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Original Article

Reproduction of *Hypoptopoma inexspectatum* (Holmberg, 1893) (Siluriformes, Loricariidae) in the Southern Pantanal Floodplain, Upper Paraguay River Basin, Brazil

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(With 9 figures)

Abstract

This work aimed to describe the reproductive biology of *Hypoptopoma inexspectatum* in southern Pantanal. A total of 538 individuals were sampled and analyzed from February 2009 through January 2011 in southern Pantanal. We did not observe differences in sex-ratio, and both sexes presented positive allometric length/weight relationship (LWR). Reproduction occurs mainly from January to February. Females reached first maturation (L_{50}) with 37.80 mm and males with 45.80 mm. Absolute fecundity is estimated in mean=177.43 (sd±127.06) oocytes and relative fecundity in 3.12 (sd±2.23) oocytes/mg. Fecundity is positively correlated with standard length (Spearman r= 0.43; p=0.013), and total spawning is a used spawning strategy for *H. inexspectatum*.

Keywords: size at first maturation, gonadosomatic index, reproductive period, spawn type.

Reprodução de *Hypoptopoma inexspectatum* (Holmberg, 1893) (Siluriformes, Loricariidae) na planície de inundação do Pantanal Sul, bacia do alto rio Paraguai, Brasil

Resumo

Este trabalho teve como objetivo descrever a biologia reprodutiva de *Hypoptopoma inexspectatum* na região do Pantanal Sul. Foram amostrados e analisados entre fevereiro de 2009 a janeiro de 2011 um total de 538 indivíduos. Não foi observada diferença na proporção sexual e ambos os sexos apresentam relação alométrica de peso/comprimento positiva. A reprodução ocorreu principalmente entre os meses de janeiro e fevereiro. Fêmeas atingiram o tamanho de primeira maturação (L_{50}) com 37,80 mm e machos com 45,80 mm. A fecundidade absoluta média foi 177,43 (dp±127,06) ovócitos e a fecundidade relativa foi de 3,12 (dp±2,23) ovócitos/mg. A fecundidade foi positivamente correlacionada com o comprimento padrão (Spearman r= 0,43; p=0,013) e a desova parcelada foi a estratégia de desova utilizada por *H. inexspectatum*.

Palavras-chave: tamanho de primeira maturação, índice gonadossomático, período reprodutivo, tipo de desova.

1. Introduction

The Upper Paraguay Basin has a diversified and relatively well-preserved ichthyofauna, mainly in the Pantanal floodplains that present differences in flood pulse dynamics among subregions and along longitudinal gradient. For small fish species, little information is available about biological traits in the context of adjustment to seasonal variations in the Pantanal (Junk et al., 1989; Alho and Sabino, 2011).

It is expected that the life cycle of fishes adjusts to flood pulse as a strategy to optimize reproductive success in floodplain river systems (Junk et al., 1989). This means that the increase of river level would allow for the expansion of aquatic habitats and offer resources otherwise unavailable before such increase. These conditions would also increase recruitment success (Junk et al., 1989; Freitas et al., 2015).

Siluriforms are the main Neotropical freshwater fish group with diversified biological characteristics (Reis et al., 2016). For *Hypoptopoma*, 15 species are valid (Fricke et al., 2019) with seven (46.7%) described in the last ten years. Only *Hypoptopoma inexspectatum* is registered occurs outside the Amazon basin and frequently sampled in association with macrophyte beds in the main channel of larger rivers. Species of this group are commonly used for ornamental purposes. Yet, the absence of biological data makes it difficult to propose policies aimed at the conservation and sustainable use of these resources.

Therefore, to understand the effect of temporal variation on reproductive and population characteristics of *Hypoptopoma inexspectatum* in the southern Pantanal region, the present work describes the effect of seasonality on reproduction, as well as reproductive characteristics, such as sex-ratio, size at first maturation, fecundity, and spawning type.

