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CARACTERÍSTICAS DE HISTÓRIA DE VIDA DE PEIXES DE PEQUENO PORTE SOB O EFEITO DE DIFERENTES REGIMES HIDROLÓGICOS EM PLANÍCIE DE INUNDAÇÃO TROPICAL

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Não é o mais forte que sobrevive, nem o mais inteligente, mas o que melhor se adapta às mudanças.

(Charles Darwin)

Dedico este trabalho a minha amada mãe Aparecida e aos meus avós Dominizia e Elpidio que foram meus alicerces em todas as conquistas.

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Resumo

O presente trabalho tem como objetivo avaliar traços de história de vida de peixes de pequeno porte sob o efeito de diferentes regimes de inundação no Pantanal. As amostragens foram realizadas nas regiões Norte (Rio Cuiabá) e Sul do Pantanal (Rio Paraguai), que apresentam regimes hidrológicos diferenciados. Inicialmente, foram obtidos dados de 623 indivíduos da espécie *Odontostilbe pequira* no Pantanal Sul, para análise de estrutura populacional e traços reprodutivos. Não foi observada variação significativa na distribuição de comprimento entre os sexos. O período reprodutivo foi longo para ambos os sexos (10 meses), com maior intensidade entre os meses de Junho e Julho. Não ocorreu correlação entre o índice gonadossomático (IGS) de ambos os sexos com a temperatura da água e pluviosidade temporalmente. Os machos não apresentaram associação entre o IGS e o nível do rio, mas uma correlação marginalmente significativa foi observada nas fêmeas. Contudo, foi observado o efeito do nível histórico do rio sobre o IGS para ambos os sexos, indicando que o regime de inundação tem influência decisiva na atividade reprodutiva de *O. pequira*, proporcionando a ocorrência de desovas mesmo que a pluviosidade e temperatura apresentem baixos valores. *O. pequira*, pode ser caracterizada como uma espécie de "estratégia oportunista", apresentando longo período reprodutivo, desova parcelada e elevada fecundidade, com atividade reprodutiva fortemente associada com o regime de inundação. Posteriormente, foram utilizados dados de comprimento de 977 indivíduos de *O. pequira* no Pantanal Sul, para análises adicionais de traços de história de vida entre os sexos. O comprimento assintótico ($L\infty$) estimado para fêmeas foi maior (39,59mm) que para os machos (37,57mm). As fêmeas também apresentaram maior taxa de crescimento (k=0,93 ano^{-1}) e mortalidade natural (Z=1,56 ano^{-1}) em relação aos machos (k=0,82 ano^{-1}; Z= 1,45 ano^{-1}). Através das curvas de crescimento foram registrados 3 coortes completas para as fêmeas, com longevidade estimada em 3,22 anos, e, 4 coortes para os machos, com longevidade de 3,65 anos. O padrão de recrutamento foi longo para ambos os sexos, não sendo observada variação significativa na forma da distribuição do recrutamento entre os sexos. Constatamos correlação entre o recrutamento e o nível do rio para ambos os sexos, com pico de recrutamento em Julho e Junho para fêmeas e machos, respectivamente, corroborando com o período reprodutivo da espécie e com a associação com o regime de inundação no Pantanal Sul. Finalmente, foram obtidos dados de comprimento das espécies *Bryconamericus exodon, Hyphessobrycon eques, O. pequira, Moenkhausia dichroura, Hypoptopoma inexpectatum* e *Eigemnannia trilineata*, nas regiões norte e sul do Pantanal,

para realizar as comparações intra e interespecífica. As espécies não apresentaram diferença significativa na forma de distribuição de comprimento entre as regiões. O $L\infty$ das espécies apresentou variação intraespecífica entre as regiões, com os maiores valores para as populações da região norte (exceção, *E. trilineata*). A taxa de crescimento (k) e mortalidade (Z) apresentou variação intraespecífica entre as regiões, com quatro espécies (*B. exodon, H. eques, O. pequira* e *M. dichroura)* demonstrando menores k e Z, e maiores $L\infty$ na região Norte, sugerindo que a região norte oferece condições mais favoráveis em relação à região Sul. Não ocorreu variação intraespecífica entre as regiões para o número de coortes e longevidade. O padrão de recrutamento não apresentou variação intraespecífica entre as regiões, apresentando longo período de recrutamento e picos para todas as espécies entre Junho e Agosto. Na região Norte, o padrão de recrutamento de quatro espécies (*B. exodon, H. eques, M. dichroura* e *H. inexpectatum*) não apresentou correlação significativa com o nível histórico do rio Cuiabá, entretanto, essas espécies apresentaram covariação negativa, além de duas espécies (*O. pequira e E. trilineata*) apresentarem correlação negativa significativa, apresentando picos de recrutamento com a diminuição do nível da água. Na região Sul, cinco espécies (*B. exodon, H. eques, M. dichroura, H. inexpectatum e O. pequira*) estiveram associadas significativamente com o nível histórico do rio Paraguai, com picos de recrutamento em níveis mais elevados de água, indicando que o regime de inundação tem influência decisiva no padrão de recrutamento (exceção, *E. trilineata*). Enfim, as espécies apresentaram variação intraespecífica na maioria dos traços de história de vida, mas não há ampla variação, inclusive no padrão de recrutamento que não se altera intra e interespecificamente, evidenciando tanto a força da ancestralidade de táxon (filogenia), como das condições ambientais locais regidas pelo regime de inundação, respectivamente.

Abstract

The present study aimed to evaluate life history traits of small sized fish according to different flooding regimes in the Pantanal. Samplings were performed in Northern (Cuiabá River) and Southern Pantanal (Paraguai River), which present distinct hydrological regimes. First, data of 623 individuals of *Odontostilbe pequira* in Southern Pantanal were analyzed as for population structure and reproductive traits. No significant variation was found in length distribution between sexes. The reproductive period was long for both sexes (10 months), with higher intensity between June and July. No correlation was detected between the gonadosomatic index (GSI) of both sexes with water temperature and rainfall over time. Males presented no association between GSI and river water level, but a marginally significant correlation was observed for females. However, it was verified the effect of the historical river level on the GSI for both sexes, indicating that the flooding regime has a decisive influence on the reproductive activity of *O. pequira*, by promoting spawning even if rainfall and temperature present low values. *O. pequira* can be characterized as an opportunistic species, presenting a long reproductive period, multiple spawning and high fecundity with reproductive activity strongly associated with the flooding regime. Afterwards, length data from 977 individuals of *O. pequira* in Southern Pantanal were used for additional analysis on life history traits between the sexes. The asymptotic length ($L\infty$) estimated for females was higher (39.59mm) than for males (37.57mm). Females also presented higher growth rate ($k=0.93$ year^{-1}) and natural mortality ($Z=1.56$ year^{-1}) than males ($k=0.82$ year^{-1}; $Z=1.45$ year^{-1}). By means of growth curves, 3 cohorts were recorded for females, with longevity estimated at 3.22 years, and 4 cohorts for males, with longevity of 3.65 years. The recruitment pattern was long for both sexes, without significant variation in recruitment distribution between the sexes. There was a correlation between recruitment and river water level for both sexes, with a recruitment peak in July and June for females and males, respectively, corroborating with the reproductive period of the species and with the association with the flooding regime in Southern Pantanal. At last, length data of *Bryconamericus exodon, Hyphessobrycon eques, O. pequira, Moenkhausia dichroura, Hypoptopoma inexpectatum* and *Eigemnannia trilineata*, in Northern and Southern Pantanal, were used for intra- and interspecific comparisons. Species have not presented significant difference in length distribution between regions. The $L\infty$ of species exhibited an intraspecific variation between the regions, with higher values of the populations from the Northern Pantanal (except for *E. trilineata*). The growth (k) and mortality (Z) rates presented

intraspecific variation between the regions, with four species (*B. exodon*, *H. eques*, *O. pequira* and *M. dichroura*) revealing lower values of k and Z, and higher $L\infty$ values in Northern Pantanal, suggesting that this region provides more favorable conditions than the Southern region. There were no intraspecific variations between the regions for the number of cohorts and longevity. The recruitment pattern also had no intraspecific variation between the regions, presenting a long recruitment period and greater peak for all species between June and August. On the Northern region, the recruitment pattern of four species (*B. exodon, H. eques, M. dichroura* and *H. inexpectatum*) showed no significant correlation with historical level of the Cuiabá River, but these species presented a negative covariation; besides that, two species (*O. pequira* and *E. trilineata*) presented a significant negative correlation, with recruitment peaks with decreasing water level. In the Southern Pantanal, five species (*B. exodon, H. eques, M. dichroura, H. inexpectatum* and *O. pequira*) have been significantly associated with the historical level of the Cuiabá River, with recruitment peaks at higher water levels, pointing out that the flooding regime has a key influence on the recruitment pattern (except for *E. trilineata*). Finally, species presented intraspecific variations in most of life history traits, but there is no wide variation, including in the recruitment pattern that does not change intra- and interspecies, evidencing both the control of the taxa ancestry (phylogeny) and of local environmental conditions ruled by the flooding regime, respectively.

Introdução Geral

A evolução ocorre através do processo de seleção natural que se revela a nível populacional nas espécies (Begon et al., 2006). Portanto, o conhecimento da biologia populacional das espécies ainda é um dos maiores desafios na ictiologia (Lowe-McConnell, 1999), principalmente em espécies de pequeno porte, que são menos conhecidas, desde o ponto de vista taxonômico, até a quantificação de aspectos básicos da sua ecologia. Assim, pesquisas em nível populacional são de extrema importância para entendermos os processos evolutivos que alteram padrões ecológicos em peixes.

Neste sentido, a compreensão da história de vida dos organismos, ou seja, do conjunto de traços co-adaptados e "projetados" pela seleção natural para um determinado ambiente (Stearns, 1992; Rochet, 2000), apresenta-se como um dos focos no entendimento da ecologia populacional em peixes. Isto porque, Nikolskii (1969) relata que, a ecologia e dinâmica populacional é centrada geralmente em nascimento, crescimento e morte: a reprodução compensa a perda por mortalidade e o crescimento controla as taxas de reprodução e mortalidade na população. Desta forma, se o crescimento contribui para a abundância da espécie, fazendo com que ela atinja a fase de reprodução num curto tempo e entre no ciclo reprodutivo, a mortalidade controla a abundância dessa espécie (Nikolskii, 1963). Portanto, os traços de história de vida, como a taxa de crescimento, mortalidade, aspectos reprodutivos, entre outros, podem ser determinantes na persistência de espécies ou populações, sob condições ambientais específicas. Salientando que, essas espécies e/ou populações apresentam sucesso caso ocorra plasticidade fenotípica em seus traços, mantendo populações viáveis, do contrário, elas são extintas localmente (Winemiller, 1989; Wotton, 1998).

Entre os inúmeros traços de história de vida, a estrutura em comprimento de população é um aspecto relevante, pois segundo Pauly (1998) o tamanho dos indivíduos determina grandemente a natureza das suas interações com outros organismos e suas características demográficas. Ainda, a estrutura em tamanho pode ser particularmente importante em populações onde o crescimento é flexível e a alimentação e a vulnerabilidade à predação dependem do comprimento (Wootton, 1998). Isto porque, os indivíduos pertencentes às classes de comprimento menores sofrem maior pressão de predação, comparada com os indivíduos maiores de uma população (Reznick et al., 1996).

Outro traço importante é a taxa de crescimento, que em muitas espécies de peixes variam acentuadamente de acordo com as condições ambientais (Nikolskii, 1969). Acredita-se que em regiões temperadas a taxa de crescimento dos peixes seja afetada principalmente

pela temperatura, enquanto que em regiões tropicais os recursos alimentares atuem como fatores decisivos ao crescimento (Boujard et al., 1991). Estas taxas também podem variar durante o ciclo de vida, sazonalmente e em cada habitat ocupado pela espécie (Lowe-McConnell, 1999). Dessa forma, nos últimos anos tem-se destacado, de maneira muito ampla, a importância dos estudos de crescimento em peixes, sendo considerado um aspecto fundamental para o conhecimento da dinâmica populacional e manejo das espécies (Froese & Binohlan, 2000), inclusive para espécies não alvo da pesca, mas que estão inseridas numa matriz altamente fragmentada e impactada pelas ações antrópicas.

Para qualquer taxa de crescimento ou comprimento assintótico, altos valores de mortalidade natural é comum em peixes tropicais (Pauly, 1998). As variações nas taxas de mortalidade são adaptações ao ambiente em que vivem e que interferem na biomassa dessas populações. Os principais fatores naturais de mortalidade são a predação e as doenças, que apresentam intensidade de ação com tendências divergentes em função da idade, isto é, indivíduos maiores e mais velhos sofrem menor mortalidade por predação, mas são mais suscetíveis a doenças devido à degeneração dos tecidos e menor aproveitamento dos elementos nutritivos (Fonteles-Filho, 1989).

Nas pesquisas com animais aquáticos os parâmetros de crescimento têm sido estimados indiretamente, por meio da distribuição temporal da frequência de dados de comprimento (Basson et al., 1988), método alternativo sugerido como uma boa alternativa para a determinação dos parâmetros de crescimento. Esta forma de análise é realizada frequentemente utilizando-se o programa FISAT (FAO-ICLARM Stock Assessment Tools) (Gayanilo & Pauly, 1997), com inúmeros trabalhos em regiões tropicais e temperadas utilizando este método em espécies de peixes para estimar as taxas de crescimento, mortalidade, longevidade e recrutamento (Lizama & Ambrósio, 2003; King & Etim, 2004; Gomiero et al., 2006; Mateus e Penha, 2007; Lourenço et al., 2008a; Vásquez et al. 2009; Close et al., 2010; Vasconcelos et al., 2011; Grabowska et al., 2011; Tondato et al., 2012; Mazel et al., 2012; Vicentin et al., 2013).

