic rates registered in these experiences characterize the behavior of the species in their natural environment, there are only approximations, since it is not possible to describe exactly the natural conditions.

The data obtained by Parma de Croux (1981, 1983a, 1983b, 1994) and Montagna and Parma de Croux (2001) showed that the metabolic rate of *Hoplias malabaricus*, registered at different temperatures, was lower than that registered for *Pimelodus maculatus*, *Pimelodus albicans* and *Prochilodus lineatus* (Table 12.2). *Hoplias* consumption was 25–39% lower than *P. maculatus*, and 15–31% lower than *Prochilodus* at 15–20°C and 40% lower at 30°C. Some ecological characteristics of *Hoplias*, such as that it is considered to be a non-active and non-migratory species, typical of lentic environments (Bonetto et al. 1971; Cordiviola de Yuan 1977), solitary and sit-and-wait (Winemiller 1989a; Oliveros and Rossi 1991), may explain its low metabolic rate and situate this species in energetic advantage over other neotropical fish.

*Pimelodus maculatus* registered the greatest metabolic rate at the lowest temperature, but showed a significant decrease at 30°C. When compared with *Prochilodus*, it is considered to be a species with little migratory behavior,

**Table 12.2** Mean metabolic rate (mgO<sub>2</sub>/h) for different fish of the Paraná River

Species	Weight (g)	15°C	20°C	24–26°C	30°C
<i>Hoplias</i>	10	1.30	2.05		3.01
<i>malabaricus</i>	50	2.98	4.92		9.01
<i>Pimelodus</i>	10	1.75	2.92		4.94
<i>maculatus</i>	50	4.41	7.35		12.08
<i>Prochilodus</i>	10	1.52	2.43		5.05
<i>lineatus</i>	50	3.93	7.15		13.70
<i>Leporinus</i>	10	1.30	2.20		
<i>obtusidens</i>	50	3.76	6.34		
<i>Pimelodus</i>	10	1.64	3.27		5.22
<i>albicans</i>	50	3.91	7.80		14.65
<i>Salminus</i>	10			4.14	
<i>brasiliensis</i>	50			12.79	

bottom frequenter and more active in fall and winter (Ringuelet 1975; Tablado et al. 1988). *Prochilodus* makes important trophic, reproductive and thermal migrations (Bonetto et al. 1981), and appears in great shoals in spring and summer; then, the important increase in the metabolic rate between 20 and 30°C shows that this range is the most favorable for the development of its activities, mainly those concerning feeding. *Salminus brasiliensis* is considered to be an active fish with predatory and migratory habits; then, the high and continuous activity requires a higher respiratory rate than that measured for other Neotropical fish species (Parma de Croux 1997).

### 12.6.2 Responses to Hypoxia

Reduction in the level of available oxygen has a marked effect on many physiological, biochemical, and behavioral processes in fish. Restrictions in this supply for metabolic processes, including swimming, migrating and feeding, are likely caused by hypoxia. Adequate oxygen levels for such activities are necessary for survival of fish populations.

Fishes can develop diverse mechanisms to subsist with small amounts of oxygen, although there is controversy and doubt about how they are done. Kramer (1987) describes four response categories to low oxygen availability: (1) changes in activity; (2) increase in the aerial respiration, only possible to some fishes; (3) utilization of the oxygen-rich surface film, known as “aquatic surface respiration”, and (4) horizontal and vertical changes of habitat. In behavioral ecology, the optimality theory assumes that an organism will maximize the net rate of resource uptake or minimize the cost of obtaining a required amount of that resource.

Very little has been done in terms of measurements of minimum oxygen requirements in tropical and temperate fish. The main interest has always been air-breathing fish species (Val and Almeida-Val 1995); consequently, requirements of water-breathing fish of the Paraná River are little known.

In the studied species, the data obtained showed that the lethal oxygen level oscillated between 0.3 and 0.8 ppm for *Hoplias malabaricus*, *Pimelodus maculatus*, *Pimelodus albicans* and *Prochilodus lineatus*, with no significant differences detected among species (Parma de Croux 1987, 1994).