2. Material and Methods

2.1. Study area

The Pantanal is the greatest floodplain area in the world (140,000 km^2). It is located in the Upper Paraguay River Basin (Junk et al., 2006; Súarez et al., 2017), mainly in Brazilian territory, but also Bolivia and Paraguay. The Porto Murtinho region represents approximately 2.8% of Brazilian Pantanal, one of the smallest areas (Silva and Abdon, 1998), and marks the southern limit of the Brazilian Pantanal. In Porto Murtinho Pantanal, the river level historically peaks from May to July, and dry season occurs from October to December (Tondato et al., 2018; Santana et al., 2019).

The Paraguay River is the main watercourse of the Pantanal, and the Amonguijá River is one of its tributaries in the Porto Murtinho region. The lower part of the Amonguijá River is a wide floodplain with narrow areas covered by macrophytes. In the Paraguay River, macrophytes are restricted to the river banks (Scanferla and Súarez, 2016; Súarez et al., 2017).

Samples of *Hypoptopoma inexspectatum* were collected from beds of aquatic macrophytes along 25 km of the Paraguay and Amonguijá Rivers in the Pantanal at Porto Murtinho (Figure 1). Captures were performed monthly from February 2009 through January 2011. In each month, approximately six sampling stations, distributed in the Paraguay and Amonguija Rivers, were sampled, totaling 109 sampling stations in two years. In some cases, the same sampling stations were repeated, but in different months. The repeated months over the two-year period were grouped for statistical analysis.

