

## INFLUENCE OF THE FLOOD REGIME ON THE REPRODUCTION OF FISH SPECIES WITH DIFFERENT REPRODUCTIVE STRATEGIES IN THE CUIABÁ RIVER, UPPER PANTANAL, BRAZIL

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### ABSTRACT

This study evaluated the influence of the flood regime of the Cuiabá River on the reproductive dynamics of fish species with different reproductive strategies. Sampling was carried out at ten sites in the basin, between March 2000 and April 2004. The reproductive strategies evaluated were long-distance migrant (LM), short-distance migrant (SM), sedentary with parental care (PC) and sedentary or SM with internal fertilization (IF). Period, duration and intensity of floods were the flooding attributes considered. Duration and time of spawning were evaluated using the index of reproductive activity (IRA), and inferences concerning reproductive allocation were based on the analysis of gonad weight. Reproductive success was evaluated based on the annual catch of young-of-the-year of each species. Reproductive dynamics and flood regime were closely correlated; the reproductive peaks of fishes using all four strategies always preceded flood peaks. Intense floods favoured gonadal development of LM and PC, but were less important for IF. In relation to juvenile survival, the occurrence of floods appeared to be crucial for the strategies of LM, PC and IF, because such floods increased fish survival in the period of initial development. In contrast, SM appeared to be less dependent on floods for reproduction. These results indicate that, except for SM, floods have an important role in the recruitment of species using other reproductive strategies, and influence spawning success as well as juvenile survival. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: fishes; reproductive strategy; hydrological regime; flooding attributes; floodplain; Pantanal

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### INTRODUCTION

The hydrological regime, with alternating periods of flood and drought, is the most important environmental factor in community structuring and in the functioning of river-floodplain systems (Lowe McConnell, 1987; Junk *et al.*, 1989; Neiff, 1990). Artificial regulation in this regime affects biotic integrity (Agostinho *et al.*, 2001; Welcomme *et al.*, 2006; Thomaz *et al.*, 2007) and perhaps is the greatest anthropogenic impact on the functioning of large river ecosystems (Bunn and Arthington, 2002; Hoeinghaus *et al.*, 2007).

Seasonal flooding increases the connectivity among water bodies, allowing for the exchange of propagules, nutrients and organisms among habitats (Thomaz *et al.*, 2007); some of these are essential for connecting the life cycle stages of several species.

The synchrony between the major events in fish reproductive cycles and the fluctuations in hydrometric level has been discussed at length (Godoy, 1975; Lowe McConnell, 1987; Winemiller, 1989; Gomes and Agostinho, 1997; Humphries *et al.*, 1999; Agostinho *et al.*, 2003; Agostinho *et al.*, 2004a, 2004b). However, for migratory species, the environmental factors that stimulate spawning, gonad maturation and migratory movements are still not entirely clear. Quite possibly, a combination of factors such as photoperiod, temperature, water conductivity, increase in water level and the availability of food associated with physiological changes in the individual may be involved in these processes by regulating different stages of the reproductive cycle. Increases in photoperiod and temperature have been associated with gonadal maturation (Suzuki *et al.*, 2004). The beginning of the flood cycle is considered

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to be the synchronizing trigger for spawning events. Peak flood level appears to signal the cessation of spawning (Suzuki *et al.*, 2004). Therefore, floods play an essential role in the stimulation of spawning (Godoy, 1975), whereas the first rains following the dry season are considered the stimulus for the formation of schools of long-distance migratory fish species and their subsequent movements (Agostinho *et al.*, 2003). Biological factors associated with limitations of space and food during the dry season are also considered vital components of migration (Duque *et al.*, 1998). At latitudes where seasonal fluctuations of temperature are small, floods are the principal trigger for the reproduction of many species of fishes. Small flood events or the lack of a flood can limit or even frustrate the reproductive processes of many fish species (Agostinho *et al.*, 2004a).

Anatomical, physiological and behavioural adaptations resulting from selection promote the adjustment of life strategies of fish species to the cyclical events of flood and drought, and facilitate their survival in the sometimes inhospitable conditions of flooded environments, especially those related to decomposition of the biomass produced in the dry season, as reported for the Pantanal of Mato Grosso (Ferraz de Lima, 1999; Severi, 1999).

However, floods appear to affect the reproduction and recruitment of species with different reproductive strategies in various ways; this leads to interannual variation in the composition and structure of the fish assemblages (Agostinho *et al.*, 2004a). The major inundations tend to favour the reproduction of long-distance migratory species, which spawn in the uppermost regions of the basin and use flooded environments in their early developmental stages (Nakatani *et al.*, 1997; Baumgartner *et al.*, 2004; Agostinho *et al.*, 2004a). For these species long-lasting floods can maximize recruitment (Gomes and Agostinho, 1997). According to Agostinho *et al.* (2004a, 2004b), sedentary species with parental care (PC) or internal fertilization (IF) appear to reproduce independently of the flood regime, whereas short-distance migrants (SM) show intermediate tendencies.