The registry of frequency and amplitude of ventilatory movements is a good documented change of activity in response to reduced levels of dissolved oxygen (Doudoroff and Sumway 1970; Saint-Paul 1984). The normal operculum movements of these species at 20–27°C range from 16–30/min for *Hoplias*, 100/min for *Pimelodus*, and 90–100/min for *Prochilodus*, and, at critical concentrations, they were increased to 104–108 for *Hoplias*, 200–230 for *Pimelodus*, and 210–220 for *Prochilodus*, for similar temperature ranges.

There is some evidence that the decision of staying in habitats with lower oxygen or moving to one with higher oxygen availability depends on the relative costs of these alternatives. The studied species have neither air breathing



nor adaptations for the aquatic surface respiration, but they showed high tolerance to low oxygen concentrations. The characteristics of *Hoplias*, such as its low metabolic rate, large respiration surface (Fernández 1985) and other physiological measurements (Hochachka et al. 1978b; Rantin and Johansen 1984) increase its ability to employ successfully aquatic respiration when the environment is under periods of hypoxia.

*Prochilodus* and *Pimelodus* can decrease their metabolic rates in extreme conditions. At the same time, they show changes in some activities, e.g., the increment in the frequency and amplitude of the opercular movements. These adaptations should entail the reduction of other activities, such as feeding, which is probably the most affected one. These two species can move horizontally and vertically in the aquatic environments searching for better conditions, but both may be found in places isolated from the main channel and covered with aquatic vegetation (Cordiviola de Yuan et al. 1984), where low oxygen levels can persist for several days with summer water temperatures.

The reduction in the respiration rate and the increase in the ventilatory frequency of these important species seem to be appropriate adaptations for survival to hypoxia. A valid hypothesis to explain this situation would be the existence of hematological modifications to increase oxygen carrying capacity of blood and adapt to the scarce amount of oxygen available in the environment. Much more studies will be needed in the future to confirm this hypothesis.

## 12.7 Conclusions

The middle area of the Paraná River, with its extensive floodplain, has an enormous value for diversity and productivity of basin fish.

The life strategies of these populations are deeply adjusted to the functioning of the system. Diverse habitats of the river-floodplain complex are used by fish during their initial growth; therefore, channels are very valuable for some populations, in addition to being “nurseries” of lenitic habitats. As in other large floodplain rivers, the fluctuations of the hydrological cycle influence the structure and dynamics of fish communities, modeling temporally and spatially their trophic webs. The conservation of these populations depends, to a great extent, on actions intended to maintain the integrity of the system.

## References

- Agostinho AA, Vazzoler AEA, Gomez LC, Okada EK (1993) Estratificación espacial y comportamiento de *Prochilodus scrofa* en distintas fases del ciclo de vida, en la planicie de inundación del alto río Paraná y embalse de Itaipu, Paraná, Brasil. *Rev Hydrobiol Trop* 26(1):79–90