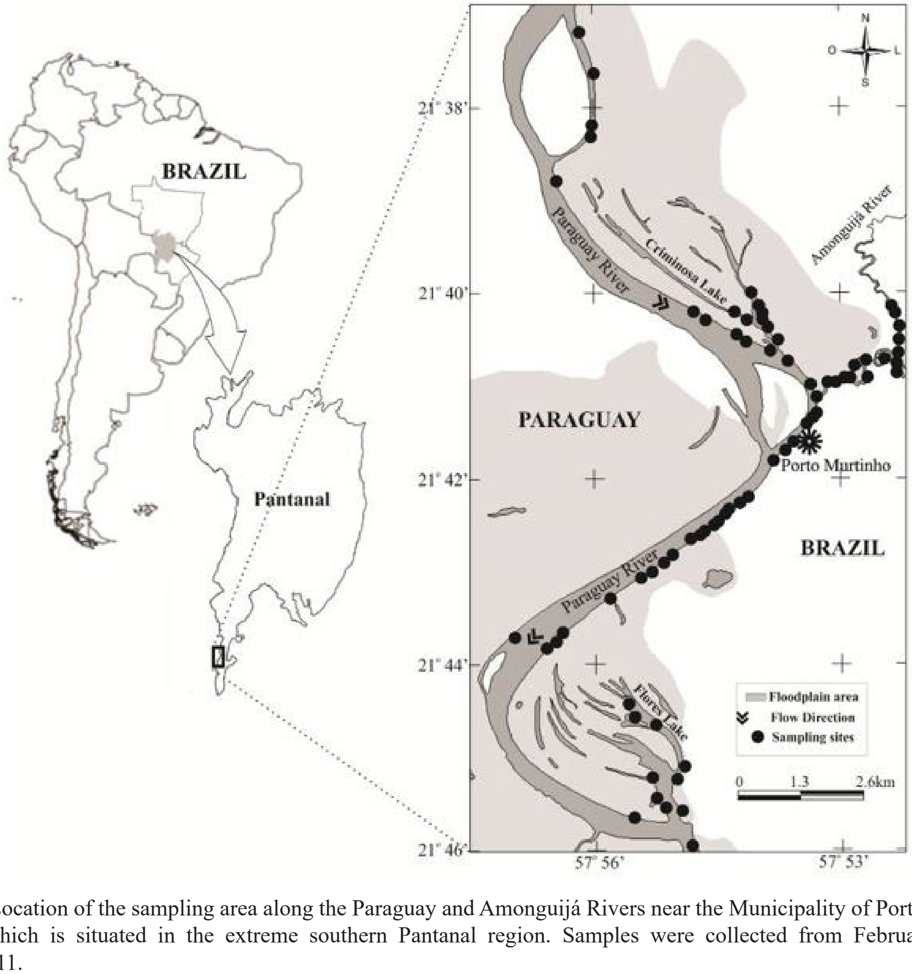

Figure 1. Location of the sampling area along the Paraguay and Amonguijá Rivers near the Municipality of Porto Murtinho (Brazil), which is situated in the extreme southern Pantanal region. Samples were collected from February/2009 to January/2011.

2.2. Data collection

Samples of *H. inexspectatum* were collected using a sieve (0.8 × 1.2 m) and drag nets (1.5 × 5.0 m) with 2 mm mesh. They were placed in 5% Eugenol solution, fixed in 10% formalin, and preserved in 70% ethanol. In the laboratory, each specimen was identified, measured for total length (mm), standard length (mm) and total body weight (g) and, after abdominal incision, the samples were sexed. Stages of gonadal maturation and gonad weight (g) were also recorded for both males and females. Gonad stages were determined macroscopically, according to Vazzoler (1996), as: A = immature, B = maturing, C = ripe, D = semi-spent and E = spent.

2.3. Data analysis

Differences in sex-ratio for the whole period and quarterly variation were quantified using the χ^2 test with Yates correction for the first case.

Linear regression was used to estimate the length-weight relationship (LWR) according to the equation TW = aTLb (Ricker, 1973) after logarithmic transformation (Froese, 2006). The degree of association between TW and TL was calculated by the determination coefficient (r^2). The confidence interval ($\alpha = 0.05$) of parameters “a” and “b” was also estimated.

The monthly variation in gonadosomatic index (GSI) was quantified through an analysis of covariance, using GSI as response variables, months as categorical variables and standard length as covariable. The correlation between female size and total fecundity was estimated using the Spearman correlation. The size of oocytes in mature females was measured by optical stereomicroscopy, and frequency distribution was used to determine if spawning was total or split.

Variance partitioning was used (Peres Neto et al., 2006) to explain the effects of environmental descriptors on female reproduction activity, using the “varpart” command in “vegan” package. Historic river level, mean water temperature during sampling, cumulative rainfall in the sampling period, and length of daylight were used as explanatory variables. Historic river level was obtained from the Brazilian Navy stationed at Porto Murtinho Municipality.

The size at first sexual maturation was estimated for males and females using a logistic regression, and then the variation in the relationship between reproductive (1) and immature individuals (0) was modeled as a function of fish size. All fishes with stage of gonadal maturation superior to immature (i.e., maturing, mature, semi-spent and spent) were considered reproductive individuals (1).

Absolute fecundity was estimated based on the total number of vitellogenic oocytes of 32 mature females, whereas relative fecundity was determined by the number of vitellogenic oocytes per milligram of body weight for these same females (Suzuki et al., 2000; Arantes et al., 2013). For bulky ovaries, only a subsample was used, and the fecundity was estimated by a simple rule of three based on the assumption that the subsample would contain the number of counted oocytes proportional to the weight of this subsample relative to full ovarian weight. Relative fecundity was obtained from the number of mature oocytes per milligram of the total weight of females. Values for absolute fecundity, relative fecundity and mean number of mature oocytes are presented.

The type of spawning was determined by analysis of the relative frequencies of diameter classes of oocytes in ten mature females. Diameters of one hundred and fifty randomly chosen oocytes were measured using a magnifying glass with an ocular micrometer. The measurements were then converted into millimeter and used to obtain occurrence frequencies for oocyte diameters, which were then used to infer the type of spawning. Hatching mode was evaluated using density plots of the frequency distribution of oocyte diameters (Vazzoler, 1981). Observation of the most advanced mode of hatching, along with the position of the ovaries, indicated developmental oocyte phases, which permitted the inference of spawning type.

