

Reproductive ecology of *Odontostilbe pequirá* (Steindachner, 1882) (Characidae, Cheirodontinae) in the Paraguay River, southern Pantanal, Brazil

Karina Keyla Tondato · Clarice Bernhardt Fialho ·
Yzel Rondon Suárez

Received: 8 November 2011 / Accepted: 18 February 2013 / Published online: 26 March 2013
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Abstract The reproductive biology of *Odontostilbe pequirá* was studied aiming to determining differences in population structure, reproductive tactics and correlating the reproductive period with rainfall, temperature and level of the Paraguay River, in the southern Pantanal, Brazil. Data were obtained for 623 individuals (366 females and 257 males), and of these, 253 females and 126 males were dissected for reproductive analysis. No significant variation was observed in the distribution of standard length and total weight between the sexes. The sex ratio was 1.42:1 (female: male), but the ratio did not differ over most months and between most length classes. The reproductive period was long (10 months). No correlation was found between the gonadosomatic index (GSI) of both sexes with water temperature and rainfall over the months analyzed. Males showed no

significant association between the GSI and river level, but a marginally significant correlation was observed for females. Moreover, an effect of the mean historical river level on GSI was observed in both sexes, indicating that the flooding regime drive the reproductive activity, which proportions spawnings even when rainfall and temperature levels are low. Length at first maturity of the females was 24.2 mm and of the males 22.2 mm, with a significant difference between the sexes. The mean absolute fecundity was 181.4 oocytes/female, while mean relative fecundity was 0.544 oocytes/mg. Absolute fecundity was positively related to total weight, gonad weight and standard length. The mean diameter of the mature oocytes was 0.46 mm and the frequency distribution of the diameters showed various modes, indicating a multiple spawning. Thus, the reproductive tactics of *O. pequirá* was characterized as “opportunistic strategist”, with reproductive activity strongly associated with the flood pulse.

K. K. Tondato (✉)
Programa de Pós-graduação em Biologia Animal,
Departamento de Zoologia, Universidade Federal do Rio
Grande Sul, Av. Bento Gonçalves, 9500,
91501-970 Porto Alegre, Rio Grande do Sul, Brazil
e-mail: ktondato@hotmail.com

C. B. Fialho
Departamento de Zoologia, Universidade Federal do Rio
Grande do Sul, Av. Bento Gonçalves, 9500,
91501-970 Porto Alegre, Rio Grande do Sul, Brazil

Y. R. Suárez
Centro Integrado de Análise e Monitoramento Ambiental,
Laboratório de Ecologia, Universidade Estadual de Mato
Grosso do Sul, Rod. Dourados-Itahum, km 12,
79804-970 Dourados, Mato Grosso do Sul, Brazil

Keywords Life history · Cheirodontinae · Population structure · Reproductive biology

Introduction

The life history of organisms is defined as “a set of co-adapted traits designed by natural selection to solve particular ecological problems” (Stearns 1992) or would simply be inherited characteristics from an ancestral taxon or population (Rochet 2000). In fishes, a

wide diversity in traits and patterns of life history has been documented (Winemiller 1989; Wootton 1998; Hutchings 2002; King et al. 2003), which by way of high phenotypic plasticity varies intra- and interspecifically in response to environmental factors (Pampoulie et al. 2000; Blanck and Lamouroux 2007; Tedesco et al. 2008; Mérona et al. 2009), altering size, growth, mortality, age and reproductive period (Wootton 1998; Lowe-McConnel 1999).

The reproduction of species with different patterns of life history is affected by local environmental conditions (Humphries et al. 1999; Magalhães et al. 2003; Zeug and Winemiller 2007), causing them to show in their reproductive strategy, a set of variable tactics which are adapted in response to the quality and variability of abiotic conditions, food availability and predation (Vazzoler 1996; Wootton 1998). Thus, the study of reproductive tactics, such as length at first maturity, sex ratio, reproductive period, type of spawning and fecundity (Vazzoler 1996; Hutchings 2002), are essential for the understanding of how these characteristics are adapted for maximizing reproductive success in a particular environment (Matthews 1998). In addition, this provides basic information for understanding the type of reproductive strategy utilized by the species, as suggested by Winemiller (1989) and Zeug and Winemiller (2007).

It is known that reproductive dynamics is intimately associated with environmental conditions favorable to the development of the progeny, such as period and locations that have greater food supply and habitat availability (Welcomme 1979; Nakatani et al. 1997; Winemiller 2005), as well as the biological characteristics of the organism such as body length and phylogeny (Alkins-koo 2000). In temperate environments, it has been documented that the reproductive period of fishes is determined mainly by the increase in temperature and photoperiod and greater availability of food (Bye 1984; Jobling 1995; Winemiller 2005). Meanwhile, in tropical environments, the periods of high rainfall and consequent elevation of the level of water bodies are considered determinant factors of reproductive seasonality (Kramer 1978; Welcomme 1979; Machado-Allison 1990; Lowe-McConnel 1999), since the beginning of the rains associated with the period of high temperatures, increases rapidly the productivity of the system (Vazzoler and Menezes 1992).

