POPULATION ASPECTS AND RECRUITMENT OF *Odontostilbe paraguayensis* (CHARACIFORMES: CHARACIDAE) IN THE PARAGUAY RIVER, PANTANAL, BRAZIL

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Abstract: Population dynamics allows comprehension on how population assures its success on continuity of the species and the balance of its population density. Thus, in order to analyze reproductive parameters (*i.e.,* gonadal maturation stages, fecundity, and recruitment) and population aspects (*i.e.,* length-weight frequency, asymptotic length, growth and mortality rates, and sex ratio) of *Odontostilbe paraguayensis* Eigenmann & Kennedy (1903) (Characiformes: Characidae) in the southern Pantanal of Brazil, samples were carried out from February 2009 to January 2011 along the main channel of the Paraguay River and its tributary, the Amonguijá River, with seine net and a rectangular sieve (0.8 x 1.2 m). To estimate population parameters, the data of 604 individuals were recorded, and for reproductive aspects, the data of 394 individuals were recorded. The sex ratio was 3:1 (females:males). The estimated asymptotic length ($L\infty$) was 36.67 mm. The population had high growth rate values ($k = 1.3$ year^{-1}) and mortality ($Z = 1.98$). Longevity was estimated as 2.3 years. The mean absolute fecundity was 420.2 oocytes/female. Absolute fecundity was positively related to total weight (g) and gonad weight (mg). For females, the standard length at first maturity (L50) was 24.1 mm, and for males, it was 27.6 mm. Reproducing females were more frequent in March and April, although females with ripe gonads were recorded nearly all year long. The recruitment pattern was long with positive correlation with the average historic level of the Paraguay River, considering seasonal flooding. The length-weight relationships were not different between the sexes, but they presented negative allometric growth. Thus, during ontogeny, the species presents more increment in length than in weight, and, consistent with the high growth rate, this may be understood as a way to reach longer lengths faster to avoid predation. The outcomes demonstrate that *O. paraguayensis* has a short life cycle with high growth and mortality rates. Together with the long recruitment pattern and high fecundity, the species may be considered an *r*-strategist.

Keywords: Cheirodontinae; floodplain; growth; reproductive biology.

INTRODUCTION

The study of fish population dynamics is an important issue in ecology (Winemiller & Rose 1992), providing knowledge about how life history traits may ensure viable populations and adaptations to different environmental requirements (Winemiller 1989). For fish species, some studies have aimed to describe the variation in life history, through traits or aspects of populations, such as recruitment pattern, growth rate, mortality, length at first maturity and reproductive activity (King *et al.* 2003, King & Etim 2004, Bailly *et al.* 2008, Close *et al.* 2010, Grabowska *et al.* 2011, Vicentin *et al.* 2012, Lima *et al.* 2017) in different environmental conditions. These traits, in addition to fecundity, offspring season and average standard length, affect life strategies in fish species (Winemiller 1989, Winemiller & Rose 1992, Zeug & Winemiller 2007).

Population studies showing variation and/ or plasticity of life history traits are found mostly between populations of the same species/genus or even between family/orders (Rochet 2000, Azevedo *et al.* 2010, Tondato *et al.* 2018). When it comes to variability between sexes, there are a lacking of studies presenting these information (Feitosa *et al.* 2004, Gomiero *et al.* 2007, Barzotto & Mateus 2017), mainly with small-sized species (Tondato *et al.* 2012, Súarez *et al.* 2017), due to its relatively unimportant status in the fishery. Nonetheless, small-sized species are essential to the base composition of the food chain for the mid- and large-sized fish, highlighting the importance of understanding their population aspects for the purposes of management and conservation of fish fauna. In addition, we see an increasing tendency to use such species for ornamentation, as suggested for Cheirodontinae species (Pelicice & Agostinho 2005, MMA 2006). Accordingly, studies like this may assist the understanding on how populations can adapt to the process of natural selection, and allow building knowledge about life history traits that can be useful for biology and population ecology.

The subfamily Cheirodontinae, as represented by 70 species (Eschmeyer *et al.* 2018), is composed of small-sized individuals described as herbivores, insectivores and omnivores, while some present semi-predatory habits (Dias & Fialho 2009, Lima *et al.* 2012) and are, therefore, considered opportunistic. As such, these species generally present earlier sexual maturation, low fecundity and low survival rates for young individuals and high growth rates (Winemiller 1989). *Odontostilbe paraguayensis* Eigenmann & Kenndy, 1903 (Characiformes: Characidae), as a Cheirodontinae, has wide occurrence in the Paraguay and La Plata River basins, occurring in Brazil, Paraguay and Argentina (Súarez *et al.* 2001, 2013, Malabarba 2003). In Brazil, it has been reported in streams and rivers in the Pantanal floodplain, and as an abundant species in these assemblages, it is considered the base in the food chain for fish fauna, reflecting its essential ecological role in rivers and ponds of this region (Súarez *et al.* 2013).

Thus, knowing that small species may be useful as food resource for higher trophic levels, it is important to understand how the population manage to perpetuate itself in environments as floodplains and how extrinsic and intrinsic factors may exert some influence on its survival. Life history traits are shaped by trade-offs that are presented as a proxy for population fitness and these traits can be different between populations in different environments or even between sexes (Tondato *et al.* 2012, 2018). Following this reason, this work aimed to provide and compare information about the life history traits of male and female *O. paraguayensis* such as length distribution, length-weight relationship, length at first maturity, stages of gonadal maturation, sex ratio and fecundity. We also estimated such parameters as asymptotic length, growth rate, recruitment, longevity and mortality for the population of *O. paraguayensis* in the floodplain of the southern Brazilian Pantanal.

MATERIAL AND METHODS

Study area

Located in the central part of South America, the Pantanal is one of the largest floodplains in the world. Paraguay River is the main river in the Pantanal, extending some 2,621 km from its headwaters in Serra de Araporé to its mouth in the Paraná River. Rainfall varies from 800 to 1400 mm/year, with 80% between November and March (Fantin-Cruz *et al.* 2011). The Pantanal of Porto Murtinho, a subregion of the Pantanal, is located along the Paraguay River, the north and south boundaries of which are the Nabileque and Apa Rivers, respectively (Silva & Abdon 1998). Flooding

in this region peaks between June and August when rainfall is low, and the level of the Paraguay River reaches almost six meters above its normal water level. Owing to its meandering course, the Paraguay River, in the analyzed region, also features some oxbow lakes formed by abandoned meanders (Figure 1) that are directly linked to the River, and thus, tightly influenced by its seasonality.