All statistical analyses were performed using the R platform (R Development Core Team, 2017). For all statistical tests, a significance level of $p<0.05$ was adopted.

3. Results

We sampled and analyzed a total of 538 individuals form the Paraguay and Amonguijá Rivers, including 231 females and 248 males. We could not identify the sex for a total of 59 individuals. The standard length varied from 28.26 mm to 81.14 mm for females and from 27.24 mm to 72.73 mm for males. Total weight varied from 0.23 g to 12.09 g for females and from 0.23 g to 7.26 g for males. While the distribution of sexes using standard length was similar between the sexes, females reached higher total weight than males (Figure 2).

We encountered no significant differences in sex-ratio for the whole samples (Chi-squared=0.60, gl=1, p=0.43), and the sex-ratio did not vary temporally (Chi-squared=17.10, gl=11, p=0.10). The general sex-ratio was 1.07 males:females, and this ratio did not vary along the year (Figure 3). On the other hand, the number of sampled individuals did present a clear temporal pattern in that we observed a decrease of sampled individuals from May to July.

The length/weight relationship (LWR) results showed that both sexes present positive allometric growth, according to the following equation describing LWR for females: $\text{Total Weight}=0.00000246*\text{Standard Length}^{3.48}$ with confidence interval ($\alpha=0.05$) for angular coefficient varying from 3.42 to 3.53. For males, the equation was $\text{Total Weight}=0.00000332*\text{Standard Length}^{3.40}$ with confidence interval for angular coefficient varying from 3.36 to 3.46. In spite of the overlap of confidence interval, no significant differences in angular coefficient were found for either sex (Figure 4).

Females of *H. inexspectatum* presented higher GSI from January to February (F=10.12, p<0.001). Males also presented higher GSI values in the same period (F=8.95, p<0.001). Importantly, the higher GSI values occur in months with higher temperatures and greater precipitation

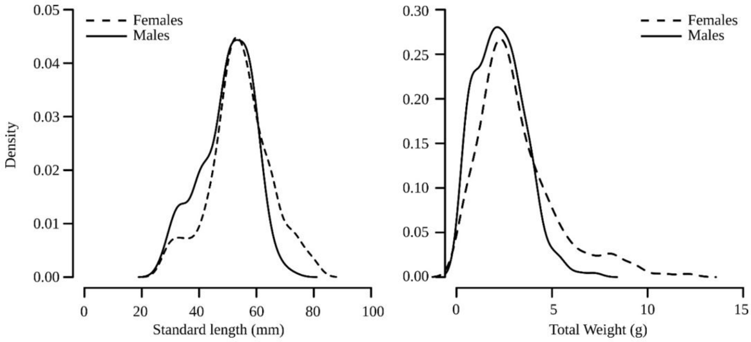

Figure 2. Density plot of standard length and total weight for females and males of *H. inexspectatum* in the southern Pantanal region where samples were captured from February/2009 through January/2011.

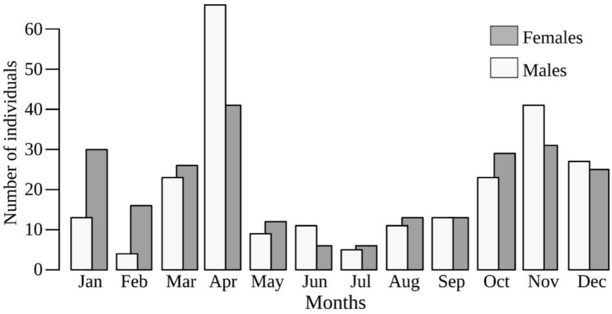

Figure 3. Number of individuals by sex analyzed for females and males of *H. inexspectatum* in the southern Pantanal region where samples were captured from February/2009 through January/2011.