In the Pantanal, as in other tropical floodplains, reproduction is seasonal and the majority of the fishes spawn when the water level begins to rise, preceding the peak of the rains, because the overflow of the main river on the plain promotes access to new habitats, offering greater availability of food and shelter to the larvae and juveniles (Junk et al. 1989; Baumgartner et al. 1997; Lowe-McConnel 1999; Agostinho et al. 2004; Bailly et al. 2008; Tondato et al. 2010). In these environments, the flooding period coincides with high photoperiod and temperature levels, which also favor spawning of the species (Bailly et al. 2008), following that proposed by one of the aspects of the “flood pulse concept” (FPC), which relates better conditions and advantages for the spawning of fish when flooding coincides with high temperatures, due to the increase in productivity (Junk et al. 1989; Winemiller 2005). On the other hand, if high temperatures and flooding are not coincident, it can be advantageous for fish to spawn in low water levels in the main channel of the river, when the food resources are concentrated, as proposed in the “low flow recruitment” (LFR) hypothesis of Humphries et al. (1999), which questions pre-suppositions of the FPC. Therefore, in the Pantanal of Porto Murtinho (southern Pantanal), where there is asynchrony between the period of greatest rainfall and temperature with the period of highest level of the river, there is the possibility of determining the effects of these variables on reproduction of the species of fishes, identifying which variable is key to reproductive activity. The small-sized specie, *Odontostilbe pequirá* (Steindachner, 1882), widely distributed in rivers and lakes of the Pantanal (Súarez et al. 2001; Veríssimo et al. 2005), although is not of interest for fisheries, is of great importance as the basis of the food chain of the ichthyofauna. Besides, it shows economic potential (ornamental), as suggested by Pelicice and Agostinho (2005) in species of the same subfamily. Therefore, given the evolution of the reproductive strategies in heterogeneous environments and based on the hypothesis that reproductive traits of *O. pequirá* respond in a singular way and adaptive to the flooding regime, the objective of this work was to evaluate the relationship between the reproductive period of *O. pequirá* and environmental factors (rainfall, temperature and river level). Additionally, we examined the reproductive tactics (reproductive period, length at first maturity, fecundity, oocyte diameter, type of spawning) and population structure of this species (standard length and sex ratio).

Methods

Study area

The Pantanal is a sedimentary floodplain with an area of approximately 140 000 km², part of the basin of the upper Paraguay river. Shows variation in the intensity of rains, oscillating between 800 and 1,400 mm/year, where 80 % of rains occur from November to March (Fantin-Cruz et al. 2011). This floodplain shows a unimodal flooding regime, which is essential to all the functions of the system (Junk et al. 1989), since the high evapotranspiration does not allow local rainfall to contribute significantly to the fluvimetric variations (Hamilton et al. 1996).

The study region is in the Pantanal of Porto Murtinho, located in the extreme south of the Pantanal (Fig. 1). According to Silva and Abdon (1998), the Pantanal has as its southern border the confluence of the Apa River with the Paraguay River, which also divides the upper Paraguay River and the middle Paraguay River. Due to its geographical position and low declivity of 1 cm/km (Hamilton et al. 1996), the Pantanal of Porto Murtinho is characterized by asynchrony between the period of greater rainfall and temperature (November to March) and the period of flood (June to August). Flooding begins to the north of the floodplain together with the rainy period, draining slowly toward the south due to the low declivity in the north-south direction, which results in discrepancies of 3 to 6 months between the peak of the rains in the springs and the maximal flooding in the southern part, generally in June, outside the rainy season (Hamilton et al. 1996; Gonçalves et al. 2011). By having a sinuous course, the Paraguay River in the region studied shows innumerable marginal lakes formed by abandoned meanders (Fig. 1), which are directly connected to the river and therefore strongly influenced by its seasonality level. These water bodies show a wide variation in size, shape and cover of aquatic macrophytes, represented mainly in this region by *Eichhornia azurea*, *Eichhornia crassipes* and *Salvinia* sp.. These aquatic environments are important, because they provide reproduction sites and growth for many species (Lowe-McConnel 1999).

Collection and analysis of data

The samples were collected monthly between February 2009 and January 2010 on the banks of aquatic

macrophytes in 42 sites along the channel of the Paraguay River, in the marginal lakes Criminosa and Flores and in the affluent Amonguijá, totaling 53 samples, because in some sites the samples were repeated (Fig. 1). In addition, the distance between sampling sites is small not reaching 25 km between the most distant points, there is no physical barrier and no physical-chemical differences between the points, besides flood which homogenizes the distribution of fish, being considered a single population. Fish were collected with drag nets (1.5×5 m) and sieve nets (0.8×1.2 m) both with 2 mm mesh, being carried out at least 5 drags and twenty throws close to the littoral zone covered with aquatic macrophytes. Fish were fixed in 10 % formalin and preserved in 70 % ethanol for identification, count and for obtaining biometric and biological data of the species *Odontostilbe pequirá*. In the laboratory, identification was carried out with the help of the Fishes of the Pantanal identification key (Britski et al. 2007), and voucher specimens were catalogued (11167) in the collection of fishes of the Department of Zoology, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. After identification, all individuals were pooled from several points of each month into a single monthly sample, and from each monthly sample a random sub-sample was selected with at least 30 individuals in each month to obtain the following data: sex, total weight (g), weight of the gonads (g), standard length (mm) and stage of gonadal maturation. For the analyses of the population structure by length and sex ratio, 20 or more individuals random were added per month. The stages of gonadal maturation were determined based on macroscopic characters according to Vazzoler (1996), and later confirmed and revised by histological analysis of gonads previously selected from both sexes. For the females, the following stages were stipulated: immature (juveniles), maturing (adults), mature (ready for spawning) and semi-spent (spawning), while for males the stages were defined as: immature (juveniles), maturing (adults) and mature (reproducing).

