LIFE HISTORY TRAITS OF *ODONTOSTILBE PEQUIRA* (STEINDACHNER, 1882) IN THE PANTANAL OF PORTO MURTINHO, MATO GROSSO DO SUL STATE, BRAZIL

Karina Keyla Tondato[1]*, Clarice Bernhardt Fialho[1] & Yzel Rondon Súarez[2]

[1] Universidade Federal do Rio Grande Sul (UFRGS), Instituto de Biologia, Departamento de Zoologia, Programa de Pós-graduação em Biologia Animal, Av. Bento Gonçalves, 9500, Porto Alegre, Rio Grande do Sul, RS, Brasil. CEP: 91501-970.

[2] Universidade Estadual de Mato Grosso do Sul (UEMS), Centro Integrado de Análise e Monitoramento Ambiental, Laboratório de Ecologia, Rod. Dourados-Itahum, km 12, Dourados, Mato Grosso do Sul, MS, Brasil. CEP: 79804-970.

E-mails: ktondato@hotmail.com, cbfialho@pro.via-rs.com.br, yzel@uems.br

ABSTRACT

This study aimed to analyze the life history traits of females and males of *Odontostilbe pequira*, and correlate the recruitment of both sexes with the variation in the flood pulse of Paraguay River. The samplings were performed every month between February 2009 to January 2011, along the main channel of Paraguay River and its tributary (Amonguijá River) and the marginal lakes Criminosa and Flores. Length data were taken from 977 individuals of *Odontostilbe pequira* (564 females and 413 males). The equation that describes the relationship weight/length for females is Total weight=0.0000183*Standard length$^{2.95}$, and for males, Total weight=0.0000105*Standard length$^{3.10}$, with isometric growth for females and positive allometric for males. The asymptotic length (L∞) estimated for females was greater (39.59mm) than for males (37.57mm). Females also had higher growth rate (k=0.93 year^{-1}, Rn=0.35) and natural mortality rate (Z=1.56 year^{-1}) than males (k=0.82 year^{-1}, Rn= 0.27, Z= 1.45 year^{-1}). Through the growth curves, generated by the distribution of length classes, it was registered 3 complete cohorts for females, with longevity estimated at 3.22 years, and 4 cohorts for males with longevity of 3.65 years. The growth performance index values (φ) were close to 3 and similar between females (φ= 3.16) and males (φ= 3.06). The recruitment pattern was long for females and males of *O. pequira*, without significant variation in the recruitment distribution (p=0.77) between sexes. The recruitment peak occurred in July and June, for females and males, respectively. There was correlation between the recruitment and the water level of the river for both sexes (females: r=0.91, p<0.001, males: r=0.67, p=0.02).
Keywords: intraspecific variation; population biology; cheirodontinae; growth rate; recruitment.

RESUMO

TRAÇOS DE HISTÓRIA DE VIDA DE *ODONTOSTILBE PEQUIRA* (STEINDACHNER, 1882) NO PANTANAL DE PORTO MURTINHO, MATO GROSSO DO SUL, BRASIL. O presente trabalho tem como objetivo analisar os traços de história de vida de fêmeas e machos de *Odontostilbe pequira*, bem como, correlacionar o recrutamento de ambos os sexos com a variação no pulso de inundação do rio Paraguai. As coletas foram realizadas mensalmente entre Fevereiro/2009 e Janeiro/2011, ao longo da calha do rio Paraguai e seu afluente (Rio Amonguijá) e nas lagoas marginais Criminosa e Flores. Foram obtidos dados de comprimento de 977 indivíduos de *Odontostilbe pequira* (564 fêmeas e 413 machos). A equação que descreve a relação peso/comprimento para fêmeas é Peso total=0,0000183*Comprimento padrão^{2,95} e para machos Peso total=0,0000105*Comprimento padrão^{3,10}, com crescimento isométrico para as fêmeas e alométrico positivo para os machos. O comprimento assintótico (L∞) estimado para fêmeas foi maior (39,59mm) que o estimado para os machos (37,57mm). As fêmeas também apresentaram maior taxa de crescimento (k=0,93 ano^{-1}; Rn=0,35) e mortalidade natural (Z=1,56 ano^{-1}) em relação aos machos (k=0,82 ano^{-1}; Rn= 0,27; Z= 1,45 ano^{-1}). Através das curvas de crescimento, geradas pela distribuição por classes de comprimento, foram registrados 3 coortes completas para as fêmeas, com longevidade estimada em 3,22anos, e, 4 coortes para os machos, com longevidade de 3,65anos. Os valores de índice de performance de crescimento (φ) foram

próximos de 3 e semelhantes entre fêmeas (φ= 3,16) e machos (φ= 3,06). O padrão de recrutamento foi longo para fêmeas e machos de *O.pequira*, não sendo observada variação significativa na forma da distribuição do recrutamento (p=0,77) entre os sexos. O pico de recrutamento ocorre em Julho e Junho, para fêmeas e machos, respectivamente. Constatamos correlação entre o recrutamento e o nível do rio para ambos os sexos (fêmeas: r=0,91; p<0,001; machos: r=0,67; p=0,020).

Palavras-chave: variação intraespecífica; biologia populacional; cheirodontinae; taxa de crescimento; recrutamento; diferença sexual.

RESUMEN

ESTRATEGIAS DE VIDA DE *ODONTOSTILBE PEQUIRA* (STEINDACHNER, 1882) EN EL PANTANAL DE PORTO MURTINHO, ESTADO DE MATO GROSSO DEL SUR, BRASIL. El presente estudio tiene como objetivo analizar las estrategias de vida de hembras y machos de *odontostilbe pequira* y la correlación entre el reclutamiento de ambos sexos y la variación en el pulso de inundaciones del Río Paraguay. El muestreo fue llevado a cabo mensualmente entre Febrero de 2009 y Enero de 2011 a lo largo del canal principal del Río Paraguay y su afluente (Río Amonguijá) y los lagos marginales Crimosa y Flores. La información de la longitud fue obtenida de 977 individuos de *odontostilbe pequira* (564 hembras y 413 machos). La ecuación que describe la relación peso/longitud para las hembras es Peso total=0,0000183*Longitud estándar^{2,95}, y para los machos es Peso total=0,0000105*Longitud estándar^{3,10}, con un crecimiento isométrico para las hembras y alométrico positivo para los machos. La longitud asintótica (L∞) estimada para las hembras fue mayor (39,59mm) que la estimada para los machos (37,57mm). Las hembras también presentaron una mayor tasa de crecimiento (k= 0,93 año^{-1}, Rn= 0,35) y de mortalidad natural (Z= 1,56 año^{-1}) respecto a los machos (k= 0,82 año^{-1}, Rn= 0,27, Z= 1,45 año^{-1}). A través de las curvas de crecimiento, generadas por la distribución de clases de longitud, se registraron 3 cohortes completas para las hembras, con una longevidad estimada en 3,22 años, y 4 cohortes para los machos con una longevidad de 3,65 años. Los valores del índice de performance de crecimiento (φ) fueron cercanos a 3 y similares entre hembras (φ= 3,16) y machos (φ= 3,06). El patrón de reclutamiento fue largo para hembras y machos de *O. pequira*, sin registrarse una variación significativa entre sexos (p= 0,77). El pico de reclutamiento ocurrió entre Julio y Junio, para hembras y machos respectivamente. Se registró una correlación entre el reclutamiento y el nivel de agua del río para ambos sexos (hembras: r= 0,91, p< 0,001, machos: r= 0,67, p= 0,02).