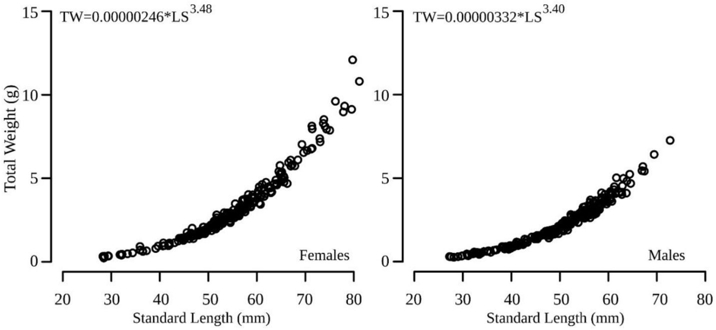

Figure 4. LWRs for females and males of *H. inexspectatum* captured in the southern Pantanal region from February/2009 through January/2011.

(December to February). Our data also suggest that larger females and males have higher GSI values (F=84.98; $p<0.001$; $r^2=0.53$ and F=8.01; p=0.005; $r^2=0.36$, respectively), suggesting that the increase of size allows a corresponding increase in reproductive investment (Figure 5). River level and day length were the best predictors of temporal variation of gonadosomatic index for *H. inexspectatum* in southern Pantanal (Figure 6).

The estimated size at first maturation for females (L_{50}) was estimated to be 37.8 mm ($IC_{(\alpha=0.05)}$= 35.7 to 39.9 mm), and 100% of females reached sexual maturity (L_{100}) with 47.7 mm ($IC_{(\alpha=0.05)}$= 43.5 to 51.9 mm). For males, we estimated that 50% would be sexually mature with 45.8 mm ($IC_{(\alpha=0.05)}$= 44.02 to 47.6 mm), and 100% of males reached sexual maturity (L_{100}) with 78.3 mm ($IC_{(\alpha=0.05)}$= 70.2 to 86.5 mm). The size at first maturation for females represents 46.6% of their maximum observed standard length, while males represent 62.9% of their maximum observed standard length (Figure 7).

Absolute fecundity varied from 16 to 595 vitellogenic oocytes (mean=177.43±127.06). Relative fecundity varied from 0.28 to 10.47 oocytes/mg (mean=3.12±2.23). Total fecundity is positively correlated with standard length (Spearman r= 0.43, p=0.013), indicating that larger females have higher fecundity (Figure 8).

Oocyte diameters showed two peaks, the first representing reserve oocytes and the second varying from 0.9 to 1.5 mm as mature oocytes ready to spawn. Thus, our results suggest a total spawning for *H. inexspectatum* in the southern Pantanal region (Figure 9).

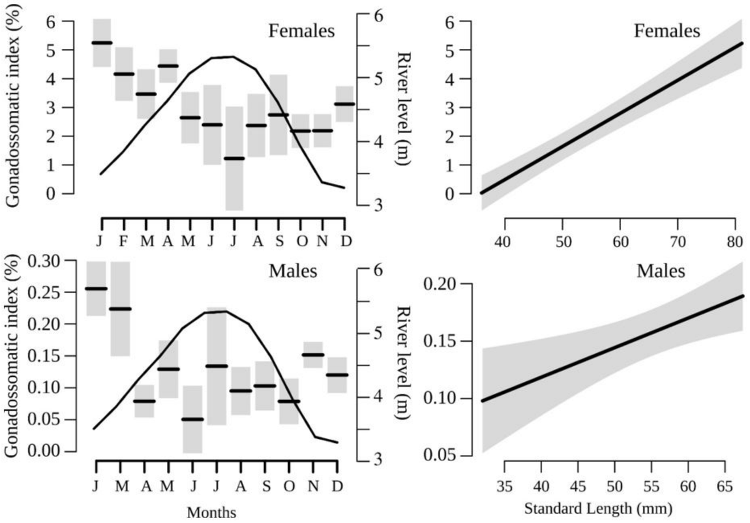

Figure 5. Frequency distribution of GSI (Mean±Confidence Interval) values relative to river level for females and males of *H. inexspectatum* in the southern Pantanal region where samples were captured from February/2009 through January/2011.