No que se refere à reprodução, o comportamento reprodutivo varia entre ambientes e é amplamente dependente das variáveis ambientais locais (Humphries et al., 1999; Magalhães et al., 2003; Zeug & Winemiller, 2007). Segundo Wootton (1998), o início da reprodução representa uma fase crítica na vida de um indivíduo, pois se antes o recurso era destinado apenas para o crescimento e sobrevivência, passa a existir, em seguida, um conflito potencial entre a alocação de tempo e o recurso para a reprodução, ou para sobrevivência e crescimento. Deste modo, para que os organismos estejam aptos a desafios ecológicos e se

adaptem a condições específicas do ambiente, a história de vida das populações enfrenta restrições entre variáveis demográficas e com características associadas à reprodução através do *trade-off*, onde o investimento em um atributo causaria a redução dos recursos disponíveis para investimento em outro (Winemiller & Rose, 1992). Portanto, *trade-offs* entre os investimentos energéticos no crescimento, reprodução e sobrevivência é responsavel pela evolução e diversidade das *estratégias de história de vida* adaptadas ao ambiente para manter a existência de populacões ao longo das gerações e garantir o equilibrio populacional (Stearns, 1992; Winemiller & Rose, 1992; Winemiller, 2003). Salientando que, o sucesso de uma população ou espécie de peixe depende do desenvolvimento destas estratégias, ou seja, do conjunto de características que deverá se manifestar em seus indivíduos para que se adequem ao ambiente e tenham sucesso na reprodução, deixando descendentes de modo a garantir o equilíbrio da população (Wootton, 1984). Essas características são conhecidas como táticas reprodutivas e podem ser variáveis adaptativas e sofrerem variações devido às alterações ambientais (Vazzoler, 1996; Wootton, 1998). Essas táticas reprodutivas possuem efeitos tanto diretos quanto indiretos na reprodução e no *fitness* dos peixes (Winemiller, 2003). Vários autores (Welcomme, 1979; Vazzoler, 1996; Lowe-McConnell, 1999;) enumeram várias táticas em populações de peixes, dentre elas: desenvolvimento de cuidado parental, alteração na proporção sexual, redução no tamanho e idade de primeira maturação gonadal, aumento da fecundidade e do número de períodos reprodutivos, aumento da taxa de crescimento e tempo de incubação.

Vazzoler (1996) relata que os teleósteos alcançaram sucesso em ambientes distintos por apresentarem várias estratégias reprodutivas que englobam táticas extremas de reprodução. Essas táticas reprodutivas estão associadas a condições ambientais favoráveis ao desenvolvimento da prole, como época e locais que apresentam maior disponibilidade de alimento e abrigo (Welcomme, 1979; Lowe-McConnell 1999; Agostinho et al., 2004). Sendo resultados tanto de forças evolucionarias quanto de respostas imediatas a pressões ambientais, alterando a alimentação, a movimentação, o crescimento e a época de reprodução das espécies (Lowe-McConnell, 1999). Portanto, a análise das táticas reprodutivas são fundamentais para compreender como essas características se adaptaram para maximizar o sucesso reprodutivo de uma espécie em um determinado ambiente levando a sobrevivência das populações (Matthews, 1998).

Em relação aos fatores ambientais que afetam a dinâmica da reprodução, sabe-se que a variação da intensidade reprodutiva e da sua sazonalidade em regiões tropicais tem sido determinada pelas altas pluviosidades, que refletem na variação dos níveis hidrométricos,

associados à elevação da duração do dia e da temperatura da água (Lowe-McConnell, 1999). Quando se trata de peixes de planície de inundação, a reprodução também é altamente sazonal e a maioria dos peixes desovam quando o nível da água começa subir, garantindo a produção de jovens peixes no período em que as condições são mais favoráveis para sua sobrevivência (Welcomme, 1979; Bailly et al., 2008).

Neste sentido, Junk et al., (1989) propuseram o "Conceito de Pulso de Inundação", que considera os aspectos hidrológicos juntamente com os aspectos geomorfológicos, produzindo picos de inundações e secas, com diferentes amplitudes e períodos ao longo da bacia hidrográfica e consideram esta sazonalidade a maior força controladora da biota nos rios com planície de inundação. A influência do pulso de inundação sobre as comunidades aquáticas é resultado do acesso a novos habitats com o transbordamento de água do leito principal sobre a planície, bem como da maior oferta de abrigo e alimento (Junk et al., 1989; Winemiller, 2005), resultante do aumento da área disponível para exploração de recursos alimentares interagindo com a maior oferta de alimento, uma vez que, usualmente o período de maior pluviosidade é sincronizado com o de temperaturas mais elevadas. Além disso, o ciclo hidrológico sincroniza eventos biológicos como maturação gonadal, migração, desova e desenvolvimento larval, crescimento e alimentação (Winemiller, 1989; Lowe McConnell, 1999). Nas latitudes em que as flutuações sazonais na temperatura são pequenas, as cheias se constituem o principal gatilho para a reprodução de várias espécies de peixes (Welcomme, 1979), sendo que cheias ausentes ou reduzidas limitam ou até mesmo frustram o processo reprodutivo de muitas delas. Suzuki et al. (2004) relacionando a intensidade reprodutiva com variáveis ambientais na planície de inundação do Alto rio Paraná concluíram que: i) a temperatura e o foto-período constituem gatilhos preditivos que desencadeiam o processo de maturação gonadal; ii) o início das cheias é o gatilho sincronizador da desova; iii) o pico das cheias é o gatilho finalizador do período reprodutivo.

No Pantanal, a maior planície de inundação do mundo (aproximadamente 140.000 km^2), declarada Reserva da Biosfera em outubro de 2002, onde ocorrem mais de 260 espécies de peixes (Britski et al., 2007), o comportamento reprodutivo não é diferente. Bailly et al. (2008) estudando a influência do regime de inundação sobre a reprodução de várias espécies no Alto Pantanal, evidenciaram que, com a exceção dos migradores de curta distância, as cheias têm papel relevante no recrutamento de espécies das demais estratégias reprodutivas, apesar de ressaltarem que independentemente da estratégia, os picos reprodutivos das espécies antecedem os picos das cheias, estando a reprodução associada com o início da inundação. A associação da reprodução com início da inundação na mesma região do

Pantanal também foi relatada por Lourenço et al. (2008b) e Tondato et al. (2010). Contudo, esta região (Norte do Pantanal), o período de inundação coincide com altos valores de fotoperíodo e temperatura que também favorecem a desova das espécies, seguindo o que propõe um dos aspectos do "Conceito do pulso de inundação" (CPI).

Por outro lado, em planícies de inundação em que as altas temperaturas e as inundações não são coincidentes, pode ser vantajoso para um peixe desovar em baixos níveis de água no canal principal do rio, quando os recursos alimentares estão concentrados, como propõe a hipótese do "Recrutamento em baixo fluxo"(RBF) de Humphries et al. (1999). Esta teoria pode ser testada no Sul do Pantanal, onde ocorre assincronia entre o período de maior pluviosidade e temperatura (novembro a março) e o período de cheia (junho a agosto), questionando os pressupostos do CPI. Assim surge uma pergunta extremamente interessante na análise das populações de peixes: O que atua como display reprodutivo para as espécies de peixes nesta região, o aumento da pluviosidade e temperatura no início do verão? Ou o aumento do nível do rio no inverno?

Neste contexto, uma das áreas de estudo se encontra no Sul do Pantanal, especificamente Pantanal de Porto Murtinho, onde ocorre a falta de sincronia entre o período de maior pluviosidade e temperatura com o período de inundação, devido a sua posição geográfica e a baixa declividade de 1cm/km (Hamilton et al., 1996). A inundação tem início ao norte da planície juntamente com o período de chuvas, escoando lentamente em direção ao sul, o que resulta em defasagens de 3 a 6 meses entre o pico das chuvas nas nascentes e a inundação máxima na parte sul, geralmente em Junho, fora da estação chuvosa (Hamilton et al., 1996; Gonçalves et al., 2011). Além disso, esta região apresenta importância biológica, uma vez que, representa o "final" do Pantanal, onde os impactos ambientais que atuam na bacia (desmatamento, assoreamento, entre outros) bem como os previstos (eg. Aumento da vazão pelo projeto da Hidrovia Paraguai-Paraná) devem se manifestar de forma mais explícita. O rio Apa, logo abaixo da região de Porto Murtinho atua como limite entre o médio rio Paraguai e Alto Rio Paraguai, desta forma, a compreensão da dinâmica de peixes nesta região também assume uma importância biogeográfica, permitindo a comparação com outros trechos e regiões do Pantanal de forma mais robusta.

Associado a esta assincronia, outra questão importante em todo o Pantanal é a possível exploração dos estoques das espécies de pequeno porte, que além de serem pouco conhecidas, muitas espécies apresentam potencial econômico (ornamental) (Súarez et al., 2001). Pelicice & Agostinho (2005) analisando o potencial da ictiofauna na planície do alto rio Paraná para a captura de peixes ornamentais constataram que 40,6% das espécies

capturadas são citadas como ornamentais na literatura e outros 42,6% foram definidas como potencialmente ornamentais.

Desta forma, espécies como *Odontostilbe pequira*, *Hyphessobrycon eques*, *Moenkhausia dichroura*, *Hypoptopoma inexpectatum*, *Bryconamericus exodon*, entre outras, que são muito comuns nos bancos de macrófitas aquáticas, são comumente encontradas em lojas especializadas em aquariofilia em vários municípios de Mato Grosso e Mato Grosso do Sul e apesar disto, inexistem informações sobre a sua captura nos rios destes estados e mesmo informações sobre aspectos populacionais destas espécies. Por outro lado, a captura de iscas vivas, como da espécie *Eigemnannia trilineata* que ocorre através da remoção dos peixes dos bancos de macrófitas aquáticas tanto na calha dos rios, quanto das lagoas marginais, altera a estrutura física destes bancos de macrófitas e possivelmente interfere nos padrões naturais de mortalidade e recrutamento desta espécie, pelo menos em nível local.

Diante do exposto o presente trabalho tem como objetivo geral avaliar traços de historia de vida de espécies de peixes de pequeno porte em diferentes regiões do Pantanal, enfocando a influência da assincronia entre pluviosidade, temperatura e nível do rio na região Sul do Pantanal. Para isto o estudo foi dividido em três capítulos:

1) O primeiro capítulo analisa a ecologia reprodutiva de *Odontostilbe pequira* (Steindachner, 1882) no Pantanal Sul, com o objetivo de verificar as diferenças na estrutura populacional e nas táticas reprodutivas entre os sexos, além de correlacionar o período reprodutivo com a pluviosidade, temperatura e nível do rio;

2) O segundo capítulo apresenta os traços de história de vida de *O. pequira* no Pantanal Sul, com o objetivo de analisar as variações nos traços de história de vida entre fêmeas e machos, bem como, correlacionar o padrão de recrutamento de ambos os sexos com a variação do regime de inundação;

3) O terceiro capítulo abordada os traços de história de vida e recrutamento de seis espécies de peixes sob o efeito de diferentes regimes hidrológicos no Pantanal, com o objetivo de analisar a variação intra e interespecífica nos traços de história de vida e no padrão de recrutamento, além de correlacionar o recrutamento de cada espécie com o regime de inundação de cada região (Norte e Sul).

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REPRODUCTIVE ECOLOGY OF *ODONTOSTILBE PEQUIRA* (STEINDACHNER, 1882) (CHARACIDAE, CHEIRODONTINAE) IN THE PARAGUAY RIVER, SOUTHERN PANTANAL, BRAZIL

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Abstract: The reproductive biology of *Odontostilbe pequira* 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 24.2mm and of the males 22.2mm, 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 0.46mm and the frequency distribution of the diameters showed various modes, indicating a multiple spawning. Thus, the reproductive tactics of *O. pequira* was characterized as "opportunistic strategist", with reproductive activity strongly associated with the flood pulse.

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- McConnell 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-Alisson 1990; Lowe- McConnell 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-McConnell 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 presuppositions 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 pequira* (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. pequira* 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. pequira* 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 km^2, part of the basin of the upper Paraguay river. Shows variation in the intensity of rains, oscillating between 800 and 1400 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 fluviometric 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-McConnell 1999).
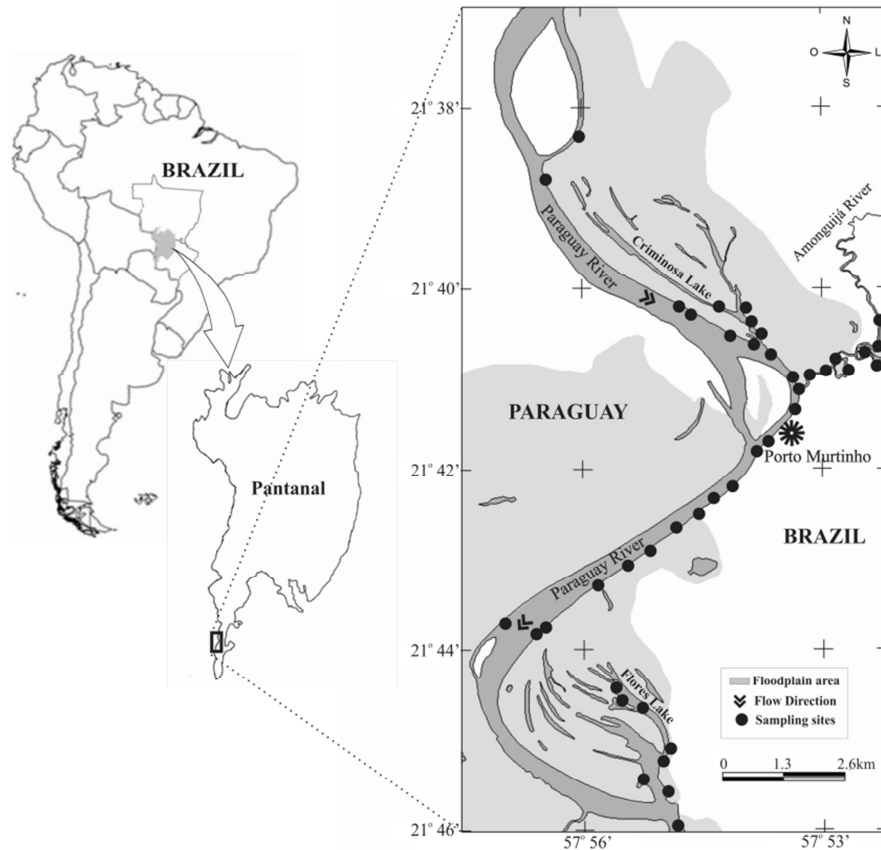
Fig 1 Location of the sampling area along the Paraguay River, next the city of Porto Murtinho (Brazil), extreme southern Pantanal (Pantanal de Porto Murtinho), sampled from February/2009 to January/2010

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 (1.5x5m) and sieve nets (0.8x1.2 m) both with 2 mm mesh, being carried out at least 5 drags and 20 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 pequira. 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 Metereologia (INMET).