Palabras clave: variación intraespecífica; biología poblacional; cheirodontinae; tasa de crecimiento; reclutamiento; variación sexual.

INTRODUCTION

Understanding the variations in life history traits is a key issue in the different ecology areas (Roff 2001, Stearns 1992), being used to describe reproductive strategies, 'trade-offs', and basic parameters of population dynamics (Winemiller 1989, Winemiller & Rose 1992). High plasticity and/or variation inter- and intraspecific in life history traits is widely reported for fish, with significant differences in reproductive aspects, variation in asymptotic length, in the growth rate and in longevity of populations in response to environmental variations (Stearns 1989, Wotton 1998, Rochet 2000, Mazzoni & Iglesias-Rios 2002, Blanck & Lamouroux 2007).

Although most studies have focused on variations between populations at species level (Winemiller & Rose 1992, King & McFarlane 2003, Mérona *et al.* 2009), the life history traits may vary between individuals (Hartz *et al.* 1998, Becker *et al.* 2003) and between other levels, according to the degree of analysis comparison. However, few studies on fish fauna have examined the trait variability at different levels, as for example, between orders and between latitudes (Rochet 2000, Blanck & Lamouroux 2007). Despite these detailed studies, analyses of trait variability between sexes are scarce (Barbieri *et al.* 2001, Martin-Smith & Armstrong 2002, Feitosa *et al.* 2004, Gomiero *et al.* 2007), and this difference is evidenced only in ecological theories (Vazzoler

1996, Wotton 1998, Lowe-McConnell 1999) and speculated in several studies on populations that sought to understand the trend and particularity of their results (Braga 2006, Abilhoa 2007), as observed for *Odontostilbe pequira* (Steindachner, 1882) in Southern Pantanal (Tondato *et al. in press*). The significant variation in life history traits, like in the growth rates between sexes, may be a result from trade-offs among reproductive investment, growth and mortality (Stearns 1992, Hutchings & Jones 1998). Thus, by understanding the variation in life history aspects within a species provides knowledge on how natural selection works in natural populations (Roff 2002) and through the analysis between sexes, can show how sexes get adapted to conditions imposed, according to their portion, in the maximization of reproductive success, survival and population balance.

The species *Odontostilbe pequira* belongs to the subfamily Cheirodontinae, and has little sexual dimorphism. This subfamily is composed of small freshwater fish that reach a maximum of 40 mm standard length, mainly found in lentic environments and floodplains, and inhabits the majority of catchment areas of Central and South Americas (Malabarba 1998). Although having no relevance to fisheries, it has great importance for the food chain of fish fauna, besides economic potential (ornamental), as suggested by Pelicice & Agostinho (2005) for species of the same subfamily. In Brazil, studies on Cheirodontinae species examined the reproductive biology (Gelain *et al.* 1999, Oliveira *et al.* 2002, Gomiero & Braga 2007, Azevedo *et al.* 2010), diet aspects (Casatti *et al.* 2003, Pelicice & Agostinho 2006, Dias & Fialho 2009) and population biology (Lizama & Ambrósio 1999, Piana *et al.* 2006, Lourenço *et al.* 2008, Benitez & Súarez 2009). Nevertheless, only two studies were undertaken with *O. pequira*, investigating its reproductive aspects in Southern Brazil (Rio Grande do Sul State, Ibicuí-Mirim River) (Oliveira *et al.* 2010) and Southern Pantanal (Mato Grosso do Sul State, Paraguay River) (Tondato *et al. in press*), with no information about its population dynamic. In this way, the analysis on the dynamics of *O. pequira*, considered an opportunistic species (r-strategist) (Tondato *et al.in press*), aimed to provide effective information about the life history traits of females and males (weight/length relationship, asymptotic length, growth rate, mortality

and longevity), enabling the comparison between sexes and among phylogenetically related species, in addition the understanding of the influence of the flood (river level) on the recruitment of both sexes.

MATERIAL AND METHODS

The Pantanal is a sedimentary floodplain with an area of about 140,000 km^2, part of the Upper Paraguay River basin (Adámoli 1982). The rainfall ranges from 800 to 1,400 mm/year, with 80% between November and March (Fantin-Cruz *et al.* 2011). Also, the flood regime is unimodal, of essential importance for all system functions (Junk *et al.* 1989), since the high evapotranspiration prevents a significant contribution of the local rainfall to river level variations (Hamilton *et al.* 1996).

The study region is within the Pantanal of Porto Murtinho, located in southernmost region of Pantanal (Figure 1), municipality of Porto Murtinho, Mato Grosso do Sul State, Brazil. Given its geographical position and low slope of 1cm/km in the North-South direction (Hamilton *et al.* 1996), the Pantanal of Porto Murtinho is characterized by the asynchrony between the period with the highest rainfall and temperature (November to March) and the flood period (June to August). The flood begins in the North of the floodplain (Cáceres, Mato Grosso State) along with the rainy period, slowly flows southward, resulting in lags from 3 to 6 months between the peak rainfall in the springs and the maximum flood in the Southern part, usually in June, out of the rainy period (Hamilton *et al.* 1996, Gonçalves *et al.* 2011). Once the Paraguay River has a meandering course in the study region, it also has marginal lakes formed by abandoned meanders (Figure 1), which are directly connected to the river and strongly influenced by its seasonality.

Monthly samplings were conducted between February 2009 and January 2011, under macrophyte stands along the main channel of the Paraguay River and in one of its tributary, the Amonguijá River, and in the marginal lakes Criminosa and Flores (Figure 1). Fish were collected using drag nets and sieve nets (80x120cm) with 2 mm mesh size, fixed in 10% formaldehyde and preserved in 70% ethanol for identification, count, and obtaining biometric and biological data. In laboratory, the identification

was made using specialized literature (Britski *et al.* 2007) and voucher specimens were cataloged (11167) in the fish collection of the Department of Zoology, Federal University of Rio Grande do Sul, Porto Alegre, Brazil. After the identification, a casual subsample was selected with at least 30 individuals per month, to get the following data: sex, total weight (g), and standard length (mm). For the analyses, the data of months repeated on the two consecutive years were summed up, because we assumed that the analyzed parameters have no significant interannual variation.
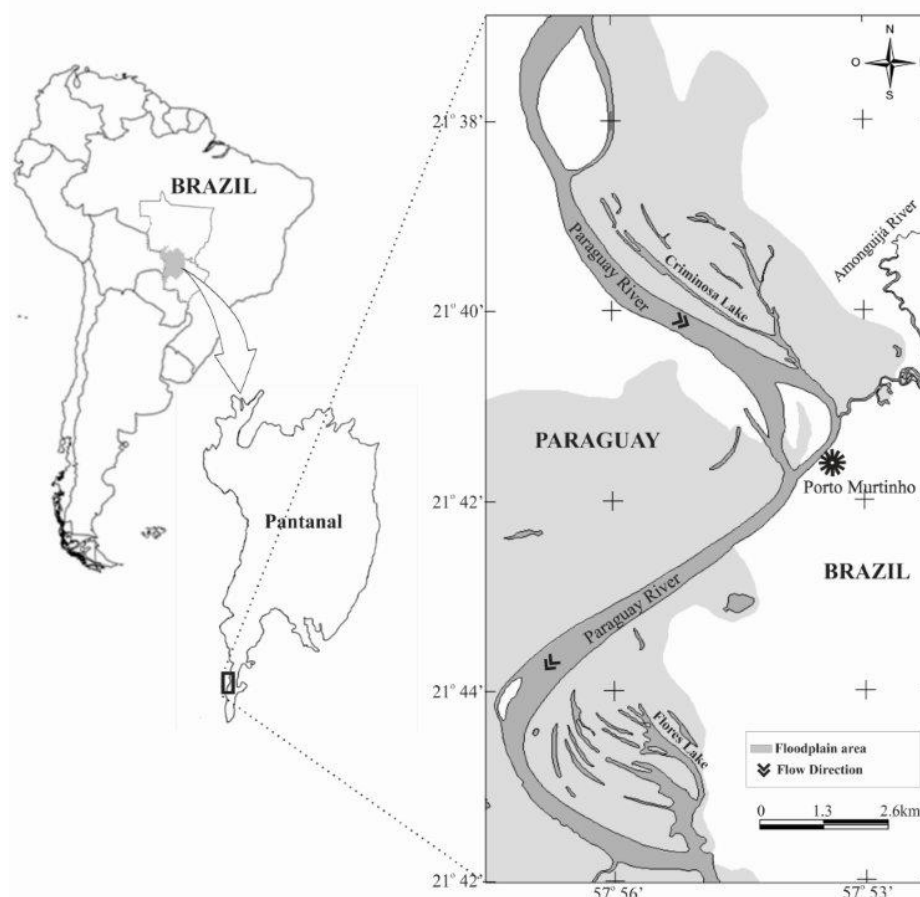