During the collections, water temperature data were obtained at the points sampled and river level data in the base of the Marinha do Brasil in the city of Porto Murtinho (Station 67100000). The historical river levels were provided by the Agência Nacional das Águas (ANA) referring to the same station and rainfall data for the period sampled was supplied by the Instituto Nacional de Meteorologia (INMET).

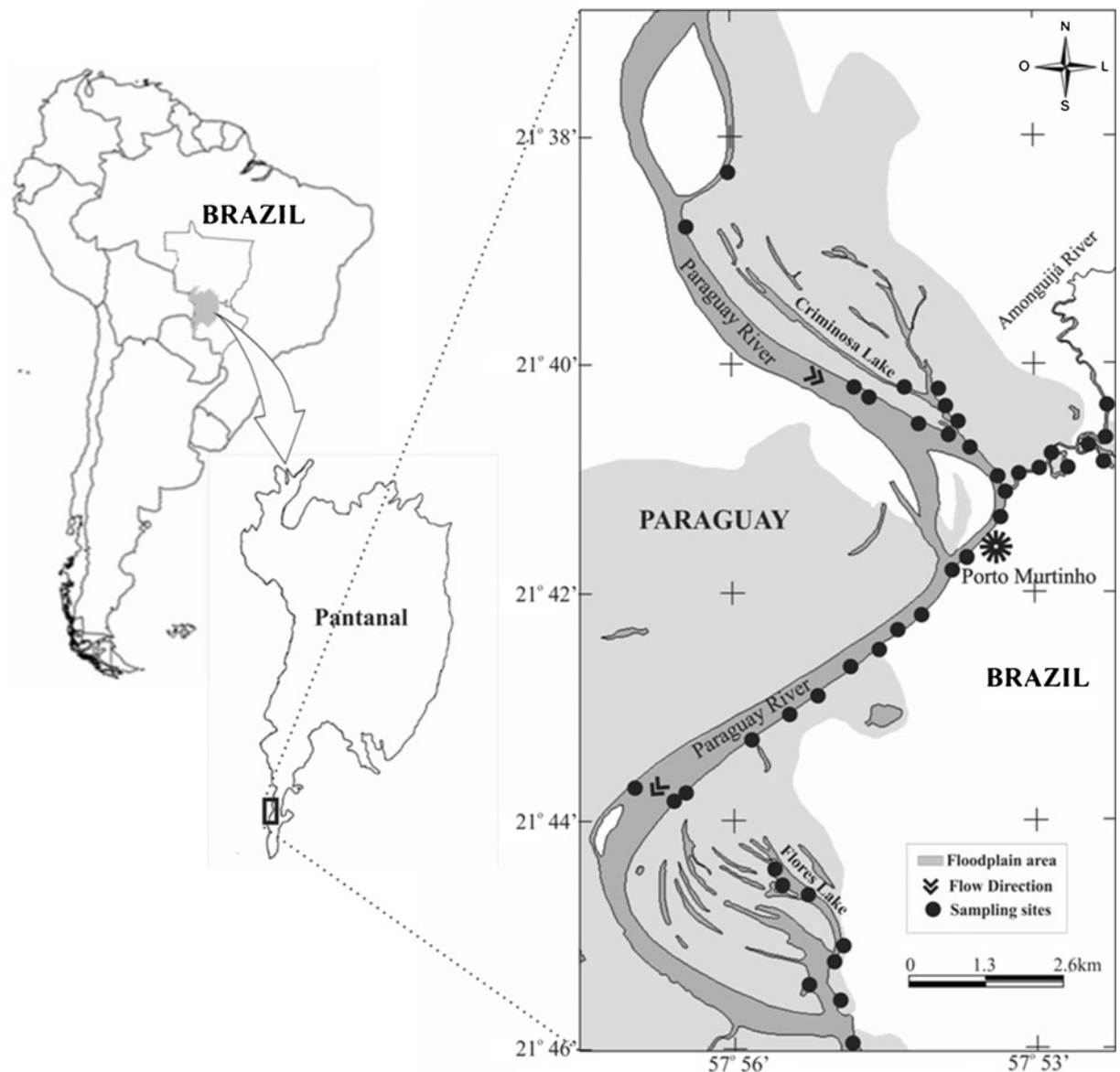


Fig. 1 Location of the sampling area along the Paraguay River, next the city of Porto Murtinho (Brazil), extreme southern Pantanal (Pantanal de Porto Murtinho), sampled from February/2009 to January/2010

The population structure by length was analyzed by visual inspection of the distributions of frequency of the standard length of the population between the sexes, besides utilization of the Kolmogorov Smirnov test to assess the difference between the distribution curves of the length and weight between the sexes, since a large quantity of data and non-standardization in the number of males and females could result in type I error. The distribution of the frequency of individuals of both sexes per length classes of 2 mm and the weight classes of

0.05 g was determined, in order to standardize the data for analysis and graphic representation. Sex ratio was determined according to monthly distributions and by length classes of males and females during the period of study. In addition, the chi-squared test (χ^2) was used to determine if the sex ratio differed significantly from the expected 1:1 ratio between the months sampled and per length class.

The reproductive period was established based on the distribution of the monthly frequency of the

gonadal maturation stages and by the variation in the gonadosomatic index (GSI) (%)=(gonad weight/total weight)*100, during the period studied. To determine if the GSI of the females and males varied between the months sampled, the Kruskal-Wallis test was applied, since the presumption of normality was not attained even after data transformation. Graphic inspection was used to determine the patterns of variation in GSI of the females and males between the months analyzed. The correlation between the abiotic variables (water temperature, level of the river-2009/2010, historical mean of the river level-1939/2009 and rainfall) and the gonadosomatic index of females and males between the months was determined after initial transformation of all variables to $\log(x)$, in order to linearize the correlations, later employing Pearson's correlation.