Data sampling

Odontostilbe paraguayensis individuals were sampled monthly in the southern Pantanal from February 2009 to January 2011, under macrophyte banks, along the shore zone of the Paraguay and Amonguijá River and in marginal ponds. Samples were collected with seine nets (1.5 x 5 m) and a sieve (0.8 x 1.2 m) with mesh of approximately 2 mm. In the field, fish were anesthetized with eugenol, fixed in 10% formalin, and labeled for subsequent analysis in the laboratory where they were transferred to 70% alcohol. Identification was carried out in the laboratory, and voucher specimens (#11163) were deposited in the fish collection of the Zoology Department, Universidade Federal do Rio Grande do Sul, Brazil.

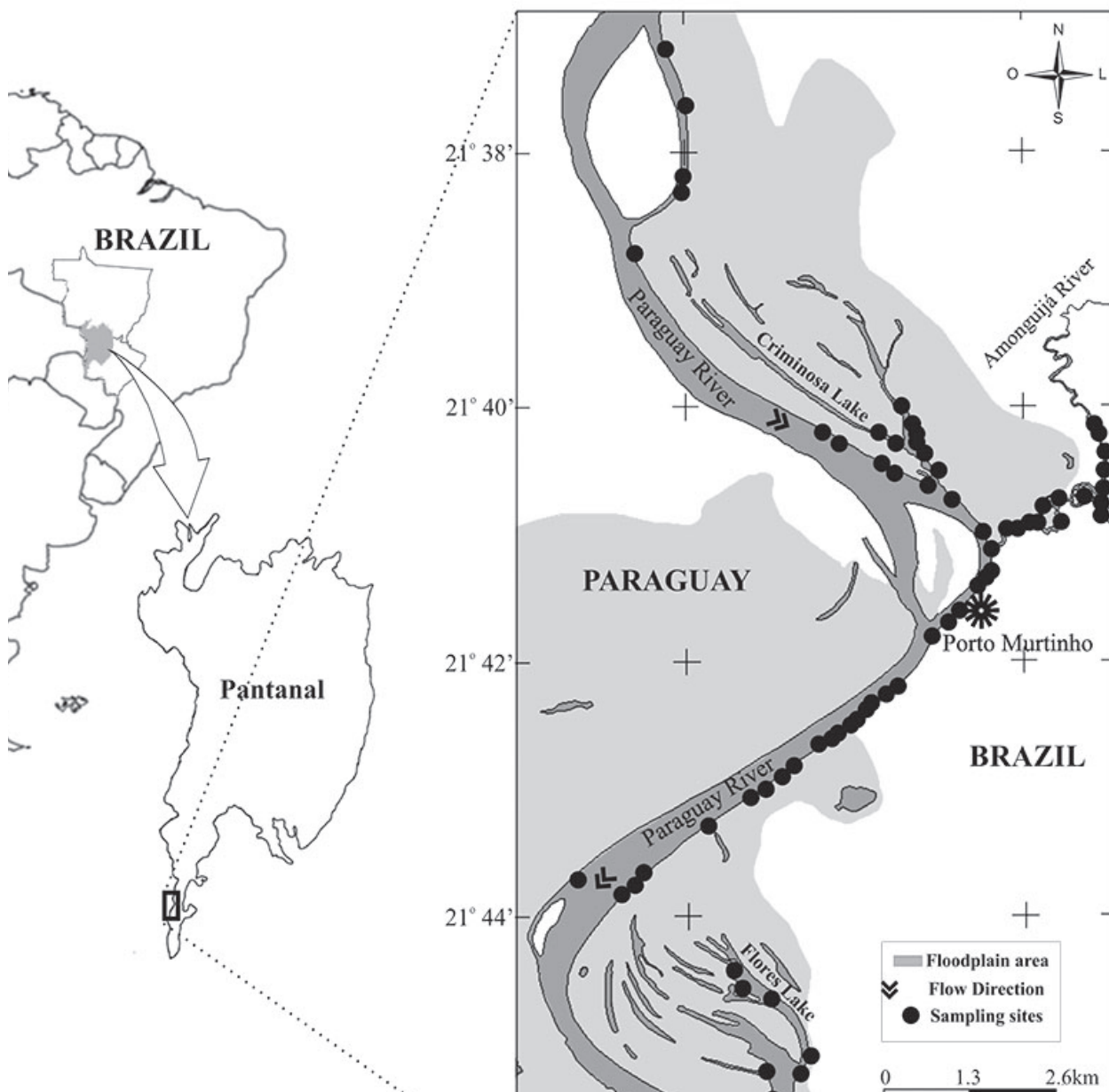From each specimen the following biometric

Figure 1. Location of the study area in the subregion of the Pantanal of Porto Murtinho, Brazil, from February 2009 to January 2011.

data were obtained: total weight (g), standard length (mm), sex, and gonadal maturation stages of females (immature, maturing, mature and semi-spent) (Vazzoler 1996). In this procedure, approximately 30 fish per month were dissected for reproductive analyses, and data from equivalent months of both years were grouped. For analyses based on length-frequency data, more individuals had their standard length measured, in order to have a better representation of the length classes by month and all over the year. The data of the months repeated in consecutive years were also grouped.

The gonadal maturation stages were macroscopically determined according to Vazzoler (1996): immature, maturing, mature and semi-spent. Some gonads of females identified macroscopically as each maturation stage were checked through histological analysis in paraffin. The frequency of gonadal stages was grouped bimonthly for visual inspection of stage distribution over time and to determine the reproductive period of the species.

Absolute fecundity was estimated by counting all the vitellogenic oocytes present in ovaries of 15 previously selected females classified as mature, and relative fecundity was determined by the number of oocytes per milligram of total weight of the female.

During collections, river levels were provided by the Brazilian National Water Agency (*Agência Nacional das Águas*) from the 67100000 station in Porto Murtinho municipality.