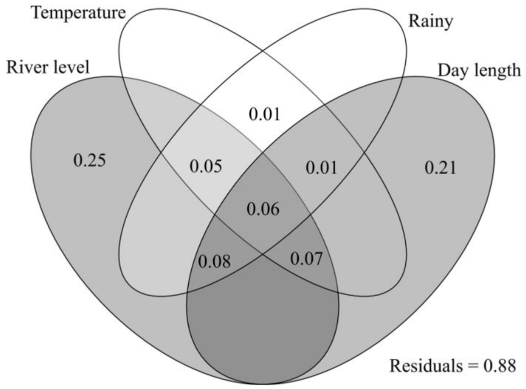

Figure 6. Variance partitioning of river level, water temperature, cumulative rainfall, and day length all influence the gonadosomatic index for females of *H. inexspectatum* in the southern Pantanal region where samples were captured from February/2009 through January/2011.

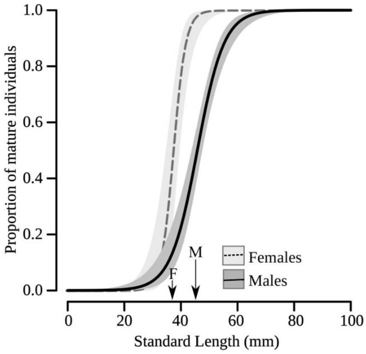

Figure 7. Proportion of mature *H. inexspectatum* females and males as a function of standard length for samples collected in the southern Pantanal region from February/2009 through January/2011. The arrow indicates size at first maturation (L50) for Females (F) and Males (M).

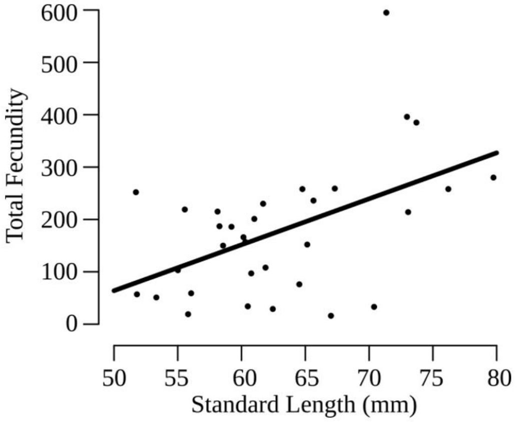

Figure 8. Variation in fecundity, as a function of standard length of females of *H. inexspectatum*, for samples captured in the southern Pantanal region from February/2009 through January/2011.

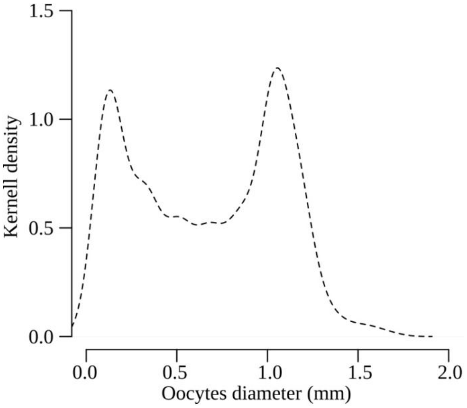

Figure 9. Density graph of oocyte diameter of females of *H. inexspectatum* for samples captured in the southern Pantanal region from February/2009 through January/2011.