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-standardizaton 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 2mm and the weight classes of 0.05g 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 (X^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. pequira* 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 ovelap 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, 7471 individuals of *Odontostilbe pequira* 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 36.3mm (median = 25.2mm) and of the males from 14.4 to 33.0mm (median = 23.8mm) (Fig. 2A). Total weight for females varied from 0.042 to 0.74g (median = 0.265g) and for the males from 0.047 to 0.541g (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).
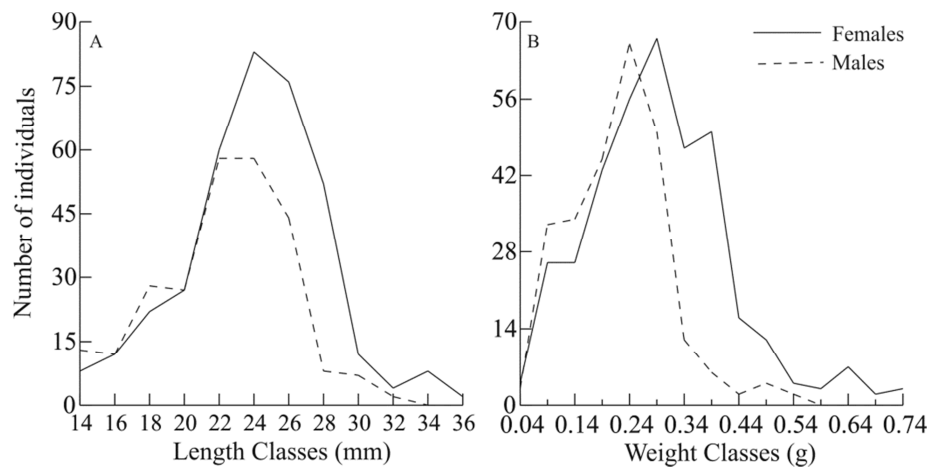
Fig 2 Histogram of number of individuals for standard length classes (A) and total weight classes (B) for females and males of *O. pequira* in the Paraguay River in the period February/2009 to January/2010

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. pequira*, 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 males in the maturing and immature stage, with the last only with immature individuals (Fig. 3B).
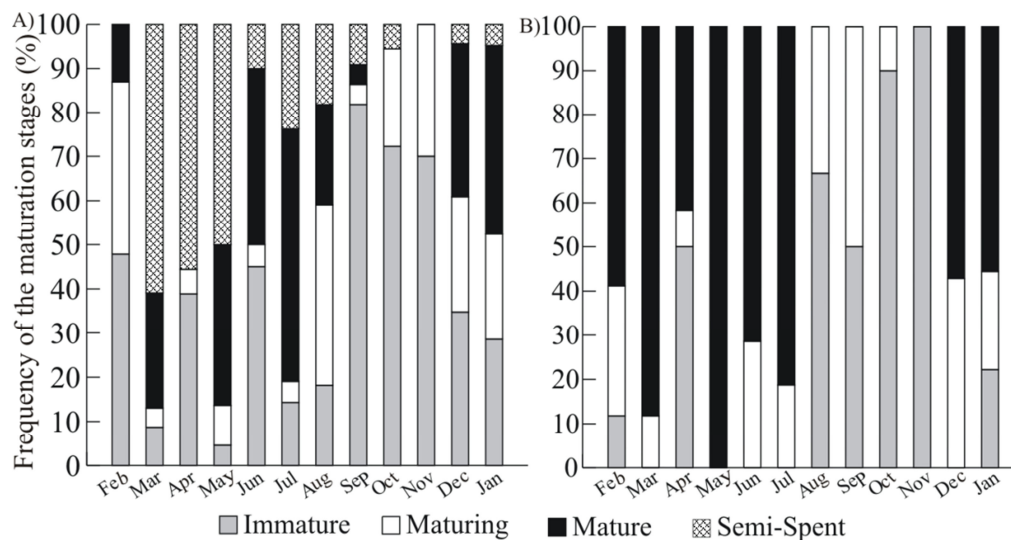
Fig 3 Temporal variation in the frequencies of maturation stages of A) female and B) males of *O. pequira* in the river Paraguay between February/2009 and January/2010

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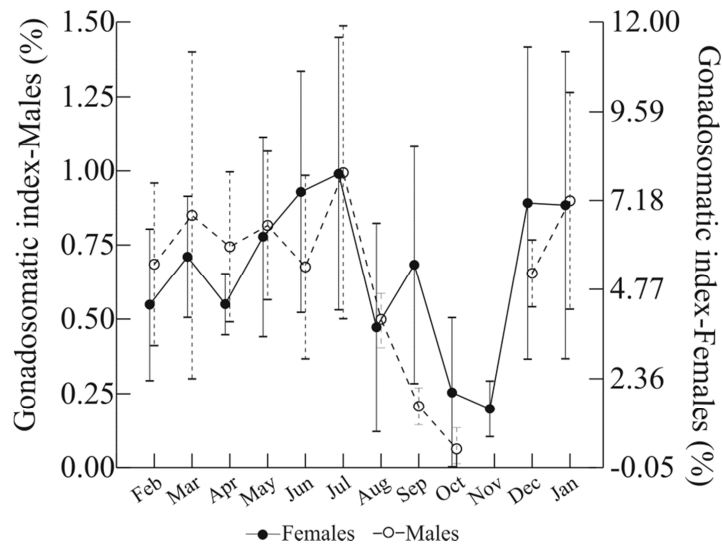
Fig 4 Temporal covariation between the mean (± standard deviation) gonadosomatic index (%) of females and males of *O. pequira* in the Paraguay river between February/2009 and January/2010

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 rainfall and temperature, however, these variables had not been statistically correlated with reproduction (Fig. 5A and C).
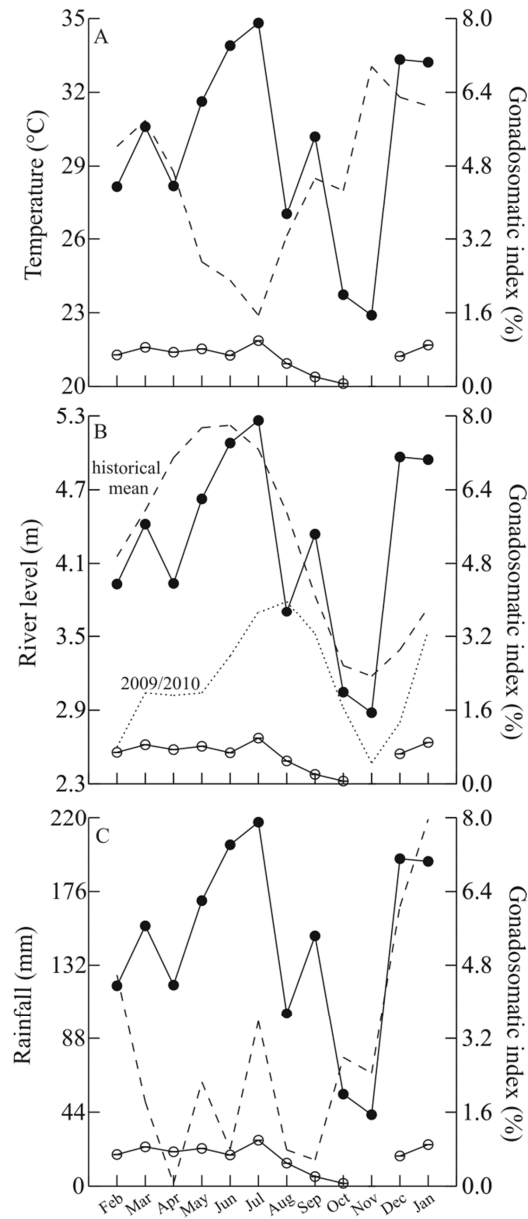
Fig 5 Temporal variation of the mean gonadosomatic index (%) of females and males *O. pequira* and (A) mean temperature (B) river level (2009/2010) and historical mean river level (1939/2009) of the Paraguay river and (C) mean rainfall from February/2009 to January/2010

The length at first maturity of the females (L_{50}) was estimated to be 24.2mm with a confidence interval of 23.7 to 24.6mm and L_{100} of 30.6mm, considering all the females analyzed (Fig. 6). For the males, L_{50} was 22.2mm with a confidence interval of 21.3 to 22.9mm 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.
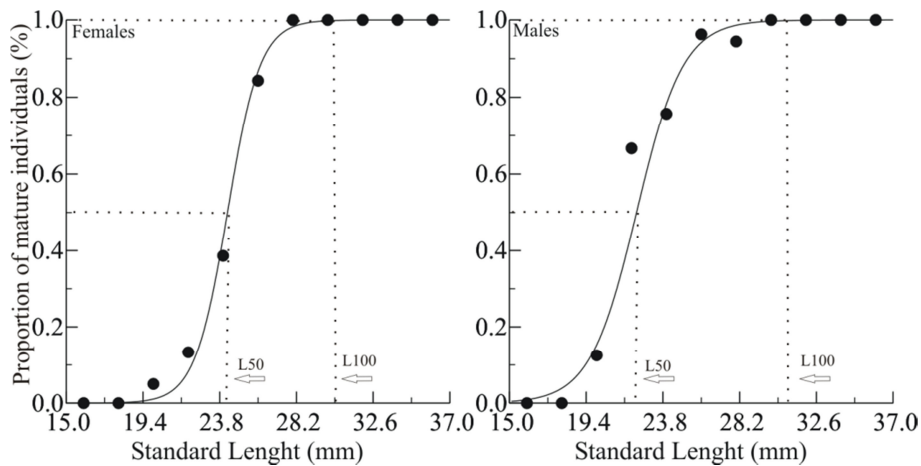
Fig 6 Relation between the proportion of females and males mature sexually and standard length (mm) of *O. pequira* in the Paraguay river in the period February/2009 to January/2010. L_{50} (Length at which 50% of individuals are reproduced) and L_{100} (length in which 100% of individuals are reproduced)

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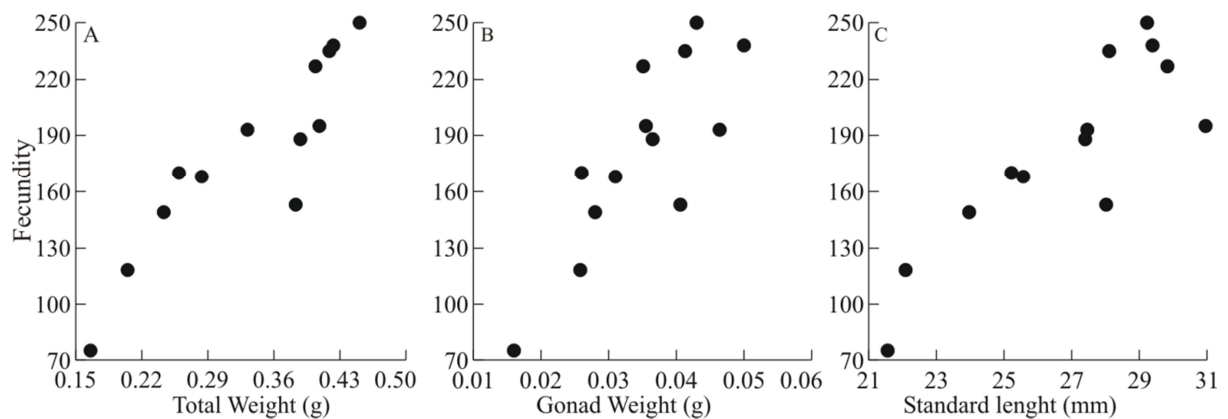
Fig 7 Relation of the fecundity of females of *O. pequira* in the Paraguay river from February/2009 to January/2010 as a function of total weight (g), gonad weight (g) and standard length

The diameter of mature oocytes varied between 0.38 and 0.61mm, with mean of 0.46mm (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).
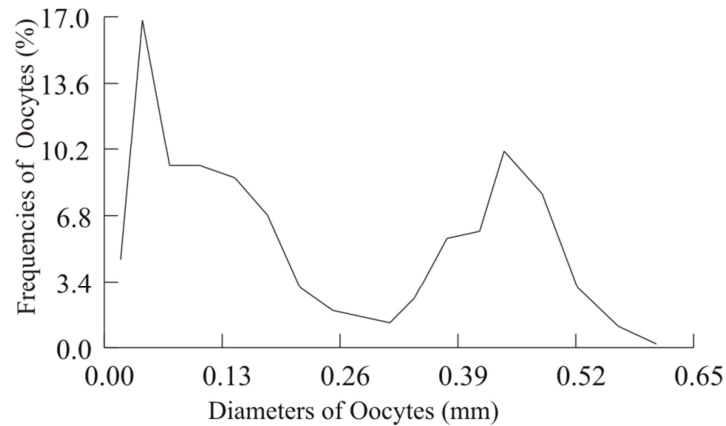
Fig 8 Distribution of the relative frequencies of the oocyte diameters of *O. pequira* the Paraguay River from February/2009 to January/2010

Discussion

Despite the mean length of *O. pequira* being similar to those found in other Cheirodontinae fishes in tropical regions of Brazil (Silvano et al. 2003; Lourenço et al. 2008b; Benitez and Súarez 2009), the median length of the females and males is similar to the minimal lengths found by Oliveira et al. (2010) for *O. pequira* 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 5mm 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. pequira* 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. pequira* (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 (Wooton 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. pequira*, with predominance of females. The predominance of females is common in fish (Abilhoa 2007; Súarez 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 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; Hojo et al. 2004; Mazzoni et al. 2005), 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; 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. pequira* 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. pequira*, 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. pequira* 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. pequira* 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. pequira*. However, the LFR hypothesis was tested in temperate environments, which could have been very important for the partial observation in the results, since in the southern Pantanal (tropical region) the mean annual temperatures vary between 22.5ºC and 26.5ºC, with a minimal mean of 21ºC, 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-McConnell 1999), appear to be evolutionarily important in the adaptability of the reproductive strategy of *O. pequira*, 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. pequira* 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. pequira* 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. pequira* (0.54) is similar to that of various Cheirodontinae fishes, such as *Macropsobrycon uruguayanae* (0.53) and *Cheirodon ibicuhiensis* (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; Oliveira et al. 2010). Despite the intraspecific difference in relative fecundity, *O. pequira* 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 (Silvano et al. 2003, Mazzoni et al. 2002).

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 (Nikolskyy 1963). The analysis *O. pequira*, 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. pequira* shows a long reproduction, it is possible to suppose that the females have a high reproductive investiment, spawning several batches the whole year, which also compensates for the apparently low fecundity. The diameter of *O. pequira* 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 (Nikolskyy 1963; Lowe-McConnel 1999). An analysis of the reproductive tactics of *O. pequira* 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.pequira* 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

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CAPÍTULO 2

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

Karina Keyla Tondato, Clarice Bernhardt Fialho e Yzel Rondon Súarez

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 ($L\infty$) 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).

Key words: intraspecific variation; population biology; cheirodontinae; growth rate; recruitment.