Data analysis

Length data were analyzed by visual inspection of standard length frequency distribution by sex. The Kolmogorov Smirnov test was used to compare the length and weight distributions between the sexes. Sex ratio was analyzed, distributing the individuals by length classes (3 mm) and along the months. Chi-square test was applied to verify whether sex ratio was consistent with the expected ratio of 1:1.

The length-weight relationship (LWR) was fitted to each sex by nonlinear regression such that total weight (TW) and standard length (SL) were adjusted by the power function, as TW = a * SL^b, where a = intercept constant and b = angular coefficient. The superposition of the confidence interval (CI) (± 0.95; p = 0.05) of parameter b was realized in order to verify differences in the increment rate of weight over the length between the sexes and to observe if b is statistically different from three (isometric growth), *i.e.*, $b > 3$ indicates positive allometric growth, whereas $b < 3$ indicates negative allometric growth.

In order to estimate growth rates, a monthly frequency distribution of length classes with interval of 3 mm was used allowing to obtain a better distribution along the year. According to Pauly & David (1981), it was assumed that fish with the same length in a sample would be at the same age and differences in length could be attributed to differences in age. The population parameters were estimated by the updated version of the electronic length frequency analysis (ELEFAN) method (Pauly 1980) with new optimization techniques using the TropFishR package (Mildenberger *et al.* 2017a,b). Asymptotic length (L∞, mm), growth rate (k), time of year when the von Bertalanffy growth function (VBGF) crosses length = 0 for a given cohort (t-anchor), and the growth performance index (φ) were all estimated by the ELEFAN_SA function, which is based on Simulated Annealing (SA) (Taylor & Mildenberger 2017). The curve was obtained by the growth function of von Bertalanffy, as L(t) = L∞ (1 - exp[-k(t-t0)]), where L∞ = asymptotic length, k = growth rate (year-1), t = age (month/year), and t_0 = theoretical age at length zero (Bertalanffy 1938, Gulland 1977). This last parameter is a mathematical artifact to improve de adjustment of the growth formulae (Moreau 1987), has no biological meaning and in this study was considered equal to zero.

Since *O. paraguayensis* is not commercially fished, the total mortality (Z) here is equal to natural mortality (M) obtained by the empirical formula of Pauly (1980), using the parameters (L∞ and k) and the average temperature (°C) of the environment where the specimens was caught, following the equation $\ln M = -0.0152 - 0.279 \ln L\infty + 0.6543 \ln k + 0.463 \ln T°C$. Longevity was estimated using the equations of Taylor (1958), as $t_{max} = t_0 + 2.996/k$, and by the number of cohorts (1 cohort = 1 year) from the von Bertalanffy model. For all population parameters, a bootstrap procedure was employed in order to have Confidence Intervals (CI) for the estimated values.

The recruitment pattern along the year was established through the monthly length-frequency distribution, growth rate (*k*) e asymptotic length (*L∞*), using a FISAT routine (FAO-ICLARM Stock

Assessment Tools) (Gayanilo & Pauly 1997). To determine any relationship between recruitment and variation of historic river levels, a Spearman's correlation was performed.

Logistical regression was used to estimate the probability of females being mature. Immature gonads were considered non-reproductive (0), and those that showed gonadal maturation stage of "maturing", "mature" and "semi-spent" were classified as reproductive animals (1). In this way, the frequency of mature individuals was used as a response variable to the total length as explanatory variable (Roa *et al.* 1999). The estimated mean total length at first maturity (L50) indicates the size at which 50% of the fish are mature and L100 indicates the size at which all fish are mature. L50, L100 and their confidence intervals (CI; p < 0.05) were estimated using the MASS package (Venables & Ripley 2002) in R software (R Core Team 2018). The superposition of the estimated Confidence Interval was performed to observe a possible intraspecific difference of L50 between the sexes.

Possible relationships between absolute fecundity and standard length (mm), as well as total weight (g) and standard length, were all determined using Spearman's correlation. The R program (R Core Team 2018) was also used for the analysis.

RESULTS

A total of 604 specimens had their length measured for the analyses of population aspects. For reproduction analyses, 394 specimens were recorded for gonadal data (291 females, 96 males and 7 of undetermined sex), and also had their length and weight measured.

The standard length ranged from 16.02 to 34.83 mm for females and from 10.89 to 33.22 for males. The total weight ranged from 0.07 to 0.81 g for females and from 0.03 to 0.62 for males. No significant differences in the length and weight distribution were found between the sexes (p = 0.52 and p = 0.59, respectively).

The sex ratio for the whole period was 3:1 (χ^2 = 98.25; p < 0.001), indicating that females were significantly predominant. Sex ratio along the length classes demonstrated that females predominated significantly in most classes (χ^2 = 30.20; p < 0.001), and the same pattern was recorded for the sex ratio along the year (χ^2 = 19.49; p < 0.001) (Figure 2).