Figure 1. Location of the sampling area along the Paraguay River, near to the city of Porto Murtinho (Brazil), extreme southern Pantanal (Pantanal de Porto Murtinho), during the study period.
Figure 1. Localização da área de amostragem ao longo do Rio Paraguai, próximo à cidade de Porto Murtinho (Brasil), extremo sul do Pantanal (Pantanal de Porto Murtinho), durante o período de estudo.

The relationship between weight and length was obtained for each sex through a non-linear regression analysis, where the data of weight and length were directly adjusted by the power function: Total weight = a*standard length^b, where: a = constant, and b= allometric coefficient of growth. The parameters *a* and *b* were estimated by a non-linear regression for each sex. The type of growth was determined by analyzing the confidence interval of the growth coefficient (b): (1) if b=3, the growth is isometric, (2) if b>3, the growth is positive allometric, (3) if b<3, the growth is negative allometric (Orsi *et al.* 2002). Then, the difference in the growth type between females and males was estimated through overlapping the respective confidence intervals of the coefficient 'b'. In this way, given no overlap in the confidence intervals between the sexes, these are considered statistically different. The asymptotic standard length for each sex was estimated from the largest individual caught, using the equation of Pauly (1983): $L\infty = L_{max} / 0.95$.

In order to analyze the growth rate, initially for each sex we built a bimonthly frequency distribution of individuals into length classes with interval of 3

mm. The growth curve with the respective growth rate (k) was obtained using the method ELEFAN I (Eletronic Lengths-Frequency Analysis) (Pauly & David, 1981), through the growth model of Von Bertalanffy: $L(t) = L\infty (1 - exp[-k(t-t0)])$, wherein: $L\infty$=asymptotic length, k=growth rate (year^{-1}), t0= nominal age at which the length is zero, t=age (months/ year) (Bertalanffy, 1938, Gulland 1977). The ELEFAN I method is inserted in the FISAT software (FAO-ICLARM Stock Assessment Tools) (Gayanilo & Pauly 1997), which seeks the best combinations in estimating the parameters, based on the best fit, i.e., best values of Rn (goodness of fit index). This method uses an alternative technique suggested as a good option to determinate the growth parameters, based on the temporal distribution (displacement) of the modes of the growth frequency (Gomiero *et al.* 2007).

The total mortality (Z) defined here as equal to natural mortality (M) was achieved according to the empirical formula of Pauly (1980), using the information of growth parameters (L∞ and k) and the mean temperature (°C) of the environment where the species was collected, following the equation: $\ln M = -0.0152 - 0.279\ln L\infty + 0.6543\ln k + 0.463\ln T°C$. The longevity for each sex was calculated by the value estimated according to the equation proposed by Taylor (1958): $t\max = t_0 + 2.996/k$, with t_0=0, and, by observing the number of cohorts (1 cohort = 1 year) previously generated by the Von Bertalanffy model. The FISAT also provided the growth performance index (φ) for each sex using the equation proposed by Pauly & Munro (1984): $\phi = \log k + 2\log L\infty$. The growth performance index allows us to know about the possibility to compare estimate parameters with parameters of other species or phylogenetically related groups, and should present values close to 3 and similar between sexes or related species as an indicative that the population parameters were properly estimated.

The recruitment pattern for each sex was obtained through the monthly frequency distribution of the standard length and of growth parameters (L∞ and k) previously estimated, using the routine included in the FISAT(Gayanilo & Pauly 1997). The analysis of the recruitment pattern for each sex was carried out through visual inspection throughout the year. Moreover, the Kolmogorov-Smirnov test was used to compare the distribution of recruitment between the sexes.

To check a possible relationship between the recruitment of each sex and variation in the historical river level (provided by the Agência Nacional das Águas-ANA), we used a Spearman correlation, once the assumption of data normality was not reached.

RESULTS

Length data from 977 individuals of *Odontostilbe pequira,* 564 females and 413 males, ranged from 13.7mm to 37.61mm. For females, it was possible to predict with accuracy of 94.8% the weight of individuals, with the model Total weight=0.0000183*Standard length$^{2.95}$, with confidence interval estimated for the coefficient (b) varying between 2.89 and 3.01 (α=0.05). For males, it was possible to predict with accuracy of 93.1% the weight of individuals, and the model generated was Total weight=0.0000105*Standard length$^{3.10}$, with confidence interval estimated for the coefficient (b) varying between 3.03 and 3.18 (α=0.05) (Figure 2).
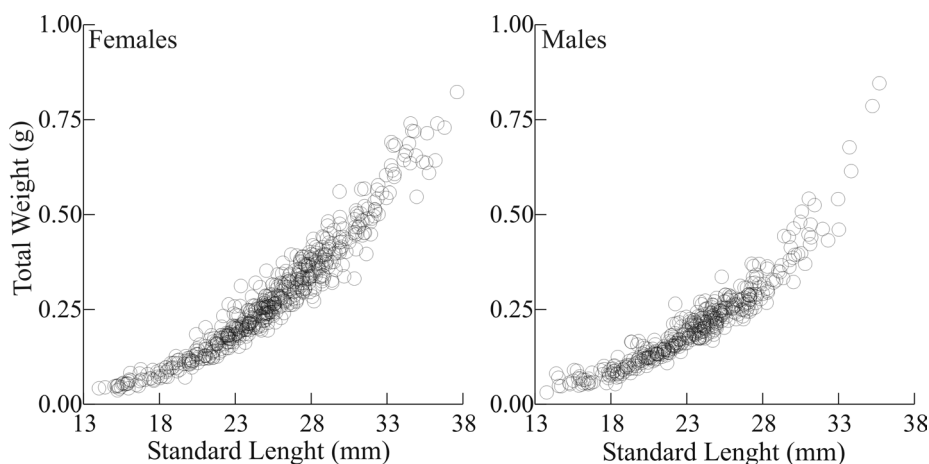

Figure 2. Weight/length relationship for females and males of *O. pequira* in Paraguay River during the study period.
Figura 2. *Relação peso/comprimento para fêmeas e machos de* O. pequira *no Rio Paraguai durante o período de estudo.*

There was no overlap between confidence intervals of the allometry coefficient (b) fitted by the non-linear regression between the sexes, indicating a significant difference in the growth type between females and males. For females, the growth can be considered isometric, where the speed of increase in weight is equal to length, once the confidence interval of 'b' (2.89-3.01) was not statistically different from 3. On the other hand, for males, the growth type can be considered positive allometric, where the speed of increase in weight is higher than in length, since the confidence interval of 'b' (3.03-3.189) was statistically higher than 3 (Figure 2).