RESUMO

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-chaves: variação intraespecífica, biologia populacional, cheirodontinae, taxa de crescimento, recrutamento, diferença 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.
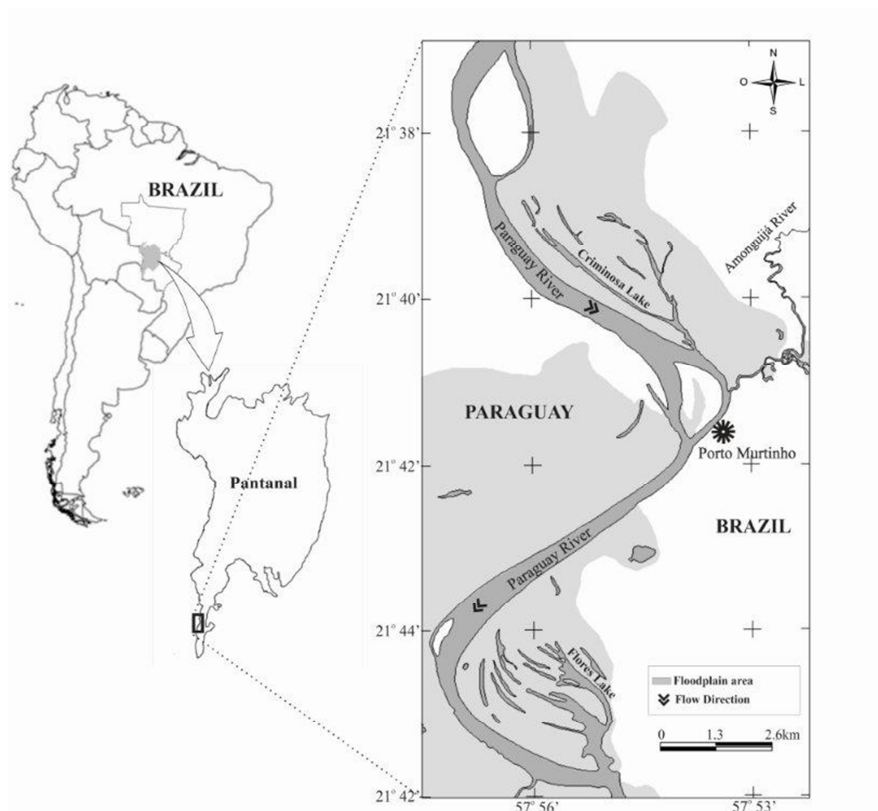
Figure 1. Location of the sampling area along the Paraguay River, near to the city of Porto Murtinho (Brazil), extreme southern Pantanal (Pantanal de Porto Murtinho), sampled from February/2009 to January/2011.

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 ($L\infty$ 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 ($L\infty$ 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).

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).
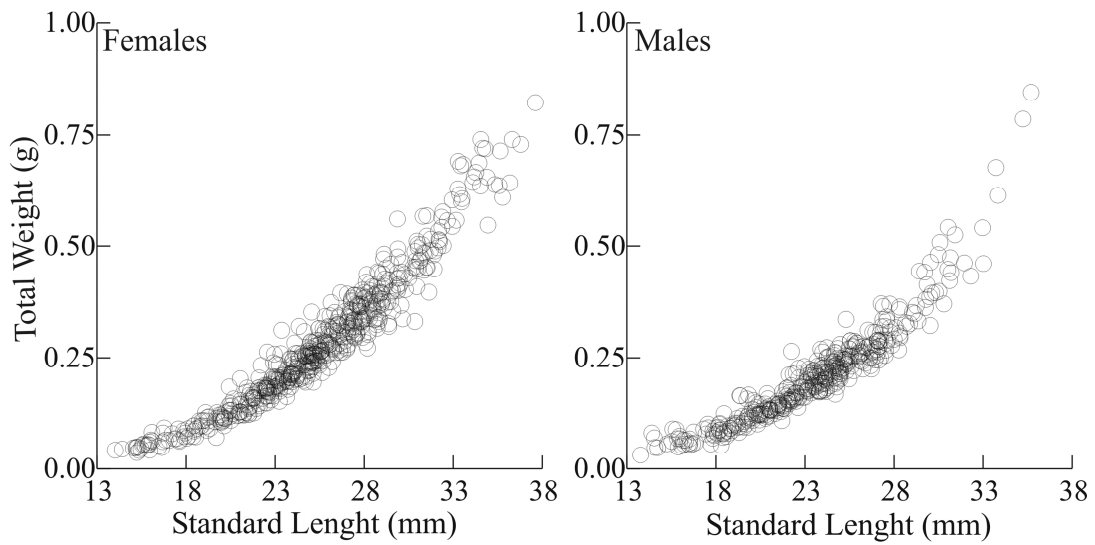
Figure 2. Weight/length relationship for females and males of *O. pequira* in Paraguay River during the study period.

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.
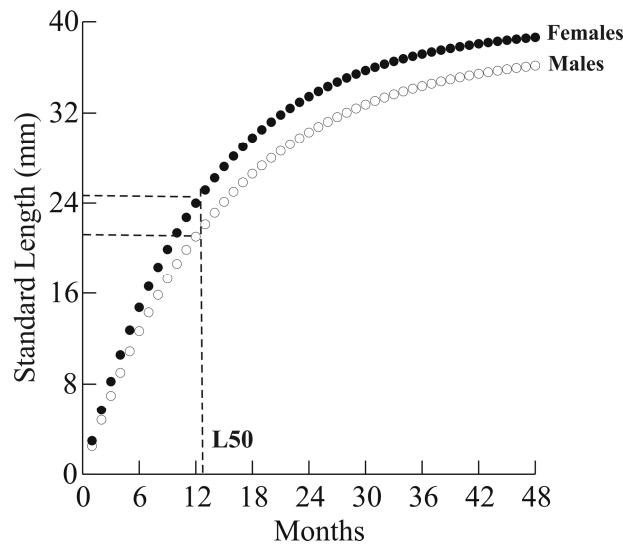
Figure 3. Von Bertalanffy growth curve fitted for the estimated ages in months of females and males of *O. pequira*, in Paraguay River. L_{50} = first maturity length.
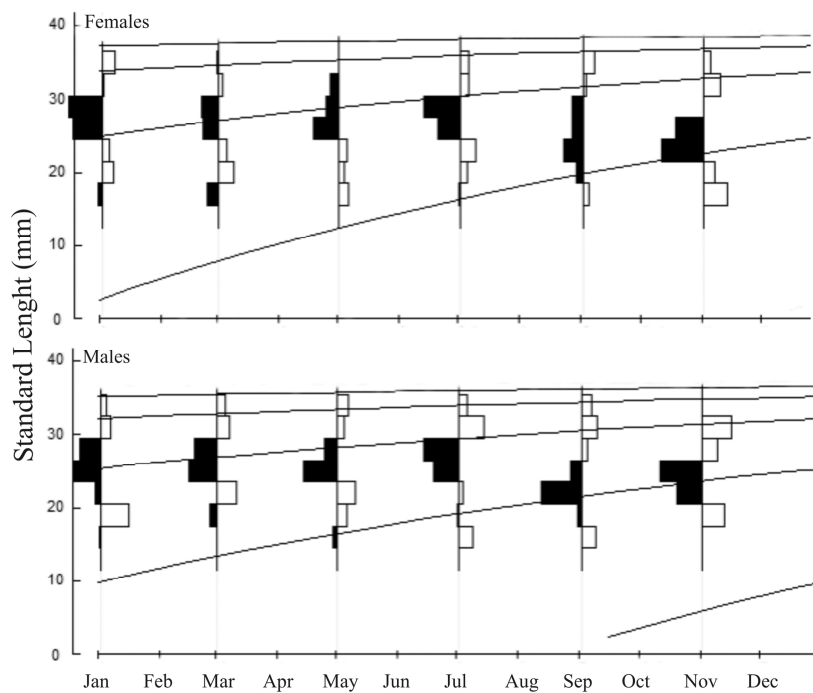
Figure 4. Growth curves of the cohorts of females and males of *O. pequira*, in Paraguay River between February 2009 and January 2011.

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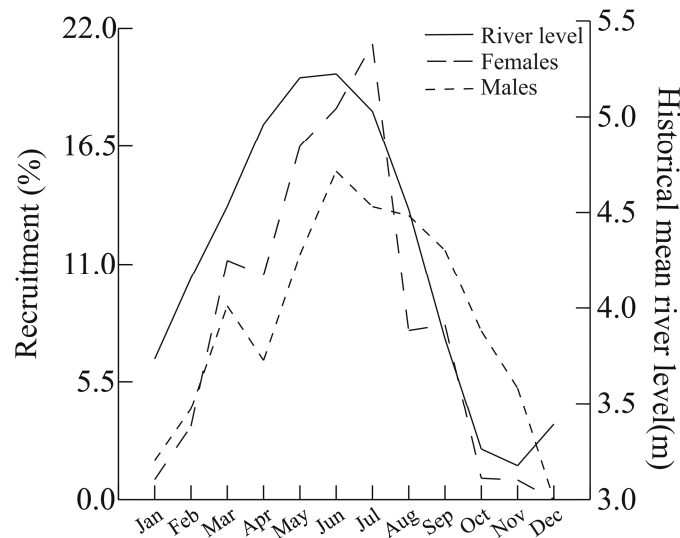
Figure 5. Temporal variation of the recruitment (%) of females and males of *O. pequira* from February 2009 to January 2011 and of the historical level of Paraguay River.

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. in press*), 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. in press*), 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 $L\infty$. 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 $L\infty$ 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. in press*). Furthermore, the highest growth rate observed for females of *O. pequira* leads to its shorter longevity in relation to males, despite males have shorter $L\infty$ 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.

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CAPÍTULO 3

LIFE HISTORY CHARACTERISTICS AND RECRUITMENT OF FISH UNDER THE EFFECT OF DIFFERENT HYDROLOGICAL REGIMES IN A TROPICAL FLOODPLAIN

Karina Keyla Tondato, Yzel Rondon Súarez e Clarice Bernhardt Fialho

Summary:

1. The intraspecific variation in the life history characteristics and pattern of recruitment of six fish species was analyzed in different regions of the Pantanal, besides correlating the recruitment of each species with variation in flooding regime in each region.

2. In the northern region (synchronous regime), the combined data collected between the years 2005 and 2010 in Rio Cuiaba and marginal lakes were utilized. In the southern region (asynchronous regime), the collections were made between 2009 and 2011, in Rio Paraguai and marginal lakes.

3. Data on the length of the species *Bryconamericus exodon, Hyphessobrycon eques, Odontosltilbe pequira, Moenkhausia dichroura, Hypoptopoma inexpectatum* and *Eigemnannia trilineata* were obtained.

4. The species did not show any difference in length structure between the hydrological regimes, nor was there intraspecific variation between the populations the synchronous regime and asynchronous.

5. The asymptotic length ($L\infty$) of the species displayed intraspecific variation between the hydrological regimes, with the highest values for the populations of the synchronous regime (northern region) (except for *E. trilineata*). Growth rate (*k*) and mortality (*Z*) showed intraspecific variation between the hydrological regimes, with four species (*B. exodon*, *H. eques*, *O. pequira* and *M. dichroura)* demonstrating lower *k* and *Z* and higher $L\infty$ in the synchronous regime , suggesting that this regime in the northern region offers more favorable conditions compared with the asynchronous regime the southern region. There was no intraspecific variation between the regions for the number of cohorts and longevity, with equal or similar values between the populations.

6. The recruitment pattern did not show intraspecific variation in the form of recruitment distribution for each species between the hydrological regimes, with long period of recruitment displaying a greater pulse for all species between June and August, which also confirms the lack of interspecific variation.

7. In the synchronous regime (northern region), the recruitment pattern of four species (*B. exodon, H. eques, M. dichroura* and *H. inexpectatum*) did not show a significant correlation with the historic level of Rio Cuiaba, but these species did show a negative covariation, besides the other species (*O. pequira* and *E. trilineata*) demonstrating a significant negative correlation with recruitment peaks at low water levels. In the asynchronous regime (southern region), five species (*B. exodon, H. eques, M. dichroura, H. inexpectatum* and *O. pequira*) were significantly associated with the historic level of Rio Paraguai, with recruitment peaks

at the highest water levels, indicating that flooding regime has a decisive influence on the pattern of recruitment (except for *E. trilineata*).

8. The species exhibited intraspecific variation in the life history characteristics, indicating phenotypic plasticity, despite the range of variations not having been sufficient to differentiate the recruitment patterns intra- and interspecifically, demonstrating the strength of specific characters each taxon (intraspecific) as well as local environmental conditions governed by the flooding regime (interspecific). Thus, the populations "fluctuate" characteristics in each hydrological regime (region), but maintain a pattern of life history between the populations of the same species.

Key words: population dynamics, growth rate, mortality, Pantanal, Fisat.

Introduction

In fish, the wide variety of characters of life history and the diverse responses of these organisms to particularities of the environment constantly challenge ecologists to formulate models and theories at the inter- and intraspecific levels that can describe the general patterns within a evolutionary and phylogenetic perspective (Wootton, 1984, 1998; Winemiller and Rose, 1992; Zeug and Winemiller, 2007; Mims and Oldem, 2012). Therefore, information on the self-ecology of species is fundamental as initial and primary knowledge in comparative ecology, since the reproductive strategy of each fish species results from a trade-off between their life history characteristics (Winemiller, 1989; Stearns, 1992), altering length structure, reproductive period, recruitment pattern, growth rate, mortality and longevity of their populations through phenotypic plasticity (Stearns, 1989; Pampoulie *et al.*, 2000; King, Humphries & Lake, 2003; Merona, Vigouroux & Chavez, 2009).

The intra- and interspecific variations in life history characteristics can be determined by the spatial and temporal variability of environmental characteristics (Winemiller, 1989; Blanck & Lamouroux, 2007; Olden & Kennard, 2010), influencing evolution through behavior, physiology and life history characteristics of species, according to the theory of "habitat template" (Southwood, 1988, Townsend and Hildrew, 1994) or by historic and phylogenetic attributes that could limit some specific characters, independent of habitat (Rochet, 2000; Blanck & Lamouroux, 2007), representing an ancestral heritage of the taxon (Coddington, 1988).

Among the environmental factors, the flooding regime is well documented as one of the determinant factors in the ecology of fish in temperate and tropical floodplain regions (Welcomme, 1979; Lowe-McConnell, 1999; Agostinho *et al.*, 2004; Zeug and Winemiller, 2008; Súarez, Petrere Junior & Catella, 2001; Fernandes, Machado & Catella, 2010). However, the large rivers that comprise these floodplains can exhibit a wide gamut of hydrological regimes and innumerous spatial units of habitat that influence and diversify the life history strategies of fish (Winemiller, 1989; Zeug & Winemiller, 2007; Tedesco *et al.*, 2008; Olden & Kennard, 2010), where research is constantly needed aimed at learning more about the ecology of species with broad distribution for a better understanding of their dynamics according to differences in hydrologic cycle and formulation of conceptual models (Winemiller and Rose, 1992; Humphries, King & Koehn, 1999; Mims & Olden, 2012).