The determination coefficient of LWR for females explained 95.4% of the data variation (TW = $0.00008*SL^{2.58}$), while for males, the coefficient explained 96.8% (TW = $0.00024*SL^{2.24}$). No significant differences were noted for angular
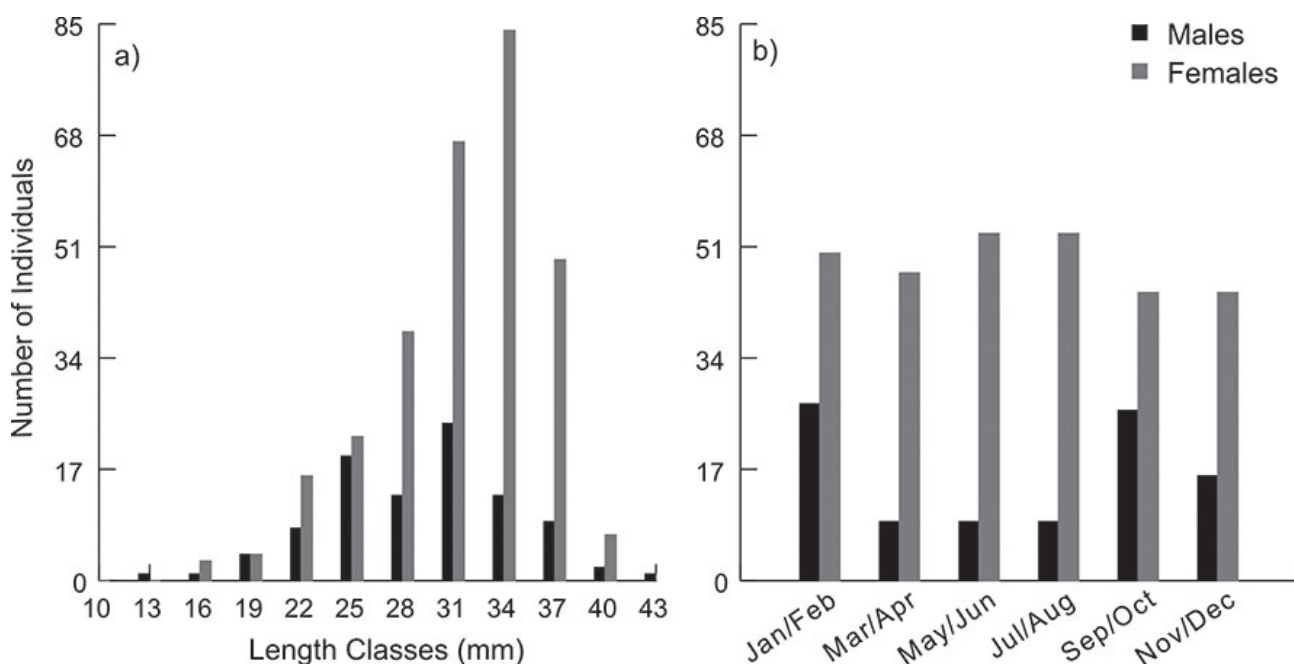

Figure 2. Sex ratio along the length classes (a) and along the year (b) for *Odontostilbe paraguayensis* (Characiformes: Characidae) in the Paraguay River, Brazil.

coefficient between female (b = 2.58; IC = 2.30-2.86) and male (b = 2.24; IC = 1.94-2.53), and both sexes presented a significant negative allometric growth with more increment in length than in weight.

The frequency of gonadal stages revealed that reproductive activity occurred during almost the whole period, peaking in March/April and July/August for mature females (Figure 3). The occurrence of semi-spent females in several months evidenced prolonged reproductive activity (Figure 3). A large number of young individuals were also registered in September/October and May/June interspersing monthly with high frequency of mature females.

The estimated standard length at first maturity (L50) for females was 24.1 mm (CI = 23.04 – 24.83), and the estimated standard length where all females reach maturity (L100) was 35.7 mm (CI = 33.48-39.45). For males, the estimated L50 was 27.6 mm (CI = 24.64 – 26.40), and L100 was 38.4 (CI = 34.33-49.49). Considering that the Confidence Intervals for L50 were not overlapped between the sexes (Figure 4), the length at first maturity for females was significantly smaller compared to males.

The estimated population parameters were as follows: asymptotic length ($L\infty$) = 36.66 cm (CI = 36.56-36.75), growth rate (k) = 1.182 (CI = 1.11-1.25), natural mortality (Z) = 1.88 (CI = 1.81-1.95). The best adjustment (Rn) was 0.382 (CI = 0.350-0.414). With the length-frequency data, three cohorts were verified (Figure 5), and corroborating this result, longevity was estimated at 2.53 years.

The performance index (φ) was 3.19 (CI = 3.17-3.22). By plotting the von-Bertalanffy growth curve, it was estimated that *O. paraguayensis* reached Lmax between the 30th and 31th month of relative age (Figure 6). Females reached L50 between the 10th and 11th month, while males reached L50 between the 13th and 14th month (Figure 6).

The recruitment pattern was long with a peak in May and June (Figure 7). A positive correlation was detected between recruitment and the historic average river level (r = 0.77; p = < 0.01), and the entrance of new individuals followed the increase in the river level. Juvenile and immature individuals were recorded in several months along the year, giving evidence that the entrance of new
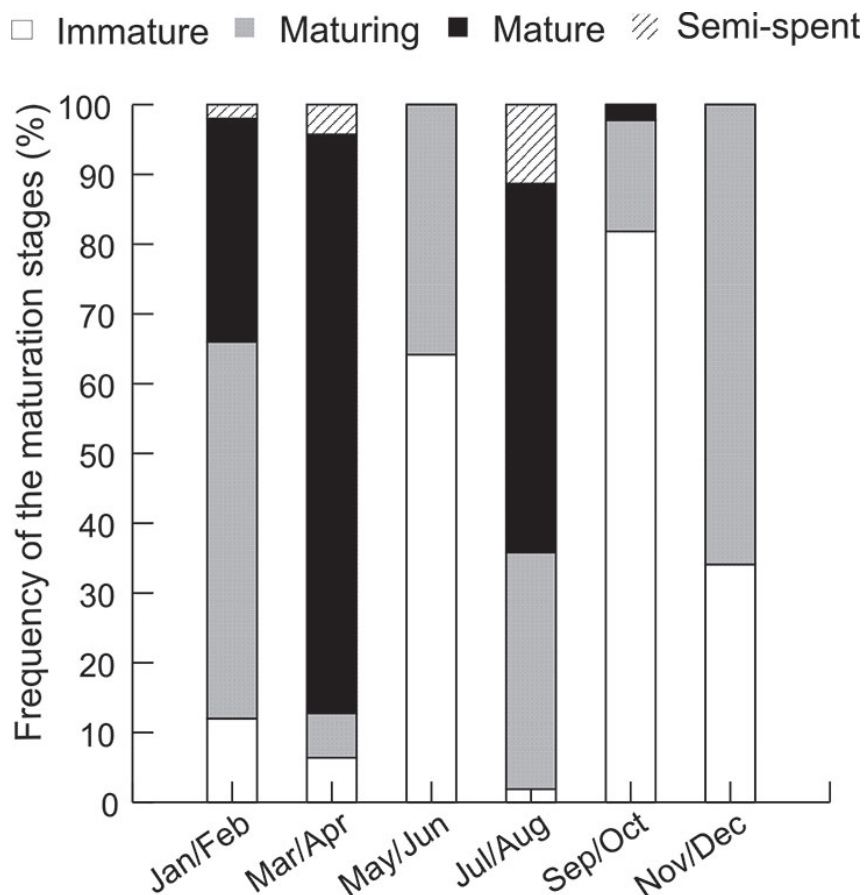

