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Flood regime, dam regulation and fish in the Upper Paraná River: effects on assemblage attributes, reproduction and recruitment

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Abstract

The flood regime is the most important force determining seasonality in neotropical rivers. In the Upper Paraná River floodplain, it is the primary factor influencing biological processes. The aim of this paper is to summarize information on the influence of dam-controlled floods on some fish assemblage attributes, reproduction and recruitment in the Upper Paraná River floodplain, providing preliminary guidelines for dam operation upstream. Fish were collected in different habitats of the Upper Paraná River floodplain (river, channels and lagoons) in the period from 1986 to 2001. The high water period in the Paraná River usually occurs from November/December to April/May. Annual variation in the hydrograph affects species with distinct life history strategies differently, and influences the composition and structure of fish assemblages. Large floods were associated with higher species richness. Frequencies of individuals with ripe and partially spent gonads, which indicate spawning, were higher during the period of increasing water level. Dependence on floods seems to be lowest in sedentary species that develop parental care, and highest in large migratory species that spawn in the upper stretches of the basin and use flooded areas as nurseries. Migratory fishes were favored by annual floods that lasted more than 75 days, with longer floods yielding larger populations. The occurrence of high water levels at the beginning of summer is fundamental to the spawning success of migratory species. However, the flood may be less important for recruitment of juveniles if it is of short duration. Dam operation upstream (releasing more water during the raining season) has potential to promote greater floods with appropriate duration improving recruitment, particularly for migratory species.

Introduction

The flood regime is the most important force determining seasonality in neotropical rivers (Lowe-McConnell, 1987). In fact, the biogeochemical cycles on the Upper Paraná River floodplain are strongly influenced by periodic increases in water level (Thomaz et al.,1992, 1997). Besides the direct exchange of nutrients resulting from this dynamic, floods promote pulses of nutrients from the decomposition of inundated floodplain vegetation (Pagioro and Thomaz, 1999). Primary productivity and the biophysical responses of aquatic macrophytes and several taxa of invertebrates are also dependent on the flood pulse (Bini, 1996).

The importance of flooding on the alluvial plain for the life cycles of fishes has been discussed elsewhere (Lowe-McConnell, 1964; Welcomme, 1979; Winemiller, 1989; Machado-Allison, 1990). As for other tropical floodplains, the flood regime of the Upper Paraná River is the primary factor influencing fish life histories, ecology and regional fisheries (Agostinho and Zalewski, 1996; Gomes and Agostinho, 1997; Agostinho et al., 2000, 2001). The hydrological cycle is thought to play a significant role in cueing various biological attributes such as gonad maturation, migration, spawning and larval development, growth and feeding (Welcomme, 1979; Lowe-McConnel, 1987; Junk et al., 1989; Winemiller,1989; Machado-Allison, 1990; Agostinho et al., 1993, 1995; Vazzoler, 1996, Gomes and Agostinho, 1997).

The regulation of flow by upstream dams has modified the structure and function of the Upper Paraná River floodplain and negatively impacted the fish fauna (Agostinho et al., 2000, 2003). However, the results of this regulation on the hydrograph of this floodplain are predictable. Thus, management of the quantity and quality of the water passing through the dams to maintain hydrology close to the natural regime has great potential to reduce impacts on the fish assemblages. However, the efficacy of flow management requires detailed information about its effect on floodplain functioning and assemblage responses. This information does not exist in this area and dam operation usually serves only the interest of the hydropower companies. Therefore, to change this situation, a compelling conservation goal with regulatory support is required, which is already in progress with the creation of three conservation units in the region (a protected area, a state and a national park).

The aim of this paper is to summarize information on the influence of dam-controlled floods on some fish assemblage attributes, reproduction and recruitment in the Upper Paraná River floodplain and provide preliminary guidelines for dam operation upstream, in order to promote floods. To achieve this we will use a descriptive approach. Firstly, we broadly describe the area and the flood cycle (natural and regulated). Then, we review the literature on the subject and provide some unpublished data in support of our observations.