Another important factor in studies of population ecology in fish is the pattern of recruitment, which refers to the entry of young individuals into the population, allowing the

population to be constantly renewed (King *et al.*, 2003). The recruitment pattern represents the dynamic interaction between reproductive success, regulation and population variability (Wootton, 1998; Agostinho *et al.*, 2004). It should be noted that hydrology, heterogeneity of habitats and strategy of life history can simultaneously determine the ideal conditions for recruitment (Zeug & Winemiller, 2008; Gorski *et al.*, 2011), since the conditions of river flow influence species differently, providing a condition beneficial to recruitment success for one species and not another (Humphries *et al.*, 1999; King *et al.*, 2003).

In the northern region of the Brazilian Pantanal, as in other floodplains, there is a wide variety of reproductive strategies (Bailly, Agostinho & Suzuki, 2008), but reproduction is seasonal and the majority of species of fish spawn at the beginning of flooding, because water overflow from the principal river onto the plain promotes access to new habitats, offering greater availability of food and shelter for fish larvae and juveniles (Wootton, 1998; Lowe-McConnell, 1999). In this environment, the period of flooding coincides with long photoperiod and higher temperature, according to the "flood pulse concept" (FPC), which holds that conditions and advantages for spawning and recruitment of fish are better when flooding coincides with high temperatures, due to the increase in productivity (synchronous regime) (Junk, Bayley & Sparks, 1989). On the other hand, in the southern region of the Brazilian Pantanal, high temperatures and flooding are not coincident (asynchronous regime), which can be advantageous for a fish spawning in low water levels in the main channel of the river, when food resources are concentrated, as proposed in the hyposthesis of "low flow recruitment" (LFR) proposed by Humphries *et al.* (1999). Thus, the analysis of life history characteristics and recruitment of fish comparing the different regions of the Pantanal is essential for understanding the responses and adaptive evolution of these characteristics. Consequently, it will be possible to project patterns of reproductive strategies in fish exposed to different flooding regimes, besides defining which key factor (environment versus taxon) will determine life history characteristics and recruitment in a tropical floodplain, in the same manner as proposed for floodplains of temperate regions (Winemiller & Rose, 1992; Humphries *et al.*, 1999; Zeug & Winemiller, 2008; Mims & Oldem, 2012). In addition, there are no works comparing life history characteristics on a regional scale in the Pantanal, rather studies only on a local scale, focusing on species of economic interst or evaluation of fishery stocks (Mateus & Petrere, 2004; Mateus & Penha, 2007; Peixer, Catella & Petrere Junior, 2007; Costa & Mateus, 2009; Vicentin, Costa & Súarez, 2012a, 2013; Vicentin *et al.*, 2012b), and also scarce are analyses involving small-sized species (Cunha, Catella & Kinas, 2007; Lourenço, Mateus & Machado, 2008a; Tondato, Fialho & Súarez, 2012, 2013).

Accordingly, we chose for this work six species of small-sized fish, *Bryconamericus exodon* Eigenmann, 1907, *Hyphessobrycon eques* (Steindachner, 1882) ("Mato-grosso"), *Odontostilbe pequira* (Steindachner, 1882), *Moenkhausia dichroura* (Kner, 1858) ("pequira"), *Hypoptopoma inexpectatum* (Holmberg, 1893) and *Eigenmannia trilineata* Lopez and Castello, 1966 ("Tuvira"), because of their wide distribution and abundance in the Pantanal (Súarez et al., 2001, 2012, In press; Verissimo et al., 2005) and because they represent the 3 principal orders of the Neotropical region (Characiformes, Siluriformes and Gymnotiformes). However, despite not being important for fishing, with exception of *E. trilineata* which is utilized as bait, all these species are of great importance as the base of the food chain of icthyofauna and show substantial economic potential (ornamental), as suggested by Pelicice and Agostinho, (2005). It should be noted that small-sized species generally show an opportunistic strategy, with short longevity, high growth rate and mortality, precocious sexual maturation and long reproductive period (Winemiller & Rose, 1992), similar to the classic selection of r-strategists (Pianka, 1970).

In the Brazilian Pantanal, works on the reproductive biology or life history characteristics of the species cited above are scarce, but include the studies of Cunha *et al.* (2007) and Santos & Súarez (2012) with *M. dichroura*, Santana, Tondato & Súarez (2012) with *H. eques* and Tondato *et al.* (2012, 2013) with *O. pequira*. Thus, based on the hypothesis that the life history characteristics of each species under heterogeneous environmental conditions respond in a singular and adaptive way, the objective of this work was to address the following questions: 1) Is there intra- and interspecific variation in length structure, asymptotic length (L∞), growth rate (*k*), natural mortality (Z) and longevity (years) for each species between the hydrological regimes (synchronous and asynchronous regime) of the Pantanal? 2) Does the recruitment pattern of each species vary between the synchronous and asynchronous regime (northern and southern region) of the Pantanal? 3) Is there a correlation between the recruitment patterns of each species in each region with the hydrologic regime of the corresponding river? 4) Is there interspecific variation in recruitment pattern in both hydrological regimes?

Methods

Study area

The Pantanal is a sedimentary floodplain with an area of approximately 140,000 km^2, part of the Upper Rio Paraguai basin, with about 80% of its territory in Brazil, while entering in small parts of Bolivia and Paraguay (Adamoli, 1982). It is characterized by a unimodal

flooding regime, which is essential for all the functions of the system (Junk *et al.*, 1989), since the high rate of evapotranspiration does not allow the local rainfall to contribute significantly to the variations in river level (Hamilton, Sippel & Melack, 1996).

The study area is located in the extreme northern and south regions of the Pantanal (Fig. 1). In the northern Pantanal, the sub-region studied is known as Pantanal de Pocone, and this is located in and around the Reserva Particular de Patrimônio Natural do SESC (SESC/RPPN), next to the margins of the Rio Cuiaba, in the state of Mato Grosso, Brazil (Fig.1). Rio Cuiaba is the principal affluent of Rio Paraguai and is approximately 850 km long (Cavinato, 1995), where there is a complex of marginal lakes in its lower portion, which can show a direct connection with the river channel or be connected through temporary channels in the flooded period. In the high-water season (January to March), the rivers overflow and flood the low areas, and in the low-water season (April to June), the waters return to the main channel of the river. The dry season (July to September) is represented by a period of little rainfall, while the flood season (October to December) is marked by the beginning of the rains and elevation of the water level of Rio Cuiaba (Da Silva & Esteves, 1995), demonstrating a synchronous regime.

In the southern Pantanal, the sub-region studied is known as Pantanal de Porto Murtinho, and this is located along the margins of the Rio Paraguai, in the state of Mato Grosso do Sul, Brazil (Fig. 1). Due to its geographic position and low declivity of 1cm/km in the north-south direction (Hamilton *et al.*, 1996), Pantanal de Porto Murtinho is characterized by the asynchrony between the period of greatest rainfall and temperature (November to March) and the high-water period (June to August). Flooding begins to the north of the plain close to the rainy period, moving slowly southward resulting in a lag of 3 to 6 months between the peak of rains in the riverheads and maximal flooding in the southern part, generally in June, outside the rainy season (Hamilton *et al.*, 1996; Goncalves, Mercante & Santos, 2011), demonstrating an asynchronous regime.
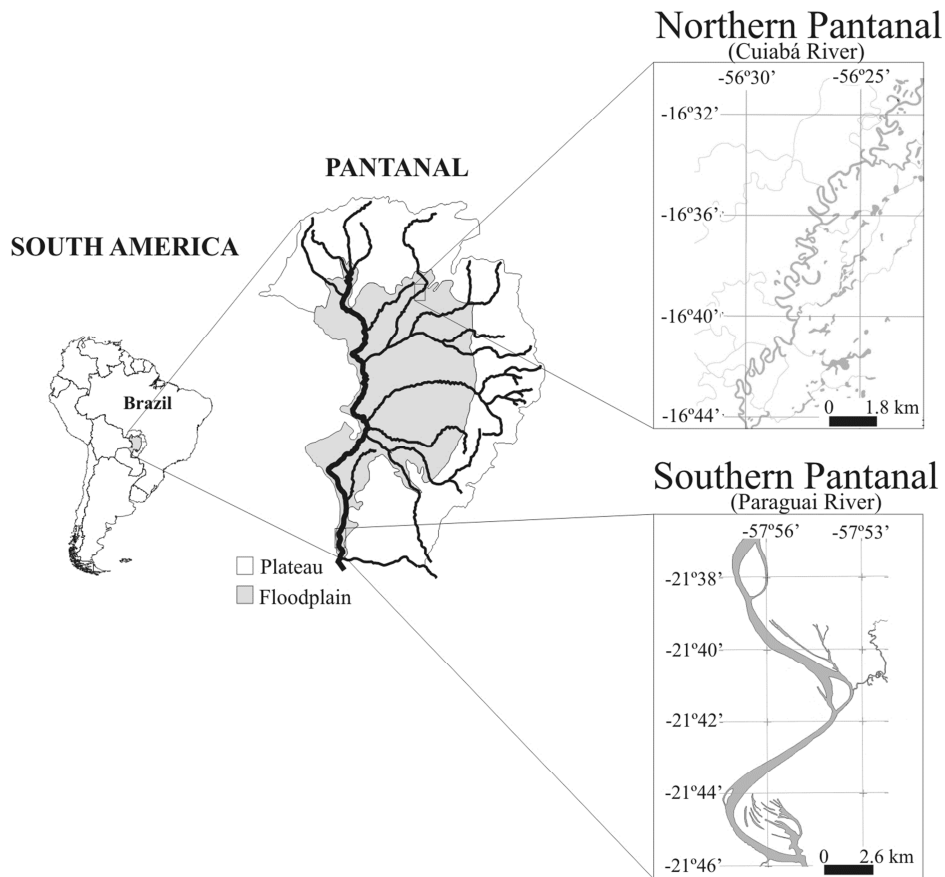
Figure 1. Location area of study.

Collection of data

In the northern Pantanal, we utilized data obtained in the monthly collections of June to December (dry and flooded periods) between the years of 2005 and 2010 and in the month of March (flooded period) only in 2005 and 2006, under the banks of aquatic macrophytes in the littoral zone of the Rio Cuiaba and in the marginal lakes, located within and around the Reserva Particular de Patrimônio Natural-SESC. In total, 44 locations were sampled, including 18 along Rio Cuiaba and 26 lakes, totaling 252 samples. The lakes sampled, for the most part, are on the sides of the river, at a distance of 1 to 5 km (Fig. 1). The fish were collected with the help of a sieve net (1 x 1 m) with 1.5 mm mesh and dragnets.

In the southern Pantanal, the collections were carried out monthly between February 2009 and January 2011 also under the banks of aquatic macrophytes, totaling 109 sample units along the littoral zone of Rio Paraguai and in the marginal lakes (Fig. 1). In this region, the fish were collected with the help of dragnets (1.5 x 5.0 m) and sieve nets (0.8 x 1.2 m), both with 2 mm mesh and non-standardized sampling effort. The fish of both regions were fixed in 10% formalin and stored in 70% ethanol for identification, counting and obtaining

biometric data. In the laboratory, identification was done using the identification key Peixes do Pantanal (Britski, Silimon & Lopes, 2007) and voucher specimens were deposited in the Universidade Federal de Mato Grosso - Laboratório de Ecologia e Manejo de Recursos Pesqueiros -LEMaRPE and in the fish collection of the Universidade Federal do Rio Grande do Sul - Departamento de Zoologia (UFRGS/14065; UFRGS/11169; UFRGS/11167; UFRGS/1170; UFRGS/11166; UFRGS/11172), respectively.

In the northern Pantanal, all length data (mm) available for the six species analyzed in the sampled years were utilized. However, in the southern Pantanal, after identification, a random sub-sample of at least 30 individuals per month was selected, to obtain length data (mm). For the analyses of both regions, the data of the months repeated in consecutive years were summed, because it was assumed that the parameters analyzed do not show significant interannual variation.

The historic levels of the Cuiaba and Paraguai rivers were furnished by the Agência Nacional das Águas (ANA), in reference to the station of Porto Cercado 66280000 and station 67100000, respectively.

Analysis of data

Length structure was analyzed by visual inspection of distributions of frequency of standard length of the population between the regions, besides the utilization of the Kolmogorov-Smirnov test to determine intraspecific difference between the curve of length distribution between the regions, since the large quantity of data and non-standardization of the number of individuals of each species in each region could result in a type I error. Therefore, the frequency distribution was initially determined for individuals of *O. pequira* and *H. eques* per classes of 3mm, *M. dichroura* and *B. exodon* per classes of 4mm, *H. inexpectatum* per classes of 5mm and *E. trilineata* per classes of 10mm, to standardize the data between the regions for analysis and graphic representation.

The asymptotic standard length for each species in each region was estimated on the basis of the largest individual caught utilizing the equation of Pauly (1983): $L\infty = L_{max} / 0.95$. For each species in each region, the growth curve with the respective growth rate (k) was obtained utilizing the ELEFAN I (Electronic Length Frequency Analysis) method (Pauly and David, 1981), according to the growth function of Von Bertalanffy: L(t) = L∞ (1 - exp[-k(t-to)]), where: L∞= asymptotic length, k=growth rate (year^{-1}), t0= nominal age when the length is zero, t=age (months/year) (Bertalanffy, 1938; Gulland, 1977). The ELEFAN I method is in

the program FISAT (FAO-ICLARM Stock Assessment Tools) (Gayanilo & Pauly, 1997), which searches for the best combinations in the determination of parameters, according to the best fit or highest Rn values ("goodness of fit index"). This method utilizes an alternative technique suggested as a good option for the determination of growth parameters, based on the shift of modes of length frequency distribution temporally (Gomiero, Carmassi & Braga, 2007).

Total mortality (Z) defined here as equal to natural mortality (M) was obtained according to the empirical formula of Pauly (1980), which utilizes the information of growth parameters (L∞ and k) and mean temperature (°C) of the environment in which the species was collected, according to the equation: $\ln M = -0.0152 - 0.279\ln L\infty + 0.6543\ln k + 0.463\ln T°C$. However, longevity was calculated by the value estimated according to the equation proposed by Taylor (1958): $t\max = t_0 + 2.996/k$, where $t_0=0$, and by the observation of the number of cohorts (1 cohort= 1 year) generated by the model of Von Bertalanffy carried out previously. FISAT provided the growth performance index (φ), which was obtained using the equation proposed by Pauly and Munro (1984): $φ = \log k + 2\log L\infty$. The growth performance index allows us to see if it is possible to compare the estimated parameters with parameters of other species or phylogenetically related groups, which should provide values close to 3 and similar between the sexes and/or relateed species as an indication that the population parameters were estimated adequately.

