Reproductive biology of pacu *Piaractus mesopotamicus* (Holmberg, 1887) (Teleostei: Characidae) in the Cuiabá River Basin, Mato Grosso, Brazil

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The purpose of this study was to analyze the reproductive strategy and life-history traits involved in the reproductive processes of *P. mesopotamicus* in two regions of the Cuiabá River basin, the first of these encompassing its headwaters (Cuiabazinho River - Rosário Oeste) and the other the flood area of the Cuiabá River (Porto Cercado - Poconé). A total of 391 individuals were sampled monthly from August 2006 to July 2007, 159 from the headwaters and 232 from the flood area. The size structure indicated that the females in the headwaters attain longer lengths than the males, while no differences in length were found in the flood area. Females predominated in the headwaters, while males outnumbered females in the flood area. The reproductive period in the headwaters extended from October to March, but was restricted to October and November in the flood area. Feeding activity showed significant differences in both sexes between the stages of gonadal maturation, with the highest values recorded in stages of gonadal inactivity. The length at first maturity was 34.89 cm and the length at which all specimens were ready for reproduction was 44 cm at both sampling sites. The spawning type was total and fecundity was positively correlated to the size of the female.

O presente estudo teve como objetivo analisar a estratégia reprodutiva e os traços de história de vida relacionados aos processos reprodutivos de *P. mesopotamicus* em duas regiões da bacia do rio Cuiabá: uma que representa a região das cabeceiras (rio Cuiabazinho - Rosário Oeste) e outra que abrange a área de inundação do rio Cuiabá (Porto Cercado - Poconé). Indivíduos foram amostrados, mensalmente, no período de agosto de 2006 a julho de 2007. Foram amostrados 391 indivíduos, sendo 159 de ambiente de cabeceira e 232 de área alagada. A estrutura de tamanho mostrou que em ambiente de cabeceira as fêmeas atingem comprimentos maiores que os machos, enquanto que em área alagada não houve diferença nos comprimentos. Ocorreu predomínio de fêmeas em ambiente de cabeceira, e de machos em área alagada. O período reprodutivo para o ambiente de cabeceira estendeu-se de outubro a março e para a área alagada foi restrito a outubro e novembro. A atividade alimentar apresentou diferenças significativas para ambos os sexos entre os estádios de maturação gonadal com os maiores valores encontrados em estádios de inatividade gonadal. O comprimento de primeira maturação foi de 34,89 cm e o comprimento em que todos estão aptos a reproduzirem foi de 44 cm para ambos os locais. O tipo de desova é total e a fecundidade foi positivamente relacionada ao tamanho da fêmea.

Key words: Reproduction, Size at first maturity, Sexual proportion, Pantanal.

Introduction

Piaractus mesopotamicus (Holmberg, 1887), popularly known as *pacu*, belongs to the family Characidae, subfamily Myleinae (Britski *et al*., 1999). Geographically, it is widely distributed in the La Plata River basin formed by the Paraguay, Paraná and Uruguay rivers and their tributaries (Reis *et al*., 2003; Romagosa *et al*., 1988). This fish lives in lotic environments and spawns after a period of migration upriver (Ferraz de Lima & Chabalin, 1981).

Migration plays a fundamental role in the reproductive success of fishes, because it allows for the search for suitable environments for egg fertilization (the gathering of large numbers of individuals of both sexes), initial development (high oxygenation and food availability), and conditions of low predation rates (Agostinho *et al*., 2007; Godin, 1997). These regular seasonal changes in population distribution can frequently lead to major implications for commercial fishing (Metcalfe *et al*., 2002), since migration is a common trait in the life-history of many economically important fish

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species. For example, one of the behavioral traits of large migratory freshwater fish is the temporal and spatial separation of the habitats they use for reproduction, growth and feeding during different stages of life (Agostinho *et al.*, 2007).

The beginning of reproduction is a critical phase in the life of an individual, because the energy heretofore directed at growth and survival is now spent in a potential conflict between the time and resources allocated for reproduction, or for survival and growth (Wootton, 1998). This event is related to growth rate, which in turn depends on environmental conditions and individual characteristics (Nikolsky, 1969).

According to Donald & Winemiller (1989), tropical fishes of seasonal environments can be divided into three major groups: (I) equilibrium strategists - associated with local sedentary populations with few fluctuations, prolonged reproductive seasons and care of offspring; (II) opportunistic strategists - characterized by small fish, rapid maturation, multiple spawning and high capacity to recolonize disturbed habitats; (III) seasonal strategists - which may attain large sizes, have high fecundity and do not show parental care. These last exploit the periodic expansion of the aquatic environment through reproductive migration and total spawning at the onset of the rainy season.

Among the main aspects that comprise the reproductive strategy of fish species are sex ratio, egg size, fecundity and the reproductive period (Nakatani *et al.*, 2001; Hutchings, 2002). Understanding these aspects can be considered the first step in establishing the principal life-history patterns of fish species and in determining recurrent patterns, which normally facilitate the prediction of behavior in a given period and geographic area (Matthews, 1998; Mazzoni & Silva, 2006).

Individuals must reach a given age or size before they are able to reproduce. This size is the mean length at first maturity, defined as the length at which 50% of the individuals of a population are sexually mature (King, 1995). This is an important life-history trait, information that must be known for successful fish management, since it is fundamental for the establishment of measures that avoid the exploitation of juveniles and the resulting depletion of spawning stock (Hilborn & Walters, 1992).

Piaractus mesopotamicus is a highly important species in the Paraguay River basin due to its commercial value, and is one of the species most sought after by amateur and professional fishermen (Catella, 2001; Vaz, 2001). It is the most frequently caught species in Mato Grosso do Sul, representing almost 1/3 of the total production of professional fishing between 1994 and 1999 and corresponding to 2,393.8 tons (30.2%) of the total catch (Catella, 2001). In the Cuiabá River in the State of Mato Grosso, the species represented 13.52 tons (8%) of the commercial catch in 2001 and 2002 in Cuiabá, occupying the fourth position in landings (Mateus *et al.*, 2004). However, statistical fisheries data from the 1980's indicate that the species ranked third in landings from the Cuiabá River (Ferraz de Lima, 1986; Silva, 1986). Moreover, some studies indicate that the pacu fish stock is overexploited in the Cuiabá River (Vaz, 2001) and in the southern reaches of

the Pantanal of Mato Grosso (Catella, 2001; Peixer & Petrere, 2007). Despite the species economic importance, more detailed data about its reproductive strategy in natural environments are scanty, making it difficult to take effective management measures to ensure the maintenance of its stock.