Figure 3. Seasonal frequency of gonadal stages for *Odontostilbe paraguayensis* (Characiformes: Characidae) in the Paraguay River, Brazil.
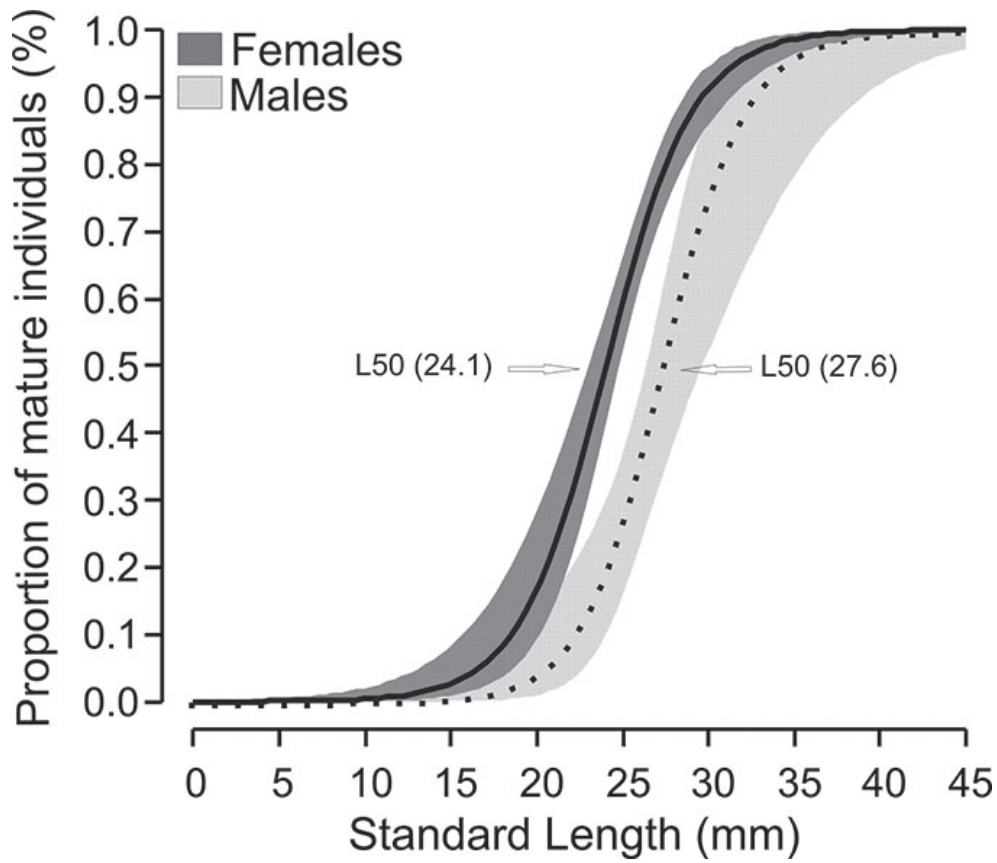
Figure 4. Proportion of mature females in function of standard length (cm) for both sexes of *Odontostilbe paraguayensis* (Characiformes: Characidae) in the Paraguay River, Brazil.
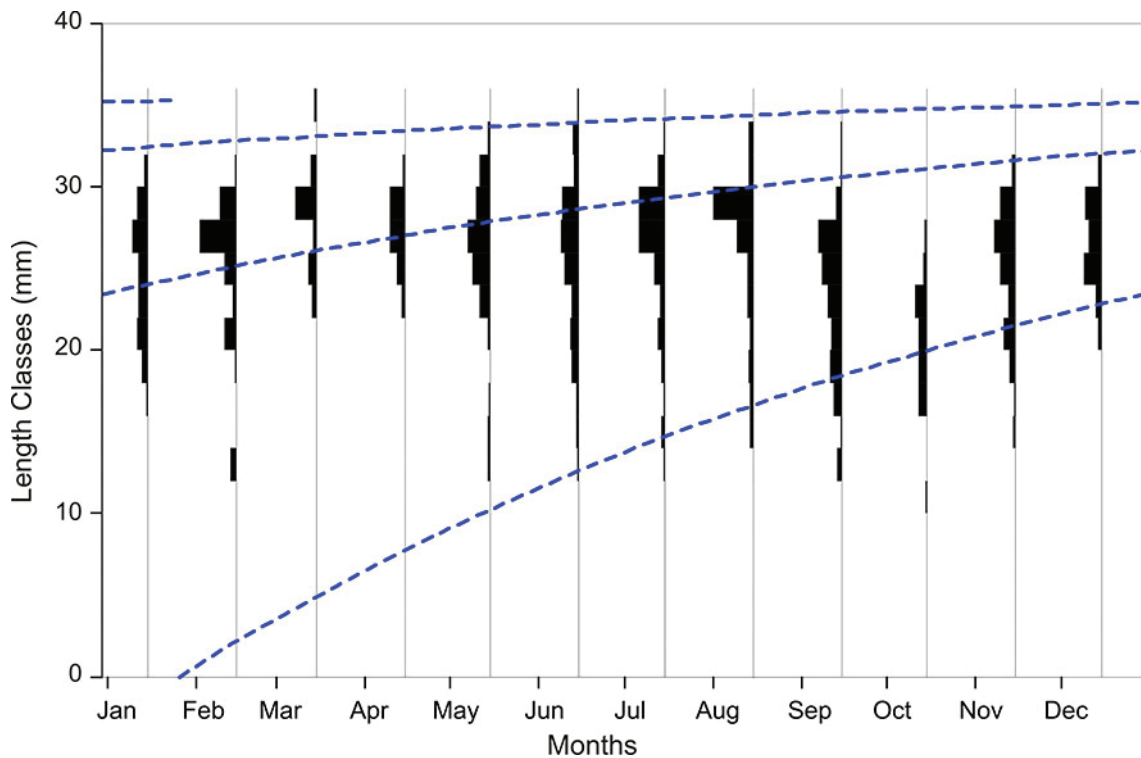