Based on the hypothesis that species with different reproductive strategies respond differently to the flood regime, the present study attempted to evaluate the reproductive responses of 16 species of fish grouped into four categories of strategies, with respect to the intensity, duration and seasonality of floods, during different hydrological cycles. Specifically, we intended to answer the question of whether the duration and seasonality of spawning and weight allocation in gonads varied with the annual flood regime. We also wanted to investigate the influence of the floods on the survival of juveniles.

## MATERIALS AND METHODS

### *Study area*

The Cuiabá River, which is about 850 km long and occupies a drainage basin of about 100 000 km<sup>2</sup>, is formed by the confluence of the Manso and Cuiabazinho Rivers (Severi, 1999). The Cuiabá and Paraguai Rivers are the main watercourses forming the Pantanal of Mato Grosso. The geological formation of this basin and the predominant regional climate (i.e. a hot rainy summer and a dry, relatively mild winter) lead to a seasonal pattern of periods of high rainfall that causes floods that affect the Upper Pantanal (Severi, 1999). The local climate is marked by a dry season from May through September, and a rainy season from October through April. Monthly mean temperatures near the city of Cuiabá ranging from 21.4°C in July to 27.4°C in December. However, short-term incursions of polar air masses during winter may lower the temperature to nearly 0°C (Girard *et al.*, 2003).

The database used for this study was generated during the course of the project 'Biologia Pesqueira e Pesca na área de influência do APM-Manso', carried out by the Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura/UEM-Furnas Centrais Elétricas. Data obtained at ten sampling stations located at different points in the Cuiabá River basin, between 14° 41'20''S/56° 13'51''W and 16° 21'32'' S/55° 57'20'' W were used.

### *Sampling*

Experimental fishing was carried out monthly from March 2000 through April 2004, except for the period between March 2001 and July 2002 when collections were made every 3 months. The fishing gear consisted of gillnets, longlines, cast nets and seine nets, with sampling effort standardized. Nets and longlines were set out for 24-h periods at each sampling locality, and checked at 7:00, 17:00 and 22:00 h. Cast nets and seine nets were operated during the morning and at night. After removing the fish from the nets, for each individual we recorded the

total length (cm), standard length (cm), total weight (0.01 g), weight of the gonads (0.01 g), sex and stage of gonadal maturation (immature, resting, beginning of maturation, maturing, mature, semi-spent, spent and recovering) adapted from Vazzoler (1996).

### Data analysis

For the analyses, the fish species of the basin were classified into four groups according to their reproductive strategy. Based on the regularity of their occurrence in the samples, four species from each group were selected. The criteria for classification were based on Vazzoler (1996), Agostinho *et al.* (2003), Agostinho *et al.* (2004a) and Suzuki *et al.* (2005).

*Group long-distance migrators (LM)—with external fertilization, without parental care.* This category includes species that carry out extensive longitudinal migrations (travelling more than 100 km). These species use more than one habitat during their life cycle and migrate upriver to spawn in specific localities, whereas the juveniles use the lower parts of the basin, especially lakes, for their initial development. Generally, they are large in size, and have seasonal and total spawning, high fecundity, small oocytes and rapid embryonic development. The eggs are free, which facilitates their passive transport and access to nursery areas. This category was represented by *Prochilodus lineatus* (Valenciennes, 1836), Prochilodontidae, Characiformes; *Rhaphiodon vulpinus* Spix and Agassiz, 1829, Cynodontidae, Characiformes; *Pterodoras granulosus* (Valenciennes, 1821), Doradidae, Siluriformes and *Hemisorubim platyrhynchos* (Valenciennes, 1840), Pimelodidae, Siluriformes.

*Group short-distance migrators (SM)—with external fertilization, without parental care.* These are species that carry out migrations of less than 100 km, with primarily lateral movements. They have relatively high fecundity and small oocytes. Spawning may be total or partial, and the reproductive period may extend over several months. This category was represented by *Acestrorhynchus pantaneiro* Menezes, 1992, Characidae, Characiformes; *Hemiodus orthonops* Eigenmann and Kennedy, 1903, Hemiodontidae, Characiformes; *Pachyurus bonariensis* Steidachner, 1879, Scianidae, Perciformes and *Trachydoras paraguayensis* (Eigenmann and Ward, 1907), Doradidae, Siluriformes.

*Group parental care (PC)—sedentary, with external fertilization.* Fish in this category predominantly spawn multiple times over a long period of time, have low fecundity, and large adhesive eggs with prolonged embryogenesis. PC is well developed including the construction of nests and transport of eggs adhered to the body. These species invest a large amount of energy per individual in their offspring. In this study, this category was represented by *Serrassalmus marginatus* Valenciennes, 1837; *Serrassalmus maculatus* Kner, 1858 and *Pygocentrus nattereri* Kner, 1858, belonging to the family Serrasalminae, order Characiformes; and *Loricariichthys labialis* (Boulenger, 1895), Loricariidae, Siluriformes.

*Group internal fertilization (IF)—sedentary or short-distance migrators, without parental care.* These fishes may show sexual dimorphism and mating rituals associated with reproductive behaviour. Fecundity is relatively low, with medium-sized eggs, and they generally conceal their offspring. In the case of the species analysed here, development is external. Representing this category were *Auchenipterus osteomystax* (Ribeiro, 1918), *Auchenipterus nigripinis* (Boulenger, 1895) and *Parauchenipterus galeatus* (Linnaeus, 1766), belonging to the family Auchenipteridae, order Siluriformes; and *Ageneiosus inermis* (Linnaeus, 1766), Ageneiodidae, Siluriformes.