The recruitment pattern for each species in each region was obtained by the distribution of monthly frequency of standard length and of growth parameters (L∞ and k) previously estimated, utilizing the routine included in FISAT for the time axis (Gayanilo and Pauly, 1997). According to these cited authors, this manner of calculating generally allows the identification of the number of seasonal pulses of recruitment, which have been generated by the population represented in the data of length frequency. In addition, the analysis of recruitment pattern was done by visual inspection over the year. Next, the Kolmogorov-Smirnov test was utilized with the aim of comparing the shape of the distribution of recruitment of each species between the regions.

Spearman's correlation was performed to determine if there was a relation between the recruitment of each species and the variation in the historic water levels of the river in each region, since normality of the data was not fulfilled.

Results

Length structure

Data were obtained on the length of 15381 individuals, including 1868 specimens of the species *B. exodon,* 3586 of *H. eques,* 3773 of *O. pequira,* 2396 of *M. dichroura*, 1422 of *H. inexpectatum* and 2336 of *E. trilineata.* For all the species analyzed, the range of standard length showed variation between the hydrological regimes (regions), with greatest lengths and maximal length of each species observed in the populations of the synchronous regime (northern region), with exception of *E. trilineata* whose largest individual was recorded in the asynchronous regime (southern region) (Table I and Fig. 2). However, no significant difference was observed for all species (Table I) in the shape of the distribution of standard length between the hydrological regimes (regions) analyzed, demonstrating similarity in length structure between the populations (synchronous and asynchronous regime) of each species (Fig. 2).

Table I. Data standard length and result of the Kolmogorov Smirnov test for six species of small fish in the different hydrological regimes (synchronous and asynchronous regimes) of the Pantanal, Brazil.

Species	Synchronous regime (Northern Pantanal)		Asynchronous regime (Southern Pantanal)		Synchronous vs. Asynchronous Ls (mm)
	N	Ls (mm) min-max	N	Ls (mm) min-max	p
B. exodon	1131	7,7 - 53,4	737	8,4 - 44	0,85
H. eques	3066	9,2 - 36,7	520	12,4 - 30,6	0,77
O. pequira	2347	11 – 41,7	1426	11,2 – 37,7	0,99
M.dichroura	1776	12,7 - 83,3	620	10,4 - 58,8	0,49
H. inexpecatatum	884	13,6 – 90,4	538	15 – 81,2	1,0
E. trilineata	1636	21,6 - 154	700	19 - 182	0,22
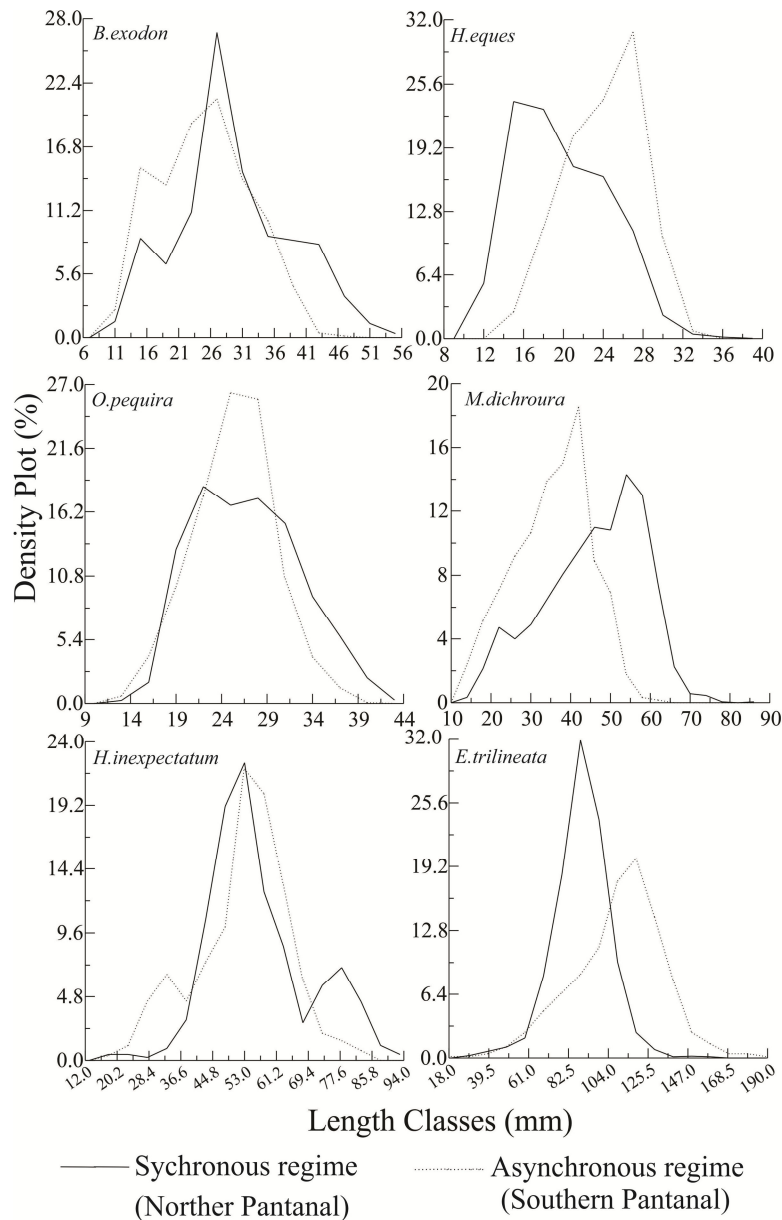
Figure 2. Density plot (%) of standard length classes for six species of small fish in the different hydrological regimes (synchronous and asynchronous regimes) of the Pantanal, Brazil.

Population parameters

The asymptotic length of all species showed intraspecific variation between the hydrological regimes (regions), where the populations of the synchronous regime (northern region) had the highest values of L∞, with exception of the species *E. trilineata* (Table II and Fig. 3). The inverse relation between the asymptotic length and growth rate between the hydrological regimes was observed for *B. exodon*, *H. eques*, *O. pequira* and *M. dichroura*, which showed for the synchronous regime (northern region) a lower growth rate, greater

asymptotic length and lower mortality. However, in the same regime, the species *H. inexpectatum* demonstrated a higher growth rate and higher mortality, showing a direct and positive relation between L∞ and k between the hydrological regimes (regions) (Table II). On the other hand, *E. trilineata* displayed the greatest asymptotic length in the asynchronous regime (southern region), directly related to a low growth rate and low observed mortality (Table II). Thus, of the six species, four showed a low growth rate and mortality, and five species showed a large asymptotic length in the synchronous regime (northern region) (Table II).

Table II. Population parameters of the six species of small fish in different hydrological regimes (synchronous and asynchronous regimes) of the Pantanal.

Species	Pantanal regimes	L∞ (mm)	k (year^{-1})	Ø	Rn	Z (year^{-1})	tmax (years)	Nº of Cohorts
B. exodon	Synchronous	56,18	0,95	3,47	0,53	1,42	3,2	4
	Asynchronous	46,29	1,5	3,50	0,26	2,03	2	3
H. eques	Synchronous	38,64	1,7	3.4	0,18	2,32	1,7	3
	Asynchronous	32,19	1,8	3,27	0,50	2,53	1,7	3
O. pequira	Synchronous	43,79	0.7	3.1	0,27	1,24	4,2	5
	Asynchronous	39,59	0,77	3,08	0,28	1,37	3,9	5
M. dichroura	Synchronous	87,65	0,77	3,77	0,28	1,09	3,9	5
	Asynchronous	61,89	0,97	3,57	0,21	1,41	3,1	4
H. inexpecatatum	Synchronous	95,16	0,81	3,86	0,60	1,10	3,7	5
	Asynchronous	85,42	0,75	3,73	0,22	1,09	4	5
E. trilineata	Synchronous	162,11	0,7	4,26	0,21	0,86	4,3	6
	Asynchronous	191,58	0,57	4,32	0,20	0,72	5,3	7

L∞= Asymptotic lenght, k= Growth rate, Ø= performance growth, Rn= Adjustment index,
Z= Natural mortality e tmax= Longevity
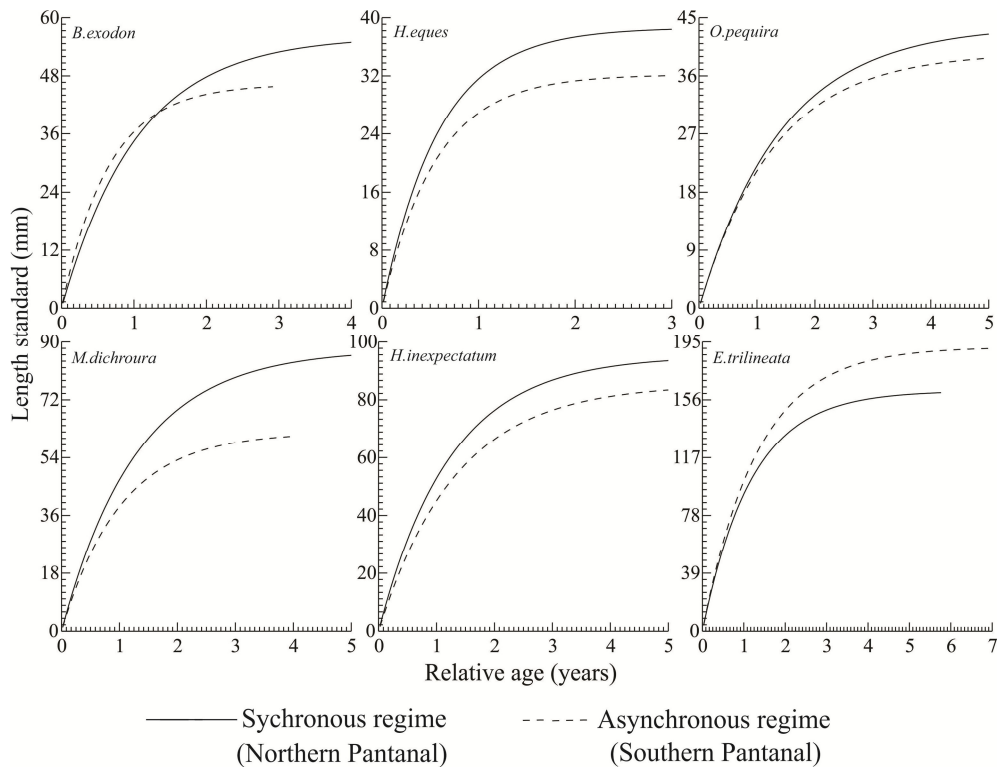
Figure 3. Growth curve of Von Bertalanffy adjusted for the estimated ages (years) of six species of small fish in different hydrological regimes (synchronous and asynchronous regimes) of the Pantanal.

Using growth curves of cohorts generated by the distribution of length classes and by adjusting the Von Bertalanffy growth curve to relative ages estimated in years, there was no evidence of a wide intraspecific variation in the quantity of cohorts and longevity of each species between the hydrological regimes (regions). Between the hydrological regimes, the number of cohorts and longevity showed equal or very close values between the populations of species analyzed (Table II and Fig. 3). The species *H. eques*, *O. pequira* and *H. inexpectatum* displayed the same number of cohorts and similar longevity between the synchronous and asynchronous regimes (northern and south regions) (Table II and Fig. 3). Growth performance index (φ) was close to 3 and similar between the populations (synchronous and asynchronous regimes) of each species (Table II), indicating that the parameters estimated differed little between them, allowing them to be analyzed comparatively.

Recruitment

Recruitment pattern did not show intraspecific variation between the synchronous and asynchronous regimes (northern and south regions), since no significant variation was

observed in the shape of the recruitment distribution of each species between the regions (Table III and Fig. 4). Thus, recruitment over the year was similar between the populations of the synchronous and asynchronous regimes (northern and south regions) in all species, occurring gernerally with greater intensity between the months of February and October, which resulted in specific monthly variations for each species between the hydrological regimes (regions) (Fig. 4). In addition, the greatest pulse (peaks) of recruitment for all species occurred between June and August, demonstrating the similarity in the period of recruitment between the hydrological regimes (regions) (Fig. 4). The recruitment pattern of the species *B. exodon, H. eques, M. dichroura* and *H. inexpectatum* did not show a significant correlation in the synchronous regime (northern region) with the historic level of Rio Cuiaba, but in the asynchronous regime (southern region) it was significantly associated with the historic level of Rio Paraguai, with pulses of recruitment at higher water levels (Table III and Fig. 4). On the other hand, for the species *O. Pequira,* a marginally significant and positive correlation was observed (p=0.09) in the asynchronous regime (southern region) between recruitment and the historic level of Rio Paraguai and a significant and negative correlation (p=0.003) in the synchronous regime (northern region) with the historic level of Rio Cuiaba. Thus, in the synchronous regime, the peaks of recruitment occur with the retreat of waters, the period in which waters rise and there are peaks of recruitment in the asynchronous regime (Fig. 4). For *E. Trilineata*, there was no significant correlation in the asynchronous regime (southern region) between recruitment and the historic level of Rio Paraguai, but rather recruitment correlated significantly with historic level of Rio Cuiaba in the synchronous regime (northern region), with elevation and peaks of recruitment occurring with the decline in water level (Table III and Fig. 4).

Table III. Results of Spearman correlation and Kolmogorov Smirnov in relation to the recruitment of six species of small fish in the different hydrological regimes (synchronous and asynchronous regimes) of the Pantanal, Brazil.