Length at first maturity for females and males of *O. pequirá* was estimated using logistic regression, according to the method proposed by Roa et al. (1999). The comparison of length at first maturity between males and females was done by overlapping the confidence intervals of the sexes obtained by logistic regression. In this way, the lack of overlap of confidence intervals of L_{50} would indicate a statistically significant difference.

Absolute fecundity was estimated by counting all the vitellogenic oocytes present in the ovaries of 13 previously selected females with high GSI values, classified as mature. Relative fecundity was determined by the number of oocytes per milligram of total weight of the female, as suggested by Adebisi (1987). The possible relations between fecundity and standard length (mm), total weight (g) and gonad weight (g) were determined using Spearman's correlation. All statistical analysis were carried out with the help of the Systat software version 12 (Wilkinson 2007).

The type of spawning was determined using the same gonads selected for analysis of fecundity. A sub-sample was obtained from each gonad selected, and the diameter of 100 random oocytes was obtained with the help of a stereomicroscope with a graduated ocular (mm) (Vazzoler 1996). The values obtained were grouped in classes of oocyte diameter, and the distribution of the frequencies of these classes was determined to establish by means of visual inspection how the females release mature oocytes during a reproductive period, seeing if spawning is total or partial (Vazzoler 1996).

Results

Population structure

In the period of February 2009 to January 2010, 7,471 individuals of *Odontostilbe pequirá* were captured, where the weight and length data of 623 individuals (366 females and 257 males) were obtained for analysis of the population structure between the sexes.

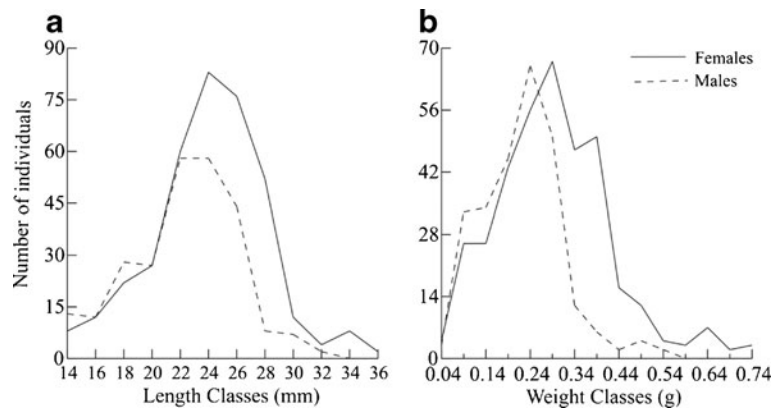
The standard length of the females varied from 14.0 to 36.3 mm (median=25.2 mm) and of the males from 14.4 to 33.0 mm (median=23.8 mm) (Fig. 2a). Total weight for females varied from 0.042 to 0.74 g (median=0.265 g) and for the males from 0.047 to 0.541 g (median=0.211 g) (Fig. 2b). There was no significant variation in the shape of the distribution of standard length (Ls) ($p=0.98$) and total weight ($p=0.34$) between females and males, but there was a slight asymmetry to the right, with females more frequent in the greater lengths and weights, besides reaching maximal length and weight in relation to males (Fig. 2).

The sex ratio in the period analyzed was 1.4:1 ($X^2=19.07$; $p<0.001$), so the population was mostly composed of females. Over months, sex ratio did not differ, maintaining the highest proportion of females, with exception of August ($X^2=12.30$; $p<0.001$) and January ($X^2=5.56$; $p=0.018$), whose dominance of females significantly exceeded. A significant difference in the sex ratio was found only for the length classes of 24 mm ($X^2=4.43$; $p=0.035$), 26 mm ($X^2=8.53$; $p=0.003$) and 28 mm ($X^2=32.26$; $p<0.001$), with predominance of females, while absence of males was observed in the classes of 34 and 36 mm. Thus females predominated in the largest size classes.

Reproductive aspects

Reproductive aspects were examined in 412 individuals of *O. pequirá*, including 253 females, 126 males and 33 whose sex was undetermined. In relation to the gonad maturation stages of the females, a greater frequency of mature and semi-spent individuals was observed between March and August and later in December and January (Fig. 3a). A similar temporal variation was found for the maturation stages of the males, with a predominance of mature males from February to July and in December to January. From August to November, there was a large proportion of

Fig. 2 Histogram of number of individuals for standard length classes (a) and total weight classes (b) for females and males of *O. pequirá* in the Paraguay River in the period February/2009 to January/2010



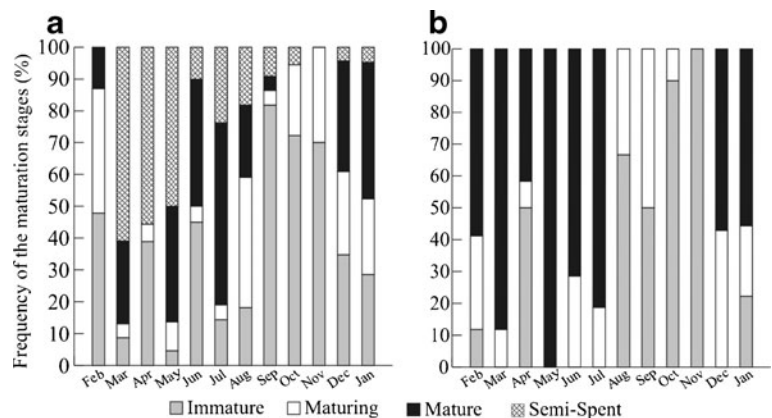
males in the maturing and immature stage, with the last only with immature individuals (Fig. 3b).