Description of the floodplain and the flood cycle

Before 1998, the Upper Paraná River had an extensive floodplain between the cities of Três Lagoas, Mato Grosso do Sul State and Guaira, Paraná State (a 480 km stretch, ≤20 km wide). This section was the only remaining dam-free stretch of the Paraná River in Brazil, except for 30 km downstream from the Itaipu Dam (Agostinho and Zalewski, 1996). Despite being one of the most regulated river stretches in the world (more than 46 large dams), the flood regime in the study area did not change drastically because of several important tributaries in this stretch. In 1998, Porto Primavera Dam, located in the middle part of this dam-free stretch, was closed, which reduced the floodplain to 230 km between the Itaipu Reservoir and the Porto Primavera Dam (Figure 1).

In this segment, the river has a wide-braided channel, with a low slope (0.09 m km^{-1}) and a great accumulation of sediments on its bed that give rise to sandbanks and small islands. Secondary channels, the Baía River, and the lower courses of rivers entering on the west bank (e.g. Ivinheima, Amambai, and Iguatemi rivers) form complex anastomoses in this section. The east margin of the river is higher and tributaries have higher slopes (Paranapanema, 0.6 m km^{-1}; Ivai, 1.30 m km^{-1}; Piquiri, 2.2 m km^{-1}) with smaller floodplains (Agostinho et al., 1995).

The area of this study is located along the lower third of the Upper Paraná River between the mouths of the Paranapanema and Ivinheima rivers. At this point, the Paraná River channel is 3.4–4.0 km wide, with an extensive alluvial plain on its west margin. Annual water temperatures fluctuate between 10.3 and 33.6 °C, with an average of 22.0 °C (Stevaux, 1994). The pluvial regime in the region is marked by a wet season from October to February when monthly rainfall averages more than 125 mm, and a dry season from June to September when rainfall is less than 80 mm. Average annual rainfall reaches 1500 mm, characterizing the climate of the region as tropical–subtropical (IBGE, 1990).

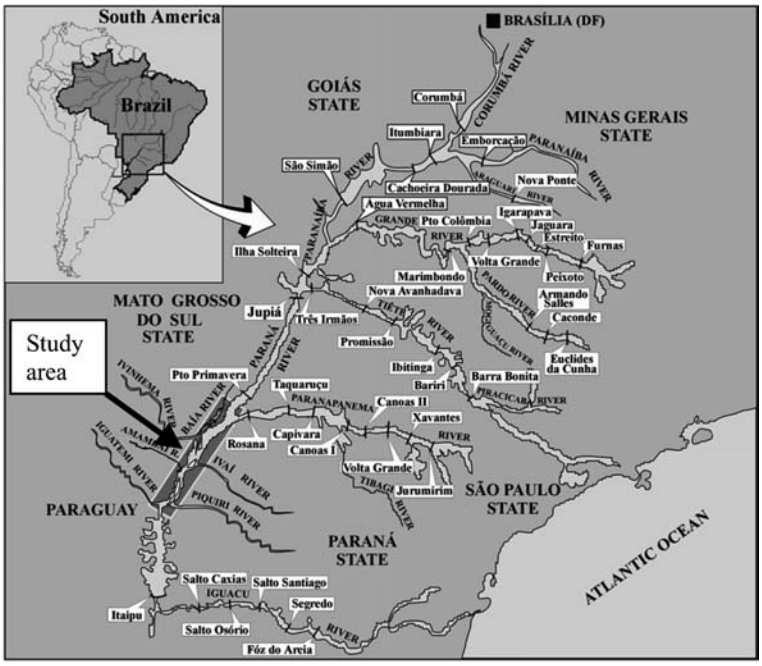

Figure 1. Upper Paraná River basin, reservoirs and location of the study area (arrow).

The high water period in the Paraná River usually occurs from November/December to April/May. High water levels characterize this phase and some pulses occur with amplitudes of up to 2–3 m. Occurrence of two or three annual flood pulses is quite common during high water levels, and they have been recorded even in the Middle Paraná River in Argentina (Carignan and Neiff, 1992). Smaller pulses (< 0.5 m) occur weekly during the dry season (Thomaz et al., 1992) and they are caused by the operation of the upstream reservoirs. Therefore, the seasonal water level fluctuation in the upper Paraná River floodplain is not continuously sinusoidal (i.e., it presents several pulses) like those of other large rivers such as the Amazon (Rai and Hill, 1982), and uninterrupted periods of falling and rising water are rarely observed (Agostinho et al., 2000). On average, the water level of the Paraná River fluctuates about 2.5 m during each seasonal cycle, but considerable interannual variation may be observed. The flood amplitude may reach up to 7.5 m, but years with almost no flooding have been recorded (e.g. 1986–1987; Figure 2).