- Agostinho AA, Segatti Hahn N, Gomes LC, Bini LM (1997) Estructura trófica. In: Vazzoler AE, Agostinho AA, Segatti Hahn N (eds) A planície de Inundação do Alto Rio Paraná: Aspectos físicos, biológicos e socioeconômicos. Universidade Estadual de Maringá. Maringá
- Agostinho AA, Gomez LC, Ferreira Julio Jr H (2003) Relações entre macrófitas acuáticas e fauna de peixes. In: Thomaz SM, Bini LM (eds) Ecología e Manejo de Macrófitas Aquáticas. Editora da Universidade Estadual de Maringá. Maringá, pp 261–279
- Amoros C, Roux AL (1988) Interaction between water bodies within the floodplains of large rivers: function and development of connectivity. Proceeding of the 2nd International Seminar of the International Association for landscape Ecology, pp 125–130
- Araujo Lima CA, Oliveira EC (1998) Transport of larval fish in the Amazon. *J Fish Biol* 53:297–306
- Arias JD, Rossi LM (2005) Dieta y estrategia alimentaria de *Pyrrhulina australis* (Pisces, Lebiasinidae). *Rev FABICIB* 9:197–205
- Bayley PB (1995) Understanding large river–floodplain ecosystems. *BioScience* 45(3):153–158
- Bialetzki A, Sanchez PV, Cavicchioli M, Baumgartner G, Pereira R, Nakatani K (1999) Drift of ichthyoplankton in two channels of the Paraná River, between Paraná and Mato Grosso do Sul States, Brazil. *Braz Arch Biol Technol* 42(1):53–60
- Bechara J, Sanchez S, Roux J, Terraes J, Flores Quintana C (1999) Variaciones del factor de condición relativo de la ictiofauna del río Paraná aguas debajo de la represa de Yacyretá, Argentina. *Revista de Ictiología* 7:75–89
- Bonetto AA (1976) Calidad de las aguas del río Paraná. Introducción a su estudio ecológico. Corrientes, Argentina, Instituto Nacional de Construcciones Portuarias y Vías Navegables Instituto de Ciencias y Técnica Hídrica
- Bonetto AA, Canon Veron M, Roldan D (1981) Nuevos aportes al conocimiento de las migraciones de peces en el río Paraná. *Ecosur* 8(16):29–40
- Bonetto AA (1986) Fish of the Paraná system. In: Davies BR, Walker KF (eds) The ecology of river systems. DW Junk Publishers, Dordrecht, pp 573–588
- Bonetto AA, Cordiviola de Yuan E, Pignalberi C, Oliveros O (1969) Ciclos hidrológicos del río Paraná y las poblaciones de peces contenidas en las cuencas temporarias de su valle de inundación. *Physis* 29:213–223
- Bonetto AA, Cordiviola de Yuan E, Pignalberi C (1970) Nuevos datos sobre poblaciones de peces en ambientes leníticos permanentes del Paraná medio. *Physis* 30(80):141–154
- Bonetto AA, Pignalberi C, Cordiviola de Yuan E, Oliveros O (1971) Informaciones complementarias sobre migraciones de peces de la Cuenca del Plata. *Physis* 30(81):505–520
- Brett JR, Zala CA (1975) Daily patterns of nitrogen excretion and oxygen consumption of sockeye salmon under controlled conditions. *J Fish Res Bd Can* 32:2479–2486
- Cordiviola de Yuan E (1977) Poblaciones de peces del río Paraná. IV Fluctuaciones en la composición íctica de la laguna “Los Matadores” (Isla Clucellas), Santa Fe. *Neotrópica* 23(69):17–25
- Cordiviola de Yuan E (1980) Campaña “Keratella I” a lo largo del río Paraná medio: Taxocenosis de peces de ambientes leníticos. *Ecología* 4:103–113
- Cordiviola de Yuan E (1992) Fish populations of lentic environments of the Paraná River. *Hydrobiologia* 237:159–173
- Cordiviola E, Oldani N, Oliveros O, Pignalberi de Hassan C (1984) Aspectos limnológicos de ambientes próximos a la ciudad de Santa Fe (Paraná Medio): Poblaciones de peces ligadas a la vegetación. *Neotrópica* 30(84):127–139
- Cordiviola de Yuan E, Pignalberi de Hassan C (1985) Fish populations in the Paraná River: lentic environments of Diamante and San Pedro areas (Argentine Republic). *Hidrobiología* 127:213–218
- Cox Fernandes C (1997) Lateral migration of fishes in Amazon floodplains. *Ecol Freshw Fish* 6:36–44
- del Barco DM, Panattieri AE (1986) Variaciones de la densidad relativa de peces en el Paraná medio en relación con factores ambientales. *Rev Asoc Cien Nat Litoral* 17(1):127–136