The reproductive period observed through the temporal variation in the gonadal maturation stages was confirmed by the variation in the gonadosomatic index (GSI) for both females ($H=41.98$; $p<0.001$) and males ($H=25.94$; $p<0.003$) throughout the year, showing higher values in the same period as evidenced by the stages for the females (February to September and December to January) and males (February to July and December to January), and reduction in values in October and November for both sexes (Fig. 4). In addition, the GSI of the females and of the males showed similar variation, indicating that gonadal development occurred in a synchronous way between the sexes in the period analyzed, co-varying along the year (Fig. 4). The lack of a mean GSI for males in November was due only to the presence of immature individuals.

The correlation between the mean values of abiotic variables and gonadosomatic index (GSI) of females

and males indicated that water temperature ($r=-0.14$, $p=0.68$ and $r=-0.06$, $p=0.84$, respectively (Fig. 5a) and rainfall ($r=0.08$, $p=0.79$ and $r=0.05$, $p=0.86$, respectively) (Fig. 5c) were not significantly associated with the GSI of both sexes during the months analyzed. Although the males showed no significant association between the GSI and the river level ($r=0.10$, $p=0.76$), a marginally significant correlation for the females GSI was observed ($r=0.53$, $p=0.07$) (Fig. 5b). Moreover, a correlation was observed between the historical river level and the mean GSI of females ($r=0.58$ and $p=0.04$) and males ($r=0.61$ and $p=0.04$) (Fig. 5b). The reproductive activity was positively correlated with historical and current variation in the river level. There was a greater frequency of immature and maturing individuals during the period of low levels (Fig. 3), with lower GSI values, although reproductive females have also occurred (Fig. 5b). The greater reproductive activity occurred in months with little rainfall and mild temperatures, although the reproduction had also been observed in December and January, with high values of

Fig. 3 Temporal variation in the frequencies of maturation stages of a female and b males of *O. pequirá* in the river Paraguay between February/2009 and January/2010



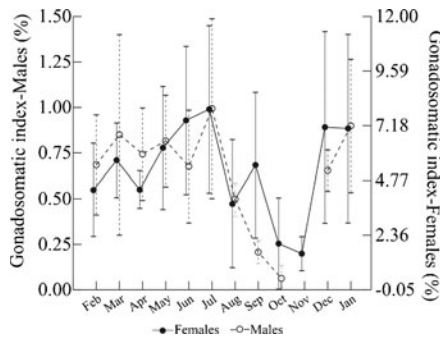


Fig. 4 Temporal covariation between the mean (\pm standard deviation) gonadosomatic index (%) of females and males of *O. pequirá* in the Paraguay river between February/2009 and January/2010

rainfall and temperature, however, these variables had not been statistically correlated with reproduction (Fig. 5a and c).

The length at first maturity of the females (L_{50}) was estimated to be 24.2 mm with a confidence interval of 23.7 to 24.6 mm and L_{100} of 30.6 mm, considering all the females analyzed (Fig. 6). For the males, L_{50} was 22.2 mm with a confidence interval of 21.3 to 22.9 mm and L_{100} of 31.4 mm (Fig. 6). The lack of overlap of the confidence intervals of L_{50} of females and males indicated a significant difference in L_{50} between the sexes.

Absolute fecundity varied between 75 and 250 vitellogenic oocytes, with a mean of 181.4 (SD=50.6). The mean relative fecundity was 0.544 oocytes/mg (SD=0.07), varying 0.39 to 0.65. Absolute fecundity was positively related to total weight ($r=0.945$; $p<0.001$) (Fig. 7a), gonad weight ($r=0.785$; $p=0.002$) (Fig. 7b) and standard length ($r=0.846$; $p<0.001$) (Fig. 7c), demonstrating that these parameters are possible indicators of fecundity.

The diameter of mature oocytes varied between 0.38 and 0.61 mm, with mean of 0.46 mm (SD=0.05). The distribution of the frequencies of the oocyte diameters showed various modes, where the first was formed by the reserve oocytes, the intermediate by oocytes in different phases of development and the last by large, mature oocytes, indicating multiple spawning (Fig. 8).

Discussion

Despite the mean length of *O. pequirá* being similar to those found in other Cheirodontinae fishes in tropical regions of Brazil (Silvano et al. 2003; Lourenço et al.

2008b; Benitez and Suárez 2009), the median length of the females and males is similar to the minimal lengths found by Oliveira et al. (2010) for *O. pequirá* in southern Brazil (sub-tropical region). This observation can be explained by two hypothesis: 1) The samples of Oliveira et al. (2010) has biased to higher individuals, in response to the use of 5 mm mesh size of the net, which influenced the sampling of smaller individuals or 2) The high temperatures during most of the year that lead to high productivity in the southern Pantanal, would result in rapid growth up to sexual maturity and consequent decrease in growth after the L_{50} , leading to a greater representativeness in small-sized classes.

The larger body size reached by the females of *O. pequirá* in relation to the males is a common characteristic for many fish species (Mazzoni et al. 2005; Mazzoni and Silva 2006), including Cheirodontinae fishes (Gelain et al. 1999; Oliveira et al. 2002) such as *O. pequirá* (Oliveira et al. 2010). In the females, the advantage of attaining greater lengths is mainly related to the fact the fecundity increases with the size of the individual (Wootton 1992), and thus, the production of a larger number of oocytes should assure the survival of the species. However, the similar distribution in length and weight observed for both sexes, suggested that, despite of higher fitness associated with the larger size females, the general pattern of size distribution between sexes was not altered in this population.