The asymptotic length (L∞) for females of *O. pequira* was estimated at 39.59mm (lmax=37.61mm), while for males it was lower, estimated at 37.57mm (lmax=35.69mm). Females presented higher growth rate (k=0.93 year^{-1}, Rn=0.35) and natural mortality (Z=1.56 year^{-1}) than males (k=0.82 year^{-1}, Rn= 0.27, Z= 1.45 year^{-1}). The fit of the Von Bertalanffy growth curve for the estimated ages in months for each sex indicated that females and males spend around 12 months to reach the first maturity length (L$_{50}$) (females=24.2mm, males=22.2mm, Tondato *et al. in press*) (Figure 3). Also, through the growth curves, generated by distributing the length classes along the year, it was registered 3 complete cohorts for females, and 4, for males (Figure 4). Furthermore, for females

it was estimated longevity of 3.22 years, while for males, the longevity estimated was 3.65 years. The values of the growth performance index (φ) were close to 3 and similar between females (φ= 3.16) and males (φ= 3.06), pointing out that the estimated parameters differ little from each other, and can be comparatively analyzed.
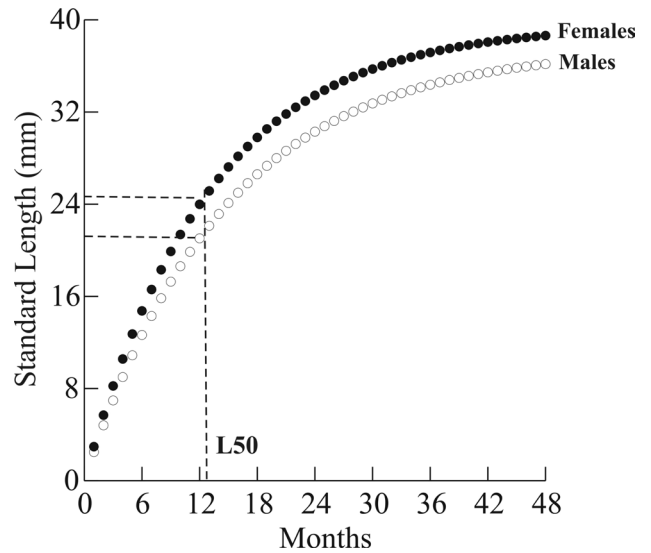

Figure 3. Von Bertalanffy growth curve fitted for the estimated ages in months of females and males of *O. pequira*, in Paraguay River. L$_{50}$ = first maturity length.
Figura 3. Curva de crescimento de Von Bertalanffy ajustada para as idades estimadas em meses de fêmeas e machos de O. pequira, *no Rio Paraguai. L$_{50}$ = comprimento de primeira maturação.*
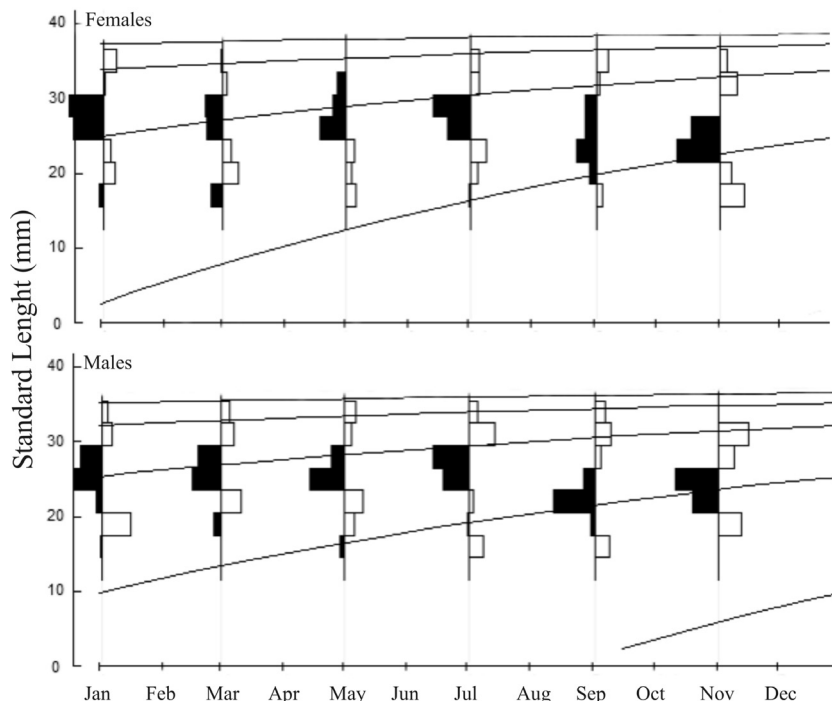

Figure 4. Growth curves of the cohorts of females and males of *O. pequira*, in Paraguay River between February 2009 and January 2011.
Figura 4. Curvas de crescimento dos cortes de fêmeas e machos de O.pequira, *no Rio Paraguai entre Fevereiro/2009 e Janeiro/2011.*

The recruitment pattern of females and males of *O. pequira* was similar, without significant variation in the recruitment distribution (p=0.77) between the sexes over the year. Through graph analysis, it was verified that in both sexes the recruitment is long, although the period with the highest intensity is between March and September (Figure 5). For females, the maximum recruitment takes place between May and July, and for males, between May and August. Importantly, the highest recruitment for females occurs in July, whereas for males, in June (Figure 5).

A correlation was detected between the recruitment of both sexes and the historical river level (Females r=0.91, p<0.001 and Males r=0.67, p=0.020), suggesting that the entry of juveniles in the population is strongly associated with the river level, with the most intense pulse of recruitment of both sexes occurring with the highest river levels (Figure 5).
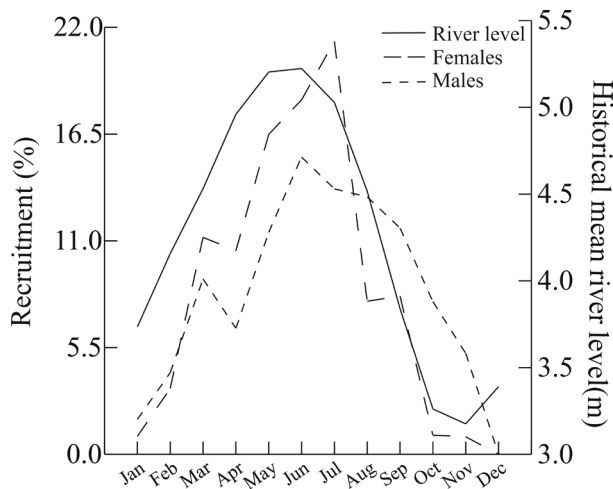

Figure 5. Temporal variation of the recruitment (%) of females and males of *O. pequira* from February 2009 to January 2011 and of the historical level of Paraguay River.