	Synchronous regime		Asynchronous regime		Synchronous vs. Asynchronous
	Northern Pantanal		Southern Pantanal		Northern vs. Southern
Species	**Recruitment vs. River Level Cuiabá**		**Recruitment vs. River Level Paraguai**		**Recruitment**
	r	p	r	p	P
B. exodon	-0,34	0,26	0,90	**0,001**	0,98
H. eques	0,09	0,78	0,87	**<0,001**	0,76
O. pequira	-0,79	**0,003**	0,50	**0,09**	0,98
M. dichroura	-0,49	0,10	0,69	**0,01**	0,42
H. inexpecatatum	0,27	0,37	0,73	**0,006**	0,98
E. trilineata	-0,76	**0,005**	-0,26	0,40	0,76
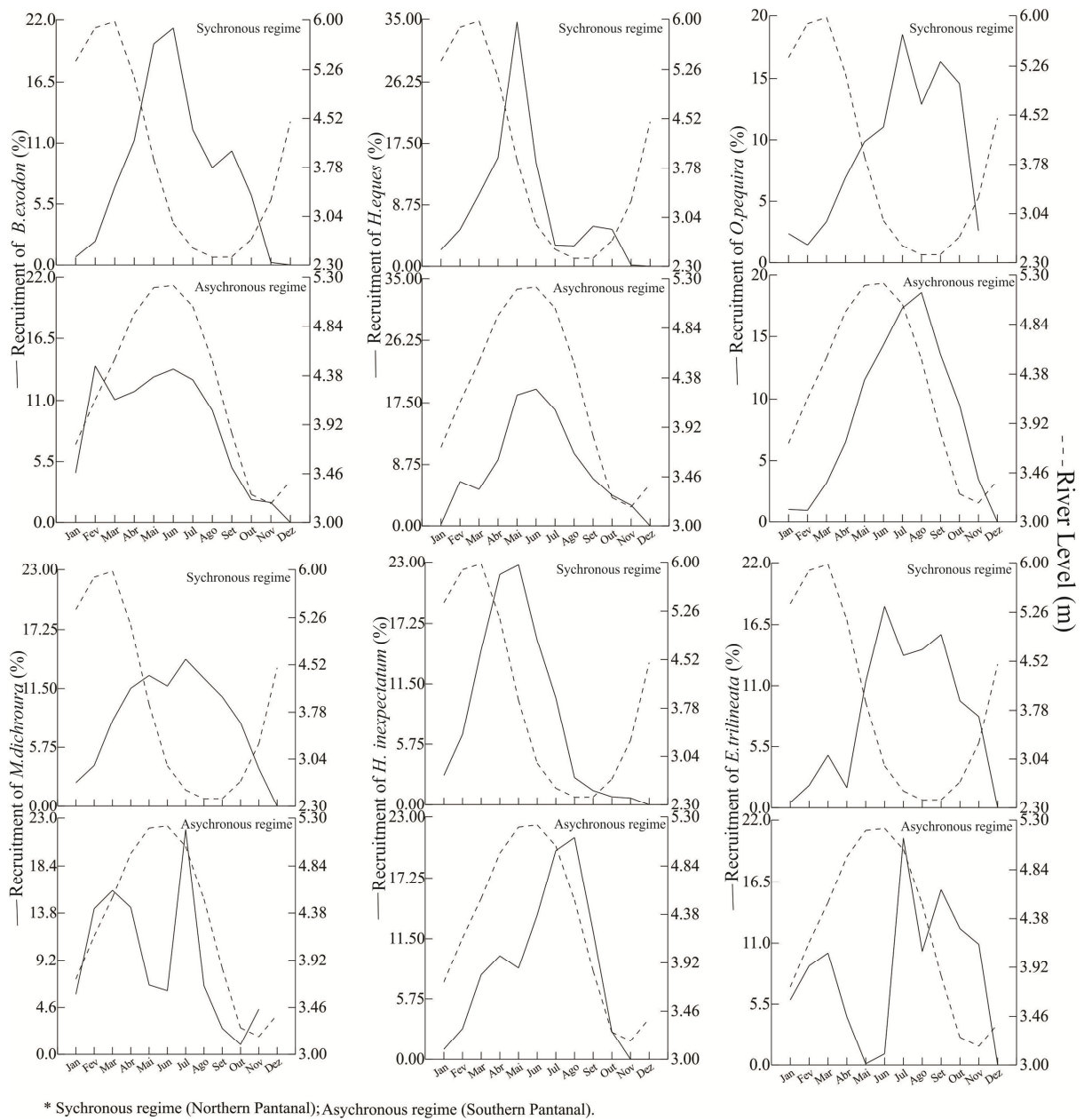
Figure 4. Temporal variation of recruitment (%) of six species of small fish and the historical level of the Cuiabá Rivers (Synchronous regime) and Paraguay (Asynchronous regime) in the Pantanal, Brazil.

Discussion

Length structure

Since the lifespan of the majority of fish species is highly variable, size structure between locations or periods has a decisive influence on population dynamics (De Angelis *et al.*, 1993), determining the nature of many interactions (Pauly, 1998) and the conditions of survival (Nikolskii, 1969). Thus, the maximal length observed in all populations of species in

the region with synchronous regime of the Pantanal, with exception of *E. trilineata*, suggests that the environmental conditions are more favorable for growth in relation to the asynchronous regime, possibly because of the synchrony between the flooding period, high temperature and rainfal, in addition to the greater number of lakes in the northern than southern region, which makes shelter and food more widely available. This result also corroborates the work of Prestes *et al.* (2010), who found that the greater heterogeneity of the habitat in lakes provides conditions that favor the presence of individuals of the larger size classes.

The polymodal appearance of the distribution of lengths of all species in the two hydrological regimes of the Pantanal, indicates the occurrence of various reproductive events over the year and of various cohorts in the populations analyzed, as suggested by Lourenço, Súarez & Florentino (2008b) and Benitez & Súarez (2009) in studying *Serrapinnus notomelas* in Brazilian streams and Tondato *et al.* (2013) for *O. pequira* in the region sampled in this work. This is because size structure in intimately linked to the processes of feeding and reproduction (Lizama & Ambrosio, 2003). Besides, the occurrence of various modes suggests the the species are well established in the habitat, as proposed by Cunha *et al.* (2007) for *M. dichroura* in the Pantanal de Aquidauana (central region- synchronous regime), pointing out the high abundance observed in this work for this species.

According to Orsi, Carvalho & Foresti (2004), the differences in the distribution of lengths of the same species sampled in different regions, can be related to local environmental characteristicas, as well as predation, availablity of food, fecundity and mortality. Therefore, the similar shape of length distribution between the regions (hydrological regimes), observed in all species, gives evidence of a general pattern in structure that does not significantly change, even though the synchronous regime in the northern region shows individuals reaching a greater length and the populations of each regime (region) are under a different flooding regime and environmental conditions, suggesting a strong influence of phylogenetic and taxon characteristics, as reported by Coddington (1988), Rochet (2000) and Blanck & Lamouroux (2007).

Population parameters

Life history characteristics such as growth rate and mortality are strongly influenced by interactions with other species through competition and predation (Sparre & Venema, 1992), varying with availability of food and factors that affect its utilization, such as temperature (Black, Bohlert & Yoklavich, 2008) and with the population density (Lowe-

McConnell, 1999). It should be pointed out that growth rate in fish is also determined genetically and/or physiologically, while L∞ is influenced by the food supply and population density (Beverton & Holt, 1957; Sparre & Venema, 1992), there being a mathematical interaction between the two parameters, where the value of *L∞* influences the value of k, and vice-versa. With exception of the species *H. inexpectatum*, all species showed the expected mathematical interaction of the greater the L∞ the lower the *k,* and concomitantly the lower the natural mortality (Z). Besides the greater maximal lengths having been recorded in the synchronous regime (exception of *E. trilineata*), L∞ also showed the same expected pattern for the populations of these species with the greater values in the synchronous regime, since the parameters are correlated. Additionally, four (*B. exodon*, *H. eques*, *O. pequira* and *M. dichroura*) of the six species showed a lower *k* and Z in the synchronous regime (northern region) of the Pantanal, confirming that this regime shows favorable characteristics in the interactions between food availability and population density in relation to the higher L∞ which lowers *k*. These results suggest that the period of flooding in northern region (Rio Cuiabá) which forms and/or connects the numerous marginal lakes, increasing the area for exploration of food resources, associated with high temperatures (synchronous regime), results in higher L∞, lower *k* and lower Z, in relation to the southern region of the Pantanal, where there is asynchrony between the period of flooding and elevated temperature and rainfall. Corroborating our results, Grabowska *et al.* (2011) in studying *Perccottus glenii* in Poland, also observed variation in growth rates along its geographic distribution, where these differences are considered a common phenomenon in species of fish that are widely distributed (Mann, 1991; Lobon-Cervia *et al.*, 1996). Thus, the results suggest that during flooding the greater expanse of habitats rich in food in the synchronous regime (northern region) guarantees more favorable conditions in comparation with the asynchronous regime (southern region), resulting in higher values of L∞ and lower values of *k.*

On the other hand, the lower *k* and lower Z for *H. inexpectatum* and the lower *k* and lower Z and higher L∞ for *E. trilineata* in the asynchronous regime, suggest that these species have a strategy of life history different from the other species, adapting to guarantee the population balance under the environmental conditions favorable for both species in the southern region, which has a more voluminous river, flooding in the period of mild temperatures and few marginal lakes.

The values of *k* (between 0.57 and 1.8) and of the majority of Z (beween 0.72 and 2.53) were elevated for all species in the two regimes, as considered by Prestes *et al.* (2010) in analyzing three species of *Triportheus*, in lakes of the Central Amazon, whose values of *k*

varied between 0.6 and 0.8 and Z between 1.4 and 1.7. Therefore, at high temperatures, typical of tropical regions, growth rates are high, allowing fish to reach sexual maturity earlier (Hutchings & Jones, 1998), as an adaptive response to rapidly restore their stocks due to high mortality.

Despite the variations in L∞, k and Z between the synchronous and asynchronous regimes of the Pantanal, the longevity of all species was very similar, with only one cohort with greater longevity for *B. exodon* and *M. dichroura* in the synchronous regime and for *E. trilineata* in the asynchronous regime. Therefore, life history characteristics of species between the regions showed intraspecific variation, but the results did not indicate wide differences, showing the same estimate of longevity.

Despite the little information at the species and/or genus level, among the Characiformes (*B. exodon, H. eques*, *O. pequira,* and *M. dichroura*), Cunha *et al.* (2007) analyzed *M. dichroura* in the Pantanal de Aquidauana (central region - synchronous regime) showing a similar value of φ (3.75) and k (0.85) and intermediate L∞ (81 mm) and lower quantities of cohorts (3) compared to values observed in the populations of this species in this work. This result indicates that despite that values vary intraspecifically, occurs at small range not altering a possible pattern in these characteristics for *M. dichroura* in all the Pantanal. Still, the high growth rate for *M. dichroura* and high natural mortality, characterize it as an r-strategist, as suggested by Cunha *et al.* (2007). According to Pauly (1980), r-strategist species are generally small-sized and show high growth rates and natural mortality, noting that *H. eques* can also be considered an r-strategist, because it was the species showing the highest k and Z among all those analyzed.

To better understand the estimated characteristics of *B. exodon*, we refer to the studies of the population aspects of *Bryconamericus stramineus* in tropical streams by Lourenço *et al.* (2008b) and Vasconcelos, Súarez & Lima-Junior (2011), which revealed evident intraspecific variation in life history characteristics. In the work of Lourenço *et al.* (2008b) the value of L∞ (54.7 mm) is similar to the that of the population of *B. exodon* in the northern region of the Pantanal (L∞=56.18 mm), but the value of k (0.54) and longevity (5.54 years) was less than the values of both regions (k=0.95 and 1.5; longevity=2 and 3.2 years, northern and southern, respectively), possibly occurring because of the difference in Z (0.93), which was much less than that recorded for both regions of Pantanal (Z= 1.42 and 2.03). Vasconcelos *et al.* (2011) showed a higher value of L∞ (62.8 mm), but values of k (0.76), longevity (3.94 years) and Z (1.18) were more similar to those found for *B. exodon* in the Pantanal, indicating that phenotypic plasticity affects the life history characteristics of

phylogenetically close populations. These could show more evident differences when compared to the results of Lourenço *et al.* (2008b) or show more similar values when compared to the results of Vasconcelos *et al.* (2011), both in streams, whose environmental and hydrologic conditions are particularly different from floodplains environments.

In relation to the cheirodontines, such as *O. pequira,* the results obtained also showed intraspecific variation when compared to the works of Lourenço *et al.* (2008b) and Benitez & Súarez (2009) with the cheirodontine *Serrapinnus notomelas* in tropical streams. L∞ (42.1 mm), *k* (0.60) and longevity (4.9 years) in the work of Lourenço *et al.* (2008b) were more similar to the values for *O. pequira* (L∞=43.79 mm) of the synchronous regime of the Pantanal, and longevity (3.9 years) and *k* (0.7 and 0.77) in both regimes (regions), while the values of Z (1.08 and 1.61, respectively) were similar for *O. pequira* (1.37 and 1.09) in the two works cited, respectively. Tondato *et al.* (2012) analyzed the variation in life history characteristics between the sexes of *O. pequira* in the asynchronous regime (southern region) of the Pantanal and found values of *k*, Z and longevity very close to the results of both regions in this work, with exception of higher L∞ (females=39.5 mm) differing from L∞ (43.79 mm) of the synchronous regime (northern region). Finally, the high natural mortality of *O.pequira*, compensated by the high growth rate, consequent early maturity (around 12 months), long reproductive period and multiple spawning (Tondato *et al.,* 2013), demonstrates adaptive advantages that can be expanded to the other species (exception *H. inexpecatum* and *E. trilineata*), characterizing them as r-strategists. Fish species that are r-strategists display a relative advantage in the regions where an annual flood pulse occurs, because they are capable of establishing more rapidly in the water bodies and adapting to variations in the availability of resources, in comparison with the k-strategist species (Lae, 1997). A similar situation was described by Junk, Soares & Saint-Paul (1997) for the Amazon plain, demonstrating that the pulse of flooding causes the increase in nutrients necessary for r-strategist fish.

On the other hand, the lower value of *k* and Z for the siluriforme *H. inexpectatum* and the lower *k* and Z and higher L∞ for the gymnotiforme *E. trilineata* in the asynchronous regime (southern region), indicates that these species show a strategy of life history better adjusted to these local environmental conditions, resulting from flooding in the period of mild temperatures and few existing lakes. Braga, Gomiero & Souza (2009) studied in tropical streams the species *Pareiorhina rudolphi,* belonging to the same family (Loricariidae) as *H. inexpectatum*, and observed a lower L∞ (72 mm), slower growth (*k*= 0.35), greater longevity

(8.6 years), and similar mortality (Z=1.1) in relation to *H. inexpectatum* in both regions, indicating an interspecific adaptive variation. In addition, in this same work and that of Braga, Gomiero & Souza (2008), studying *Neoplecostomus microps* (Loricariidae), both species were found to have low fecundity, greater diameter oocytes and long reproductive period, suggesting parental care, characterizing them as k-strategists, since species with low fecundity are associated with an equilibrium strategy (Winemiller & Rose, 1992). Thus, *H. inexpectatum* despite showing interspecific variation in its values because of phylogenetic proximity can express the equilibrium strategy of k-strategists, where more studies of its reproductive biology are necessary to confirm these observations. This strategy proposed by Winemiller & Rose (1992) favors the occupation of environments subject to stable population densities or stressing habitats, which maintain population equilibrium and not abundance (Braga *et al.*, 2008), aimed at greater efficiency in adapting to or exploiting its environment . In relation to the species *E. trilineata,* studies indicate that it shows parental care (Vazzoler, 1996; Giora & Fialho, 2009), which explains the lower *k* and Z and greater longevity recorded for all the species analyzed here, providing evidence that this species is also a k-strategist, following a equilibrium strategy in the Pantanal.

