

Chapter 6

Cyclic behaviour of potamodromous fish in large rivers

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Abstract

Potamodromous fish species have evolved under natural river conditions, and have usually keyed migrations and spawning behaviour to coincide with high-water events. Knowledge of riverine fish populations has increased significantly over the past decade, but advancement in the study of potamodromy is lagging behind. However, potamodromy is strongly represented in large South American rivers. Over the past 30 years the upper Parana basin has been highly regulated, and damming has altered flow regimes, especially between 1985 and 1990. To study the effects of river regulation on fish movements, a site situated in the main channel of the lower middle Parana River was studied for fish abundance twice a week during that period. The fish species have changed their abundance cyclically in the main channel. Moreover, the potamodromous fishes maintained their seasonal position in the main channel, despite huge flow regulation by upper basin dams. Most fish species maintained seasonal cycles similar to those evident in the pre-regulation period. Potamodromous fishes have retained the migration patterns evolved in the pristine riverine system. Consequently, it may be that factors other than water level and temperature trigger upstream migration of potamodromous fish in large river-floodplain systems.

6.1 Introduction

Because the best breeding habitat rarely coincides with the best feeding habitat, most fish species inhabiting large river-floodplain systems have two distinct centres of concentration and fish migrate between the two (Welcomme 1985). Longitudinal migrations take place within the main river channel, sometimes over long distances. Potamodromy is strongly represented in large river-floodplain systems from the warm temperate zone and the tropics. In South America, a number of medium-sized river-floodplain systems seem to have migratory fish populations showing similar characteristics, with a single seasonal movement to and from a downstream feeding zone and an upstream breeding zone (e.g. Bayley 1973; Godoy 1975; Paiva & Bastos 1982). This pattern is presumably repeated throughout most moderate size river-floodplain systems of the continent which carry characin and siluroid populations (Welcomme 1985). However, for the middle Parana river the migration patterns

obtained using tagging methods are more complex (see Espinach Ros & Delfino (1993) for an overview).

Oscillating cycles of abundance between spawning and feeding areas have been shown for potamodromous fishes in the lower Rio de la Plata basin (Bonetto & Pignalberi 1964; Bonetto *et al.* 1971). Because of the close relationship between water level fluctuations and rainfall, cyclic fish behaviour in seasonal comparisons was assigned to water level variations in the Parana River (Quiros & Cuch 1989). However, river regulation through damming in the headwaters has changed the flow regime, especially for the period 1985–1990 (Fig. 6.1) and provided the opportunity to test the effects of flooding as an onset for fish upstream movements.

Potamodromous fish species have coevolved with the system under natural river conditions and usually keyed their movements to coincide their spawning with high-water events. Some examples from natural undeveloped river–floodplain systems support this statement (Welcomme 1985). But what happened when the flood pulse changed its seasonal variability by human intervention, assuming all the other characteristics remained constant? To respond to this question would help to clarify the main determinants of upstream potamodromous fish movements. Therefore, the main objective of this chapter was to study patterns in riverine fish abundance within and between years in a regulated, but highly variable, river floodplain system, and to compare cyclic fish patterns for years with moderate to unusually high discharge manipulations. The aim was to test the hypothesis that potamodromous fish move into the main channel for spawning or feeding according to the river discharge,

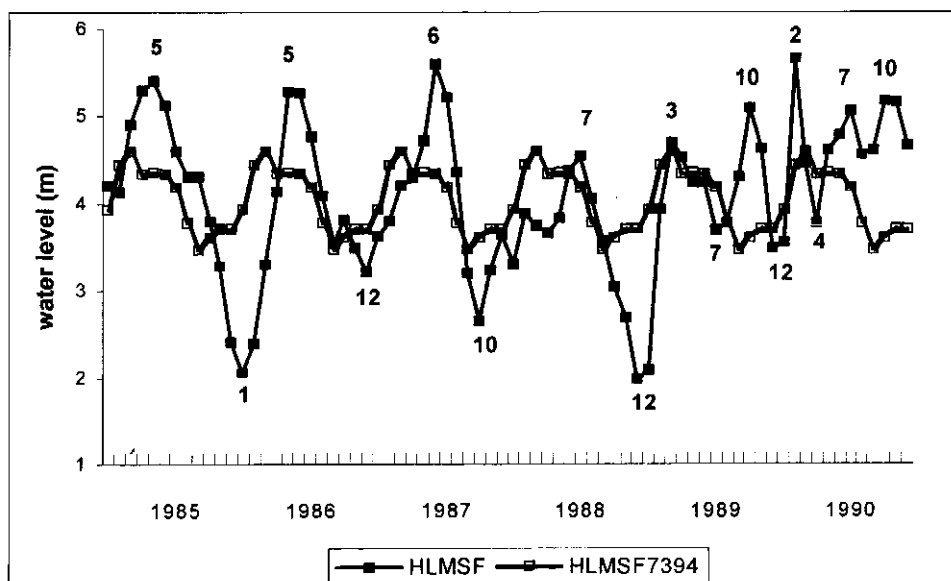


Figure 6.1 Water level: monthly mean of daily averages for the period 1985–1990 (HLSFM) and monthly for the 1973–1994 post-dam period (HLMSF7394). Figure numbers indicate month of the year

independent of the cyclic patterns they have inherited through coevolution with the unaltered environment.