Figura 5. Variação temporal do recrutamento (%) de fêmeas e machos de O.pequira *entre Fevereiro/ 2009 e Janeiro/2011 e do nível histórico do Rio Paraguai .*

DISCUSSION

The significant variation in the growth type between the sexes of *O. pequira* indicates that females and males develop differently, characterizing an intraspecific phenotypic plasticity in response to adaptive variations of each sex to environmental conditions. A similar pattern is commonly found in

fish population (Campos *et al.* 1993, Mazzoni & Silva 2006), being evidenced that differences between sexes in the values of 'b' can mean mere presence of a greater weight gain by one sex or sexual dimorphism (Menezes & Caramaschi, 1994). In addition, the isometric growth in females of *O. pequira* suggests that the energy gained is directed to a balanced investment in growth and weight, given the no-need to reserve energy due to the high availability of food resources and favorable temperature practically continuous in the study area. However, even under lower food supply, the amount of stored energy, proportional to the weight, increasing to a factor 3 with the body size, enables a greater resistance to food shortage periods (Metcalfe & Monaghan 2003). According to Lizama & Ambrósio (1999), species of the family Characidae tend to present an isometric growth, maintaining the shape throughout the life cycle. On the other hand, the positive allometric growth in males of *O. pequira* seems the most plausible in Cheirodontinae, since in Brazilian rivers and streams of the Upper Paraná River it was observed the same type of growth for *Serrapinnus notomelas* (Lizama & Ambrósio 1999, Lourenço *et al.* 2008, Benitez & Súarez 2009), supporting similarities related to phylogenetic proximity in different environments.

There is an inverse relationship between the allometry coefficient and the intercept of the adjusted line, the intercept being the condition factor, i.e., the parameter 'a' (Braga 1997). In females and males of *O. pequira*, the values of 'a' were similar (0.000018, 0.000015, respectively) to those found by Lourenço *et al.* (2008) and Benitez & Súarez (2009) for *S. notomelas* in streams of the Upper Paraná River basin (0.0000191, 0.0000007, respectively). Although the parameter 'a' can vary in fish of the same species or between species, according to location, average length of the population, and age (Gurgel 2004), the results did not indicate interspecific variability of the parameter 'a' between *S. notomelas* and *O. pequira* evidencing the strong expression of phylogenetic proximity which characterizes similarities in life history traits.

Differences in the parameters of growth and mortality can lead to different characteristics and strategies in life history of fish species (Nikolskii 1969, Heibo & Vøllestad 2002), with spatial variations according to environmental conditions,

such as food availability, temperature, and population density (Lowe-McConnell 1999). Spatial variation in population parameters has been reported with different growth patterns exhibited by the same species in different environments (Wootton 1998, Benitez & Súarez 2009). For *O. pequira*, in Southern Pantanal, it was observed high values of growth and mortality rates, with values higher than recorded for the Cheirodontinae *S. notomelas* in streams of the Upper Paraná River basin, as well as a shorter longevity (Lourenço *et al.* 2008). This pattern was expected, since higher growth rates are common in species inhabiting floodplains, which can be related to the intense predation suffered from the moment of hatching (Lowe-McConnell 1999). Therefore, the faster they reach the theoretical maximum length the higher the chances for survival, once the smaller individuals are more vulnerable to predation (Reznick *et al.* 1996). Additionally, the high natural mortality of *O. pequira*, common in tropical fishes (Pauly 1980), is also offset by the high growth rate, consequent early maturity (around 12 months) and long reproductive period (Tondato *et al. submitted*), which corroborate adaptive advantages (Smith & Armstrong 2002) common to opportunistic species (r-strategist) (Winemiller 1989).

Once the growth rate of a population is directly influenced by offsets between fecundity, survival, and the mean generation time (Winemiller & Dailey, 2002), it is suggested that these parameters may work differently between the sexes (Braga *et al.* 2006). So the higher rates of growth and mortality observed in females explain their smaller length of first maturity, in relation to males, and the lack and/or lower proportion of females in the first length classes in this population (Tondato *et al. submitted*), considering that the fast growth decreases the probability of capture in the smaller size classes and anticipate the sexual maturity. The higher growth rate in females was also observed in other studies (Barbieri *et al.* 1986, 2001), and may be a result of trade-offs between costs (e.g. increased predation pressure) and benefits (increased rate of food acquisition) (Smith & Armstrong 2002). Thus, the highest growth rate in females of *O. pequira* was associated with fitness and survival, in order to minimize the effects of the high mortality, rapidly reaching larger lengths and maximizing the reach of sexual maturity in a shorter time period, as suggested by Blanck & Lamouroux (2007).

The growth rate presented by a species is usually opposite to the value of asymptotic length and longevity, regarding that, the higher the growth rate, the smaller is the asymptotic length and shorter longevity (Lizama & Vazzoler 1993, King 2007). Nevertheless, as observed above, females of *O. pequira* had higher growth rate, shorter longevity, highlighting the larger asymptotic length in relation to the males, without opposite relationship between k and L∞. Feitosa *et al.* (2004) and Gomiero *et al.* (2007) studying growth rates of *Salminus brasiliensis* and *Brycon opalinus*, respectively, also registered the highest growth rate and larger asymptotic length for females, but the k values were slightly higher (e.g.: female=0.56 and males=0.54, Gomiero *et al.* 2007). In this way, the highest k and L∞ in females of *O. pequira* can be explained by two hypotheses: 1) the difference in the growth rate between the sexes, with the higher value for females was not enough to reduce the asymptotic length of the females in relation to males, 2) the females maximize the reproductive investment, exceeding not only the males length, but also the maximum length, since in females of this species, the length is positively related to fecundity (Tondato *et al. submitted*). Furthermore, the highest growth rate observed for females of *O. pequira* leads to its shorter longevity in relation to males, despite males have shorter L∞ in a longer life period, suggesting that males have a lower investment in length, and direct the energy gained to participate in another reproductive year of the life cycle.

On the other hand, the energy expenditure of females on the reproduction and lower growth rate, lead to an earlier senescence than males, decreasing the longevity and justifying the high mortality. This may occur because according to Fonteles-Filho (1989) the major natural factors for mortality are predation and diseases, which have action contrary according to the age, i.e., larger and older individuals are less predated, but are more susceptible to diseases, due to tissue degeneration and lower use of nutritive elements.

Despite the variations in population parameters between the sexes of *O. pequira*, the distribution way of entry of females and males in the population was not different suggesting that this recruitment pattern is similar between the sexes throughout the year. This result justifies the similar length

distribution between the sexes of *O. pequira* and its balanced sex ratio over time in the study of Tondato *et al.* (*in press),* because females and males recruit proportionally along the year. The long recruitment in females and males of *O. pequira*, with the maximum in July for females, and June, for males, also corroborated Tondato *et al.* (*in press*) for the same species, which evidenced a long reproductive period, with the highest reproductive intensity in July. Meanwhile, Oliveira *et al.* (2010) investigating the reproductive period of the same species in Southern Brazil (subtropical region) found two reproductive stages, one from September to October, and another from January to February, being evidenced spatial intraspecific variation in the recruitment of *O. pequira,* once the recruitment and reproduction are distinctly influenced by environmental conditions (Olden *et al.* 2006).