4. Discussion

According to the theory of sexual selection, a 1:1 sex-ratio is a stable evolutionary strategy (Fisher, 1930). From this perspective, the analyzed population of *H. inexspectatum* presented an expected result in equilibrium conditions. Although sex-ratio is an important biological characteristic, it has been largely neglected in fish population studies; however, it remains an important descriptor of reproductive potential of a population (Marshall et al., 2006).

Temporal variation in the number of sampled individuals was measured by a non-standard method. Nonetheless, this parameter was still difficult to calculate in months with a higher river level, suggesting that the increase in river level leads to a reduction in sampled individuals. This is an understandable result considering the occurrence of individuals at the edge of macrophyte beds, which become less accessible during peak flooding. This contributes to less capture frequency, as well as the natural reduction of fish density when the river levels rise. This result can also be explained by increase of habitat availability and resultant refuge for the species. Temporal variation in species abundance is common in many environments and is considered fundamental to defining species diversity in communities (Shimadzu et al., 2013). In our study area, the variation in flood pulse is an important determinant of variation in the abundance of aquatic species (Junk et al., 1989; Scarabotti et al., 2011).

The larger size of females is also observed in other Loricariidae species, such as *Loricariichthys castaneus* (Gomes et al., 2011), *Hypostomus affinis* (Duarte et al., 2011), and *Hypostomus francisci* (Sales et al., 2016). This difference is usually explained by the need of females to invest in fecundity, and larger females can produce more oocytes, a phenomenon observed in our study (Dala-Corte and Azevedo, 2010; Sales et al., 2016).

We observed that both sexes presented positive allometric growth, suggesting a higher investment in mass increase relative to length. This result can be considered a strategy to rapidly accumulate energy before the reproductive phase of life, leading to higher fitness (Froese, 2006). Some species show differences in LWR between sexes, as observed for *Odonstostilbe pequira* and *Astyanax lacustris*, also found in the southern Pantanal region (Tondato et al., 2012; Súarez et al., 2017). For other species, both sexes can present the same weight increment rate as that observed for *H. inexspectatum* (our data) and also for *Hyphessobrycon eques* in the southern Pantanal region (Santana et al., 2019). Again, while energy allocation schemes are fundamental to understand the life cycle histories of fish, few studies reporting on this can be found in the literature (Olsson and Gislason, 2016). Notwithstanding the lack of previous literature, our studies lead us to propose that *H. inexspectatum* allocates similar energy in proportion to weight and length along size growth in the southern Pantanal region.

The higher GSI values at the beginning of the year, followed by higher temperature, pluviosity and day length, are inconsistent with the idea that flood pulse plays a key role in the life cycle of fish in the southern Pantanal region where flooding peaks from June to July. Therefore, our results suggest that river level does not trigger reproduction in *H. inexspectatum* individuals, but rather presents an inverse correlation with gonadosomatic index. While few studies have reported on Loricariidae reproduction, higher reproductive intensity during a period of higher temperatures and pluviosity can also observed in such species as *Loricariichthys platymetopon* (Marlucci et al., 2005), *Loricariichthys castaneus* (Gomes et al., 2011), *Loricariichthys melanocheilus* (Zardo and Behr, 2015), and *Farlowella hahni* (Figueiredo et al., 2019). Thus, the short reproductive period concentrated in the summer appears to be a more common strategy in Loricariidae. Water temperature is considered one of the important factors for the reproductive period of fish, acting as a trigger for hatching eggs and larvae. Conversely, *Otocinclus vittatus*, also found in the southern Pantanal region, has a different reproductive seasonality with a longer reproductive period following the flood pulse (Pereira and Súarez, 2019). Multicolinearity of environmental variables is commonly used to explain fish reproduction. However, we used a variance partitioning method that estimates the individual fraction of the influence to each environmental variable. Thus, our results showed that river level and day length play important roles in *H. inexspectatum* spawning in southern Pantanal.

