



Life history traits of the glass knifefish *Eigenmannia desantanai* (Gymnotiformes: Sternopygidae) in the Southern Pantanal, Brazil

Características de história de vida da tuvira *Eigenmannia desantanai* (Gymnotiformes: Sternopygidae) no Pantanal Sul, Brasil

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Abstract: Aim: This study investigated life-history traits of *Eigenmannia desantanai* in the southern Pantanal floodplain. **Methods:** Fish were collected beneath stands of aquatic macrophytes using seine nets and rectangular sieves with a 2 mm mesh size in the Paraguay and Amonguijá rivers between February 2009 and January 2011. **Results:** A total of 484 individuals were sampled, including 351 females, 113 males, and 20 individuals of undetermined sex. Females predominated in the population (3.1:1), and no significant differences were observed in total weight or standard length between sexes. Both sexes exhibited negative allometric growth. Females reached sexual maturity at an estimated standard length of 63.06 mm, and males at 59.58 mm. Mean absolute fecundity was 305.3 oocytes (mean relative fecundity = 0.17), with no significant correlation with female body weight or standard length. The frequency distribution of oocyte diameter indicated batch spawning. Females showed a prolonged reproductive period, with two peaks in gonadosomatic index (GSI) values: the first from January to April, and the second including June, August, and September. GSI was correlated with river level and temperature. In contrast, males reproduced throughout the year, with no influence from environmental variables. **Conclusions:** The results indicate that *E. desantanai* responds to immediate environmental conditions and demonstrates high reproductive investment through a prolonged breeding period. Reproductive peaks occurred during the hydrological phases of rising waters and flood, associated with high or increasing temperatures. Additionally, the species exhibits low fecundity, batch spawning, and an extended reproductive period, characterizing it as an equilibrium strategist.

Keywords: reproductive biology; population biology; small fish; Paraguay river; tuvira.



Resumo: Objetivo: Este estudo investigou características de história de vida de *Eigenmannia desantanai* no Pantanal Sul. **Métodos:** Os peixes foram coletados sob bancos de macrófitas aquáticas utilizando redes de arrasto e peneiras, com malha de 2 mm, nos rios Paraguai e Amonguijá entre fevereiro de 2009 e janeiro de 2011. **Resultados:** Um total de 484 indivíduos foi amostrado, incluindo 351 fêmeas, 113 machos e 20 indivíduos de sexo indeterminado. As fêmeas predominaram na população (3,1:1) e não foi observada diferença significativa na distribuição do peso total e comprimento padrão entre os sexos. Ambos os sexos apresentaram crescimento alométrico negativo. As fêmeas atingiram a maturidade sexual com comprimento padrão estimado em 63,06 mm, enquanto os machos em 59,58 mm. A fecundidade absoluta média foi de 305,3 ovócitos (fecundidade relativa média = 0,17), sem correlação significativa com o peso total ou o comprimento padrão das fêmeas. A distribuição da frequência do diâmetro dos ovócitos indicou desova parcelada. As fêmeas tiveram um período reprodutivo prolongado, com dois períodos com valores elevados de Índice Gonadossomático (IGS), sendo o primeiro de janeiro a abril e o segundo incluindo junho, agosto e setembro. O IGS foi correlacionado com o nível do rio e com a temperatura. Em contrapartida, os machos se reproduziram durante o ano todo, sem influência de variáveis ambientais. **Conclusões:** Os resultados indicam que *E. desantanai* responde às condições ambientais imediatas e demonstra um alto investimento reprodutivo com um período reprodutivo prolongado. Apresentaram picos de reprodução nos meses que correspondem ao período hidrológico de enchente e cheia, associado a temperaturas elevadas ou em elevação. Além disso, a espécie apresenta baixa fecundidade, desova parcelada e um longo período reprodutivo, caracterizando-se como uma estrategista de equilíbrio.

Palavras-chave: biologia reprodutiva; biologia populacional; peixes pequenos; rio Paraguai; tuivira.