The data for the hydrological cycle of the Cuiabá River were provided by the National Water Agency (Agência Nacional de Águas, ANA), and were obtained at the Hydrological Station of Cuiabá-MT. The data obtained from the hydrograph, as attributes of the flood regime, were *duration of the floods* (number and % of days in which the river level remained above flood stage), *time of year* or *delay of the floods* (initial month of the floods, in relation to the historical mean) and *intensity of the floods* (annual maximum level and mean level in the flood period). The threshold value for flood stage was considered as the mean of the daily river levels from January 1933 to March 2004. Initial letters were used to summarize the yearly variations on these hydrographic attributes (duration of flood: Ds = short, Dm = moderated, Dl = long, timing of the floods: To = on time, Tl = little late, Td = delay; intensity of the floods: Ih = high, Im = medium, Il = low).

The duration and time of year of spawning were established for the four reproductive strategies from the values of the index of reproductive activity (IRA, Dei Tos *et al.*, 2002). Moderate activity was considered as  $5 \leq \text{IRA} < 10$ ,

and intense activity as  $IRA \geq 10$ . This index is given by the equation:

$$IRA = \frac{\ln N_i \left( \frac{n_i}{\sum n_i} + \frac{n_i}{N_i} \right) \frac{GSR_i}{\overline{GSR}_e}}{\ln N_m \left( \frac{n_m}{\sum n_i} + 1 \right)} \times 100$$

where  $N_i$  is the no. of female individuals in sample unit  $i$ ;  $n_i$  the no. of breeding female individuals in sample unit  $i$ ;  $N_m$  the no. of female individuals in sample unit with highest  $n$ ;  $n_m$  the no. of breeding female individuals in sample unit with highest  $n$ ;  $GSR_i$  the gonado-somatic relationship average of breeding female individuals in sample unit  $i$  and  $\overline{GSR}_e$  is the highest individual value of GSR (weight of gonads  $\times$  100/total weight).

Inferences on the reproductive allocation of the species with different strategies were based on the gonadal weight of females in reproductive activity caught during the breeding season in years with different hydrological cycles. To remove the effect of body size, analyses of covariance (ANCOVA) were performed to obtain the adjusted means of gonadal weight. The covariate was the weight of the individuals, the response variable was gonad weight (both values were log-transformed), and the categorical variable was years. However, we found a significant interaction between years and total weight for long-distance migrants (LM), violating the assumption of parallelism, thereby precluding the use of the adjusted means. Instead, the Johnson-Neyman procedure was used for comparisons involving groups with heterogeneous slopes. This procedure identifies values of total weight that may be associated with significant differences in gonadal weights between years, and consequently allows for identification of regions of non-significance and significance (Huitema, 1980).

The duration, time of year of spawning and reproductive intensity were evaluated only for years in which the collections were made monthly (1, April 2000 to March 2001; 2, August 2002 to March 2003 and 3, April 2003 to April 2004, except March 2004).

Reproductive success was evaluated based on the annual catch of young-of-the-year of each species over the entire study period (March 2000–April 2004). Individuals with lengths less than that of first maturation were classified as young-of-the-year (UEM/Nupélia-Furnas Centrais Elétricas, 2005), except for LM (Group 1), which reached a larger size and whose size limit was that attained in 1 year, estimated from growth equations provided by Perez-Lizama (1994), Miranda *et al.* (2000), Feitoza *et al.* (2004) and Penha *et al.* (2004).

In order to assess the levels of correlation between the total catch of young individuals and the attributes of the floods (duration, time of year and intensity) for each year, Spearman (nonlinear) correlations were calculated using Statistica 7.0. We did not test the correlation significance because of the reduced number of samples (5 years).

## RESULTS

### *Hydrological cycle and attributes of the floods*

The daily variations of the level of the Cuiabá River based on historical data indicated that 240 cm was the threshold value for the flood stage, and that December was the initial month of the floods (Figure 1A). The seasonal fluctuations of the hydrological cycle showed that the Cuiabá River floods between December and April.

Analysis of five hydrological cycles during the study period indicated differences in hydrological regimes between years (Figure 1B). In 1999–2000 (DsTdIm), the hydrometric level oscillated above and below the flood stage for 39 days, i.e. a short, discontinuous flood. In the subsequent hydrological cycle (2000–2001; DsTdII), the river level exceeded flood stage for only 5 days, and therefore this was considered a period without floods. Long-lasting floods occurred in the years 2001–2002 and 2002–2003 (120 and 102 days, DIToIh and DITIIIm, respectively), especially in the former cycle, in which the floods began earlier (beginning of December) and reached the highest levels (709 cm). In the 2003–2004 cycle (DmTIIh), intense floods occurred (688 cm), although they were of moderate duration (70 days) (Table I).