Figure 5. Length frequency distribution of total length and growth curve fitted to *Odontostilbe paraguayensis* (Characiformes: Characidae) in the Paraguay River, Brazil.
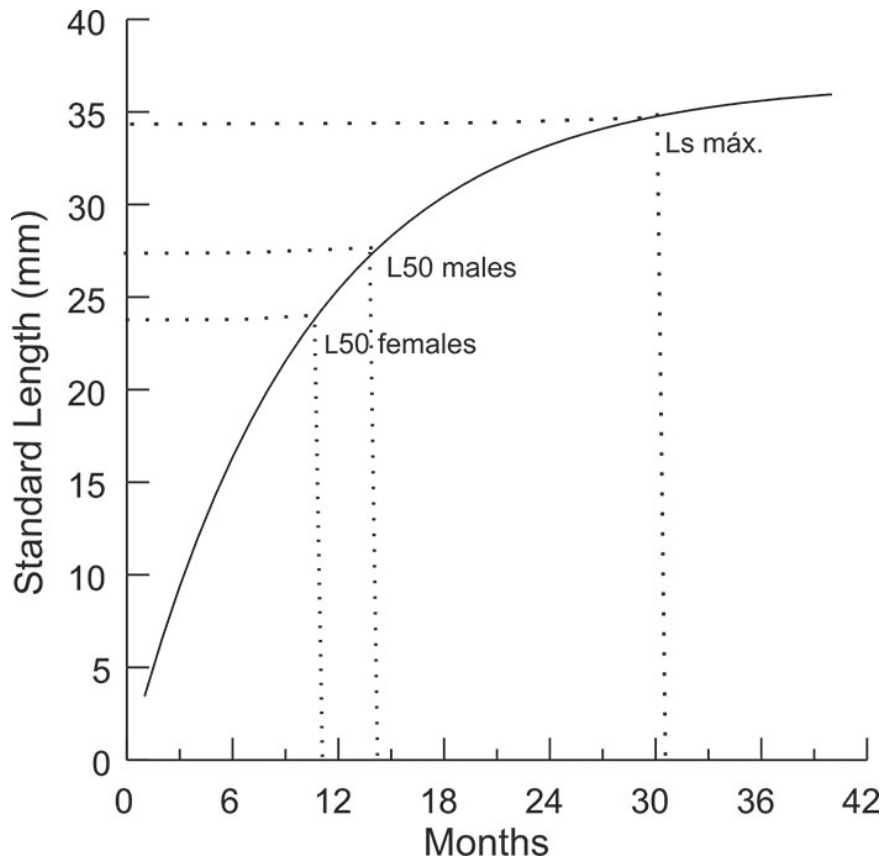
Figure 6. Von-Bertalanffy growth curve estimated in relative year for *Odontostilbe paraguayensis* (Characiformes: Characidae) in the Paraguay River, Brazil.
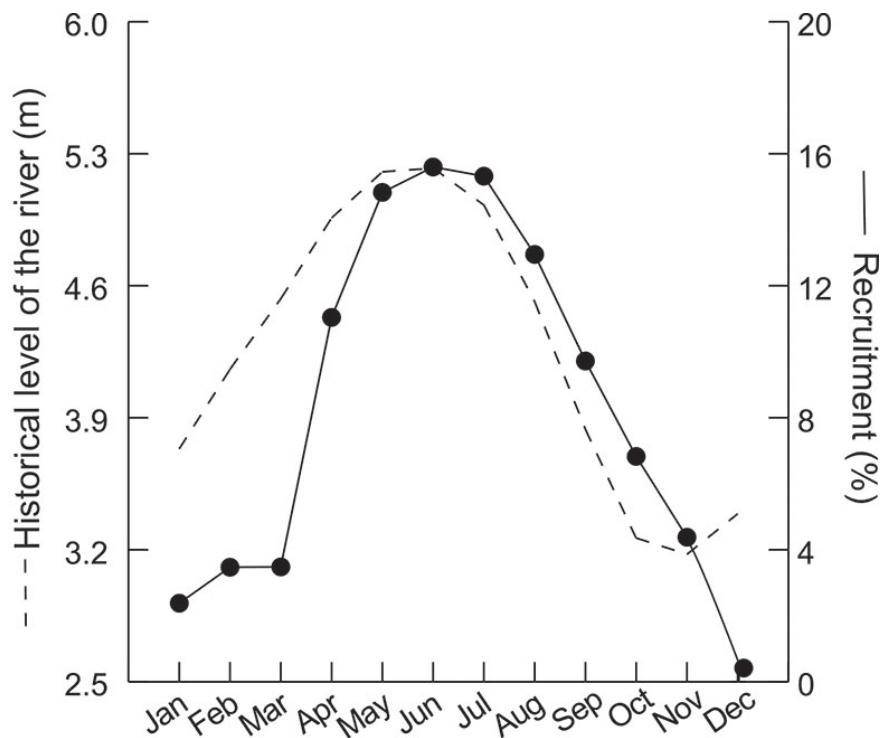