Although the pattern of long recruitment is typical of small sized species living in tropical freshwater environments (Lizama & Ambrosio 2003, Lourenço *et al.* 2008), for *O. pequira*, this pattern may indicate an adaptive variation in life history facing the uniqueness of the environment, since a long reproductive period does not correspond to the reproductive strategy for seasonal environments (Munro 1990, Vazzoler & Menezes 1992), which promotes the occurrence of species with short reproductive period associated with favorable conditions of the flood (Tedesco *et al.* 2008). However, in Southern Pantanal, the flood period does not match with rising temperature and high rainfall, suggesting that the long recruitment of *O. pequira* is related to a higher reproductive investment as an adaptive response, since according to King *et al.* (2003), for a better recruitment, fish should reproduce when the water level and temperature synchronously rise.

Also, the significant relationship between the recruitment of both sexes of *O. pequira* and the historical river level, with rise and more intense pulse in the recruitment with the increase (flood) and peak of the river level, indicates that the flood regime has a key role on the reproductive activity, as suggested by Tondato *et al.* (*in press*) for the same species in the study region, and by Bailly *et al.* (2008) for most fish species with varied reproductive strategies in the Upper Pantanal. This recruitment pattern seeks to maximize the reproductive success, given the low fecundity of the species, offset by multiple spawning and long reproductive period (Tondato *et al. in press)*, which is associated with the long flood in the Southern Pantanal (up to six months) (Gonçalves *et al.* 2011). This association is due to the expansion of the flooded area in the plain, during the flood, which promotes access to new habitats, providing greater availability of food and shelter for the development and growth of larvae and juvenile (Junk *et al.* 1989, Lowe-McConnell 1999, Agostinho *et al.* 2004, Bailly *et al.* 2008, Tondato *et al.* 2010).

Finally, the tactics comprising a strategy may differ between environments so that each species or population ensures that new individuals are recruited (Wootton 1998), indicating that the high growth rate and shorter longevity of *O. pequira*, compensate the high mortality, through an early sexual maturity and long recruitment period. It is emphasized that the analysis of life history traits between sexes are indispensable to understand the variations in the intraspecific reproductive behavior, since in *O. pequira*, the variation between the sexes provided is essential to understand its population dynamics.

REFERENCES

ABILHOA, V. 2007. Aspectos da história natural de *Astyanax scabripinnis* (Teleostei, Characidae) em um riacho de floresta com araucária no sul do Brasil. *Revista Brasileira de Zoologia*, 24: 997-1005.

ADÁMOLI, J. 1982. O Pantanal e suas relações fitogeográficas com os cerrados. Pp. 109-119. Discussão sobre o conceito de "Complexo do Pantanal". *In*: Congresso Nacional de Botânica, 32. Anais, UFPI, Piauí, Brasil.

AGOSTINHO, A.A.; GOMES, L.C.; VERÍSSIMO, S. & OKADA, E.K. 2004. Flood regime, dam regulation and fish in the Upper Parana River: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries*, 14: 11-19.

AZEVEDO, M.A.; MALABARBA, L.R. & BURNS, J.R. 2010. Reproductive biology and development of gill glands in the inseminating characidae, Macropsobrycon uruguayanae Eigenmann, *1915 (Cheirodontinae: Compsurini). Neotropical Ichthyology,* 8: 87-96, http://dx.doi.org/10.1590/S1679-62252010005000004

BAILLY, D.; AGOSTINHO, A.A. & SUZUKI, H.I. 2008. Influence of the flood regime on the reproduction of fish species with different reproductive strategies in the Cuiabá River, Upper Pantanal, Brazil. *River Research and Applications*, 24: 1218-1229, http://dx.doi.org/10.1002/rra.1147

BARBIERI, G.; BARBIERI, M.C.; MARINS, M.A.; VERANI, J.R.; PERET, A.C. & PEREIRA, J.A. 1986. Crecimiento de *Tilapia rendalli* (Boulenger, 1896) en el embalse del Monjolinho, São Carlos, Estado de São Paulo, Brasil. *Revista Latinoamericano de Acuicultura*, 27:18-28.

BARBIERI, G.; SALLES, F.A. & CESTAROLLI, M.A. 2001. Growth and first sexual maturation size of *Salminus maxillosus* Valenciennes, 1849 (Characiformes, Characidae), in Mogi Guaçu river, state of São Paulo, Brazil. *Acta Scientiarum, Biological Science,* 23:453-459.

BECKER, F.G.; BRUSCHI JR., W. & PERET, A.C. 2003. Age and growth of three Odontesthes species from southern Brazil (Atherinopsidae), with reference to phylogenetic constraints in their life-history. *Brazilian Journal of Biology*, 63: 567-578. http://dx.doi.org/10.1590/S1519-69842003000400004

BENITEZ, R.S. & SÚAREZ, Y.R. 2009. Biologia populacional de *Serrapinnus notomelas* (Eingenmann, 1915) (Characiformes, Cheirodontinae ae) em um riacho de primeira ordem na bacia do rio Dourados, Alto rio Paraná. *Pan-American Journal of Aquatic Sciences*, 4: 271-278.

BERTALANFFY, L.V. 1938. A quantitative theory of organic growth. *Human Biology*, 10: 181-213.

BLANCK, A. & LAMOUROUX, N. 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. *Journal of Biogeography*, 34:862–875, http://dx.doi.org/10.1111/j.1365-2699.2006.01654.x

BRAGA, F.M.S. 1997. Análise da equação alométrica na relação peso e comprimento e o fator de condição em *Plagioscion squamosissimus* (Teleostei, Sciaenidae). *Revista Brasileira de Biologia*, 57: 417-425.

BRAGA, F.M.S. 2006. Aspectos da reprodução no gênero *Characidium* Reinhardt, 1867 (Crenuchidae: Characidiinae), na microbacia do Ribeirão Grande, serra da Mantiqueira, sudeste do Brasil. *Acta Scientiarum, Biological Sciences*, 28: 365-371. http://dx.doi.org/10.4025/actascibiolsci.v30i4.301

BRAGA , M.R.; MENEZES, M.S. & ARANHA, J.M.R. 2006. Táticas reprodutivas de *Mimagoniates microlepis* (Steindachner, 1876) (Characidae, Glandulocaudinae) no rio Colônia Pereira, Paranaguá, Paraná. *Estudos de Biologia*, 28: 13-20.

BRITSKI, H.A.; SILIMON, K.Z. & LOPES, B.S. 2007. *Peixes do Pantanal*. Manual de identificação. 2ª Edição, Embrapa, Brasília, Brasil. 227p.

CAMPOS, E.C.; SANTOS, R.A.; CAMARA, J.J.C. & MANDELLI JR. J. 1993. Pesca seletiva da viuvinha, *Moenkhausia intermedia* Eigenmann, 1908 (Characiformes, Characidae), com a utilização de redes de emalhar, na represa de Ibitinga, Rio Tietê, Estado de São Paulo, Brasil. *Boletim do Instituto de Pesca*, 20: 21-33.

CASATTI, L.; MENDES, H.F. & FERREIRA, K.M. 2003. Aquatic macrophytes as feeding site for small fishes in the Rosana reservoir, Paranapanema river, southeastern Brazil. *Revista Brasileira de Biologia*, 63: 213-222.

DIAS, T.S. & FIALHO, C.B. 2009. Biologia alimentar de quatro espécies simpátricas de Cheirodontinae (Characiformes, Characidae) do rio Ceará Mirim, Rio Grande do Norte. *Iheringia, Série Zoologia*, 99: 242-248.