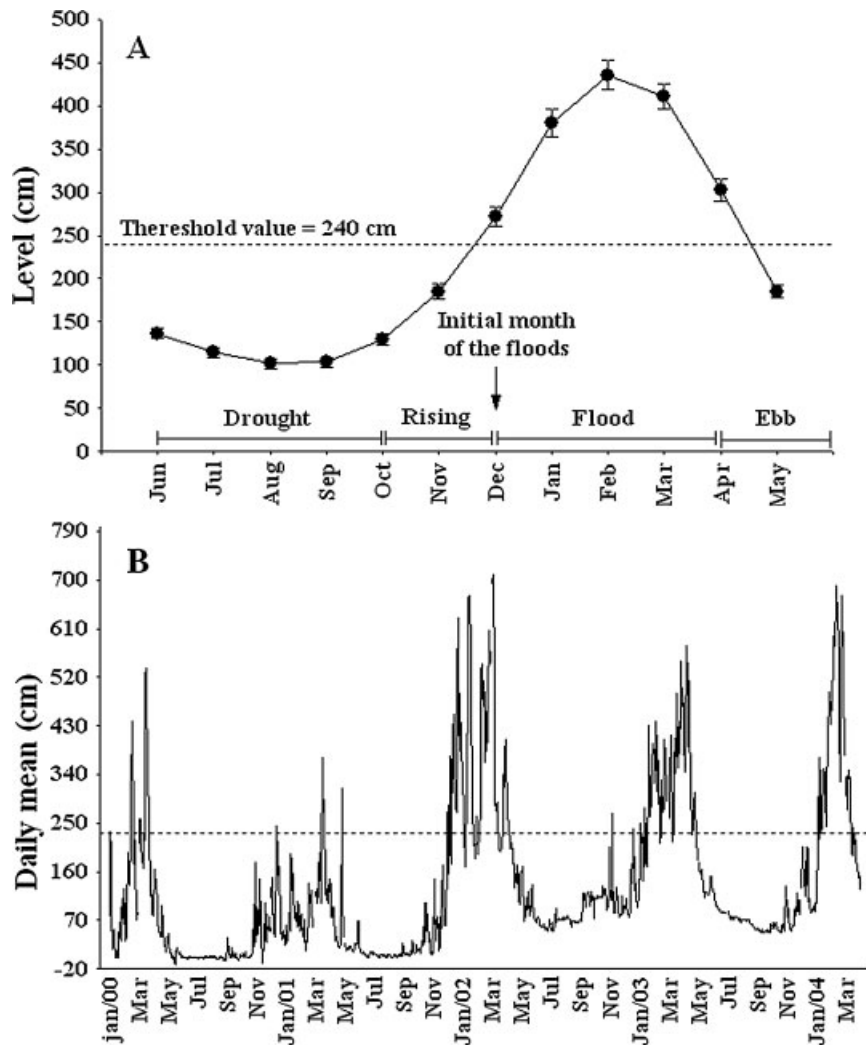


Figure 1. (A) Monthly mean levels of the Cuiabá River based on historical data (January 1933–March 2004). Vertical bar = one standard error. (B) Daily variations in water level during the study period

Table I. Values of flood attributes of the Cuiabá River in each year of the study (duration of flood: Ds=short, Dl=long, Dm=moderated; timing of the floods: To=on time, Tl=little late, Td=delay; intensity of the floods: Ih=high, Im=medium, Il=low)

Attributes of the flood	1999–2000	2000–2001	2001–2002	2002–2003	2003–2004
Duration (no. of days)	39	5	120	102	70
Duration (% days of flood in the year)	10.68	1.37	32.88	27.95	19.18
Time of year (beginning of flood)	15 February	14 March	8 December	19 January	3 January
Delay* (in relation to historical mean)	5	7	1	4	3
Intensity (annual maximum level, in cm)	520	372	709	577	688
Intensity (mean flood level, in cm)	362.22	308.80	371.10	355.29	421.29
Resume	DsTdIm	DsTdIl	DlToIh	DlTlIm	DmTlIh

\*Number of 2-week periods, based on the historical mean (first 2 weeks of December).



*Reproductive cycle*

Analysis of the mean values of the IRA revealed that in general the species of all four strategies reproduced during spring and summer (Figure 2), which are seasons with longer photoperiod and higher temperatures, although these variables did not show important variations during the year. Two patterns common to all four strategies