Water discharge measured in the Paraná River near the mouth of the Paranapanema River varies between 9200 $m^3\ s^{-1}$ (June–September) and 13,000 $m^3\ s^{-1}$ (November–March). Maximum and minimum values registered over the last 30 years were 33,740 $m^3\ s^{-1}$ in 1983 and 2550 $m^3\ s^{-1}$ in 1969. In the Upper Paraná, floodplain dams promoted alteration in discharge. They increased the minimum and reduced the maximum averages (Figure 3) and they also promoted daily and weekly pulses resulting from dam operation. However, the effect of these pulses is minimized by the interlinked functioning of the dams above and below this area, which minimizes abrupt changes

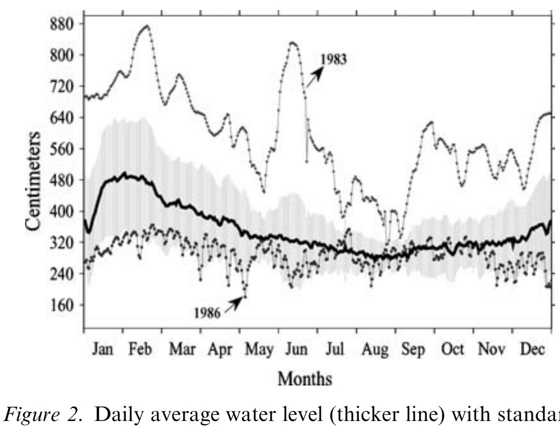

Figure 2. Daily average water level (thicker line) with standard deviation (± sd: shaded area) from 1978 to 2000 in the Upper Paraná River floodplain. The extreme cycles with pronounced floods (1983) and absence of floods (1986) are also shown (modified from Agostinho et al., 2000).

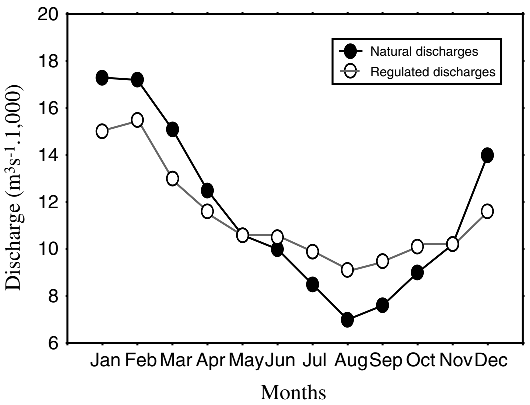

Figure 3. Comparison of the hydrologic regime of the Upper Paraná River before and after the construction of a series of reservoirs upstream (modified from Agostinho and Zalewski, 1996).

in discharge. In addition, several large tributaries in its upper basin may moderate flood pulses when their discharge is not in phase with the river mainstem (see Figure 1).

Influence of the flood regime on fish assemblages attributes

Since water level variations seasonally annex large areas of the terrestrial environment to the water bodies (flood zones), they promote great environmental fluctuations that affect biological processes and the structure and function of species assemblages. With regard to fish, fluctuations determine to a variable degree, the availability of shelter and food, reproduction, growth, mortality, competition, predation and parasitism. However, the large input of organic matter to aquatic floodplain habitats may reduce dissolved oxygen and result in the emigration or death of a great number of fishes (Winemiller, 1989, 1990; Agostinho and Julio, 1999). Annual variation in the hydrograph should affect species with distinct reproductive strategies differently, thus determining variation in the composition and structure of fish assemblages. The main hydrograph attributes that affect fishes are amplitude, duration, timing and rate of change (Agostinho et al., 2000, 2001), all of which are influenced by dams located upstream.