Therefore, based on the hypothesis that reproductive processes respond differently to different regions, the present work consisted of a comparative analysis of the reproductive strategy and life-history traits involved in the reproductive processes of *P. mesopotamicus* in two regions of the Cuiabá River basin: one encompassing the headwaters of the basin (Cuiabazinho River - Rosário Oeste) and the other the flood area of the Cuiabá River (Porto Cercado - Poconé). The reproductive process was evaluated over a one-year period in order to: (i) characterize the population structure in terms of total length and sex ratio; (ii) determine the reproductive period, considering the microscopic analysis of the stages of gonadal maturity and the gonadosomatic index (GSI); (iii) estimate the quantitative indices of the nutritional condition (stomach somatic index - IS) and energy reserves (hepatosomatic index - IH) and their correlation with the reproductive stages; (iv) estimate the length at first maturation (L_{50}); and (v) determine the type of spawning and fecundity of the species under study.

Material and Methods

Study Area

The Cuiabá River is one of the tributaries of the Paraguay River, that seasonally overflows and floods. This is due to the fact that during the rainy season, the volume of water exceeds the river's flow capacity, and because the low declivity of the floodplain, flood of extensive areas of the Pantanal Basin (Carvalho, 1986). The Pantanal of Mato Grosso is a floodplain covering 138,183 km^2 and is part of the basin of the Upper Paraguay River, which begins in the Serra dos Parecis mountain range and runs southwards until it joins the Paraná River. This floodplain lies between the 14º and 22º S parallels of latitude and 53º and 61º W meridians of longitude (Carvalho, 1986). The Upper Paraguay River drains an area of approximately 500,000 km^2, two thirds of which are located in the Brazilian States of Mato Grosso and Mato Grosso do Sul (Girard, 2002).

The Cuiabá River basin covers an area of approximately 28,732 km^2 up to the proximities of the municipality of Barão de Melgaço, MT. Its headwaters are located in the municipality of Rosário Oeste in the foothills of the Serra Azul mountain range, and it is formed mainly by the Cuiabá da Larga and Cuiabá do Bonito Rivers. The confluence of these two rivers forms the Cuiabazinho River, which then joins the Manso River, becoming the Cuiabá River. The Cuiabá River basin can be subdivided into the upper Cuiabá, which comprises the uplands region, showing a considerable difference in levels, with various streams and gradually diminishing declivity, and the middle Cuiabá in the plains region, with low declivity up to the Pantanal wetlands (Cavinatto, 1995).

Samplings were carried out in the headwaters (in the region of Rosário Oeste), about 190 km from the city of Cuiabá, and in the flood area (in the region known as Porto Cercado), situated in the northern part of the Pantanal in the municipality of Poconé, about 140 km from Cuiabá, Mato Grosso State (Fig. 1).

Data Collection

Piaractus mesopotamicus specimens were collected monthly from August 2006 to July 2007. The fish were caught using fishing nets with mesh openings varying from 17 to 20 cm, throw nets with mesh openings of 18 to 20 cm, fishing hooks, sweep nets and boulters.

Records were made of each specimen's total length (TL; cm) and total mass (TM; kg). After the biometric measurements, each specimen was subjected to a longitudinal incision along the abdominal surface from the urogenital opening to the head for inspection of the abdominal cavity and identification of the sex.

The gonads, liver and stomach of all the captured specimens were removed and weighed (g). To classify the stages of maturation and confirm the sex, the whole gonads were fixed in 10% formalin for five days, stored in 70% alcohol and subjected to routine histological techniques of paraffin embedding and staining with Hematoxilin and Eosin. The stages of gonadal development were classified as: Immature (IM, juveniles), Maturing (MG), Mature (MA), Spawned (SP),

and Rest (RE) (Vazzoler, 1996; Bazzoli, 2003). To determine the spawning period and type, the diameters of 10 ovarian follicles per female were measured randomly using the MOTIC® 3.0 program with 10x magnification.

Fecundity was estimated based on the ovaries of all the mature females, using the gravimetric method (Vazzoler, 1996): the weight of the fixed ovaries was measured and a subsample was removed from each ovary and weighed. The oocytes contained in the subsamples were dissociated in a modified Gilson solution, counted and measured, and the rule of three was applied to estimate the total number of oocytes in the ovaries. All oocytes were counted according to Ivankov's method (1985), which is based on Potential Fecundity (PF), *i.e.*, the initial vitellogenic oocyte reserve, the resource for the achievement of final fecundity by the gradual reabsorption of excess vitellogenic oocytes.

The rainfall and water flow data of the Rosário Oeste and Porto Cercado (Poconé) Station were obtained from the Civil Defense Department of the State of Mato Grosso and from Brazil's National Water Agency (ANA). That information was related to the maturation phase graphically.

Data Analysis

The data on fish length were grouped by site into classes of 5 cm intervals to determine the absolute frequency distribution of juveniles and adults during the sampling
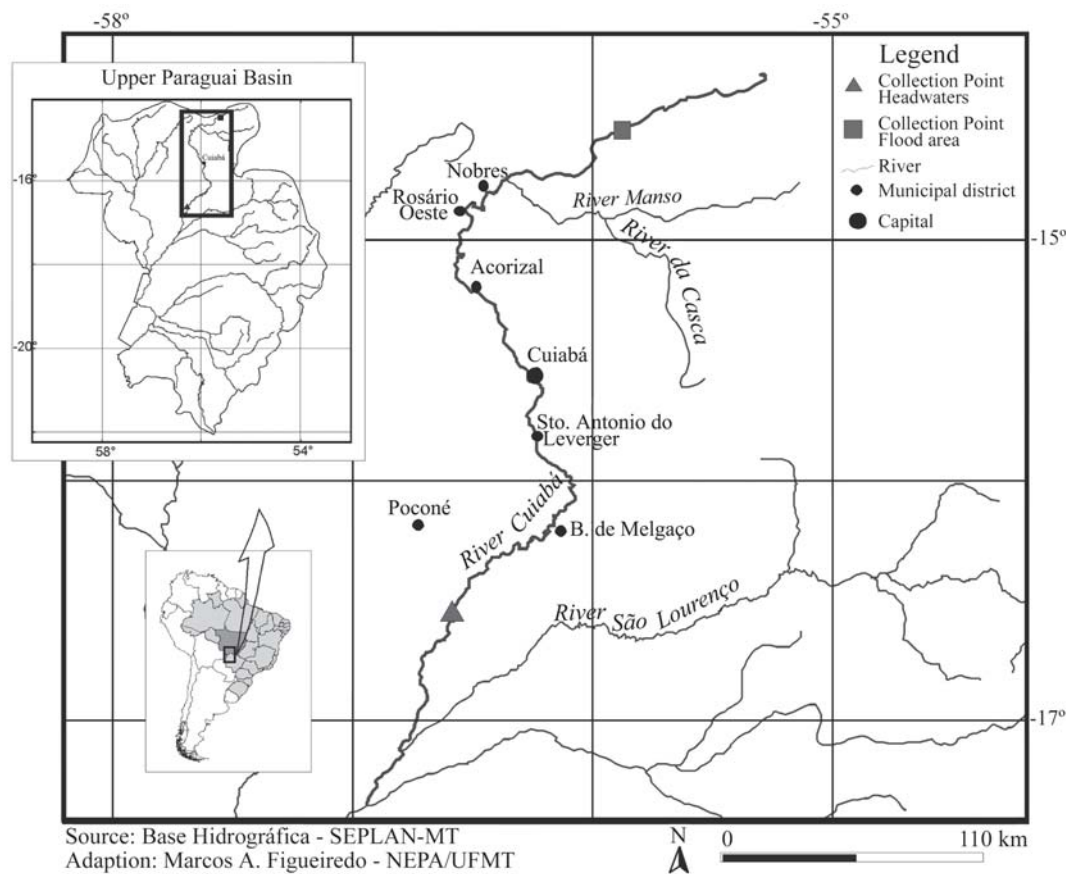