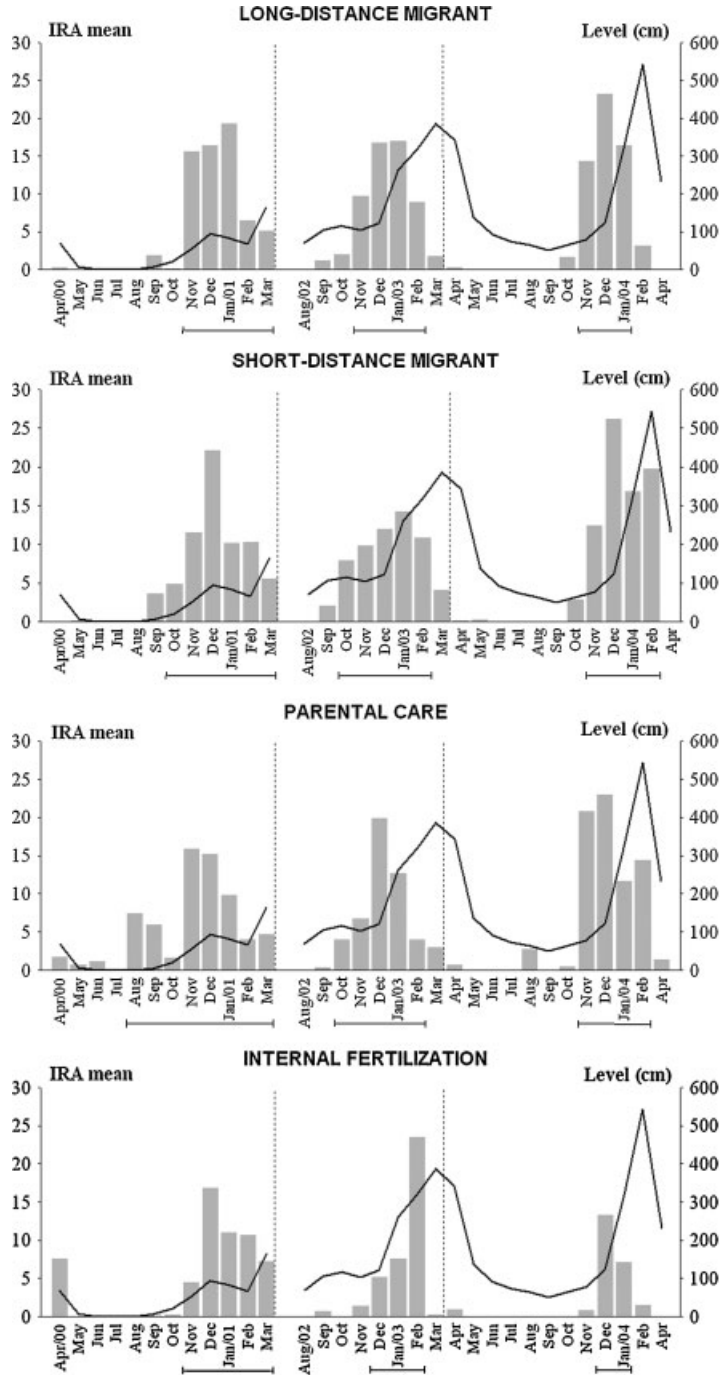


Figure 2. Monthly mean IRA values of the four reproductive strategies (vertical bars) and monthly mean river levels of the Cuiabá River (solid lines). Dashed lines = division of the study years. Horizontal bars = duration of reproductive period

emerged from this analysis: (i) the peaks of reproductive activity preceded the flood peaks and (ii) the reproductive period was shorter in the year with short intense floods, was prolonged (by a month at least) in the year with long-lasting floods, and was further extended in the absence of floods. On the other hand, the reproductive periods of the LM species and those with IF were shorter than the reproductive periods of the others, extending from November to February and from December to March, respectively. Thus, SM showed intense reproductive activity between October and March; whereas species with PC reproduced between August and March.

### Reproductive allocation

The weight allocation in gonads of fish for SM, PC and IF strategies in which it was possible to use the adjusted means followed different tendencies between years (Figure 3). The ANCOVA showed significant among-year differences in gonadal weight for all strategies, except for SM. For the PC species, allocation was greater in the year when floods were of moderate duration and high intensity (DmTIIh); intermediate allocation was observed when floods were long-lasting and of medium intensity (DITIIIm); and less allocation was seen in the year without floods (DsTdII). The inverse occurred for species with IF; their ovaries were heaviest during the years with no flood and lightest during the years with a high intensity flood.

There were heterogeneous slopes for LM. Thus, the Johnson-Neyman procedure showed that gonadal weight varied between years, depending on total weight. For the small bodied fishes (250 g) allocation was greater in the year of the high intensity and moderate duration of flood (DmTIIh cycle), intermediate when the floods were long-lasting (DITIIIm) and smaller in the year when there was no flood (DsTdII). For individuals of intermediate weight (1600 g), gonads were heavier in the year of the high intensity flood (DmTIIh). For large bodied individuals (10 000 g),