Greater habitat heterogeneity in years of large floods should increase the colonization rate by fishes and aquatic invertebrates that are food resources for these fish. It is expected that the absence of floods (accompanied by harsh abiotic conditions) might reduce species richness (Junk et al., 1989; Agostinho et al., 2000). However, variation in flood amplitude and duration, intermediate level of disturbance, should actually increase richness by preventing a competitively dominant species from excluding other species (Wootton, 1990). A study carried out by Agostinho et al. (2001) on the Paraná River floodplain during years with different flood attributes demonstrated that large floods increase the number of species. However, these authors report that this increase in species richness did not affect the diversity index (Shannon) calculated for the different habitats of that region uniformly. The diversity index may be lower as a result of reduced evenness in the distribution of individuals among species (dominance). In such cases, water ebbing after the flood periods carries large number of juveniles of dominant species into the main channel of the river. In addition, Agostinho et al. (2001) verified a tendency for greater relative density and biomass in a high water level year.

Reproduction strategies and recruitment

Four main reproductive strategies of fish from the Upper Paraná River are presented in Figure 4 (Suzuki, 1992; Agostinho et al., 1995; Vazzoler, 1996; Agostinho et al., 2000, 2003). Long distance migrants contribute with 18% of the total, and species with this reproductive strategy (i.e., migratory species such us *Salminus maxillosus*, *Pseudoplatystoma corruscans* and *Prochilodus lineatus*) are those that migrate at least 100 km and depend directly on their migration to complete the development of their gonads and the spawning process. Short distances or non-migratory species, for instance, contribute with 82% of the total. Within this group, species that present external fecundation contribute with 73%. Of this total, 52.5% are species that do not present parental care (such as *Astyanax* spp.), and they depend on migration (<100 km), and on the flood regime to complete their life cycles (i.e., short distance migratory species). The other 21% are species that present parental care and live in the floodplain (such as *Serrasalmus* spp., *Loricariichthys* spp. and *Hoplias* spp.), and they may take advantage of

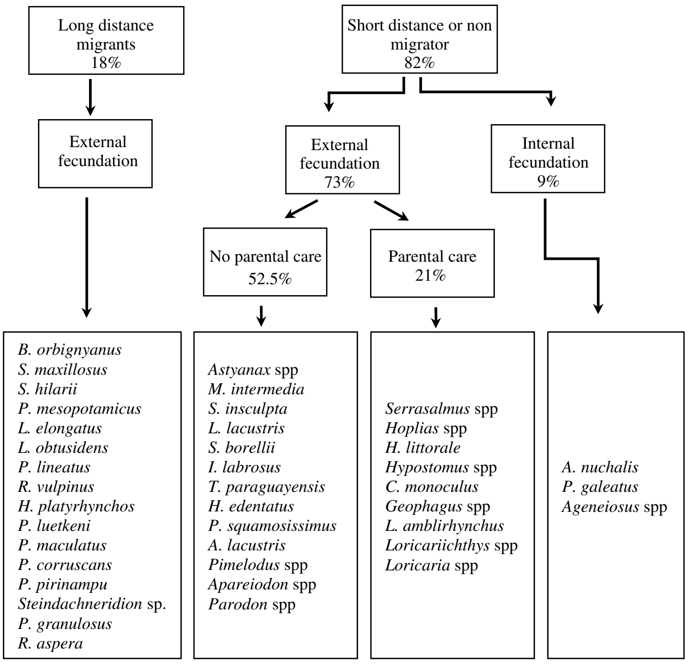

Figure 4. List of species according to their reproductive strategy, in the Upper Paraná River.

habitats when the flood is not conspicuous (i.e., sedentary species). Species that present internal fecundation (9% of the total) are more independent of the flood cycle.

The environmental factors in the Upper Paraná River basin are similar to other South American basins, in that their flood regime has great relevance in control of reproduction and recruitment success (Welcomme, 1979; Lowe-McConnell, 1987; Machado-Allison, 1990; Vazzoler and Menezes, 1992). This relationship is evident not only by the high degree of synchrony between floods and the principal events of the reproductive cycle (maturation of oocytes, migration, spawning and initial development of juveniles), but also because of the relationship between recruitment success and timing, and the duration and amplitude of floods (Agostinho, 1994; Agostinho et al., 1994; Gomes and Agostinho, 1997).