The importance of environmental variables on reproductive dynamics varies according to fish species (Araújo et al., 2012; Pessoa et al., 2013); however, the role of different responses to seasonality in the same habitat is poorly studied. Clearly, an understanding of the environmental features that drive the life cycle in the Pantanal floodplain can provide foundational knowledge that will help explain the species-specific response to seasonality among species with different life-history traits. Evaluating how fishes of different reproductive guilds respond to seasonality, Bailly et al. (2008) suggested that short-distance migration is less affected by flood pulse. While we did not consider the migration of *H. inexspectatum*, this characteristic was not evaluated in this study.

Females of *H. inexspectatum* reach larger sizes, but reach sexual maturity at smaller sizes. This suggests a lower growth rate by females when compared to males, even though females and males reach sexual maturity at the same age, but with different size. In general, it is accepted that size at first maturation is adjusted to maximize resource allocation to somatic growth and reproduction (Mazzoni et al., 2005; Karna and Panda, 2011; Lemos et al., 2011) with physiological and behavioral consequences. Comparing relative size at first maturation between sexes, we observed even greater difference in size at the beginning of reproduction. Considering stream fishes, Castro (1999) proposed that small-sized fishes reach sexual maturity early. The same conclusion was drawn by Azevedo (2010) in a meta-analysis with Characidae species. However, the phylogenetic influence on reproductive traits, as observed, along with the respective biological data, is unavailable for Loricariidae species. This means that the differences between the sexes during the early stage of reproduction need to be more intensely investigated for *H. inexspectatum*.

Larger females presented higher fecundity, which is a common pattern in fishes, and our results also showed an increase of investment in reproduction along somatic growth with larger females presenting greater GSI values. Thus, with smaller growth rate in larger females, it is plausible that a higher proportion of obtained resources could be allocated to reproduction in females of *H. inexspectatum* (Beldade et al., 2012).

Our results suggest that *H. inexspectatum* presents higher fecundity when compared to *Otocinclus vittatus* in the same region (Pereira and Súarez, 2019). Usually Loricariidae species are considered fishes with lower fecundity (Gomes et al., 2015) and greater number of oocytes (Winemiller and Rose, 1992; Kolm and Ahnesjö, 2005) when compared to Characiforms. Low fecundity can usually be explained as a strategy to compensate for higher energy allocation to parental care (Winemiller and Rose, 1992; Bailly et al., 2011; Gomes et al., 2015), and some Loricariidae species do display some parental care behavior. However, we saw no indication of parental care in *H. inexspectatum*, and the absence of data for other *Hypoptopoma* species makes it rather difficult to define quantitatively how much lower fecundity can be considered within the same species group.

We observed two synchronous peaks in oocyte size in *H. inexspectatum*, as also observed in *Hypostomus ternetzi* (Suzuki et al., 2000) and *Hypostomus francisci* (Sales et al., 2016), suggesting total spawning. This behavior can be considered a strategy that coincides with higher temperatures and increased rainfall in this Pantanal region, characteristics usually associated with a higher probability of juvenile survival (Gomes et al., 2011). The asynchronous river level flood pulse, as observed in this region (river level peaks are not coincident with higher temperatures and rainfall), can present a negative influence on growth parameters for this species (Tondato et al., 2018), resulting in smaller $L\infty$ and k when compared to species inhabiting the Cuiabá River, which shows synchronicity among water level, temperature and rainfall. On the other hand, the recruitment pattern observed in the southern Pantanal is significantly correlated with river level (Tondato et al., 2018).

To conclude, the reproductive strategy of *H. inexspectatum* in the southern Pantanal region leads to a total spawning and smaller L50 and L100 for females and reproductive success can be maximized through a greater adjustment between juvenile input and river level and longer days in this Pantanal region. Our study proposes that the correlation of reproductive seasonality with environmental variables can be evaluated, thereby removing spurious correlation by the commonly used multicolinearity of variables. As such, it is anticipated that our work will earn a place with policymakers engaged in conserving these resources.

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