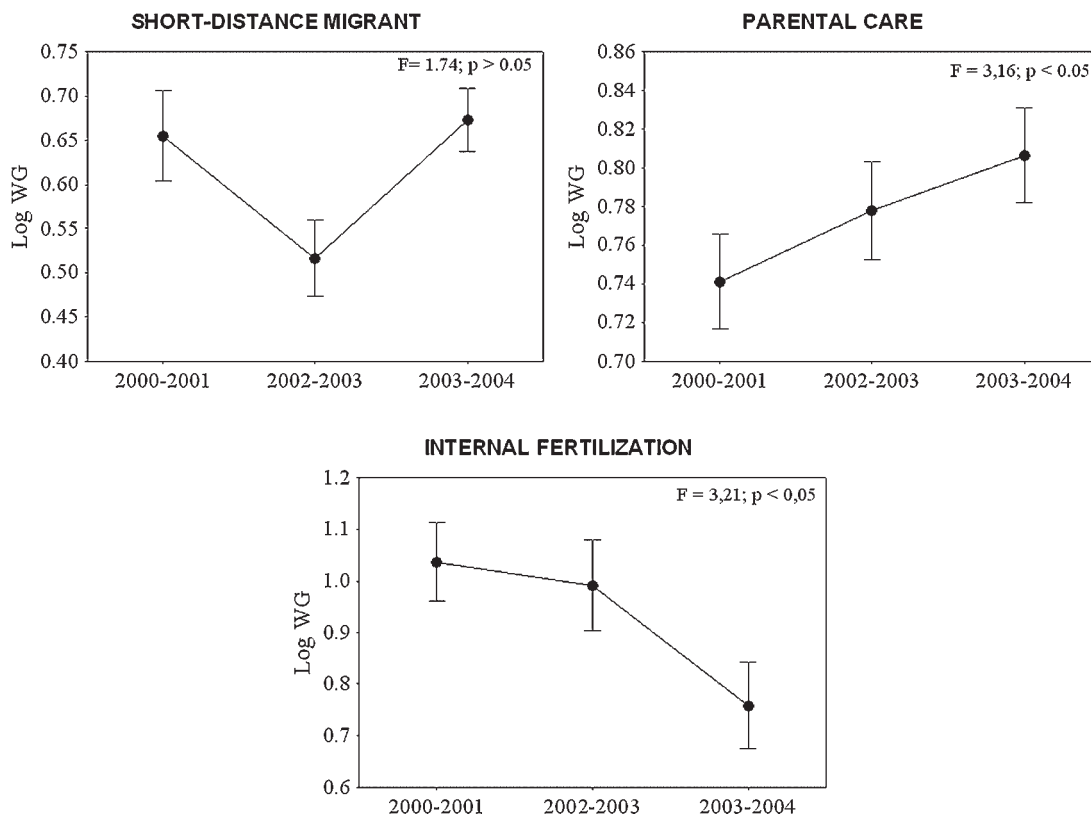


Figure 3. Adjusted mean values of the gonadal weight for the three reproductive strategies in different years. The results of the ANCOVA are included in the graphs. Vertical bar = confidence intervals

allocation of energy in gamete production was greater during the year with no flood. However, due to the low sample size, the results for the heavier fish are inconclusive.

### Reproductive success

The catch of young individuals (Figure 4) in the period following the flood stage showed that in general the floods, especially during 2001–2002 (DIToIh), favoured the survival and development of juveniles of species of all reproductive strategies, except the SM. The smallest catches occurred in the period following the absence of floods (2000–2001; DsTdII), which reinforces the importance of this event for the initial developmental stages of the species using LM, PC and IF strategies. The catch of juvenile SM showed no relationship to the flood regime: it was larger in 2000, a year with a very short, discontinuous flood (1999–2000 cycle; DsTdIm), and was similar in the years 2001 (no flooding—2000–2001 cycle) and 2004 (2003–2004; DmTIIh). For SM, the lowest abundance of juveniles was observed in 2003, in the period following a long-lasting flood (2002–2003; DITIIIm).

The general trends of correlations between the attributes of the floods and the catch of young (Table II) showed that the strategies of LM, PC and IF were positively related (Spearman's  $\rho$ ) to the duration, annual maximum river level and mean level during the floods. These correlations were, in general, highest with the duration of the floods,