The sex ratio in fish is a parameter that varies with successive events acting differently on the individuals of each sex (Vazzoler 1996). Based on the hypothesis that the sexes are not susceptible to differential effects of birth, mortality and growth, the expected ratio is 1:1 (Nikolsky 1969; Vazzoler 1996), which was not observed for *O. pequirá*, with predominance of females. The predominance of females is common in fish (Abilhoa 2007; Suárez et al. 2009), and factors like predation and variation in local environmental conditions can be involved when a difference in the sex ratio occurs (Caramaschi and Mazzoni 1995; Garcia et al. 2004). At the same time, the sex ratio observed over the months remained balanced with the greater proportion of females, little variation for almost all the months, confirming the predominance of females in the total proportion. This is possible due to the eventual spatial segregation between males and females, migrating in the search of habitats with better conditions to decrease intraspecific competition. Also, the

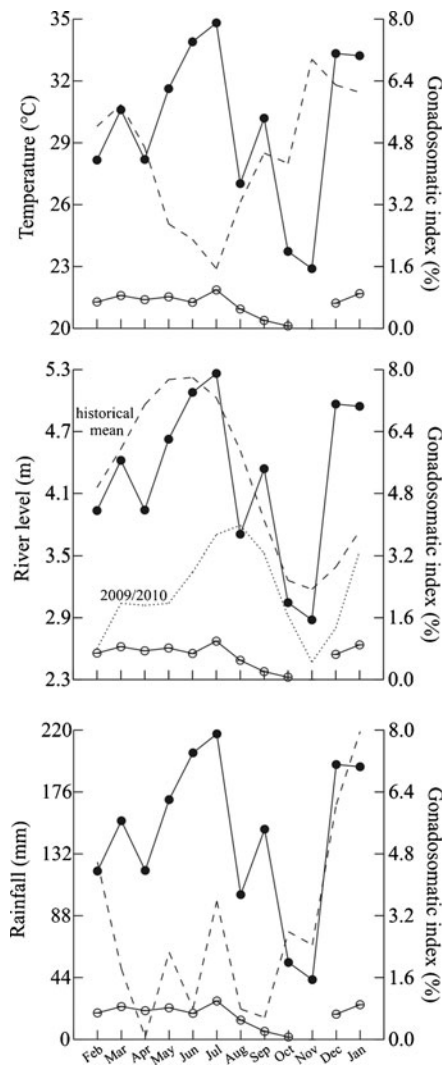
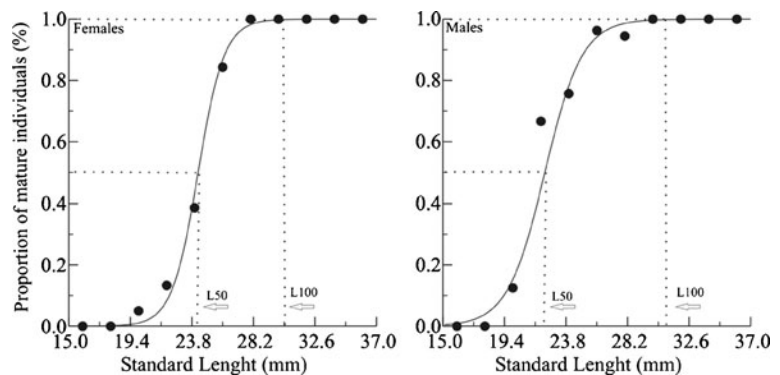


Fig. 5 Temporal variation of the mean gonadosomatic index (%) of females and males *O. pequira* and (a) mean temperature (b) river level (2009/2010) and historical mean river level (1939/2009) of the Paraguay river and (c) mean rainfall from February/2009 to January/2010

Fig. 6 Relation between the proportion of females and males mature sexually and standard length (mm) of *O. pequira* in the Paraguay river in the period February/2009 to January/2010. L_{50} (Length at which 50 % of individuals are reproduced) and L_{100} (length in which 100 % of individuals are reproduced)

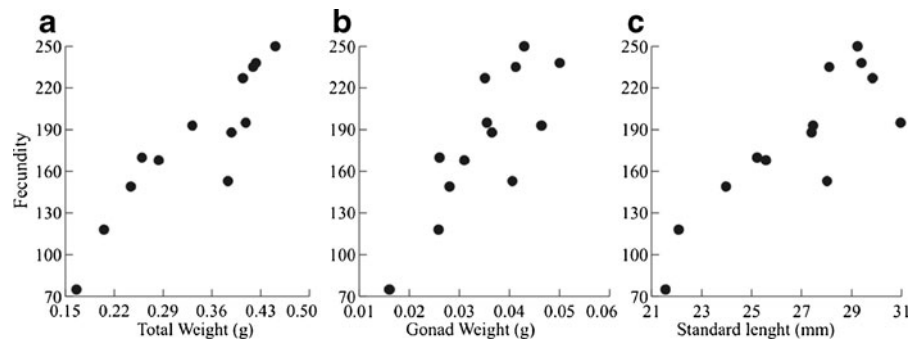


ratio had varied only in some intermediate classes, with a little dominance of males observed in the smaller classes and their absence in the larger ones. This suggests differences in the mortality rate between the length classes, since the main cause for the differential mortality of the sexes is the size specific mortality (Garcia et al. 2004).