Fig. 1. Geographic location of the sites sampled in the Cuiabá River basin, Mato Grosso State, Brazil.

period. To investigate the possible differences in TL between the sexes and sites, a bifactorial analysis of variance was applied. The hypothesis that the sex ratio differs from the expected 1:1 was tested by the chi-square test (χ^2) to verify the possible significant differences at the sampled sites.

The reproductive period was established by the monthly relative frequency distribution of the gonadal maturation stages identified considering only adult individuals (MG, MA, SP and RE) for the collection period (months), and by the monthly analysis of variation of the values of the gonadosomatic index (GSI = GM x 100/TM, where: GM is gonad mass and TM is total mass). Because the supposition of normality of the GSI data was not reached, a comparison of the months was made by the Kruskal-Wallis test (H-test).

To quantitatively analyze feeding activity during the reproductive and sampling period, a calculation was made of the stomachsomatic index (IS) and the hepatosomatic index (IH), which represent the percent of the organ's mass in relation to the total mass (TM) of the fish. Since the indices did not show a normal distribution, the Kruskal-Wallis test was applied to test differences in the values of these indices by gonadal maturation stage separately for females and males.

To estimate the mean length at first maturity (L_{50}) and the length at which all the individuals were ready to participate actively in the reproductive cycle (L_{100}), distributions were built of the proportion of adults in each total length class at both sites, including all the adult specimens (which were in the gonadal maturation stages of MG, MA, SP and RE). The resulting curve was fitted to the following expression:

$$p = \frac{1}{1+e^{\alpha(L_{50}-TL)}}$$

where, p = Proportion (number of adult individuals/total number of individuals (juveniles and adults); α = Intercept of the ratio; L_{50} = Length at first maturity; and TL = Total length. The α and L_{50} parameters were estimated by nonlinear regression (King, 1995).

An analysis was made of the relative frequency distribution of the ovarian follicle diameter grouped into classes of a 100 mm intervals. The relative frequency of the class of ovarian follicle diameter was calculated for each period and site to identify the time of gonadal maturation, to identify the type of spawning and to determine possible variations in the oocyte development phase between the sites. The relative frequency analysis of ovarian follicle diameter indicates the phase of gonadal development.

To ascertain possible fecundity (F) relationships between the TL, total fish mass and total gonad mass, by sampling site, a simple linear regression was applied, estimating coefficients *a* and *b* after log-transforming the values of the variables. To check whether there was a difference in gonad mass between the sites, an analysis of covariance (ANCOVA) was made.

All tests were performed using the statistical package Systat version 12 (Wilkinson, 2007). A confidence level of 95% (α = 0.05) was used in all the tests.

Results

A total of 391 individuals were sampled. Seven juveniles and 152 adults were captured in the headwaters. Juveniles were found in the months of September, April, May, June and July (Fig. 2a). The specimens analyzed from the flood area comprised 32 juveniles and 200 adults. Juveniles were found in all months except October, November and December (Fig. 2b). The analysis of the 159 individuals from the headwaters showed a mean TL of 47.34 cm (SD = 9.58), where the minimum was 34 cm, and maximum 75 cm. TL varied from 34 to 75 cm in females (n = 105), and from 34 to 74 cm in males (n = 54). The 232 individuals from the flood area showed a mean TL of 41.51 cm (SD = 4.90), with a minimum TL of 28 cm, and maximum of 58 cm. The TL varied from 29 to 55 cm in females (n = 89), and from 28 to 58 cm in males (n = 143). There was an interaction between the sex and site factors ($F_{1;387}$ = 10.26; p = 0.0014), with the females in the headwaters, on average, larger than the males, but no difference in length was found between females and males in the region of Porto Cercado (Fig. 2c-d).

In the headwaters there was a significant difference in the sex ratio (χ^2 = 16.35; p = 0.000, n = 159), with a predominance of females (105) in relation to males (54) in almost all the TL classes. A significant difference in the sex ratio (χ^2 = 12.56; p = 0.000, n = 232) was also found in the flood area, but here males predominated (143) over females (89) in most TL classes.

With regard to gonadal maturation stages, 178 females were analyzed, 101 from the headwaters and 77 from the flood area. In the Cuiabazinho in October and July, there was a high frequency of maturing (MG) females. Mature (MA) females were found in October, January, February and March, with the highest frequency occurring in January and the lowest in March, indicating that the reproductive period occurred from October to March. A low frequency of spawned (SP) specimens was found in February. Individuals at rest (RE) occurred practically throughout the entire year, with a low frequency in October (Fig. 3a).

In the flood area, a high frequency of maturing (MG) specimens was found in August, September, March and July. October and November were the months of high frequency of the mature (MA) stage, indicating the greater reproductive activity in those months. No individuals in the spawned (SP) stage were found. Specimens at rest (RE) were found in every month except October and November (Fig. 3b).