FANTIN-CRUZ, I.; PEDROLLO, O.; CASTRO, N.M.R. GIRARD, P.; ZEILHOFER, P. & HAMILTON, S.K. 2011. Historical reconstruction of floodplain inundation in the Pantanal (Brazil) using neural networks. *Journal of Hydrology*, 399: 376-384, http://dx.doi.org/10.1016/j.jhydrol.2011.01.014

FEITOSA, L.A.; FERNANDES, R.; COSTA, R.S.; GOMES, L.C. & AGOSTINHO, A.A. 2004. Parâmetros populacionais e simulação do rendimento por recruta de *Salminus brasiliensis* (Cuvier, 1816) do alto rio Paraná. *Acta Scientiarum, Biological Sciences*, 26: 317-323. http://dx.doi.org/10.4025/actascibiolsci.v26i3.1593

FONTELES-FILHO, A.A. 1989. *Recursos pesqueiros. Biologia e dinâmica populacional*. Imprensa Oficial do Ceará, Fortaleza, CE, Brasil.

GAYANILO JR., F.C. & PAULY, D. 1997. *The FAO-ICLARM Stock Assessment Tools (FISAT) Reference manual.* FAO Computerized Information Series (Fisheries), Roma. 262p.

GELAIN, D.; FIALHO, C.B. & MALABARBA, L.R. 1999. Biologia reprodutiva de *Serrapinnus calliurus* (Characidae, Cheirodontinae ae) do arroio Ribeiro, Barra do Ribeiro, Rio Grande do Sul, Brasil. *Comunicação do Museu de Ciências e Tecnologia*, 12: 71-82.

GOMIERO, L.M. & BRAGA, F.M.S. 2007. *Reproduction of a fish assemblage in the state of São Paulo, southeastern Brazil. Brazilian Journal of Biology,* 67: 283-292, http://dx.doi.org/10.1590/S1519-69842007000200013

GOMIERO, L.M.; CARMASSI, A.L. & BRAGA, F.M.S. 2007. Crescimento e mortalidade de *Brycon opalinus* (Characiformes, Characidae) no Parque Estadual da Serra do Mar, Mata Atlântica, Estado de São Paulo. *Biota Neotropica*, 7: 22-26.

GONÇALVES, H.C.; MERCANTE, M.A. & SANTOS, E.T. 2011. Hydrological cycle. *Brazilian Journal of Biology*, 71: 241-253.

GULLAND, J. A. 1977. *Fish populations dynamics.* John Willey & Sons, London. 372p.

GURGEL, H.C.B. 2004. Estrutura populacional e época de reprodução de *Astyanax fasciatus* (Cuvier) (Chacidae, Tetragonopterinae) do Rio Ceará Mirim, Poço Branco, Rio Grande do Norte, Brasil. *Revista Brasileira de Zoologia*, 21: 131-135.

HAMILTON, S.K.; SIPPEL, S.J. & MELACK, J.M. 1996. Inundation patterns in the Pantanal of South America determined from passive microwave remote sensing. *Archiv für Hydrobiologie*, 137: 1-23.

HARTZ, S.M.; JUNIOR, W.B. & FORMEHL, M.V. 1998. Idade e crescimento de *Gymnogeophagus lacustris* Reis & Malabarba, um Cichlldae endêmico da bacia hidrográfica do rio Tramandaí, Rio Grande do Sul, Brasil. *Revista Brasileira de Zoologia*, 15: 605-612.

HEIBO, E. & VØLLESTAD, L.A. 2002. Life-history variation in perch (Perca fluviatilis L.) in five neighbouring Norwegian lakes. *Ecology of Freshwater Fish*, 11: 270-280, http://dx.doi.org/10.1034/j.1600-0633.2002.00023.x

HUTCHINGS, J.A. & JONES, M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon *Salmo salar. Canadian Journal of Fisheries and Aquatic Sciences*, 55: 22-47, http://dx.doi.org/10.1034/j.1600-0633.2002.00023.x

JUNK, W.J. BAYLEY, P.B. & SPARKS, R.E. 1989. The flood pulse concept in river–floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 106: 110-127.

KING, J.R. & MCFARLANE, G.A. 2003. Marine life history strategies: applications to fishery management. *Fisheries Management and Ecology*, 10: 249-264.

KING, A.J.; HUMPHRIES, P. & LAKE, P.S. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 773-786, http://dx.doi.org/10.1139/F03-057

KING, M. 2007. *Fisheries biology, assessment and management.* Wiley Blackwell, Oxford. 400p.

LE CREN, E.D. 1951. The lenght-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology*, 20: 201-219.

LIZAMA, M.A.P. & VAZZOLER, A.E.A.M. 1993. Crescimento em peixes do Brasil: uma síntese comentada. *Revista Unimar*, 15: 141-173.

LIZAMA, M.A.P. & AMBRÓSIO, A.M. 1999. Relação peso-comprimento e estrutura da população de nove espécies da família Characidae na planície de inundação do alto rio Paraná, Brasil. *Revista Brasileira de Zoologia*, 16: 779-788.

LIZAMA, M.A.P. & AMBROSIO, A.M. 2003. Crescimento, recrutamento e mortalidade do pequi *Moenkhausia intermedia* (Osteichthyes, Characidae) na planície de inundação do alto rio Paraná, Brasil. *Acta Scientiarum, Biological Sciences*, 25: 328-333.

LOURENÇO, L.S.; SÚAREZ, Y.R. & FLORENTINO, A.C. 2008. Aspectos populacionais de *Serrapinnus notomelas* (Eigenmann, 1915) e *Bryconamericus stramineus* Eigenmann, 1908 (Characiformes: Characidae) em riachos da bacia do rio Ivinhema, Alto Rio Paraná. *Biota Neotropica*, 8: 1-7.

LOWE-MCCONNELL, R.H. 1999. *Estudos ecológicos de comunidades de peixes tropicais*. Edusp, São Paulo.

MALABARBA, L.R. 1998. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). Pp. 193-233. *In*: L.R. Malabarba, R.E. Reis, R.P. Vari, Z.M.S. Lucena & C.A.S. Lucena (eds.). Phylogeny and Classification of Neotropical Fishes. Edipucrs, Porto Alegre, RS, Brazil. 603p.

MARTIN-SMITH, K.M. & ARMSTRONG, J.D. 2002. Growth rates of wild stream-dwelling Atlantic salmon correlate with activity and sex but not Dominance. *Journal of Animal Ecology*, 71: 413-423, http://dx.doi.org /10.1046/j.1365-2656.2002.00609.x

MAZZONI, R. & IGLESISAS-RIO, R. 2002. Environmentally related life history variations in *Geophagus brasiliensis*. *Journal of Fish Biology*, 61: 1606-1618, http://dx.doi.org /10.1111/j.1095-8649.2002.tb02501.x

MAZZONI, R. & SILVA, A.P.F. 2006. Aspectos de história de vida de Bryconamericus microcephalus (Miranda Ribeiro) (Characiformes, Characidae) de um riacho costeiro de Mata Atlântica, Ilha Grande, Rio de Janeiro, Brasil. *Revista*

Brasileira de Zoologia, 23: 228-233, http://dx.doi.org/10.1590/S010181752006000100016

MENEZES, M.S. & CARAMASCHI, E.P. 1994. Características reprodutivas de *Hypostomus* gr *punctatus* no rio Ubatiba, Maricá-RJ (Osteichthyes, Siluriformes). *Revista Brasileira de Biologia,* 54: 503-513.