In relation to the reproductive activity, the majority of the species of Characiformes show a seasonal reproductive pattern, with spawning usually during the spring and summer (Vazzoler and Menezes 1992). However, a long reproductive period (non-seasonal) was observed for *O. pequira*, which lasted about 10 months. Nevertheless, the reproductive activity is intensified in June and July followed by December and January, and in some months there is a decrease in the proportion of reproducing females. The long reproductive period was also found by various authors in small-sized species (Mazzoni et al. 2002, 2005; Hojo et al. 2004), but not corresponding with a reproductive strategy for seasonal environments (Munro 1990; Vazzoler and Menezes 1992), characterized by species with a short reproductive period associated with the favorable conditions of flooding (Tedesco et al. 2008), as reported for *Moenkhausia sanctaefilomenae* in the northern Pantanal (Lourenço et al. 2008a). Furthermore, the long reproductive period shows a intraspecific variation in *O. pequira*, once Oliveira et al. (2010) in studying the reproductive period of the same species in southern Brazil (sub-tropical region) found two reproductive steps, from September to October and from January to February.

In relation to abiotic variables, studies suggest that reproduction in fishes in floodplain rivers is highly seasonal and coincides with the initial phases of flooding (Welcomme 1979; Agostinho et al. 2004;

Fig. 7 Relation of the fecundity of females of *O. pequirá* in the Paraguay river from February/2009 to January/2010 as a function of total weight (g), gonad weight (g) and standard length



Costa and Mateus 2009; Tondato et al. 2010), following the flood pulse concept (FPC) (Junk et al. 1989). FPC postulates that flooding in floodplain is a principal driving force for the maintenance and production of plant and animal biomass, including fish (Junk et al. 1989). On the other hand, in Australia, studies found that in rivers where the flooding regime does not coincide with the period of high temperatures, fish species reproduce in the summer, when the water levels are low (Humphries et al. 2002; King et al. 2003), as proposed in the low flow recruitment (LFR) hypothesis (Humphries et al. 1999), pointing out that under these conditions, the temperature is the dominant parameter that generally determines the spawning period (Welcomme 1985). However, in the southern Pantanal, where there is asynchrony of flooding with the increase in temperature and rainfall, the reproductive period of *O. pequirá* is not correlated with temperature and rainfall in the year sampled, but it was observed that reproductive activity is correlated with the river level, with the greater reproductive investment coinciding with the elevation of the level of the river (beginning of flooding) and decreasing with the fall of its level. This variation was evident

despite flooding being considered “light” in the year sampled (Gonçalves et al. 2011), with the level of the river reaching a maximum of 3.8 m where the mean maximum is almost 6 m. This reproductive behavior is confirmed by the clear positive correlation observed with the mean historical level of the river, indicating que the flooding regime has a decisive influence on the reproductive activity of *O. pequirá*, where spawnings occur even though rainfall and temperature show low values. Similar results were found by Bailly et al. (2008), in the northern Pantanal, who studied the influence of the flooding regime on the reproduction of various species and observed that regardless of the strategy, the reproductive peaks of the species precede the peaks of the rains, demonstrating that the association of reproduction with the beginning of flooding is a common pattern in the majority of reproductive strategies of the ichthyofauna of the northern Pantanal.

As proposed by the FPC, the greater reproductive activity of *O. pequirá* in the beginning of flooding is possibly due to the expansion of the habitats, which is important for its reproductive success, because the exploration of the new available environments as nurseries and sites of growth for the juveniles (Junk et al. 1989). However, *O. pequirá* also supports the LFR hypothesis, extending its reproductive activity with a decrease in river level, although with a smaller proportion of females reproducing, taking advantage of the elevation in rainfall and temperature, besides greater density of phytoplankton and zooplankton on which larvae can feed (documented in the northern Pantanal) (Loverde-Oliveira et al. 2009; Fantin-Cruz et al. 2011). Therefore, the results indicate an intermediate position between the applicability of the FPC and the LFR in *O. pequirá*. However, the LFR hypothesis was tested in temperate environments, which could have been very important for the partial observation in the

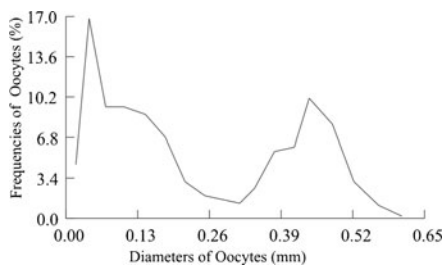


Fig. 8 Distribution of the relative frequencies of the oocyte diameters of *O. pequirá* the Paraguay River from February/2009 to January/2010

results, since in the southern Pantanal (tropical region) the mean annual temperatures vary between 22.5°C and 26.5°C, with a minimal mean of 21°C, generally in July (Gonçalves et al. 2011), where it is not considered stressing or a critical condition to reproduce in the months of pleasant temperatures. Therefore, the minimal temperatures non-limiting for reproduction in the months of flooding versus unfavorable conditions with low river level, such as fall in oxygen concentration, increase in concentrations of solutes which can be lethal (Humphries et al. 1999), and the higher levels of competition and mortality (Welcomme 1979; Lowe-McConnel 1999), appear to be evolutionarily important in the adaptability of the reproductive strategy of *O. pequirá*, resulting in a long reproductive period.

The age or size of first gonadal maturity is a reproductive tactic very unstable, intimately related to growth and in the genotype-environment interaction (Wootton 1992; Vazzoler et al. 1997), showing variation between local and intraspecific. Females and males of *O. pequirá* reach first gonadal maturity at different lengths, suggesting differences in growth rate and sexual development between the sexes, which is evident by the greater length reached by the females.