The GSI showed a significant difference among the sampling periods for females (H = 39,997; d.f. = 9; p < 0.001); (H= 39,230; d.f. = 11; p < 0.001) and males (H = 17,783; d.f. = 7; p = 0.013); (H = 83,353; d.f. = 11; p < 0.001) in the headwaters and flood areas, respectively. We found that, in the headwaters, the females displayed a higher variation in GSI in October, January, February and March, and the males in September and October (Fig. 4a-b). In the flood area, the GSI of the females showed higher variations in October and November, while that of males showed variations in September, October, November, December, January and February (Fig. 4c-d).
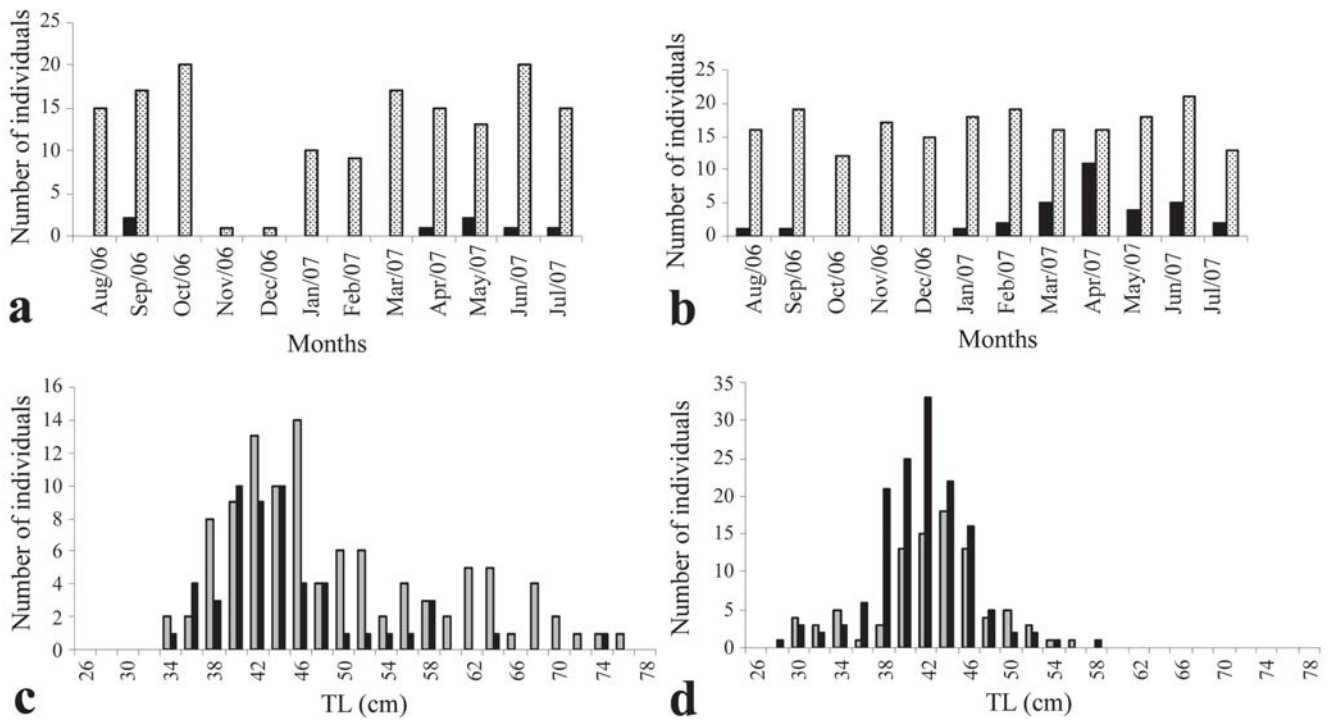
Fig. 2. Absolute frequency of young (■) and adult (▦) individuals in the headwaters - Rosário Oeste, MT (a), and in the flood area - Poconé, MT (b), and frequency distribution by class of TL (cm) of *P. mesopotamicus* females (▦) and males (■) in the headwaters (c) and the flood area (d) between August 2006 and July 2007.
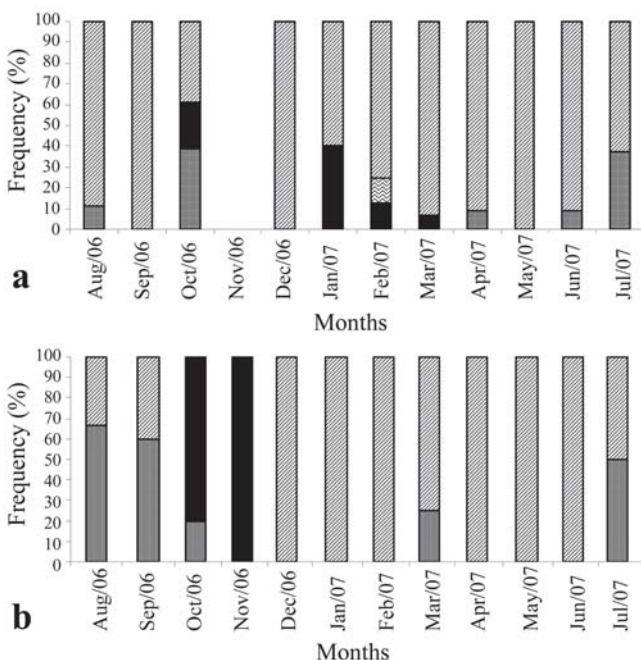

Fig. 3. Relative frequency of *P. mesopotamicus* females in the headwaters - Rosário Oeste, MT (a) and in the flood area - Poconé, MT (b) according to the stages of gonadal maturation (▦ MG; ■ MA; ▨ SP and ▨ RE) between August 2006 and July 2007.

Local rains and rising water levels are related to the maturation phase of the pacu. In the headwaters, a positive relationship was found between the rainfall index and water level, with the reproductive period of *P. mesopotamicus* males peaking in February. In the flood area, the rainfall index and water level increased in October, coinciding with the peak of the female reproductive period in October and November (Fig. 5a-d).

The IS and IH of the females showed significant differences between the maturation stages (IS: $H = 12.14$; $p = 0.017$; IH: $H = 16.29$; $p = 0.003$), with the females at rest showing a higher IS and the immature females a higher IH. The males displayed significant differences only in the IH ($H = 15.11$; $p = 0.004$), with males with spawned gonads showing a higher IH relative to the other stages of maturity (Fig. 6a-d).