The frequencies of individuals with ripe or semi-spent gonads, indicative of recent spawning, were higher during the period of increasing water level (Figure 5). Godoy (1975) monitored migratory fishes at the Cachoeira das Emas, Mogi Guaçu River from 1943 to 1970 and concluded that flooding is an important proximate factor for spawning, and the dynamics of flowing water are fundamental to oocyte fertilization, floatability and drifting. When water levels are rising, hydrated eggs drift along the river and spill over onto the floodplain, where they complete development. Godoy (1975) reported that large migratory fishes do not spawn when the river water level is stable or decreasing.

The flood regime differentially affects reproduction and recruitment of species with different life histories. Dependence on flooding seems to be lower for sedentary species with parental care

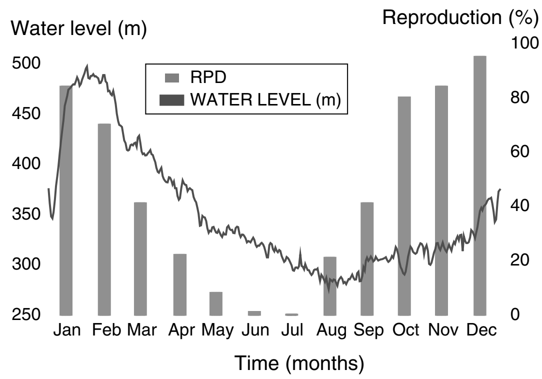

Figure 5. Daily water level average from 1978 to 2000 (line) and monthly frequency of reproductive females (ripe + semi-spent; bars) in the Upper Paraná River floodplain, during an annual cycle (modified from Vazzoler et al., 1997 and Agostinho et al., 2001).

when compared with migratory species that spawn in upper basin stretches and whose young inhabit flooded areas during their initial development. Studies carried out on the Paraná River floodplain (Agostinho et al., 2001) demonstrated that catch-per-effort of ripe and semi-spent sedentary species was greater during a drought year (1986–1987; Figure 6a). The great difference between the years may have been caused by a larger flooded area in the last 2 years affecting absolute density and catchability. On the other hand, migratory species were more abundant in the year with greatest flood. Short-distance migratory species varied in an intermediate way (Figure 6a). However, the abundance of juveniles was low in the floodless year (1986–1987), for all reproductive strategies (Figure 6b).

A 7-year survey of the biomass of species with different reproductive strategies was carried out in three lagoons in the floodplain of the Paraná River. Fishes were sampled with seine nets 6 months after the reproductive peak. These habitats are occupied by young-of- the-year of large migratory fishes, and adults and juveniles of species with other life history strategies. Flood-duration, as the main factor affecting recruitment (Gomes and Agostinho, 1997), was defined as the number of days from September to March in which water levels was higher than 3.5 m (floodplain inundation height; 221.5 m s.l. in Porto São José Hydrometric Station; Verissimo, 1999), and was correlated (Spearman ρ) with fish biomass separated by reproductive strategy (data presented in Figure 7). A significant correlation ($\rho = 0.90$; $p = 0.006$) was found for large migratory fish (ML in Figure 7). For the other reproductive strategies, correlations were not significant, with values ranging from −0.25 ($p = 0.59$) to 0.70 ($p = 0.08$). Migratory fishes were favored by annual periods of flooding greater than 75 days, as in 1998 (Figure 7). The closure of Porto Primavera Dam, in December 1998, resulted in diminished water discharge during the flood period to a level similar to those of the dry season. This event explained the low numbers of migratory fish captured in 1999 (Figure 7), despite that the duration of the flood exceeded 100 days. According to Sanches (2002), larval density of large migratory species during this period was high. It appears that larvae were not able to access the floodplain habitats, thus affecting the biomass of the cohort. After the Porto Primavera Dam closure, flooding was extremely rare. In 2000, the absence of floods can be associated with a regional drought; and in 2001, the Porto Primavera Reservoir filled completely, retaining more water. During years when the water levels in the Paraná River are held artificially low, recruitment in fish species with sedentary and parental care strategies may be associated with lateral tributaries sources not directly affected by the dams. However, when flooding is absent because of regional drought, all strategies are affected.