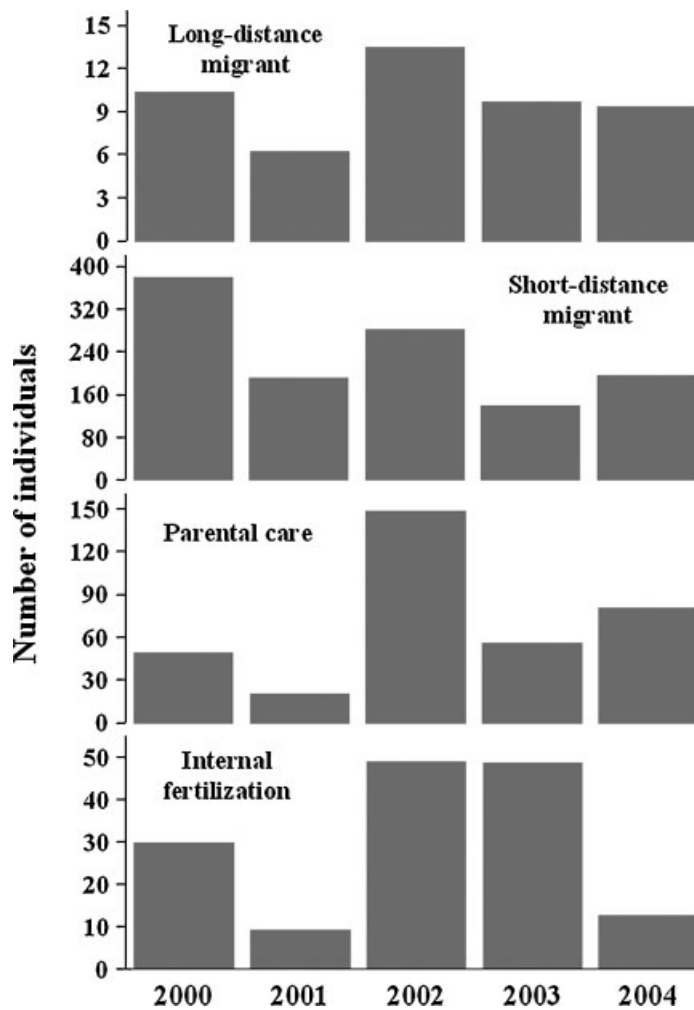


Figure 4. Catch of young individuals of the four reproductive strategies in the different years of the study. The total catches in each year were divided by the number of collections made, i.e. 10 in 2000, 7 in 2001, 6 in 2002, 12 in 2003 and 3 in 2004.



Table II. Values of Spearman correlations between the total catch of young of the four reproductive strategies and attributes of the floods

Hydrographic attributes	LM	SM	PC	IF
Duration (%)	0.70	0.00	0.90	0.90
Time of year (delay of flood)	-0.60	-0.20	-1.00	-0.70
Annual maximum water level (cm)	0.60	0.20	1.00	0.70
Mean level during flood (cm)	0.40	0.50	0.80	0.30

LM, long-distance migrator; SM, short-distance migrator; PC, sedentary with parental care and IF, sedentary or short-distance migrator with internal fertilization.

followed by the maximum river level reached and lowest with the mean level during the floods, except for species with PC, for which the abundance of young was more related to the maximum water levels. For these strategies, the abundance of young-of-the-year was negatively correlated with the time of the floods, indicating that delays in the period of the floods are deleterious to recruitment. The catches of young SM were not shown to be related to the attributes of the flood regimes considered, including the duration of these events. However, only correlations with values higher than 0.9 were significant at  $p < 0.05$  level, because of the low number of observations (5 years).

## DISCUSSION

Several studies in recent decades have demonstrated the important role played by seasonal floods on the reproduction of neotropical migratory fishes. However, the effects of floods on other reproductive strategies have not often been studied. Given the profusion of strategies shown by neotropical fishes and the marked environmental changes cyclically imposed by the inundations on floodplains, which sometimes create adverse conditions, it would be expected that species with different reproductive strategies would respond differently to the attributes of the hydrological regime.

It was observed that, independent of strategy, the reproductive peaks of the species preceded the flood peaks, showing that the association of reproduction with the beginning of the increase in water level is a pattern common to the majority of the species of the Upper Pantanal ichthyofauna. The tendency for more intense reproductive activity to precede flood peaks was also observed by Paugy (2002) in Africa, and Agostinho *et al.* (2004a) and Suzuki *et al.* (2004) in the Upper Paraná River basin.

However, the response to interannual variations in the hydrological cycle in relation to the duration of the reproductive period and weight allocation in gonads varied among the strategy groups. Thus, for the PC category and for those lighter individuals of the LM group, years with intense and moderate flood duration resulted in increased reproductive activity over a shorter time period. In years with long-lasting floods of lesser volume, the reproductive period was more prolonged, although with lower reproductive intensity. This flexibility in the spawning periods allows the species to synchronize their reproduction with environmental conditions more favourable to survival of the offspring (King *et al.*, 2003). In this manner, a sudden increase in water level, characteristic of a rapid intense flood, can trigger the final development of the gonads and immediate spawning, whereas a slow rise, characteristic of long-lasting floods, can result in more prolonged spawning, because the favourable conditions tend to persist. On the other hand, in the year when the river did not reach flood stage (DsTdII), reproductive allocation was low in species of these groups. Although gonadal maturation begins in the dry season (Por, 1995; Duque *et al.*, 1998), final maturity, responsible for a large proportion of the weight of the gonads, occurs in the period of rising water levels (Suzuki *et al.*, 2004). This may explain the low values of IRA and the relative gonadal weight. In addition, it would be expected that, in the absence of floods and with the hinderance of spawning, the maturing gametes are reabsorbed. In this regard, Humphries *et al.* (1999) noted that rheophilic species can delay spawning until the water rises, and that there may be gonadal regression through resorption of the oocytes if the flood does not occur. In contrast, for heavier individuals of the LM group, gonadal weight was higher

in years without flooding. Although this tendency was not conclusive because of the low number of large fish, it is expected because absorption of oocytes (ovary weight diminishing) happens more slowly than it does in smaller fish (Agostinho *et al.*, 1991; Agostinho, unpublished data).

The SM strategy includes a range of species with very short to moderate reproductive displacement, belonging to different phylogenetic groups. This could explain the absence of significant differences in gonad weight among years. Otherwise, the low water level during the spawning period did not affect the gonadal development of species with IF. Agostinho *et al.* (2004a) reported similar results and suggested that this strategy appears to be favoured by adverse environmental conditions, especially those of a biotic nature. Thus, IF reduces the time of exposure of gametes and eggs to predation, and assures a higher fertilization rate under conditions of high water transparency and high concentration of predators, which are adverse factors during the dry season (Agostinho *et al.*, 2004b). Three of the six most abundant species after the formation of the Itaipu Reservoir belonged to this group of fishes, although IF occurs in less than 3% of the total species of the Upper Paraná River basin (Agostinho *et al.*, 2000).