In the headwaters, the estimated L_{50} was 34.82 cm, with a confidence interval between 32.77 and 36.88 cm ($\alpha = 0.55$; $r^2 = 0.72$), and the estimated L_{100} was 40 cm. The estimated L_{50} in the flood area was 35.14 cm, with a confidence interval between 34.10 and 36.17 cm ($\alpha = 0.41$; $r^2 = 0.95$), and the estimated L_{100} was 44 cm. Because these ratios did not show significant differences considering the overlapping of the confidence intervals of the L_{50}, the data were grouped, resulting in a single expression representative of the species under study, corresponding to the total number of fish sampled in the two regions. The mean total length at first
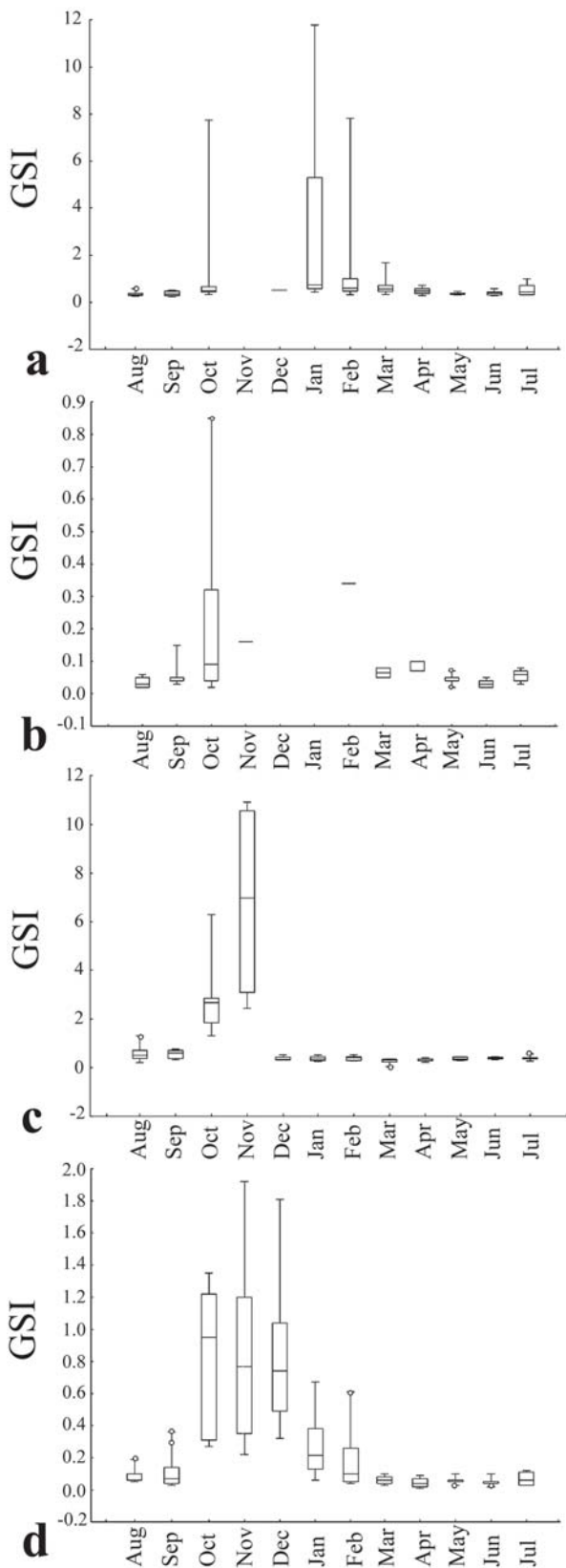
Fig. 4. Monthly variation of the gonadosomatic index (GSI) of *P. mesopotamicus* females and males in the headwaters (a,b) and the flood area (c,d), respectively, between August 2006 and July 2007.

maturity (L_{50}) was estimated to be 34.89 cm, with a confidence interval between 32.57 and 37.21 cm ($\alpha = 0.397$; $r^2 = 0.713$). The estimated mean total length at which all the individuals were ready to reproduce (L_{100}) was 44 cm.

For the headwaters, 1050 ovarian follicles from 105 females (juveniles and adults) were measured, which varied from 9.76 µm to 1023 µm. The mean follicle diameter was 156.07 µm (SD = 191.81 µm). In all the months, the relative frequency distribution of follicle diameters was concentrated in smaller diameters. In October this distribution shifted to intermediate diameters. No female specimens were caught in November. In October, January, February and March, the relative frequency of follicle diameter was distributed in larger diameters, displaying two modes that represent the peak of spawning in the headwaters (Fig. 7a).

In the flood area, 890 ovarian follicles from 89 females were measured, varying from 9.76 µm to 1016 µm. The mean follicle diameter was 165.79 µm (SD = 196.67 µm). In all months, the relative frequency distributions of follicle diameter were concentrated in smaller diameters. However, in October and November the relative frequency of follicle diameters was distributed in larger diameters, displaying two modes and indicating that spawning was total; hence, the smaller mode represented the reserve stock while the higher one corresponded to mature oocytes (Fig. 7b).

Fifteen mature females were analyzed, 7 from the headwaters and 8 from the flood area. The values of absolute fecundity, expressed as numbers of oocytes to be possibly eliminated during spawning, showed a variation of 236,147 to 1,960,970 oocytes, with a mean of 887,674 (SD = 601,040) in the headwaters, and a variation of 64,179 to 589,309 oocytes, with a mean of 258,099 (SD = 178,523) in the flood area.

In the headwaters, total length of the females analyzed varied from 41 to 73 cm, fish mass varied from 1.75 to 9.75 kg, and gonad mass varied from 55 to 775 g. Total length in the flood area varied from 38 to 52 cm, fish mass varied from 1.05 to 2.70 kg, and gonad mass varied from 34 to 352 g. Fecundity was positively correlated with total length, total mass and gonad mass at both sampling sites (Fig. 8), *i.e.*, fecundity was found to increase with body size. Gonad mass did not differ between sites ($F_{1;13} = 0.722$; p = 0.410); thus, there was no difference between the headwaters and flood area with respect to fecundity rate.