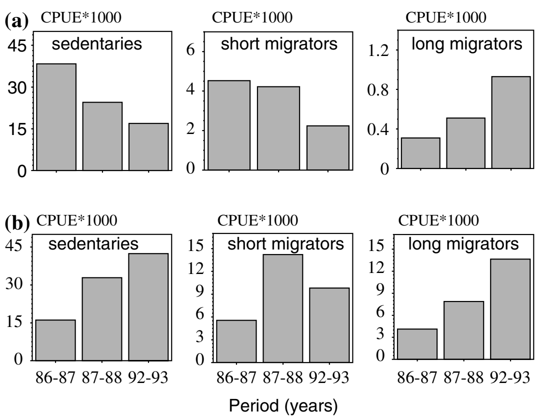

Figure 6. Annual variation in the abundance (CPUE = catch-per-unit-of-effort) of (a) reproduction stages of adult (ripe + semi-spent) and (b) juvenile fishes, according to the reproductive strategy in the Upper Paraná River during years with different flood level (1986–1987 = flood absent; 1987–1988 = moderate flood; 1992–1993 = normal flood, from Agostinho et al., 2001).

Fishery recruitment

In the Upper Paraná River, migratory species ascend the river during the beginning of the flood period and spawn in the upper stretches of tributaries (Agostinho et al., 2003). The larvae drift passively towards inundated areas. As the water recedes, juveniles are confined to lagoons and channels of the floodplain for a maximum of 2 years before they are recruited to the adult stock (Agostinho et al., 1993, 2003; Vazzoler, 1996; Gomes and Agostinho, 1997). The construction of several dams in the basin created obstacles to migration and altered the amplitude and duration of the floods as well as presenting migration barriers, thus affecting fish recruitment and survival (Agostinho et al., 2001, 2003).

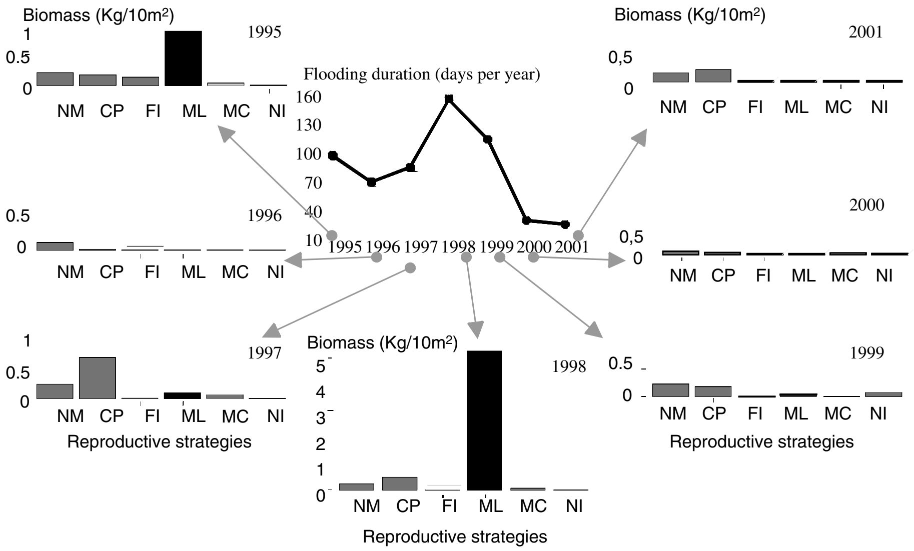

Figure 7. Average biomass estimate (kg wet mass 10 m^{-2}) of juveniles in three lagoons of the Upper Paraná River floodplain, according to reproductive strategy obtained 6 months after the peak of reproduction (NM = sedentary; CP = parental care; FI = internal fertilization; ML = long-distance migratory; MC = short-distance migratory; NI = not identified). Number of inundation days per year are represented in the upper middle graph.

In order to assess the influence of floods on fishery recruitment we focus on *Prochilodus lineatus*, one of the most studied migratory fish of the Paraná River (Sverlij et al., 1993; Agostinho et al., 1993, 2000, 2001; Gomes and Agostinho, 1997), and a regionally abundant species. Juveniles of this species use the floodplain as a nursery habitat (Agostinho et al., 1993) and are exploited by artisanal fisheries in the Paraná River and Itaipu Reservoir downstream of the last remaining major stretch of functional floodplains (Petrere and Agostinho, 1993; Agostinho et al., 1994; Okada et al., 1996; Petrere, 1996; Petrere et al., 2002).