- del Barco DM (1990) Alimentación de *Salminus maxillosus* Valenciennes 1840, en distintos ambientes de la Provincia de Santa fe (Pisces, Characidae). Rev Asoc Cien Nat Litoral 21(2):156–166
- Demonte LD, Arias JD (2005) Ictiofauna de los ríos Paraná y Uruguay en la Provincia de Entre Ríos, Argentina. In: Temas de Biodiversidad del Litoral fluvial argentino II. INSUGEO Miscelánea 1 4:355–366
- Drago EC, Ezcurra de Drago I, Oliveros O, Paire AR (2003) Aquatic habitats, fish and invertebrate assemblages of the Middle Paraná River. Amazoniana 27(3/4):291–341
- Doudoroff P, Shumway DL (1970) Dissolved oxygen requirements of freshwater fishes. FAO Fish Tech Pap 86, pp 291
- Fernández MN (1985) Morfometría branquial do Teleosteo *Hoplias malabaricus* (Bloch). Bol Fisiol Animal Univ Sao Paulo 9:57–65
- Fry FE (1957) The aquatic respiration of fish. In: Brown ME (ed) The Physiology of fishes, vol I. Metabolism. Academic Press, New York, pp 1–63
- Fuentes CM, Demonte LD, Esposti MF (1998) Temporal variation of main channel ichthyoplankton at the end of Middle Paraná River. Revista de Ictiología 6 (1/2):57–64
- Fuentes CM, Espinach Ros A (1998) Variación de la actividad reproductiva del sábalo *Prochilodus lineatus* (Valenciennes, 1847), estimadas por el flujo de larvas en el río Paraná inferior. Natura Neotropicalis 29(1):25–32
- Hochachka PW, Guppy M, Guderley KB, Storey KB, Hulbert WC (1978b) Metabolic biochemistry of water-vs. air-breathing fishes: muscle enzymes and ultrastructure. Can J Zool 56:736–750
- Gerking SD (1994) Feeding ecology of fish. Academic Press, San Diego
- Godoy MP (1975) Peixes do Brasil. Suborden Characoidei. Bacia do rio Mogi Guassu. Piracicaba, Brasil. Editora Franciscana, 4 v
- Gogniat D, Rossi L (2007) Dieta de *Thoracocharax stellatus* Kner (1860) (Pisces, Gasteropelecidae) en el Río Salado (Santa Fe, Argentina) Natura Neotropicalis 37
- Junk WJ, Soares MG, Saint-Paul U (1997) The fish. In: Junk W (ed) The central Amazon floodplain. Springer, Berlin Heidelberg New York, pp 385–405
- Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river–floodplain systems. In: Doge DP (ed) Proceedings of the International Large River Symposium. Can Spec Publ Fish Aquat Sci 106:110–127
- Junk WJ (2000) Mechanisms for development and maintenance of biodiversity in Neotropical floodplains. In: Gopal B, Junk WJ, Davis JA (eds) Biodiversity in wetlands: assessment, function and conservation. Backhuys Publishers, Leiden, The Netherlands, pp 119–140
- Kramer DL (1987) Dissolved oxygen and fish behaviour. Environ Biol Fish 18:81–92
- Leveque C (1995) L'habitat: etre au bon endroit au bon moment? Bull Fr Peche Piscic. 337/338/339:9–20
- Libertelli M, Espinach Ros A (1994) Efectos del retardo en la iniciación de la alimentación externa en la supervivencia y el crecimiento de larvas de sábalo (*Prochilodus lineatus*). Tankay 1:245–247
- Lipskaya NY (1974) Metabolic rates in the young of some tropical fish species. J Ichthyol 14(6):934–943
- Lopez HL, Miquelarena AM, Ponte Gomez J (2005) Biodiversidad y Distribución de la Ictiofauna Mesopotámica. Temas de Biodiversidad del Litoral fluvial argentino II. INSUGEO 14:311–354
- Lopez HL (2001) Estudio y uso sustentable de la biota austral: ictiofauna continental argentina. Rev Cubana Invest Pesq (Supl. Especial, e version) ISSN CUBO 138–8452
- Lowe McConnel R (1987) Ecological studies in tropical fish communities. Cambridge University Press, New York
- Mantero G, Martinez G, Retta S (1999) Distribución espacio-temporal del ictioplancton en el embalse de Salto Grande (Período 1988–1992). Bol Soc Zool Uruguay 10:72–82
- Menni RC (2004) Peces y ambientes en la Argentina continental. Monografías del Museo Argentino de Ciencias Naturales 5 Buenos Aires, Argentina