6.2 Description of the system and the main channel fishery

The Parana River flows 4000 km southwards from its sources in the Brazilian Shield to its mouth in the Pampa Plain, discharging $20\,000\text{ m}^3\text{ s}^{-1}$ in the Rio de la Plata river. From its confluence with the Paraguay River, the Parana River has extensive floodplains which widen downstream and cover more than $20\,000\text{ km}^2$. These floodplains reduce the variability and distribute the flow evenly throughout the year, suppressing sharp and pronounced flood peaks.

Before most of the upstream dams were built, the lower middle Parana River showed a regular annual cycle, usually reaching its maximum in March or April (late summer–early autumn) and its minimum flow in September. The volume of water in reservoirs in the upper basin has been increasing since the early 1950s but a sharp increase occurred from 1972–1973 up to the present. It represents more than 50% of the mean annual discharge at the mouth (Rio de la Plata) (Quiros 1990). Damming has contributed to the disappearance of large migratory fish species, mainly in the dammed upper reaches of the Parana River (Agostinho *et al.* 1994).

The flood pulse now tends to occur earlier but is more attenuated than in the unregulated river. Moreover, water remains in the floodplain for most of the year (Quiros 1990). The upper dams do not stop floods; the attenuation occurs because the water management policies of hydroelectric companies retain the water in reservoirs during high rainfall and river discharge periods and release it during low flow conditions.

However, for the 1985–1990 period, upper basin dams situated in Brazil induced huge changes in discharge, seemingly during turbine and spillway probing (Fig. 6.1). Flow variability was distinct and dramatic, involving changes of several thousands of cumecs during the years 1989 and 1990.

For the lower Parana fishery, active fishing methods are usually used, although some static gear is also used within the floodplain during high water periods. The lower middle Parana fishery takes place in the main channel all year round using drift gillnets, with panels with stretched mesh sizes ranging from 26 cm to over 34 cm. The nets are set on the bottom of the channel facing downstream and positioned in a manner considered to maximise catch efficiency. The current drags the net on the bottom in areas especially prepared for fishing (canchas). This fishing gear usually catches large fish more than four years old (Quiros & Cuch 1989).

6.3 Materials and methods

To study fish movements, changes of fish abundance over time was assessed. The fishing site was located in the main channel of the lower middle Parana River

(Rosario City). The draft gill nets catches were sampled twice a week during 1985–1990. On each sample date, the catch of 6–7 fishermen and 10–30 hauls was sampled at the landing site nearby. All fish were identified to species (Ringuelet, Aramburu & Alonso de Aramburu 1967) and individually measured for total length (mm) and weight (g). *Prochilodus lineatus* (Holmberg) (previously *platensis*) (sabalo 41.0%), *Leporinus obtusidens* (Val.) (boga 34.3%), *Pterodoras granulosus* (Bleeker) (armado 12.2%), *Pseudoplatystoma coruscans* (Eigenmann & Eigenmann) (surubi 5.2%), *Luciopimelodus pati* (Eigenmann & Eigenmann) (pati 4.8%), and *Salminus maxillosus* (Val.) (dorado 2.4%) were the principal species captured and contributed (by weight) the most to the total catch. Catch per unit effort (CPUE) was expressed as kg per net-haul for total catch and by species. Monthly mean CPUE for the large siluroids (surubi, pati, armando) and characins (sabalo, boga, dorado) are presented here.

Variability in fish abundance was large between years. For the Parana River, as for other river–floodplain systems (Welcomme 1985), fish species abundance depends on the flood conditions, flooding intensity and amount of water remaining in the system during the low flow period in the years when the fishes are born (Quiros & Cuch 1989). To analyse the relationship between the seasonal fish abundance by species and water level, the former variable was normalised, dividing it by the annual CPUE for the species. Consequently, mean monthly normalised fish abundance by species is expressed as the percentage of the annual catch per unit effort for the species.

Water level data for Santa Fe Harbor station were collected from the Nacional de Construcciones Portuarias y Vias Navegables. The monthly mean of daily averages was considered as the water level variable (HLSF). To analyse relationships between CPUE and flood regime for pre-dam (1925–1972) and post-dam (1973–1994) periods, the monthly mean water level data are presented as HLMSF25–72 and HLMSF73–94, respectively. Water temperature data for the main channel at Rosario City (TEMP) were obtained for 1985 through 1990 from the Instituto Nacional de Agua y del Ambiente.