Figure 7. Seasonal variation of estimated recruitment for *Odontostilbe paraguayensis* (Characiformes: Characidae) from February 2009 and January 2011 and the average historic level of the Paraguay River, Brazil.
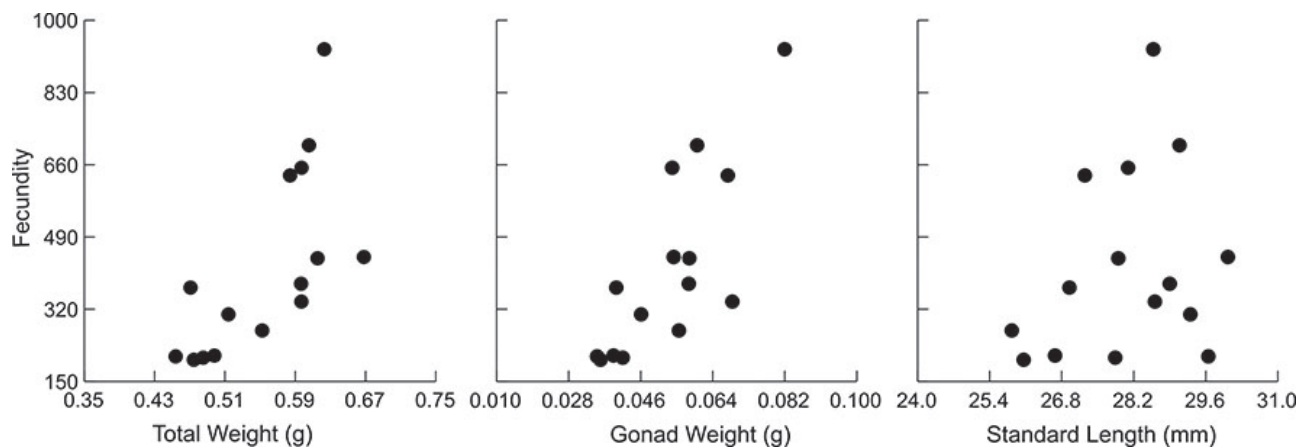
Figure 8. Total fecundity, as determined by total weight, gonad weight and standard length, for females of *Odontostilbe paraguayensis* (Characiformes: Characidae) in the Paraguay River, Brazil.

individuals may occur at any time.

Absolute fecundity varied from 201 to 932 vitellogenic oocytes, 420.2 oocytes on average (SD = 219.2), while the average relative fecundity was 0.722 oocytes/mg (SD = 0.39), ranging from 0.42 to 1.64. The total fecundity was positively correlated with total weight ($rs = 0.8$; $p < 0.001$) and gonad weight ($rs = 0.7$; $p < 0.001$), but it was not correlated with standard length ($rs = 0.3$; $p = 0.33$) (Figure 8).

DISCUSSION

The highest values of standard length recorded for males and females of *O. paraguayensis* were similar to those of other Cheirodontinae, such as *Serrapinnus notomelas* (both sexes) ($SL_{max} = 34$ mm) (Benitez & Súarez 2009), ($SL_{max} = 38$mm) (Costa & Rocha 2017) and *Serrapinnus piaba* (both sexes) ($SL_{max} = 30.18$mm) (Silvano *et al.* 2003). Nevertheless, these values were lower than the standard length reported for *Odontostilbe fugitive* (both sexes) in the Madeira River basin in Peru ($SL_{max} = 58$ mm) (Bührnheim & Malabarba 2006) and *Odontostilbe pequira* (both sexes) ($SL_{max} = 44.9$ mm) in the Ibicuí-Mirim River (Oliveira *et al.* 2010). These results were also similar to the total weight (TW = 0.74g) and standard length (SL = 36.3mm) reported for *O. pequira* (both sexes) in the Paraguay River (Tondato *et al.* 2014), demonstrating how local environmental conditions may influence the size and weight of related species, but for sure additional analyses must be performed in order to verify what has affected this results.

A greater female proportion is commonly reported for small-sized fish populations (Garcia *et al.* 2004, Súarez *et al.* 2009, Santana *et al.* 2018), including species of Cheirodontinae (Oliveira *et al.* 2010, Tondato *et al.* 2014). A greater female proportion, as found in the present study (3:1), may be interpreted as a greater reproductive investment to ensure population survival. Also, a greater proportion of females over males in length classes was registered, mainly in those where females are adults and sexually active, in other words, in greater sizes, suggesting that mortality here is more pronounced for males. Still, Cheirodontinae are known for presenting feeding plasticity, and this favors females (Dias & Fialho 2009, Fiori *et al.* 2016, Costa & Rocha 2017), since a higher diversity food acquisition can favor a greater energy intake that can be used for reproduction.

Considering the confidence intervals of the angular coefficient (*b*) for both sexes, no significant difference in the LWRs was confirmed; however, the values were significantly lower than three. Thus, a negative allometric growth was confirmed for both sexes, which means that the increment in weight is lower than the increment in length. The estimated *b* values from LWRs also diverge from other Cheirodontinae which, in general, presented isometric (Lizama & Ambrósio 1999, Lourenço *et al.* 2008, Tondato *et al.* 2012) or positive allometric growth (Benitez & Súarez 2009) in different environments. LWR may be used to indicate energetic investments in growth and/or fish reproduction (Santos *et al.* 2004).

In this way, with a greater investment in length than in weight may be suggested there is no need for saving energy due to the high food abundance and the temperature that is favorable and

practically continuous along the year as mentioned by Tondato *et al.* (2012) in the same studied area, associated to the need of reaching quickly the reproductive age. This may also be related to allocation of more energy to axial growth, rather than biomass (Mello *et al.* 2009), and it means that specimens have changed their body to become more elongated (Froese 2006). *R*-strategists, in general, are small-sized fish and occupy the base of food chains (Gubiani *et al.* 2012). They tend to present more increment in length than biomass in order to achieve longer lengths in a short time and, thus, to avoid predation pressure from large-sized fish (Walls *et al.* 1990) since vulnerability decreases as the fish grows.

The reproductive period was recorded throughout the year, as commonly reported for other Cheirodontinae (Azevedo *et al.* 2010, Oliveira *et al.* 2010, Tondato *et al.* 2014). However, it was more pronounced in March and April, suggesting that greater reproductive activity is related to the end of the dry season (rainy), as observed by Súarez *et al.* (2017) with the species *Astyanax lacustris* in the same region. This is according to the proposition by Humphries *et al.* (1998) who suggested the idea of 'low flow recruitment' (LFR) owing to the concentration of food resources and the ability to reproduce without a high degree of competition with other migrating and rheophilic species which tend to increase the abundance during the flood season, when the environmental conditions for reproducing are more suitable for them. However, reproductive activity, even with lower intensity, also occurs during flooding, indicating that *O. paraguayensis* also uses the favorable conditions of the floodplain to maximize the survival of its offspring. Small-sized species are tolerant to frequent environmental disturbances and may be prone to reproduce whenever the conditions are suitable, presenting multiple and repetitive reproduction events associated with the capacity to adapt and recolonize these habitats (Winemiller 1989, Braga *et al.* 2008).