- Merigoux S, Ponton D (1998) Body shape, diet and ontogenetic diet shifts in young fish of the Sinnamary River, French Guiana, South America. *J Fish Biol* 52:556–569
- Merigoux S, Hugueny B, Ponton D, Statzner B, Vauchel P (1999) Predicting diversity of juvenile neotropical fish communities: patch dynamics versus habitat state in floodplain creeks. *Oecologia* 118:503–516
- Montagna M, Parma de Croux MJ (2001) Consumo de oxígeno en *Pimelodus albicans* (Pisces, Pimelodidae) en relación con la masa corporal y la temperatura. *Natura Neotropicalis* 32(1):49–57
- Montalto L, Oliveros OB, Escurra de Drago I, Demonte LD (1999) Peces del río Paraná medio predadores de una especie invasora: *Limnoperna fortunei* (Bivalvia, Mytilidae) *Revista FABICIB* (3):85–101
- Nakatani K, Baumgartner G, Cavicchioli M (1997) Ecología de ovos e larvas de peixes. In: Vazzoler A, Agostinho A, Segatti Hahn N (eds) *A Planície de Inundacao do Alto Rio Paraná: Aspectos físicos, biológicos e socioeconomicos*. Universidad Estadual de Maringá: Nupelia, pp 281–306
- Neff JJ (1990) Ideas para la interpretación ecológica del Paraná. *Interciencia* 15(6):424–440
- Neff JJ (2001) Diversity in some tropical wetland systems of South America In: Gopal B, Junk WJ, Davis JA (eds) *Biodiversity in wetlands: assessment, function and conservation*, vol 2. pp 157–186
- Newmann DA, O’Conner JM, Sherk Jr JA (1981) Oxygen consumption of white perch (*Morone american*), striped bass (*M. saxatilis*) and spot (*Leiostomus xanthurus*). *Comp Biochem Physiol* 69A:467–478
- Oldani NO (1990) Variaciones de la abundancia de peces del valle del río Paraná (Argentina). *Rev Hydrobiol Trop* 23(1):67–76
- Oliveros OB (1980) Campaña limnológica “Keratella1” en el río Paraná medio. Aspectos tróficos de los peces de ambientes lenfíticos. *Ecología* 4:115–126
- Oldani NO, Oliveros OB (1984) Estudios limnológicos en una sección transversal del río Paraná. Dinámica temporal de peces de importancia económica. *Rev Asoc Cienc Nat Litoral* 15(2):175–183
- Oliveros OB, del Barco DM (1991) Aspectos de la biología de *Ageneiosus valenciennesi* (Pisces, Ageneiosidae). *Rev Asoc Cienc Nat Litoral* 22(2):43–53
- Oliveros OB, Rossi LM (1991) Ecología Trófica de *Hoplias malabaricus malabaricus* (Pisces, Erythrinidae). *Rev Asoc Cienc Nat Litoral*. 22(2):55–68
- Parma de Croux MJ (1981) Metabolismo de rutina de *Pimelodus maculatus* (Lac) (Pisces, Pimelodidae). *Rev Asoc Cienc Nat Litoral* 12:20–26
- Parma de Croux MJ (1983a) Metabolismo de rutina de *Prochilodus platensis* (Holmberg, 1889) (Pisces, Prochilodontidae) *Rev Asoc Cienc Nat Litoral* 14:1–6
- Parma de Croux MJ (1983b) Metabolismo de rutina de *Hoplias malabaricus malabaricus* (Bloch, 1794) (Pisces, Erythrinidae) *Rev Brasil Zool Sao Paulo* 1(3):217–222
- Parma de Croux MJ (1987) Nivel de oxígeno letal y mínimo de tolerancia en *Pimelodus albicans* (Pisces, Pimelodidae). *Rev Asoc Cienc Nat Litoral* 18(1):85–91
- Parma de Croux MJ (1994) Metabolic rate and oxygen consumption requirements of some fish species from the middle Paraná River. *Acta Biol Venez* 15(2):1–10
- Parma de Croux MJ (1997) Relationship between metabolic rate and body weight in *Salminus maxillosus* (Val, 1840). *J Aqua Trop* 12(1):17–22
- Quiros R, Vidal JC (2000) Cyclic behaviour of potamodromous fish in large rivers. In: Coux I (ed) *Management and ecology of river fisheries*. Fishing News Books, Blackwell Science, London, pp 71–86
- Rantin FT, Johansen K (1984) Responses of the teleost *Hoplias malabaricus* to hypoxia. *Environ Biol Fish* 11(3):221–228
- Ringuelet R (1975) Zoogeografía y ecología de los peces de aguas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de América del Sur. *Ecosur* 2(3):1–122
- Rossi LM (1989) Alimentación de larvas de *Salminus maxillosus* (Val.1840) (Pisces, Characidae). *Iheringia* 69:49–59