6.4 Results

The analyses of the fish abundance series for the 1985–1990 period indicated regular cyclic changes in abundance of fish in the main channel for most of the species studied (Figs 6.2 and 6.3). The large potamodromous fishes appear to retain seasonal movements in the main channel despite large variations in the intensity and timing of water discharges by the dams situated in the upper basin.

Normalised fish abundance by species in the main channel was slightly related to water level for the studied period. The abundance values of only two species (*Leporinus* and *Luciopimelodus*) were positively related to water level ($P < 0.01$; $n = 72$). Similar results were obtained for fish abundance in each year studied (Table 6.1). For both the pre-dam and the post-dam periods, potamodromous fishes were in the

Table 6.1 Seasonal relationships between fish abundance by species in the main channel and water temperature (climate), the mean monthly water level for the 1925–1971 period (pre-dam flood pulse), and the mean monthly water level for the studied period (flood pulse for the 1985–1990 period)

Conceptual variable	Fish species					
	<i>Prochilodus</i>	<i>Leporinum</i>	<i>Luciopermelodus</i>	<i>Salminus</i>	<i>Pterodoras</i>	<i>Pseudoplatystoma</i>
Climate	Winter	Late autumn	Late autumn/ early winter	Late summer/ early autumn	Late summer/ autumn	Summer/Early autumn
Pre-dam flood pulse	Falling	Falling	High falling	High	High	High
Flood pulse for the 1985–1990 period	High increasing, high, and high falling	High increasing, high, and high falling	High, high falling, and low	Low, low and high increasing, high and falling	Low increasing, high, and low	Low and high increasing, falling, and low
Peaking in	Increasing Spring–summer	Increasing? Spring–summer??	Spawning period ^{a, b} High increasing?? Summer??	Flood peak? Summer?	High increasing? Summer?	High increasing? Summer?
Peaking in	Increasing Spring–summer	Increasing Spring–summer	Larvae drift ^{a,b,c} High increasing?? Summer??	Flood peak? Summer?	High increasing Summer	High increasing Summer

^aOldani and Oliveros (1984). ^bCordiviola de Yuan *et al.* (1984). ^cFuentes (1998). ^dFuentes & Espinach Ross (1998).

main channel most of the year (R. Quiros unpublished data), but for the post-dam period, fish abundance varied drastically during the flood cycle (Fig. 6.2). However, for the undeveloped system, the abundance of main-channel spawners increased substantially in the main channel during the time of maximum flood (*Pseudoplatystoma*, *Pterodoras*, and *Salminus*) and during high falling waters (*Prochilodus*, *Leporinus*, and *Luciopimelodus*). From these species, the top predators *Salminus maxillosus* and *Pseudoplatystoma coruscans* have reportedly decreased in abundance in the lower middle Parana during the last twenty years. On the other hand, detritivorous and omnivorous fishes increased their relative abundance in the system (R. Quiros unpublished data).

The relationship between normalised fish abundance and water temperature describes the sequence of fish species abundance in the main channel (Tables 6.1 and 6.2). As expected, for the three species that were more abundant in the main channel during summers (*Salminus*, *Pterodoras*, and *Pseudoplatystoma*) fish abundance was positively related to water temperatures ($n = 72$, $P < 0.01$). Conversely, for the two species that were more abundant in the main channel during autumn and winter (*Leporinus* and *Prochilodus*), abundances were inversely related to water temperatures ($n = 72$, $P < 0.01$). Similar results were obtained when fish abundances were analysed for each studied year, although statistical significance was lower (Table 6.2).

However, simple correlation between these time-related variables is merely a simplified view of more complex processes. Potamodromous fishes were in the main channel when the water was both increasing and falling (Figs 6.3–6.6), indicating that they followed seasonal patterns more than flood patterns (Tables 1 and 2). During the period 1988–1990, when more dramatic changes in water level timing were expressed, fish species retained their seasonal patterns. Moreover, for the 1988–1990 period, fish cycling patterns relative to water level variability were highly chaotic, while there were highly regular cycles related water temperature variation (Figs 6.3–6.6).

Different fish species peaked in the main channel at different times, however, there was little overlap in the timing of fish movements in the main channel (Fig. 6.2). This suggests that adult potamodromous fish species maintain an independent existence in the main channel, possibly moving in distinct groups or schools.