Another factor that is related to length at first maturity is fecundity (Nikolsky 1969), which is a characteristic that is adapted the conditions of the life cycle, showing a lower intra- than interspecific variability in fish species (Blanck and Lamouroux 2007). The absolute fecundity of *O. pequirá* was low (181.4) in relation to the fecundity (795) found for the same species in southern Brazil (sub-tropical region) (Oliveira et al. 2010), as for other Cheirodontinae fishes with external fertilization (Gelain et al. 1999; Oliveira et al. 2002; Silvano et al. 2003), although such works report on seasonal reproductive periods. This behavior appears clear, because the fecundity of the inseminating Cheirodontinae *Macropsobrycon uruguayanae* was shown to have a similar value (191.08 oocytes) (Azevedo et al. 2010), which could be a viable tactic among the Cheirodontinae fishes, which have a long reproductive period, independent of the type of fertilization. However, the relative fecundity of *O. pequirá* (0.54) is similar to that of various Cheirodontinae fishes, such as *Macropsobrycon uruguayanae* (0.53) and *Cheirodon ibicuihensis* (0.5), and smaller than the value found for the species in southern Brazil, which was the highest found for Cheirodontinae fishes to date (0.80) (respectively:

Azevedo et al. 2010; Oliveira et al. 2002, 2010). Despite the intraspecific difference in relative fecundity, *O. pequirá* in the southern Pantanal demonstrates GSI values comparable to those found by Oliveira et al. (2010), indicating an equivalent reproductive investment, in view of the long reproductive period and lower fecundity observed here versus seasonal reproduction and greater fecundity in southern Brazil (sub-tropical region). Additionally, the results indicate that fecundity is related to gonad weight, standard length and especially total weight. Although individuals have been subjected to weight loss or gain, this parameter is the best indicator of fecundity, as pointed out by other works (Mazzoni et al. 2002; Silvano et al. 2003).

The type of spawning is one of the reproductive traits molded by the environment, which determines the survival of the populations (Winemiller 1989), where multiple spawning, associated with a long reproductive period, is the main reproductive characteristics of tropical fishes (Nikolsky 1963). The analysis *O. pequirá*, suggests that spawning is divided, because a polymodal pattern is observed in the distribution of oocyte width in mature females, as demonstrated in other Cheirodontinae fishes with external fertilization (Gelain et al. 1999; Oliveira et al. 2002), and in various species of small size (Hojo et al. 2004; Lourenço et al. 2008a). Since *O. pequirá* shows a long reproduction, it is possible to suppose that the females have a high reproductive investment, spawning several batches the whole year, which also compensates for the apparently low fecundity. The diameter of *O. pequirá* oocyte was smaller than observed in Cheirodontinae *Macropsobrycon uruguayanae* (Azevedo et al. 2010) and also in most of Characidae species (Kramer 1978), suggesting that the small diameter is one more attempt to increase fecundity, which is lower in relation to other Cheirodontinae fish.

Thus, in aquatic environments, the expression of the reproductive strategy of a species depends on the interaction of intrinsic factors, such as the metabolism of the organisms themselves, and on extrinsic factors, resulting from existing environmental conditions, such as the flooding regime and of interspecific relations (Nikolsky 1963; Lowe-McConnel 1999). An analysis of the reproductive tactics of *O. pequirá* characterized it as an “opportunistic strategist,” following the proposal of Winemiller (1989), since it showed a small size, rapid maturation, multiple spawning, small eggs and continuous reproduction.

Although *O. pequirá* is considered a sedentary species, its long reproductive period with greater activity at the beginning of flooding, in the winter, occurs in the period of free fishing in the Pantanal. Thus, these are previous information for the integration of conceptual models of reproduction and for future studies with the aim to improve the management strategies in fisheries of the migratory species in the region. This is because, according to the Brazilian fishing laws, fishing ban season in the study area, i.e., the period in which the activities of gathering, hunting, commercial and sport fishing are banned, corresponds to the reproductive period of most species, from November to February, needs to be changed within this basin. Thus, in large rivers with a wide range of flow dynamics, the conceptual models should be evaluated before the application of management strategies (Thorp et al. 2006), recalling the urgency of information on fish of economic interest in tropical floodplain rivers, as in the studied region, where the flood does not coincide with the period of high rainfall and temperature. Besides questioning through observations of the difference in the length at first maturity between the sexes and the lack of males in the larger length classes, possible variations in the intraspecific population parameters, raise the hypothesis widely discussed but still not confirmed that growth and mortality rates and longevity differ between females and males of the same species.

Acknowledgments The authors gratefully acknowledge the Centro de Pesquisa do Pantanal (CPP/MCT), Fundect, UEMS and UFRGS for their financial, human and logistic support. Cnpq is acknowledged for providing a doctoral grant to the author. We thank the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis - IBAMA (SISBIO # 13458-1) that authorized the scientific samples. We are indebted to Ana Paula S. Dufech e Julia Giora for his help with histological analysis of gonads and Marcelo M. Souza, Marlon C. Pereira, Fabiane S. Ferreira, Gabriela S. V. Duarte, Maiane J. Pereira, Ediléia S. Amâncio, Wagner Vicentin, Patrícia L. Rondon, for their help in the field work. Y. R. Suárez is supported by productivity grants from CNPq. Also thank Ibraim Fantin-Cruz and Luis R. Malabarba for suggestions in the text.

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