The length/size or age at first maturity may be considered as a reproductive tactic, but not a very stable one, considering the relationship to growth and genotypic interactions with the environment (Wootton 1992, Vazzoler *et al.* 1997). Males of *O. paraguayensis* reached their first size at maturity (L50 = 24.1 mm), earlier than females (L50 = 27.6 mm). Although differences in length structures have not been recorded between the sexes, this result suggests that females reach L50 more quickly (10 to 11 months), becoming adult to maximize their reproductive investment and, hence, increase their chances to leave descendants. The L50 of females is very similar to that reported for other Cheirodontinae females (also, as the current study, based on standard length), such as the L50 values obtained by Tondato *et al.* (2014) for *O. pequira* in the Paraguay River, Pantanal (L50: 23.7 and 24.6 mm) and those by Azevedo *et al.* (2010) for *Macropsobrycon uruguayanae* in the Uruguay River (L50: 24 mm) (subtropical climate), demonstrating that these fish, even under different local environmental conditions, may be influenced by the proximity of phylogenetic relatedness.

In the Paraguay Basin, *O. paraguayensis* presented high values of growth rate and natural mortality, values similar to those reported for *S. notomelas* (Cheirodontinae) ($k = 1.05$ year^{-1}; $Z = 1.61$ and longevity = 2.85 years) in streams of the upper Paraná River, Brazil (Benitez & Súarez 2009). This is usually related to an intense predation from the time of hatching (Lowe-McConnell 1999); consequently, these fish need to grow faster, reaching maturity earlier (Blank & Lamoroux 2007). As a result, they present lower asymptotic length with higher growth rate (Lizama & Ambrosio 2003). The high growth rate for *O. paraguayensis* is reflected in a trend of smaller standard length when compared to *O. pequira* in the same region (Tondato *et al.* 2012). *Odontostilbe pequira* presents smaller growth rate (females = 0.93; males = 0.82 year^{-1}) and, consequently, tend to a longer asymptotic length (females = 39.59; males = 37.57mm), as well as tend to a greater longevity (females = 3.22; males = 3.65 years) and to a lower mortality (females = 1.56; males = 1.45) under the same environmental conditions as those of the species in the current study. Therefore, the short longevity and high mortality presented by this species provide evidence of some adaptive advantages, such as reaching maturity (age/size) quickly and maintaining high reproductive activity during the year.

A long recruitment pattern is an inherent feature of small-sized species from tropical freshwater regions (Lizama & Ambrosio 2003). However, floodplains studies indicate that, even small species, have recruitment in rainy periods, as reported

by Cunha *et al.* (2007) analyzing *Moenkhausia dichroura*. This pattern is related to viable strategy for seasonal environments (Vazzoler & Menezes 1992), which, in general, favor a short reproductive period, based on the favorable flooding conditions (Tedesco *et al.* 2008), also evidenced in small-sized species (Lourenço *et al.* 2008). Therefore, the long recruitment pattern observed for *O. paraguayensis* is related to the life strategy with long reproductive activity, cited above, which uses the conditions of the dry season (rainy and high temperatures) and the flood (rainless period) to spawn. High recruitment in June suggests a response to high reproductive activity at the end of the dry season.

The significant relationship between population recruitment and historic average river level indicates that reproduction is correlated by the magnitude of flooding, as suggested by Bailly *et al.* (2008) and Tondato *et al.* (2012), even though the most intense spawning occurs before peak floods, as observed in our results. This tends to maximize reproduction success since this species has high fecundity (0.72 oocytes/mg), resulting in large populations that can be recognized as cosmopolitan in the region (Súarez *et al.* 2001). In principle, the tactics employed by a strategy may differ in each environment in a way that each species may assure the recruitment of young individuals in the population (Wootton 1999).

Fecundity, according to Nikolsky (1969), is a unique feature that may vary with growth, population density, availability of resources, and mortality rate. For *O. paraguayensis*, fecundity, as shown in the present study, can be considered high, as observed for other Cheirodontinae, such as *Serrapinnus piaba*, $F_{mean} = 0.74$ oocytes/mg (Silvano *et al.* 2003) and *O. pequira*, $F_{mean} = 0.8$ oocytes/mg (Oliveira *et al.* 2010). Nevertheless, for fish species of this family, some plasticity has been reported with lower values, such as for *Macropsobrycon uruguayanae* ($F_{mean} = 0.53$ oocytes/mg) (Azevedo *et al.* 2010), *Cheirodon ibicuhiensis* ($F_{mean} = 0.5$ oocytes/mg) (Oliveira *et al.* 2002) and *O. pequira* ($F_{mean} = 0.54$) in the same study area (Tondato *et al.* 2014). In the same regions, other small-sized species, as *Hyphessobrycon eques* and *Astyanax lacustris*, also presented lower fecundity ($F_{mean} = 0.4$ oocytes/mg and $F_{mean} = 0.6$ oocytes/mg, respectively) in relation to *O. paraguayensis*. Thus, the greater fecundity of *O. paraguayensis* in relation to *O.*

pequira in the same area suggests that the former species requires greater reproductive investment to maintain its population, even under the same extrinsic environmental conditions.

Fecundity may also vary with the female size, increasing with weight, and this is more related to length than to the individual age (Vazzoler 1996). This was partially evidenced for *O. paraguayensis*. According to our results, heavier females are more fecund, but the relationship between standard length of females and their total and relative fecundity was not verified in the present study.

In summary, *O. paraguayensis* presented multiples reproductive events throughout the year, essentially because reproducing females were recorded for almost all months and with high fecundity, compared to other Cheirodontinae and small-sized species in the same study area. Because of its occurrence in a floodplain that seasonally undergoes to physical and chemical changes in water (Junk *et al.* 1989, Resende 2008), as well as resource supplies, the strategy adopted for this species may be considered opportunistic, essentially as a mean of adjusting to an environment prone to seasonal flooding. Males and females display the same negative allometric growth; however, females reached their length earlier at first maturity, suggesting intraspecific variation in growth parameters that remain to be tested in order to better understand the life history traits of small-sized species in floodplains. Therefore, our results demonstrate that this species has a short life cycle, with high growth and mortality rates and because of that the adopted reproductive strategy of high fecundity and long recruitment period, in order to maintain the survival of the population, it may be considered an *r*-strategist species.

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