In previous studies, particularly for *Prochilodus lineatus*, the reproductive period was estimated using gonad maturity of adult fish (Bonetto 1963; Pignalberi 1965; Oldani & Oliveros 1984; Tablado, Oldani, Ulibarrie & Pignalberi de Hassan 1988). These studies showed that the reproductive period for *Prochilodus* ranges from October to April, but the months with more intense spawning activity are November and December. Larval abundance of *Prochilodus* and almost every other migratory species peaked when the water level of Parana River peaked. *Prochilodus* and *Leporinus* larvae abundance usually peak during November, while siluroids peak during February (Fuentes 1998; Fuentes & Espinach Ross 1998) (Table 6.2). It is apparent that fish larvae go into the floodplain ponds and sloughs when water rises. These areas also provide fish nursery and wintering areas when waters recede. It has

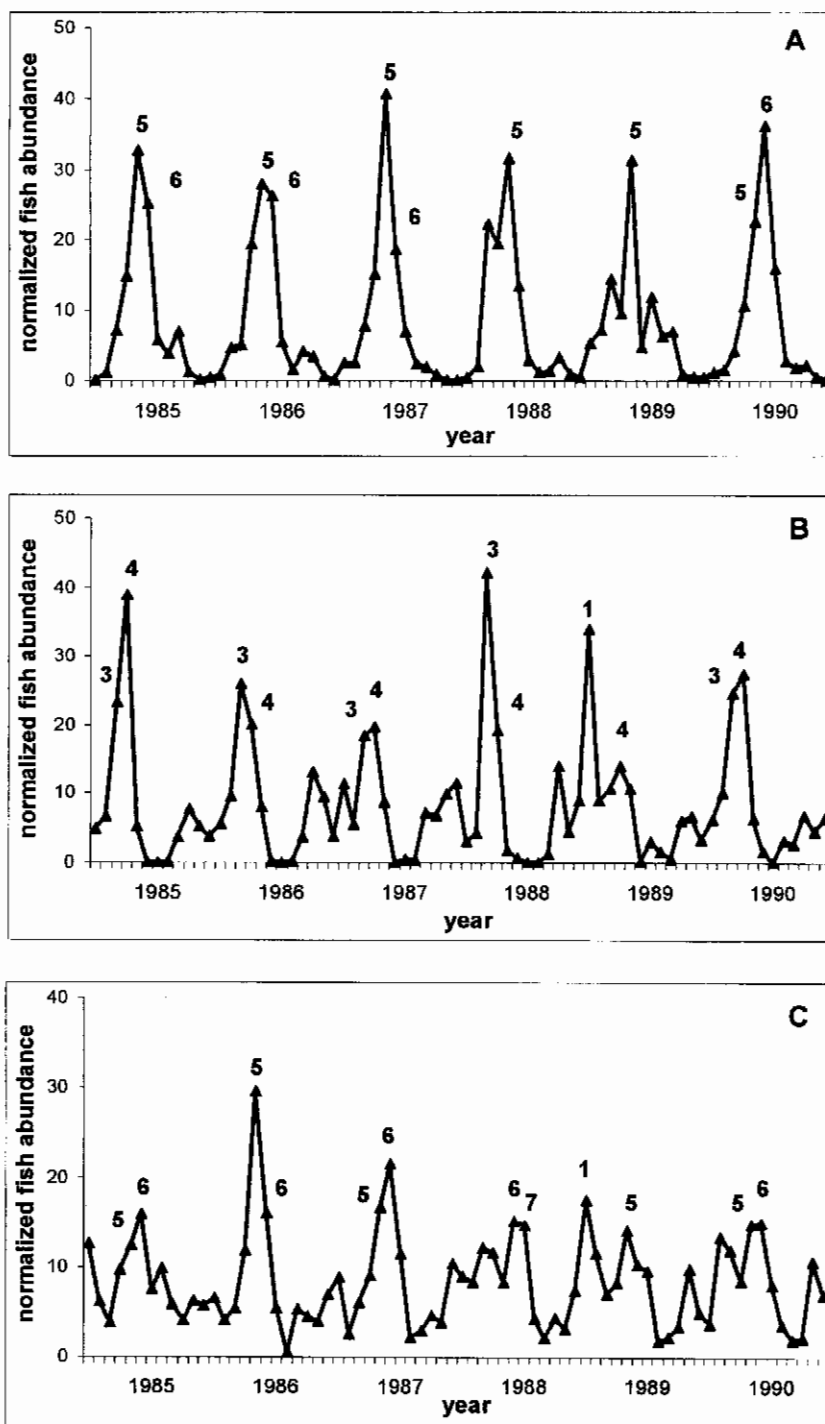


Figure 6.2 Fish abundance (normalised) for selected fish species during the period 1985–1990. A, *Leporinus obtusidens*; B, *Pterodoras granulosus*; C, *Luciopimelodus pati*.

Table 6.2 Cycling of fish abundance in the main channel and correlation coefficients^a between fish abundance by species and mean monthly water level (HLSF) and water temperatures (T_{water}) for the studied years. Direction of cycling trajectory was included between brackets (see text).