- Rossi LM (1992) Evolución morfológica del aparato digestivo de postlarvas y prejuveniles de *Prochilodus lineatus* (Val., 1847) (Pisces, Curimatidae) y su relación con la dieta. *Rev Hydrobiol Trop* 25(2):159–167
- Rossi LM, Parma de Croux MJ (1992) Influencia de la vegetación acuática en la distribución de peces del río Paraná, Argentina. *Ambiente subtropical* 2:65–75
- Rossi LM (2001) Ontogenetic diet shifts in a Neotropical catfish (*Sorubim lima*) of Paraná System. *Fish Manage Ecol* 8:141–152
- Roux AL, Copp GH (1996) Fish populations in rivers. In: Petts G, Amoros C (eds) *Fluvial hydrosystems*. Chapman and Hall, London, pp 167–183
- Saint-Paul U (1984) Physiological adaptation to hypoxia of a Neotropical characoid fish *Colossoma macropomum*, Serrasalminidae. *Environ Biol Fish* 11(1):53–62
- Segatti Hahn NA, De Fátima Andrian I, Fugi R, Lescano de Almeida VL (1997) Ecología trófica. In: Vazzoler AE, Agostinho AA, Hahn NS (eds) *A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos*. Editora da Universidade Estadual de Maringá, Maringá, pp 209–228
- Schiemer F, Zalewski M (1992) The importance of riparian ecotones for diversity and productivity of riverine fish communities. *Neth J Zool* 42(2–3):323–335
- Tablado A, Oldani N, Ulibarre L, Pignalberi de Hassan C (1988) Cambios Estacionales de la densidad de peces de una laguna del valle aluvial del río Paraná (Argentina). *Rev Hydrobiol Trop* 21(4):335–348
- Val AL, AlmeidaVal VMF (1995) *Fishes of the Amazon and their environment*. Springer, Berlin Heidelberg New York, 224 pp
- Vazzoler AE, Agostinho AA, Segatti Hahn N (1997) *A planície de inundação do Alto Rio Paraná. Aspectos físicos, biológicos y socioeconômicos* Editora da Universidade Estadual de Maringá, Maringá 460 pp
- Welcomme RL (1979) *Fisheries ecology of floodplain rivers*. Longman, London
- Welcomme RL (2000) Fish biodiversity in floodplains and their associated rivers. In: Gopal B, Junk WJ, Davis JA (eds) *Biodiversity in wetlands: assessment, function and conservation*. Backhuys Publishers, Leiden, The Netherlands, pp 61–87
- Winemiller KO (1989) Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* 81:225–241
- Winemiller KO, Jepsen DB (1998) Effects of seasonality and fish movement on tropical river food webs. *J Fish Biol* 53(Suppl.A):267–296