It is important to point out that the φ values between the populations of each region for the species analyzed were similar (φ close to 3). This is in accordance with Gayanilo & Pauly (1997), who reported that phylogenetically related species should have similar φ values, validating a reference for the estimate of growth, since the occurrence of wide variation in growth performance can be an indication of error in the estimates.

Recruitment pattern
   ✓ *Period of recruitment*

Knowledge of the parameters of growth, recruitment and mortality of fish species is very important for studies of population biology, and it is fundamental for the management of fishery stocks (Ferreira & Russ, 1994; Wotton, 1998). That is because, in floodplains, the consequences of a flooding regime are manifested through ecological alterations, capable of modifying life history characteristics by means of selection (Southwood, 1988; Townsend & Hildrew, 1994). In this work, despite the occurrence of variations in some population parameters of the species between populations of different hydrological regimes of the Pantanal, the way in which the entrance of juveniles was distributed did not differ for any of the species between the regions, demonstrating that the pattern of recruitment is similar between the populations over the year. This result also explains the similar form of

distribution in length between the populations of the hydrological regimes of the Pantanal for all species, since they recruit proportionally over the year in both regimes (regions). Besides, the period and pattern of recruitment was similar between the species, considered long for the majority of them (9 months), with the greatest pulse of recruitment for all the species between June and Agust, providing no evidence of interspecific variation in recruitment pattern between the hydrological regimes (regions), even in view of the phenotypic plasticity in the life history characteristics and differences in life strategies (r and k selection) at the species level observed. In addition, the long recruitment pattern indicates an adaptive variation in life history against the singularity of the environment, since a long reproductive period does not correspond to a reproductive strategy for seasonal environments (Munro, 1990), which leads to the occurrence of species with short reproductive period associated with favorable conditions of flooding (Tedesco *et al.*, 2008). Therefore, this result suggests that a key environmental factor unique to the Pantanal, such as the large supply of food or the environmental predictability characteristic of both flooding regimes, even though divergent, is responsible for triggering this pattern in the six species, thereby resulting in their similar recruitment.

Among all the species analyzed, there is only information on the reproductive period and/or recruitment in the Pantanal for *H. eques*, *O. pequira* and *M. dichroura*. The pattern of recruitment for *H. eques* in the asynchronous regime (southern region) is consistent with the long reproductive period observed by Santana *et al.* (2012) for the same region (January to August, with a peak in July). For *O. Pequira,* the recruitment pattern with a peak in July-August in the two regimes (regions), was observed by Tondato *et al.* (2012) for the same species in the asynchronous regime (southern region), corroborated by the long reproductive period, with greater reproductive intensity in July (Tondato et al., 2013). Cunha *et al.* (2007), in studying *M. Dichroura,* indicate on the basis of the growth curve that recruitment occurd in the middle of October, but they emphasized that there was no available information on the reproduction of the species and that this period did not concur with the reproductive biology of the majority of fish of the region (Pantanal de Aquidauana- synchronous regime) with possible spawning in December/January. These authors even considered as explanation some interference by the sampling method. However, the result observed for the pattern of recruitment of *M. dichroura* extends up to October in the northern region of the Pantanal, corroborating at least in part the results of Cunha *et al.* (2007), but it also contradicts the spawning period recorded in December for *Moenkhausia sanctaefilomenae* in the synchronous regime (northern region) of the Pantanal (Lourenço *et al.*, 2008a). For *B.*

exodon, the pattern of recruitment in the asynchronous regime begins in March and lasts until October (period of little rain), as reported by Vasconcelos *et al.* (2011) for *B. stramineus* in streams of the upper Parana basin (Brazil), with a long reproductive period, showing greater reproductive activity between April and August. For the Loriicaridae *H. Inexpectatum,* the pattern of recruitment from February to September considering both regimes (regions), is not similar to the reproductive period (September/October to February) observed fro various species of Loricariidae in streams and lakes in the Southeast and South regions of Brazil (Mazzoni & Caramashi, 1997; Querol, Querol & Gomes, 2002; Bailly *et al.*, 2011, respectivamente). For *E. trilineata*, the recruitment pattern from May to November, despite being the first period of lower intensity in the asynchronous regime (southern region) from January to March, is not consistent with the reproductive period from October to February observed by Giora & Fialho (2009) in South Brazil (sub-tropical region), where there is a lack of information for respective comparisons.

✓ *Flooding regime versus pattern of recruitment (intra- and interspecific)*

The lack of intraspecific variation in recruitment pattern between the different hydrological regimes of the Pantanal and similar interspecific pattern for the six species,, lead to divergences in relation to the influence of flooding regime on reproductive activity. In this sense, it is evident that there is a significant positive relation with the level of Rio Paraguai in the asynchronous regime in the southern region for all the species (exception of *E. trilineata*) and negative relation with Rio Cuiaba in the synchronous regime in the northern region for two species (*O. pequira* and *E. trilineata*) and negative covariation for the other species.

It is known that, in the Pantanal, as in other tropical floodplains, reproduction is seasonal and that the majority of fish spawn when the water level begins to rise, preceding the peak of rains (Lowe-McConnell, 1999; Agostinho *et al.*, 2004; Lourenço *et al.*, 2008a; Tondato, Mateus & Ziober, 2010), indicating that in the synchronous regime the variations in life history characteristics, such as lower growth rate, result in a process of slower recruitment, leading to peaks (pulses) of recruitment during the ebb and drought in this region. This result is possibly due to a concentration of food resources for the larvae, such as the greater density of phytoplankton and zooplankton documented in this region in periods of low water levels (Loverde-Oliveira, *et al.*, 2009; Fantin-Cruz *et al.*, 2011), or for example, a tactic to decrease the competition between larvae and and juveniles of other groups which can be recruited in the peak of flooding. Therefore, the species studied in the synchronous regime (northern region) show phenotypic plasticity to maximize reproductive success, spawning

possibly before the peak of flooding, but recruiting during low water, due to an adjustment of *k*, since Bailly *et al.* (2008), in studying the influence of the flooding regime on the reproduction of various species in the same region observed that independently of strategy, the reproductive peaks of the species preceded the flood peaks.

Howerver, in the asynchronous regime (southern Pantanal), , suggesting that the long recruitment of species is related to a greater reproductive investment as an adaptive response to the respective regime, since King *et al.* (2003) reported that for a better recruitment, fish should reproduce when the water level and temperature increase in a synchronous way. However, the rise and peak in recruitment with the increase (flooding) and peak of river water level, indicates that the flooding regime has a decisive influence on the reproductive activity of the species analyzed, corroborated by Tondato *et al.* (2012; 2013) for *O. pequira* and by Santana *et al.* (2012) for *H. eques* in this region, even though it is a period of mild temperatures and lower rainfall, showing that temperature and rainfall do not trigger reproductive activity in the species analyzed.

Thus, the lack of intraspecific variation in the pattern of recruitment between the regimes of the Pantanal and the correlation of four species with the level of the river in the asynchronous regime (southern region), follows the flood pulse concept (FPC), which proposes that flooding in a plains river is the principal driving force for the maintenance and production of plant and animal biomass (Junk *et al.*, 1989). However, it contrasts studies in Australia that observed that in rivers when the flooding regime does not coincide with the period of high temperatures, species of fish reproduce in the summer, when the water levels are low (Humphries *et al.*, 1999, 2002; King *et al.*, 2003), as proposed by the hypothesis of low flow recruitment (LFR) (Humphries *et al.*, 1999). In contrast, the pattern of recruitment in the synchronous regime (northern region) of the Pantanal follows the hypothesis of LFR, where it is not influenced by flooding, despite the period of high temperature and rainfall being coincident with the period of flooding. This result is evident, since the species recruit when the water level is low, even though a negative correlation with river level has been observed only with two species. In the other species, the pattern of recruitment co-varies negatively with the level of the river, with the greatest pulses of recruitment occurring with low river level values. Therefore, the pattern of recruitment that does not vary intraspecifically between the different hydrological regimes, demonstrates a controversy in relation to applicability of CPI and RBF between the regimes (regions), because the synchronous regime (northern region) does not support the CPI hypothesis and because the asynchronous regime (southern region) do not support the RBF. Thus, the results indicate a

specific adaptation in relation to recruitment, because they show plasticity in the life history characteristics, altering the growth rate and maintaining the same pattern of recruitment. The lack of observed intraspecific variation suggests that the specific characters each taxon acts more strongly on these species, but when related to the lack of interspecific variation, it is evident that local environmental conditions influenced by the flooding regime strongly determine the species that show the same recruitment pattern, even though not related.

It is important to point out that the RBF hypothesis was tested in temperate environments, which could have been important for the partial observation in the results, since the mean annual temperatures vary between 22.5 and 26.5ºC in both regions of the Pantanal (tropical region) (Goncalves *et al.*, 2011), where this situation is not considered a critical condition if reproducing in the months of mild temperatures. Nevertheless, the higher levels of competition and mortality (Welcomme, 1979; Lowe-McConnell, 1999) can be more decisive factors in the determination of this recruitment strategy, compared to flooding, temperature and rainfall.

Therefore, dynamic mathematical models based on length distribution, in which natural parameters of growth and mortality are calculated, are not only necessary for the application of various methods and actions and/or strategies of evaluation of management, but also allow tests of life history characteristics (Stergiou, 2000), such as the previous classifications presented in k- or r-strategists. Finally, the species analyzed here displayed intraspecific variation in some of their life history characteristics, demonstrating phenotypic plasticity, but remarkably, the range of variation, was not sufficient to differentiate the patterns of recruitment intra- and interspecificlly, showing evidence of the strength of specific characters each taxon and local environmental conditions, respectively. Thus, the populations "fluctuate" the characteristics in each hydrological regime (region), but maintain a pattern of life history between populations of the same species. Finally, this work emphasizes the urgent need of research on the population ecology of fish in floodplains, including those with asynchronous regime, for example the southern Pantanal, because the recruitment of the species analyzed occurs more intensively during flooding and high water, a period during which regional laws permit fishing. In addition, the models proposed in the literatura are for species of temperate environments, which are less diverse and more constant.

Acknowledgments

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Considerações Finais

História de vida de Odontostilbe pequira no Pantanal Sul.

A análise dos traços de história de vida caracterizou *O. pequira* como uma "estratégista oportunista", uma vez que, apresenta pequeno porte, maturação rápida, longo período reprodutivo, desova parcelada, elevada fecundidade relativa, altas taxas de crescimento e mortalidade e pequena longevidade. Em relação à variação dos traços de história de vida entre os sexos, os resultados deixam evidente que a diferença no comprimento de primeira maturação (Cp_{50}) entre os sexos e a ausência de machos nas maiores classes de comprimento, é resultante das diferenças dos seguintes traços, que foram mais elevados nas fêmeas: a) comprimento assintótico ($L\infty$); b) taxa de crescimento (k) e c) mortalidade natural. Adicionalmente, os machos não atingem os maiores comprimentos registrados, porém, exibem uma maior longevidade por apresentarem um menor k. Enfim, apesar das variações entre os sexos nos traços de história de vida, a estrutura em comprimento, o período reprodutivo, bem como, o recrutamento, foram semelhantes entre os sexos, indicando que a diferença observada nos traços são adaptações para garantir o equilíbrio populacional e persistência da espécie, que apresenta sincronia no padrão de recrutamento. Ressaltando que, a atividade reprodutiva e consequentemente recrutamento é influenciado pelo nível do rio, ocorrendo com maior intensidade na inundação e cheia, seguindo o "Conceito do Pulso de inundação", mesmo diante da assincronia entre o período de inundação e o período de pluviosidade e elevadas temperaturas, característico na região.

História de vida para seis espécies de peixes (B. exodon, H. eques, O. pequira, M. dichroura, H. inexpectatum e E. trilineata) sob diferentes regimes de inundação.

As espécies apresentaram variação intraespecífica entre as regiões, para o comprimento assintótico ($L\infty$), taxa de crescimento (k) e mortalidade (Z), demonstrando menores valores de k e Z, e maiores $L\infty$ na região Norte (maioria das espécies), sugerindo que a inundação sincrônica com período de elevada pluviosidade e temperatura, associada com uma maior área (maior número de lagoas marginais) abundante em alimentos garante condições mais favoráveis comparada com a região Sul. Contudo, as espécies não apresentaram variação intraespecífica na estrutura em comprimento, no número de coortes e longevidade, com valores iguais ou semelhantes entre as populações norte e sul. O padrão de

recrutamento também não apresentou variação intraespecífica entre as regiões, com longo período de recrutamento e maior pulso para as espécies entre Junho e Agosto, o que também confirma ausência de variação interespecífica.

Portanto, foi observada plasticidade fenotípica nos traços de história de vida para as espécies, apesar da amplitude das variações não ter sido suficiente para diferenciar os padrões de recrutamento intra e interespecificamente, demonstrando a forte influência das características filogenéticas e das condições ambientais locais, respectivamente. Deste modo, as populações "flutuam" os traços em cada região, mas com pouca amplitude mantendo um padrão de história de vida entre populações da mesma espécie.

Na região norte do Pantanal, o padrão de recrutamento em baixos níveis de água é possível devido às variações nos traços de história de vida, como a menor taxa de taxa de crescimento registrada, que resultou em um processo de recrutamento mais lento, atrasando e resultando em picos (pulsos) de recrutamento durante a vazante e seca na região, apoiando a hipótese do "Recrutamento em baixo fluxo" (RBF). Na região Sul, a elevação e pulsos mais intensos no recrutamento ocorreram com o aumento e pico do nível do rio para as espécies (exceção, *E. trilineata*), seguindo o CPI. Portanto, o padrão de recrutamento nas regiões norte e sul, demonstra uma controvérsia em relação à aplicabilidade do CPI e RBF entre as regiões, indicando uma adaptação específica das espécies em relação ao recrutamento, que evidencia a influência dos caracteres específicos de cada táxon (intraespecificamente) e do regime de inundação (interespecificamente).

Enfim, a análise dos traços de história de vida das seis espécies disponibiliza informações valiosas para melhor compreensão sobre dinâmica populacional e fornece subsídios para estratégias de manejo na pesca do Pantanal, ressaltando o sul do Pantanal, visto que o padrão de recrutamento longo com maior intensidade na inundação e cheia, ocorre no inverno, época de pesca livre.