Year	Fish species											
	<i>Prochilodus</i>		<i>Leporinus</i>		<i>Luciopimelodus</i>		<i>Salminus</i>		<i>Pterodoras</i>		<i>Pseudoplatystoma</i>	
	HLSF	T_{water}	HLSF	T_{water}	HLSF	T_{water}	HLSF	T_{water}	HLSF	T_{water}	HLSF	T_{water}
1985	0.03 (-)	-0.72 (-+)	0.74 (-)	-0.48 (-)	0.51 (+-)	-0.36 (-)	0.54 (+)	0.20 (-)	0.36 (+)	0.19 (-)	0.36 (+)	0.40 (-)
1986	0.79 (-)	-0.89 (-+)	0.73 (+)	-0.37 (-)	0.61 (+)	-0.19 (-)	-0.17 (+)	0.28 (-)	-0.23 (+)	0.36 (-)	-0.68 (+)	0.74 (-)
1987	0.13 (-)	-0.76 (+)	0.59 (+)	-0.32 (-)	0.73 (+)	-0.35 (-)	0.21 (+)	0.53 (-)	-0.33 (+)	0.68 (-)	-0.18 (+)	0.66 (-)
1988	-0.03 (-+)	-0.58 (-+)	0.31 (+)	-0.03 (-)	0.54 (+)	-0.15 (-)	0.11 (-)	0.43 (-)	-0.14 (chaotic)	0.53 (-)	0.07 (+)	0.57 (-)
1989	-0.13 (chaotic)	0.06 (+-)	0.07 (chaotic)	-0.23 (-)	-0.50 (chaotic)	0.36 (-)	0.04 (chaotic)	0.70 (+-)	-0.59 (chaotic)	0.59 (-)	-0.21 (chaotic)	0.33 (-)
1990	0.20 (chaotic)	-0.76 (+)	-0.01 (chaotic)	-0.63 (-)	0.27 (chaotic)	0.03 (-)	0.01 (chaotic)	0.06 (-)	-0.39 (chaotic)	0.46 (-)	-0.25 (chaotic)	0.42 (-)

^a $r = 0.71$ ($P < 0.01$, $n = 12$), $r = 0.58$ ($P < 0.05$, $n = 12$).

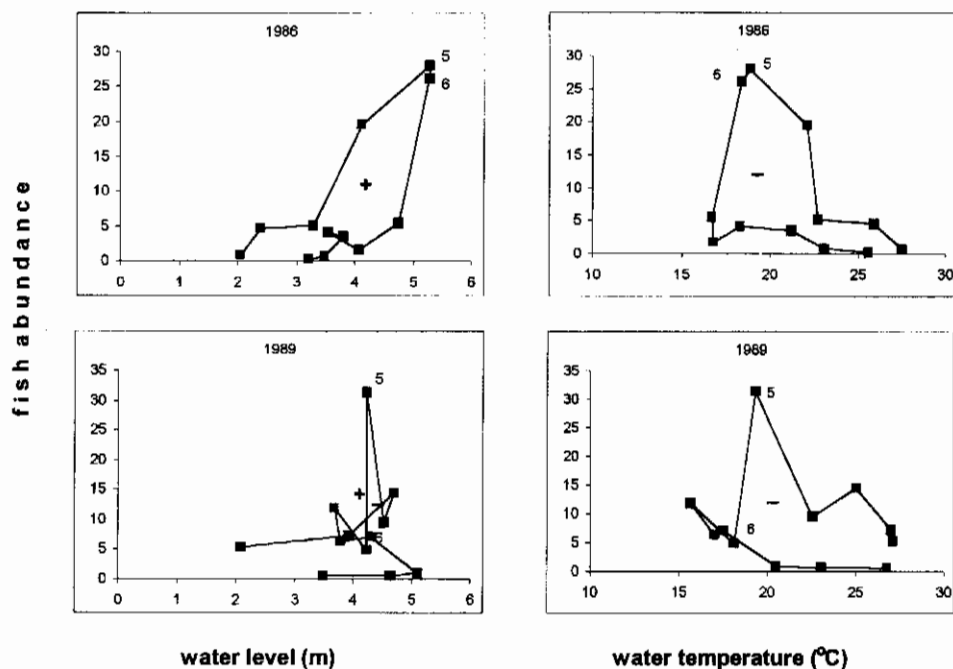


Figure 6.3 Cycling behaviour for *Leporinus obtusidens* in selected years. Figure numbers, month of the year; (+) and (-), positive and inverse direction cycling, respectively; (+-), chaotic cycling

also been suggested that fish wait for a favourable second water level increase before spawning (Fuentes & Bonetto, unpublished data).

For the studied period, fish abundance was rarely related to the flood pulse. However, fish abundances for the majority of species studied were positively related to mean monthly water levels for both the pre-dam and post-dam periods ($P > 0.01$). *Prochilodus* abundance was an exception. It was inversely related to water level for the pre-dam period (R. Quiros unpublished data). During the years when more dramatic changes to flood timing occurred the fishes approximated their pre-dam seasonal patterns in the main channel. For the study period, the main difference between *Prochilodus* and the other migratory fish species was that *Prochilodus* was present in the main channel most of all year.