Discussion

Piaractus mesopotamicus females attain longer lengths than males and occur in higher numbers in larger-size classes in the headwaters. Few individuals of larger size classes were found in the flood area and the males outnumbered the females in the intermediate classes. A larger growth attained by the females of some species may be a tactic dictated by their reproductive behavior (Veregue & Orsi 2003). The larger size of females than of males in fish species of total spawning and external fecundation may be related with sexual dimorphism (differences in body shape and size) (Chech & Moyle, 2004),
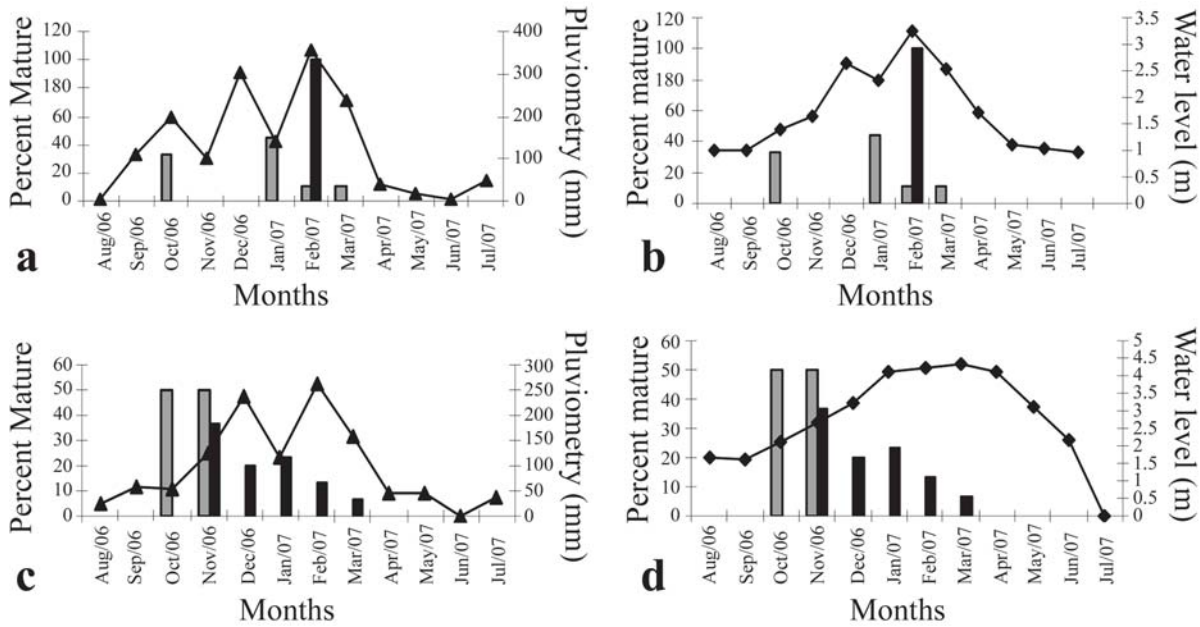
Fig. 5. Relative frequency of the stage of gonadal maturation (MA) by collection period for *P. mesopotamicus* females (▨) and males (■) with the monthly variations in rainfall (▲—) and water level (■—) in the headwaters (a, b) and the flood area (c, d), respectively, between August 2006 and July 2007.
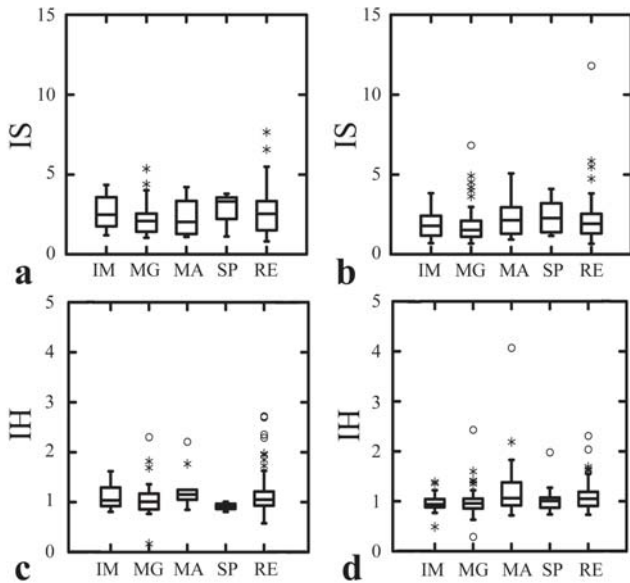

Fig. 6. Variation in the stomachsomatic index (IS) of *P. mesopotamicus* females and males (a, b) and hepatosomatic index (IH) of females and males(c, d), respectively, according to the stages of gonadal maturation between August 2006 and July 2007.

revealing a strategy for the production of larger numbers of oocytes, which would ensure the survival of the species and the maintenance of the population, aimed at overcoming the adversities imposed by the environment on ovuliparous species (Santos, 1980; Lowe-McConnell, 1999).

According to Fisher's theory (1930), natural selection is manifested equally in the production of males and females, and the expected proportion in most fish species is 1:1 (Vazzoler, 1996). However, the *P. mesopotamicus* population studied here showed significant differences in its sex ratio. This ratio may show significant differences even in analyses of different populations of the same species or at different times (Nikolsky, 1969). In the Itaipu reservoir, female *Leporinus friderici* outnumber males, while in the Corumbá reservoir (both of them in the Paraná River basin), the sex ratio is equal (Lopes *et al.*, 2000). Differences in sex ratio may reflect differential mortality or birthrates between the sexes, reproductive periods, food availability and predatory activity, or even fish shoal behavior (Araújo & Gurgel, 2002).

In the *P. mesopotamicus* population of the headwaters and flood area, the differences in the proportion of sexes may be explained by the hypothesis of the evolutionary development of reproductive strategies, which is closely linked with the environment and the selective forces in action during its history (Agostinho *et al.*, 2007). This is a large migratory species that requires wide free reaches of the basin, which enable it to roam over great distances (Ferraz de Lima, 1986).

Although the most important migrations are reproductive ones, there are also migrations of a thermal or seasonal, trophic or nutritional, and ontogenetic or growth-related nature, most of them associated with the hydrological regime.

The annual reproductive cycles are synchronized with the seasons of the year in response to the environmental conditions, whose rhythms involve endogenous and exogenous factors. Synchronization is achieved through the
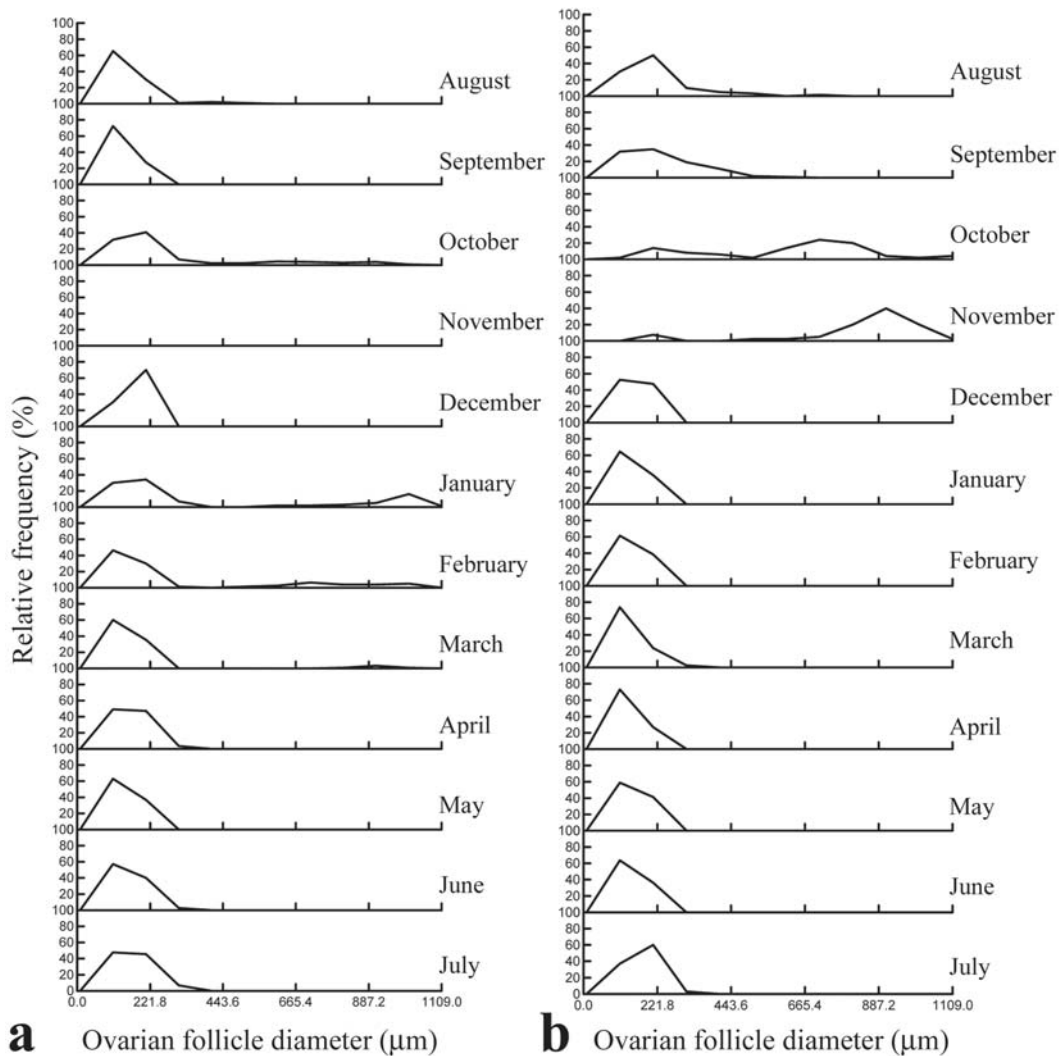
Fig. 7. Relative frequency distribution of the ovarian follicle diameter (μm) of *P. mesopotamicus* in the headwaters (a) and flood area (b) between August 2006 and July 2007.