The flood regime is one of the preponderant environmental factors in recruitment levels. In addition to affecting reproductive success, it controls the survival rates of the initial developmental stages (Lowe McConnell, 1987; Machado Allison, 1990; Agostinho *et al.*, 2004a). In the present study, the abundance of young-of-the-year of species of all reproductive strategies considered, except the SM, was correlated with the attributes of the floods. The extremes of abundance recorded in the years with no flood (minimum; DsTdII) and long-lasting and high intensity floods (maximum, DIToIh), emphasize the importance of the floods for the initial developmental stages of these species. Even species with high reproductive performance in drought years, such as those with IF, did not overcome the adverse drought conditions, and this resulted in low survival of young. The inundation of the floodplain generates a vast, highly productive environment, rich in food and shelter for young forms of many species. Thus, floodplain environments constitute natural nurseries for the larvae that hatch there as well as for those larvae that are carried by the currents from the parts of the basin farther upstream.

However, the SM species were shown to be independent of the floods for their initial development, with little or no correlation between the abundance of young-of-the-year and the intensity and duration of the floods. In contrast with fish using other strategies, the Spearman correlation between flood duration and catch of young of the SM was null. The catches after a period of drought were larger than in long-lasting and moderate intensity floods (DITIm) and equivalent to those catches during intense floods (DmTIIh) indicating that the permanence of the water within the banks during the reproductive period appears not to have affected the survival of young SM. Smaller catches of these species in the periods following long-lasting floods may be related to an increase in predation by juveniles of large piscivores, especially LM. However, the reasons for the lack of response of this group to the flood regime are unknown and will require further study. It is possible that these results were observed because this group is the most heterogeneous of the groups analysed, both phylogenetically and in feeding strategies. An analysis at the species level might be useful. In this study, however, we sought to understand the patterns at the level of groups of reproductive strategies (reproductive guilds).

King *et al.* (2003) documented these optimum flood conditions for recruitment success: (i) coincidence with high temperatures; (ii) predictability; (iii) slow rise and fall of the river level; (iv) duration from several weeks to a few months; (v) extensive floodplain area. In neotropical regions, the first condition is normally satisfied. However, the others may vary, with different characteristics each year. In temperate regions greater growth of juveniles was observed during a year when floodplain inundation persisted throughout summer, thus providing warm water coincident with floodplain inundation (Schramm and Eggleton, 2006). Interannual predictability of the floods is crucial for good recruitment, because it favours the development of morphological, behavioural and physiological adaptations in the aquatic organisms that await the flood (Junk *et al.*, 1989; Bayley, 1991). In the Pantanal, wet years can be followed by dry ones; this clearly affects the population dynamics and structure of aquatic communities (Mourão *et al.*, 2002). Gomes and Agostinho (1997) observed that the failure of recruitment of *P. lineatus* because of the lack of floods in 1986 in the Paraná River was reflected in the 1988 fishery harvest, when a dearth of 2-year-old individuals was observed.

Long-lasting floods are advantageous for recruitment, because they offer shelter and food for a longer period of time, making it possible for the species to reach sizes less vulnerable to predation (Agostinho *et al.*, 2001; Jurajda *et al.*, 2004; Agostinho *et al.*, 2004a). Agostinho *et al.* (1993) reported that the retreat of the water after long-lasting floods brought larger juveniles of *P. lineatus* into the main channel of the Paraná River than when the floods were

brief. Even in rivers of temperate regions, such as the Mississippi River, the catch of juveniles of species with PC increases in years of long-lasting floods (Sparks *et al.*, 1998). These authors reported that the flooding allows access to firm soil and recently flooded terrestrial vegetation, making available favourable substrates for nest building. Short-duration floods, however, result from a rapid increase in water level and are followed by an abrupt drop in water level (Bayley, 1991). With the rapid retreat of the water, fish can become trapped in floodplain lakes. High mortality rates may occur in these lakes in the dry season, and may worsen because of the delay of the natural floods (Agostinho *et al.*, 2000). Moreover, as previously mentioned, short flood periods bring small fish that are more subject to predation into the main river channel, suggesting that intense floods may be more or less important for recruitment depending on duration (Agostinho *et al.*, 2004a).

Although the analysis of species grouped by strategy (reproductive guilds) introduced greater variability into the responses, this option was selected in order to solve one of the greatest problems in ecosystem management, which is to consider many species simultaneously. The use of reproductive guilds, therefore, constitutes an important management tool, because functionally similar species probably respond similarly along environmental gradients or to specific disturbances (Growth, 2004).

We conclude that with the exception of SM, the floods play an important role in the recruitment of species of the other reproductive strategies, as much by influencing spawning success as through their effect on the survival of juveniles. The role of floods has profound implications for conservation of the ichthyofaunal diversity of the Pantanal, especially because of the intense use of its waters for irrigation (especially in the higher reaches of the basin in recent decades) and control of drainage by impoundments for the purposes of water supply and hydroelectric power production (Agostinho *et al.*, 2005).

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