6.5 Discussion

The abundance of potamodromous fish species in the main channel shifted in a cyclical manner with season. Although the flood pulses in the 1985–1990 period were

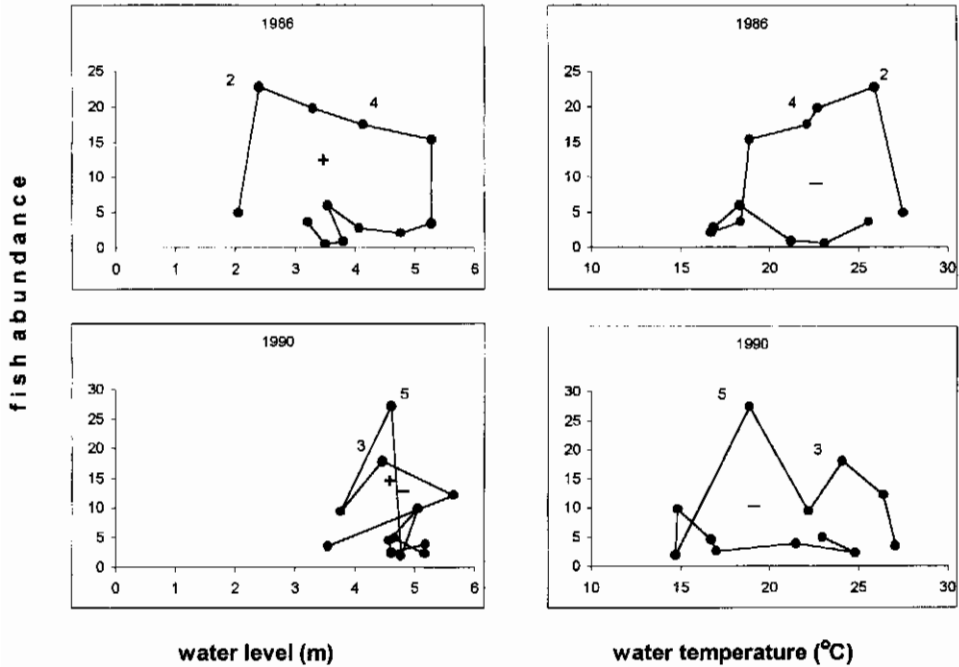


Figure 6.4 Cycling behaviour for *Salminus maxillosus* in selected years. Figure numbers, month of the year; (+) and (-), positive and inverse direction cycling, respectively; (+-), chaotic cycling

suppressed, the peak in fish abundance in the main channel was during the winter similar to before regulation of the upper river. Despite changes in the frequency and intensity of floods, fish movement has also remained similar to that observed before regulation of the upper river. Among year comparisons suggest the fishes maintained their movements on a climate basis, but not on a flood-event basis. For all the potamodromous fish species studied, fish cyclical behaviour in the main channel was more consistent when compared to water temperature than when compared to water level variability. However, the flood pattern for 1985 and 1986 were different from the flood patterns for the pre-dam period (R. Quiros unpublished data). Those results support the conclusion that flooding does not appear to be the factor determining fish movements on a seasonal basis. Furthermore, for the periods 1941–1968 and 1985–1990, changes in the time of maximum abundance have not occurred. Therefore, potamodromous fishes have retained their original migration patterns.

For many years, individuals of the large fish species in the lower Rio de la Plata basin moved upstream more than 400 km from the lower reaches of the lower basin (Rio de la Plata, lower Uruguay River, and the Parana delta) to the middle Parana during late autumn and winter to spawn in the main channel during late spring and