interaction between the neuroendocrinal system and the environmental factors (Harshman & Zera, 2006; Sumpter, 1997). The most favorable time of the year for fish reproduction is that in which the environment offers the minimal conditions necessary for the development of the juvenile phases, ensuring adequate food availability, protection against a variety of predators, and favorable abiotic conditions.

The changes occurring in the river's water levels and the sequences of dry and rainy seasons represent the principal controlling event for fish reproduction in low-latitude environments. Due to the slight variations in the temperature and photoperiod of these sites, the reproductive period of fishes in tropical regions coincides with the time of year when rainfall is at its highest (Wootton, 1998).

The reproductive period of *P. mesopotamicus* was spatially differentiated in terms of duration. In the headwaters, this period comprises the months of October, January, February and March, while in the flood area it occurs in October and November. Note that the reproductive period in the headwaters extends over two additional months. This may be due to the ovarian activity, which is reduced and remains in syntony and adjusted to the environmental conditions, thus ensuring that the release of oocytes coincides with the period when the environmental characteristics are the most favorable for the offspring's highest possible survival rate. This phase is known as the "period of dormancy", whose duration varies from one species to another and which, in Brazilian fishes, lasts from a few weeks up to several months (Zaniboni Filho & Nuñer, 2004). The reproductive periods found in this study can be attributed to the period of dormancy and the difference in local climatic and/or ecological factors, such as the rainfall and river water level that are characteristic of the sampled regions. Reproduction of mature *P. mesopotamicus* females takes place not only in the region of the headwaters but can also occur in the floodplain, although no spawned females were found.
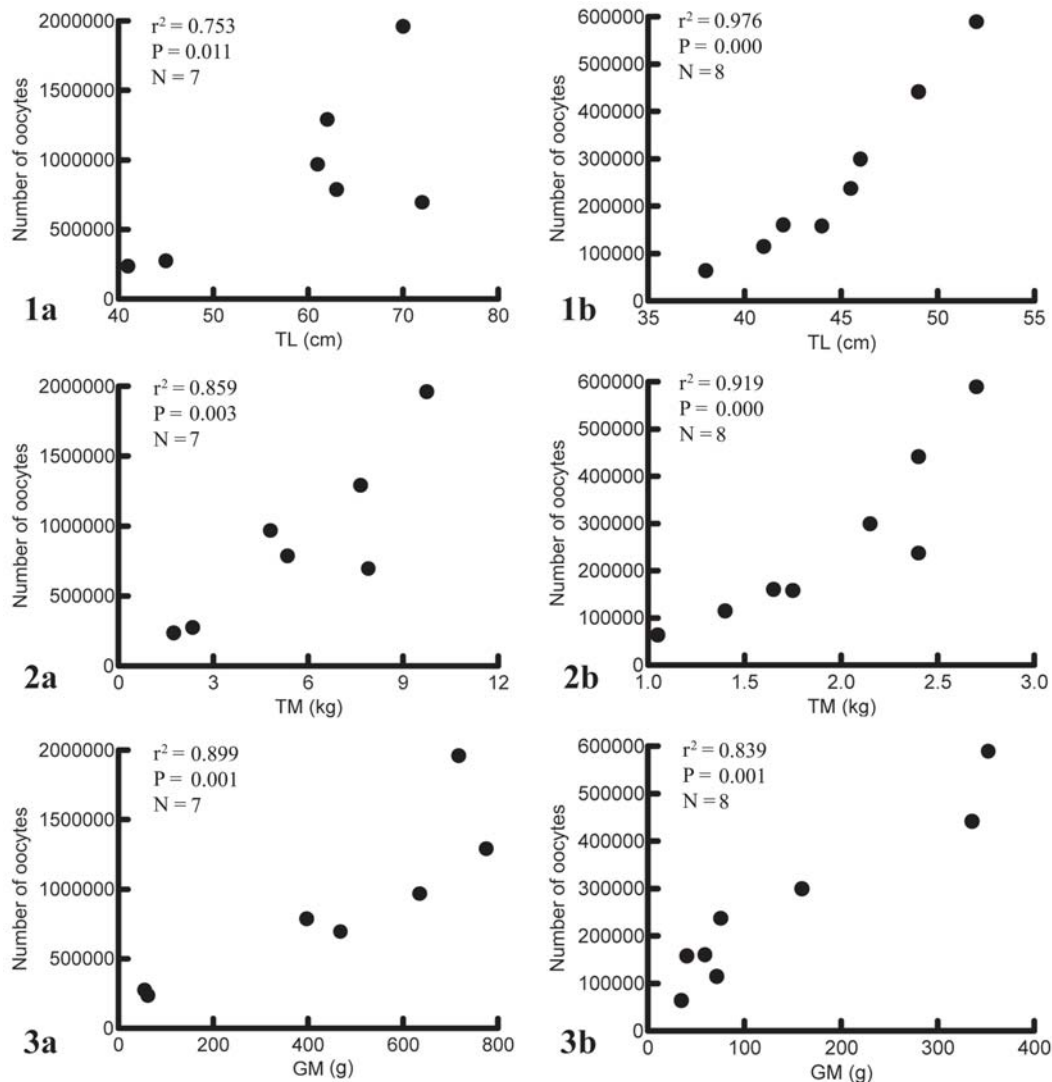
Fig. 8. Relationship between fecundity (number of oocytes) and the TL, TM and GM of *P. mesopotamicus* in the headwaters (1a, 2a and 3a) and flood area (1b, 2b and 3b), between August 2006 and July 2007.