MÉRONA, B.; VIGOUROUX, J.M.R. & CHAVES, P.T. 2009. Phenotypic plasticity in fish life-history traits in two neotropical reservoirs: Petit-Saut Reservoir in French Guiana and Brokopondo Reservoir in Suriname. *Neotropical Ichthyology*, 7: 683-692, http://dx.doi.org/10.1590/S1679-62252009000400018

METCALFE, N.B. & MONAGHAN, P. 2003. Growth versus lifespan, perspectives from evolutionary ecology. *Experimental Gerontology*, 38: 935-940, http://dx.doi.org/10.1016/S0531-5565(03)00159-1

MUNRO, A.D. 1990. Tropical Freshwater Fishes. Pp. 145-239. *In*: A.D. Munro, A.P. Scott & T.J. Lam (eds.). Reproductive Seasonality in Teleosts: Environmental Influences. CRC Press, Florida, EUA.

NIKOLSKII, G.V. 1969. *Theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources*. Oliver and Boyd, Edinburgh,UK. 323p.

OLDEN, J.D.; POFF, N.L. & BESTGEN, K.R. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs*, 76: 25-40, http://dx.doi.org/10.1890/050330

OLIVEIRA, C.L.C.; FIALHO, C.B. & MALABARBA, L.R. 2002. *Período reprodutivo, desova e fecundidade de Cheirodon ibicuhiensis Eigenmann, 1915 (Ostariophysi: Characidae) do arroio Ribeiro, Rio Grande do Sul, Brasil*. Comunicação do Museu de Ciências e Tecnologia, 15: 3-14.

OLIVEIRA, C.L.C.; FIALHO, C.B. & MALABARBA, L.R. 2010. Reproductive period, fecundity and histology of gonads of two cheirodontine (Ostariophysi: Characidae) with different reproductive strategies - insemination and external fertilization. *Neotropical Ichthyology,* 8: 351-360.

ORSI, M.L.; SHIBATTA, O.A. & SILVA-SOUZA, A.T. 2002. Caracterização biológica de populações de peixes do rio Tibagi, localidade de Sertanópolis. Pp. 425-432. *In*: M.E. MEDRI (ed.). A bacia do rio Tibagi. Universidade Estadual de Londrina, Londrina. 595p.

PAULY, D. 1980. On the interrelationships between natural mortality, growth parameters, and environmental temperature in 175 fish stocks. *Journal of Marine Science*, 39: 175-192.

PAULY, D. & DAVID, N. 1981. *ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforschung*, 28: 205-211.

PAULY, D. 1983. Some simple methods for the assessment of tropical fish stocks. *FAO Fishers Technical Papers*, 234:1-52, 1983.

PAULY, D. & DAVID, N. 1981. *ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforschung*, 28: 205-211.

PAULY, D. 1983. Some simple methods for the assessment of tropical fish stocks. *FAO Fishers Technical Papers*, 234:1-52, 1983.

PAULY, D. & MUNRO, J.L. 1984. Once more on the comparison of growth in fish and invertebrates. *Fishbyte*, 2: 1-21.

PELICICE, F.M. & AGOSTINHO, A.A. 2005. Perspectives on ornamental fisheries in the upper Paraná River floodplain, Brazil. *Fisheries Research*, 72: 109-119, http://dx.doi.org/10.1016/j.fishres.2004.09.005

PELICICE, F.M. & AGOSTINHO, A.A. 2006. Feeding ecology of fishes associated with *Egeria* spp. patches in a tropical reservoir, Brazil. *Ecology of Freshwater Fish*, 15: 10-19, http://dx.doi.org/10.1111/j.1600-0633.2005.00121.x

PIANA, P.A.; GOMES, L.C. & CORTEZ, E.M. 2006. Factors influencing Serrapinnus notomelas (Characiformes: Characidae) populations in upper Paraná river floodplain lagoons. Neotropical Ichthyology, 4: 81-86, http://dx.doi.org/10.1590/S1679-62252006000100008

REZNICK, D.N.; BUTLER, M.J.; RODD, F.H. & ROSS, P. 1996. Life-history evolution in guppies (*Poecilia reticulate*) 6. Differential mortality as a mechanism for natural selection. *Evolution*, 50: 1651-1660.

ROCHET, M.J. 2000. A comparative approach to life-history strategies and tactics among four orders of teleost fish. *ICES Journal of Marine Science*, 57: 228-239, http://dx.doi.org/10.1006/jmsc.2000.0641

ROFF, D.A. 2001. *Life History Evolution.*1nd Edition. Sinauer Associates, Sunderland, MA.527p.

SANTOS, A.L.B.; PESSANHA, A.L.M.; COSTA, M.R. & ARAÚJO, F.G. 2004. Relação peso-comprimento de *Orthopristis ruber* (Cuvier) (Teleostei, Haemulidae) na Baia de Sepetiba, Rio de Janeiro, Brasil. *Revista Brasileira de Zoologia*, 21: 185-187.

STEARNS, S.C. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience*, 39: 436-445.

STEARNS, S.C. 1992. *The Evolution of Life Histories*. University Press, Oxford. 250p.

TAYLOR, C.C. 1958. Cod growth and temperature. *Journal du Conseil International pour L'Ex-ploration de la Mer*, 23: 366 370.

TEDESCO, P.A.; HUGUENY, B.; OBERDORFF, T. DÜRR, H.H.; MÉRIGOUX, S. & MÉRONA, B. 2008. River hydrological seasonality influences life history strategies of tropical riverine fishes. *Oecologia*, 156: 691-702, http://dx.doi.org/10.1007/s00442-008-1021-2

TONDATO, K.K.; FIALHO, C.B. & SÚAREZ,Y.R. Reproductive ecology of *Odontostilbe pequira* (Steindachner, 1882) (Characidae, Cheirodontinae) in the Paraguay River, southern Pantanal, Brazil: effect of asynchronous relation between flooding regime and rainfall**.** *Environmental Biology of Fishes. (In press).*

TONDATO K.K.; MATEUS L.A.F. & ZIOBER, S.R. 2010. Spatial and temporal distribution of fish larvae in marginal lagoons of Pantanal, Mato Grosso State, Brazil. *Neotropical Ichthyology,* 8: 123-133, http://dx.doi.org/10.1590/S1679-62252010005000002

VAZZOLER, A.E.A.M. & MENEZES, N.A. 1992. Síntese dos conhecimentos sobre o comportamento reprodutivo dos Characiformes da América do Sul (Teleostei, Ostariophysi). *Revista Brasileira de Biologia,* 52: 626-640.

VAZZOLER, A.E.A.M. 1996. *Biologia da reprodução de peixes telósteos: teoria e prática*. Eduem, Maringá, PR, Brasil.

WINEMILLER, K.O. 1989. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia,* 81: 225-241.

WINEMILLER, K.O. & ROSE, K.A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Science*, 49: 2196-2218. http://dx.doi.org/10.1139/f92-242

WINEMILLER, K.O. & DAILEY, W.D. 2002. Life history strategies, population dynamics, and consequences for supplemental stocking of tarpon. *Contributions in Marine Science*, 35: 81-94, http://dx.doi.org/10.1139/f05-040

WOOTTON, R.J. 1998. *The Ecology of Teleost Fishes*. 2nd Edition. Kluwer Academic, Dordrecht, HO. 392p.