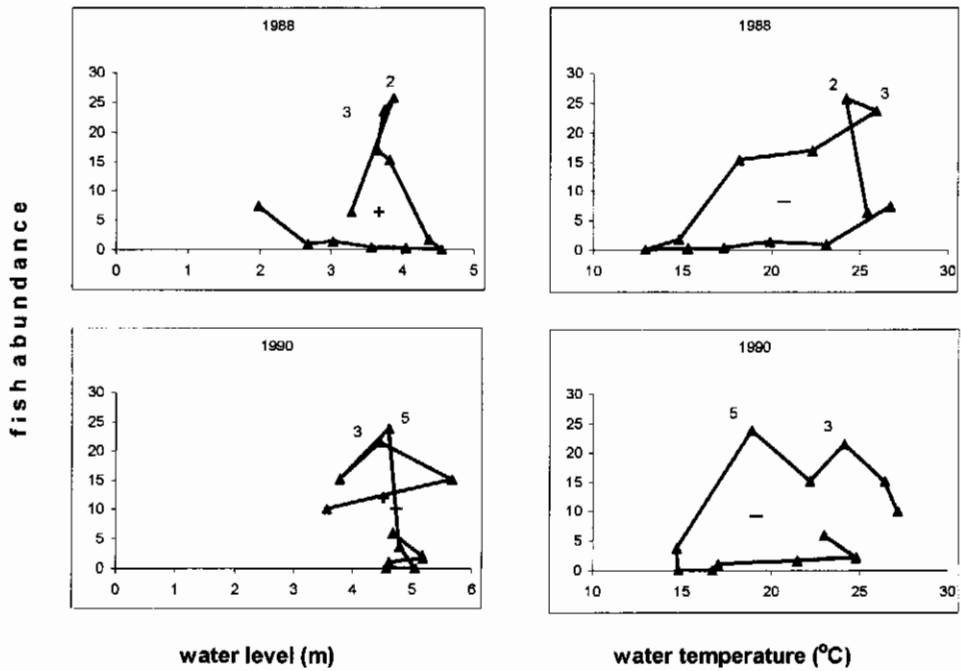


Figure 6.5 Cycling behaviour for *Pseudoplatystoma coruscans* in selected years. Figure numbers, month of the year; (+) and (-), positive and inverse direction cycling, respectively; (+ -), chaotic cycling

summer (Bonetto *et al.* 1971; Espinach Ros & Delfino 1993). Moreover, fish catches for both the Rio de la Plata and the middle Parana are inversely related (Quiros & Cuch 1989). However, other group of species appear to move from upstream areas to the middle Parana during the summers (Bonetto, Canon Veron & Roldan 1981; Oldani & Oliveros 1984). Little information exists about the migratory behaviour of individual species, but this study shows that some species, like *Prochilodus*, *Leporinus* and *Luciopimelodus* move into the lower middle Parana in winter, while other fish species such as *Pseudoplatystoma*, *Pterodoras*, and *Salminus*, move in summer. Most of those species spawn in the main channel during late spring and summer (Table 6.1). Both *Prochilodus* and *Leporinus*, and probably *Luciopimelodus*, exhibit time lags ranging from three to five months between upstream migration and spawning. Tablado *et al.* (1988) mentioned mature *Prochilodus* in a floodplain pond during late spring before spawning. For some migratory species, to rest in floodplain ponds after upstream migration and before spawning may be an explanation for the time lags between upstream movements and spawning in the main channel (C. Fuentes, personal communication). For example, *Prochilodus reticulatus* in the Sinú River move

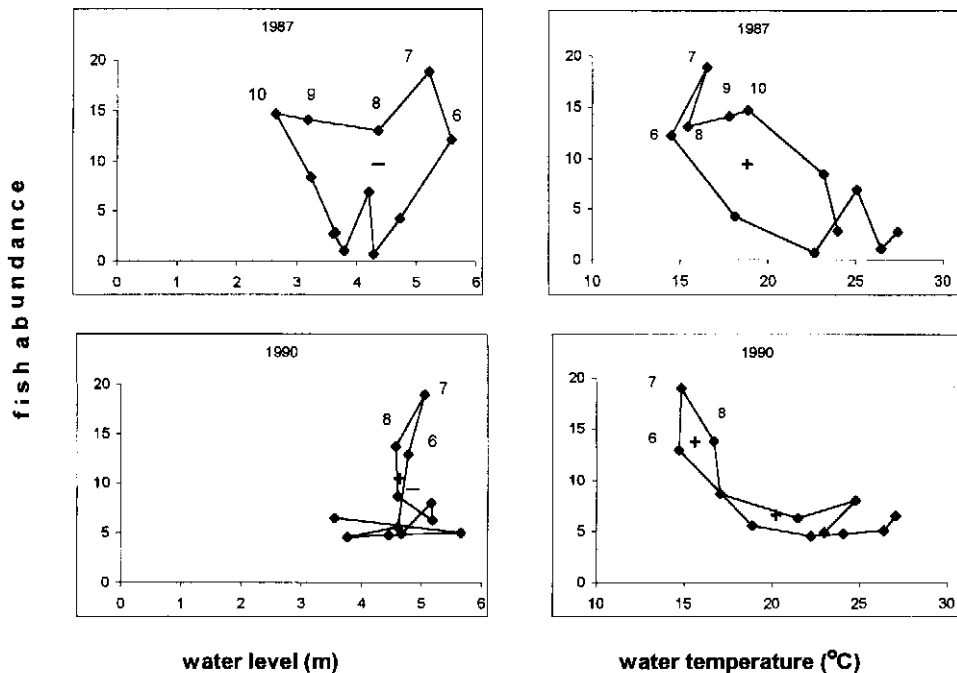


Figure 6.6 Cycling behaviour for *Prochilodus lineatus* in selected years. Figure numbers, month of the year; (+) and (-), positive and inverse direction cycling, respectively; (+-) chaotic cycling

into the upper watershed during their migration, rest for a period of time in the floodplain, and then move downstream to spawn (E. Theiss, personal communication).