Commercially exploited tropical fish species habitually reproduce synchronously with the rising waters, since these species need to migrate to their reproduction grounds, most of them spawning at the onset of the first rains while others delay their arrival at the spawning sites Thus, large shoals migrate upriver to spawn at sites where there is greater availability and better quality of food, as well as adequate shelter for protection against predators, thus ensuring the safety of their offspring (Junk *et al.*, 1997; Vazzoler *et al.*, 1997; Saint-Paul & Villacorta-Correa, 1999; Welcomme, 2001). Therefore, the beginning of migration appears to coincide with the first rains, which occur at the end of the dry season (Agostinho *et al.*, 2003).

Flooding plays an important role in the recruitment of species with other reproductive strategies, by influencing successful spawning and through the effects on the survival of juveniles (Bailly *et al.*, 2008). Rainfall and temperature are generally considered the determining factors that trigger the reproductive cycle (Menezes & Vazzoler, 1992). Some environments may sometimes not show limiting environmental factors over a given period of time, enabling reproduction to extend for several months.

Life-history strategies can be seen as mechanisms to maintain equilibrium in the amount of energy expended on reproduction, growth and metabolism (Chech & Moyle, 2004). Considering that both spawning and the processes it involves, such a gonadal maturation and migratory displacement, require the spenditure of energy, an increase in energy allocated to one of these traits should result in a decrease of energy for another (Stearns, 1992). Hence, the greater feeding activity observed in pacu in the phase of gonadal inactivity may indicate that during this period the females, especially, grow tissues for later investment in reproduction (Vazzoler, 1996).

The length at first maturity is an important life-history trait that needs to be determined for successful fish management, since it is fundamental for the establishment of measures to avoid overexploitation of juveniles and consequent reduction of the spawning stock (Wootton, 1998; Mateus *et al*., 2004). The determination of the size at first maturity serves not only to underpin management measures but also to clarify important factors of population dynamics. These factors include the genetic representativeness in future generations, provided by reproduction efficiency, which is directly correlated with the size at which the species enters reproductive maturity and with the conditions that establish this process (Begon & Mortimer, 1990). This trait is closely associated with the interaction between genotype and environment, and hence, with growth, showing spatial and temporal intraspecific variations related to the prevalent biotic and abiotic environmental conditions (Vazzoler *et al*., 1997).

As indicated by the results of this study, the mean length at first maturity, L_{50}, was estimated to be 34.89 cm and the L_{100} was 44 cm in the headwaters and flood area. Ferraz de Lima *et al*. (1984) estimated the L_{50} of *P. mesopotamicus* females at 34 cm and L_{100} at 42 cm in the flood area, in Mato Grosso. The L_{50} value estimated in the present study is consistent with that estimated by Ferraz de Lima *et al*. (1984), *i.e.*, 34 cm. The estimated L_{100} is very close to the minimum capture size of 45 cm established for *P. mesopotamicus* by State Law Nº 7155 of October 21, 1999 and CONSEMA Resolution Nº 01 of March 16, 2000.

In situations of overfishing, Gulland (1988) recommends reducing mortality by fishing and increasing the permitted age of first capture. However, increasing the age of first capture would directly affect larger individuals. Thus, due to the fact that fishing activities are highly selective, not only for reasons of yield but also because of legal restrictions (minimum capture size), fishing has led to artificial selection in populations. The law forbids the capture of juveniles, which are extremely valuable because they ensure the recruitment abundance of new cohorts in subsequent years, but the lack of control over the capture of large matrices seems damaging to the viability of the stocks (Agostinho *et al*., 2007).

The type of spawning of fishes is the way in which the females release oocytes within a reproductive period. In tropical environments, total spawning is generally observed in large migratory species. Fishes that spawn totally are characterized by the synchronous development of the oocytes (Rizzo *et al*., 1996) and by the low frequency of partially spawned females (Godinho & Tavares, 1994). Histologically, the ovaries of *P. mesopotamicus* show characteristics of "group-synchronous" oocyte development. The type of spawning can be determined through analyses of the frequency distribution of oocyte diameter as a function of the stage of gonadal maturation. This evidence refers to the occurrence of the mature (MA) stage and to the highest gonadosomatic index (GSI) values in a short period and to the bimodal distribution of the oocytes. In the other stages of the reproductive cycle, the frequency distribution of oocyte diameter displays a single mode.

Fecundity is a life-history trait that can be estimated by the number of oocytes that complete their development and are released in each reproductive period, *i.e.*, reproductive investment. This phenomenon depends, first, on the total volume of the coelomic cavity available to house the ovaries, and second, on the volume of oocytes. It is a measure of the reproductive potential of fishes (Menezes & Vazoller, 1992; Chech & Moyle, 2004).

The relationship between fecundity and the variables of length, body mass and gonad mass were linearly positive for the *P. mesopotamicus* sampled in this study. The highest correlation was found between fecundity and gonad mass in the headwaters and between fecundity and body length in the flood area. Several studies have identified a positive relationship between the number of oocytes and fish size (Adite *et al*., 2006; Brickle *et al*., 2005; Magalhães *et al*., 2003; Mazzoni & Silva, 2006; Moffett *et al*., 2006; Sato *et al*., 2006; Tarkan, 2006; Martins-Queiroz *et al*., 2008).

Older individuals of some fish species produce larvae that have a substantially greater potential for survival (Bobko & Berkeley, 2004). These new conclusions extend the knowledge that large individuals usually have exponentially high fecundity. This is important, since large fish are frequently the target of commercial and sport fishing. Older adult fish produce larvae with greater vitality; thus, older fish presumably have greater metabolic reserves, investing more energy into each progeny (Berkeley *et al*., 2004; Bobko & Berkeley, 2004).

Fecundity may show adaptive variations within the same population or in different populations, which reflect changes in life style (Niklosky, 1969). Ultimately, this variation may be due to food supply, time of the onset of sexual maturation, temperature, latitude, type of spawning and the number of times the fish has spawned, as well as the existence or absence of mechanisms of progeny protection (Niklosky, 1969). However, in this study, we found no spatial differences in fecundity, possibly because it involved a single stock (Calcagnotto, 1998) that roams widely through the basin (Ferraz de Lima, 1986).

In summary, the aspects that determine the reproductive strategy of *P. mesopotamicus* in the Cuiabá River basin reflects expressions of traits closely related to fitness, such as the reproductive period, maturation size, spawning type and fecundity in the life of the individual, according to the life-history, the trade-off between the adopted strategy and the optimal period of life ensures the maintenance of the species. These parameters are fundamentally important in the evaluation and management of the stock. Therefore, measures that ensure the stock's protection during the period of reproduction from October to March, and the size at first maturity, are crucial for the maintenance of the population in this environment, as well as for fish preservation, conservation and management.

Acknowledgements

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