Gomes and Agostinho (1997) analyzed the influence of mean annual water level (m), amplitude (maximum water level of the river in a given year; m) and flood duration (number of days above 3.5 m – yearly total and for each season, and summer and autumn together) on recruitment of *P. lineatus* for the fishery conducted at the Itaipu Reservoir. Recruitment is defined here as the amount (in kg) of immature *P. lineatus* (standard length smaller than 20 cm, i.e. less than 2 years old; Vazzoler, 1996; Gomes and Agostinho, 1997) captured in the fishery. Recruitment was 89 kg in 1988, 3335 kg in 1989, 3481 kg in 1990, 962 kg in 1991 and 1093 kg in 1992. These values ($\log_e$ transformed) were more correlated to the duration of the floods (Pearson correlation coefficient: $r = 0.80$, $p = 0.11$) than to the mean ($r = 0.75$, $p = 0.14$) and maximum water level ($r = 0.42$, $p = 0.47$) reached. Flooding during summer and autumn was more strongly and significantly correlated with $\log_e$ recruitment when these seasons were grouped together ($r = 0.92$, $p = 0.03$) than when they were examined separately ($r = 0.55$, $p = 0.33$ and $r = 0.68$, $p = 0.20$, for summer and autumn, respectively).

Since flood duration is more important to recruitment than flooding amplitude, the occurrence of high water levels at the beginning of summer, which was related to the spawning success of migratory species (Godoy, 1975; Agostinho et al., 1993; Vazzoler, 1996), may be less important to the recruitment of juveniles to the adult stock if floods are of short duration. Elevated water levels during summer and autumn favor juvenile survival by supplying shelter for a longer period, so that individuals can reach larger sizes earlier and consequently have fewer aquatic and terrestrial predators. Reduction of stress associated with the dry period also would favor survival.

Low water levels persisting for relatively long periods may result in the total absence of young-of-the-year (Welcomme, 1979). This seems to be the case for *P. lineatus* in the Upper Paraná River.

Gomes and Agostinho (1997) reported low numbers of 1-year-old individuals of this species on the Upper Paraná River floodplain in 1986–1987. These authors related the lack of recruitment to two low-water years insufficient for floodplain inundation. This prolonged period of low water levels was attributed to lack of rain (1984–1985) and retention of water by the closure of a new upstream dam (1985–1986). Then, the observed reduction of recruitment and subsequently reduction of adult stocks led to serious effects on the fishery. In fact, recruitment failure may explain reduced catches of certain species in the Itaipu Reservoir. In 1987, *P. lineatus* was the most important species in the fishery (Agostinho et al., 1994), contributing about 500 t (1.3 t $fisher^{-1}$ $year^{-1}$). In the following year, the catch was only 220 t (0.6 t $fisher^{-1}$ $year^{-1}$), stabilizing at this level in subsequent years (Gomes and Agostinho, 1997). Although other factors such as overfishing and reduction in periphyton that serves as food (algae supported by inundated vegetation) may have contributed to reductions in catches of this species in the Itaipu Reservoir, the absence of flooding certainly played an important role.

Conclusions

The maintenance of fish diversity in the last dam-free segment of the Paraná River in Brazil, especially with regard to the populations of large migratory species, strongly depends on the integrity of the land–water ecotone represented by the floodplain. The maintenance of this integrity should necessarily be linked to the disruption of the current process of human occupation in the region and especially to a greater rationalization of dam operations upstream. The maintenance of, and even an increase in the present recruitment levels that sustain the fisheries, especially the one artisanal ongoing in the Itaipu Reservoir, depends on these operations.

The artificial control of floods and discharge levels by upstream dams has great potential to improve recruitment, particularly for large migratory fishes. Dam operation has some flexibility to meet these needs, but there are some important information gaps (e.g. scarce information about South American fish biology and specific responses to floods). More detailed studies are necessary in order to assess the biological requirements of threatened and commercially important fish species and to identify the minimum level, duration and timing of floods that trigger spawning and promote reproduction, the viability of eggs, and larvae survival.

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