Fish tagging (Bonetto *et al.* 1981; Sverlij, Espinach Ros & Ort 1993) suggests the existence of different fish stocks north and south of the site where the river-floodplain geomorphology changes abruptly (Quiros & Cuch 1989). This region is situated 150 km north from the study site. Therefore, homogeneous fish stocks for the studied site can be assumed, but different overlapping stocks cannot be dismissed.

Fish movement remains similar to that observed before regulation of the upper river although changes in the intensity and timing of the flood are apparent. Moreover, cyclic patterns for water temperature were usually more regular than for water level. For the lower middle Parana River, it was suggested that higher water levels trigger reproduction of principal migratory species (Bonetto *et al.* 1981; Tablado *et al.* 1988). However, results from fish larvae studies suggest that the maturation cycle may be controlled by factors such as water temperature and photoperiod (Fuentes 1998). This study does not answer the question of why potamodromous fishes migrate. However, it supports the hypothesis that time of

migration for potamodromous fishes, and by analogy with diadromous fishes (Gross 1987), must have a genetic component. However, the influence of environmental factors cannot be rejected.

It is not known what overall effects the changes in river flow regime will have on the fish populations. In other large systems for the pre-dam period most of riverine fish species anticipate flood conditions by spawning before or during the water rise (Bayley 1995). However, it is highly probable that changes in timing of discharge have produced a disconnection between spawning period and flood conditions. This may explain the shift of potamodromous fish assemblage composition in the regulated river when compared with the unregulated river (R. Quiros unpublished data). However, it is difficult to assign a causal relationship between river regulation and change in fish assemblage (Petts, Imhof, Manny, Maher & Weisberg 1989) since other factors related to development activities may be involved. For example, previous results have supported river water pollution as a primary negative factor on fish abundance for the lower basin (Quiros 1990).

The southern portion of the Parana River has a warm temperate thermal regime, and in the middle reaches, where the current study was conducted, water temperature varies by more than 15°C over the year (Drago 1984). However, the potamodromous fish species studied and related genera are also potamodromous in tropical systems, where annual water temperature usually ranges just a few degrees (Welcomme 1985). Therefore, water temperature is probably not an important factor in triggering the start of upstream fish movement.

Fish abundance for all the species studied, with exception of *Prochilodus*, were positively related to water levels for the pre-dam period (Quiros 1990). Moreover, for the lower Parana basin, there were no noticeable climatic changes during the last centuries. Therefore, it may be supposed that the thermal regime for the 1985–1990 period was similar to that of the pre-dam river period. This is an important conclusion to support the hypothesis that factors other than flood and water temperature, trigger upstream migration for potamodromous fishes in large river–floodplain systems. As suggested for diadromy (Gross 1987), potamodromy may be a complex assortment of life history traits under competitive and environmental selection pressure.

The output of this study is important for the restoration of river–floodplain systems, and recovery and management of riverine fish populations. Potamodromous fishes have maintained their seasonal position in the main channel despite huge flow regulation. The effects of change in frequency and intensity of floods on spawning and recruitment cannot be addressed here, but some negative effects may be suspected. Periodic flooding is critical for maintaining a floodplain river's ecological integrity and biological productivity. For the maintenance of riverine fish populations however, sustaining the timing of floods appears to be as important as maintaining river–floodplain connectivity. Commonly, the spatial scale will be related to total biomass but flood timing will be basically related to healthy population life cycles. The lack of baseline data for this kind of system in developed countries presents an enormous problem to those who attempt to restore them (Bayley 1991). However, some wide generalisations, obtained from natural

fluctuations in unmodified rivers or large manipulations in relatively less developed systems, could be easily tested for developed systems. If the aim is to restore large rivers for riverine fish population, then natural flood pulses will have to be reimposed both in temporal and spatial scales (Bayley 1991). Most of the world's large rivers are greatly affected by human activity (Welcomme, Ryder & Sedell 1989). The necessity for a clear theoretical basis for how large river operate has been stressed before (Johnson, Richardson & Naimo 1995). This study also suggests that to uphold the widespread consensus on statements like 'most common fish species in river-floodplain systems are fluvial generalists well adapted to highly variable environments' would be misleading for the management of riverine populations in both developed and undeveloped systems.

Potamodromous migrations appear to have several advantages for the fish species undertaking them. In those species that are obligate main channel spawners, upstream migration by adult fish prior to spawning must have a role in counteracting downstream drift of eggs, larvae and fry (Welcomme 1985). However, this study suggests the proposed hypothesis that potamodromous fishes move in the main channel according to river discharge independent of cyclical patterns evolved within the undeveloped environment must be rejected. Potamodromous fishes retained their seasonal patterns, evolved with the pristine riverine system, despite of huge changes in water discharge.

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