1. Introduction

Gymnotiformes, commonly known as knifefish, sarapós, or electric fish, are represented by the families Apterontidae, Gymnotidae, Hypopomidae, Rhamphichthyidae, and Sternopygidae, and are widely distributed across Central and South America (Alves-Gomes et al., 1995; Albert, 2001; Peixoto & Pinna, 2022). Species within this order inhabit a diverse range of habitats, including river channels, flooded forests, forest streams, coastal creeks, estuaries, and floodplains (Albert & Crampton, 2005), often near submerged roots, aquatic plants, and floating vegetation (Peixoto et al., 2015).

Among the families, Sternopygidae displays low phenotypic variability but high ecological diversity (Cella & Crampton, 2013), with particular emphasis on the genus *Eigenmannia*, the most diverse, comprising approximately 30 valid species (Ferraris Junior et al., 2017; Dutra et al., 2021; Dutra et al., 2022). *Eigenmannia* exhibits taxonomic complexity across a wide geographical range, as evidenced by *Eigenmannia trilineata* López & Castello, 1966. Through the study of osteological, morphometric, and coloration traits, other species have been described (Peixoto & Waltz, 2017; Peixoto & Ohara, 2019). One example is *Eigenmannia desantanai* Peixoto, Dutra & Wosiacki 2015, found in the Upper Paraguay River basin, specifically within the Pantanal floodplain (Severo-Neto et al., 2015; Peixoto et al., 2022; Peixoto et al., 2022).

Eigenmannia desantanai does not exhibit secondary sexual dimorphism (Gimênes-Junior &

Rech, 2022). This species forages in areas with macrophyte beds, feeding primarily on small aquatic and terrestrial invertebrates, as well as plants (Gouveia et al., 2022). This species has significant ecological importance due to its trophic interactions and considerable economic relevance, comprising the main group (70% – knifefish) used as live bait by riverside communities and fishermen for catching large carnivorous fish (Marques & Calheiros, 2013), in addition to serving as an ornamental species (Gimênes-Junior & Rech, 2022). However, individuals are captured in an uncontrolled manner, highlighting the need for biological information to support stock maintenance and economic programs related to its captive production. According to Pelicice et al. (2017), insufficient knowledge of the biology of Neotropical fish species remains one of the main barriers to effective conservation. The authors emphasize that economic exploitation without technical guidelines may lead to stock depletion and biodiversity loss.

In this context, studies aiming to understand the life history strategies of fish through characteristics that are plastic and adaptable, such as: length at first maturation, growth, reproductive period, sex ratio, and fecundity in different environments (Vicentin et al., 2013; Tondato et al., 2014; Figueiredo et al., 2019; Lampert et al., 2022) are essential to comprehend the adaptations that ensure survival and population balance (Vazzoler, 1996; Lowe-McConnell, 1999; Wootton, 1999). Therefore, a detailed study of *Eigenmannia desantanai*

is crucial to ensure the sustainability of its natural stocks, to support appropriate management and conservation practices, and to enable its economic use in a responsible manner.

The Pantanal floodplain is considered an important model for ecological studies due to its well-defined hydrological cycles, which serve as key factors in maintaining biological populations and act as selective forces for strategies related to feeding, growth, and reproduction (Junk & Cunha, 2005; Schulz et al., 2019). Fish species in this floodplain have their reproductive activity linked to the hydrological cycle (rising river levels and/or high precipitation), and their biological responses to these fluctuations vary according to their position along the continuum of the three life history strategies (opportunistic, equilibrium, and periodic) as defined by Winemiller & Rose (1992).

In this floodplain, reproductive success is evident across different strategies, with opportunistic species exhibiting prolonged spawning periods and little or no parental care; equilibrium species displaying extended reproductive periods with developed parental care; and periodic species characterized by short reproductive periods with little or no parental care (Bailly et al., 2008; Barzotto et al., 2017; Tondato et al., 2018; Rauber et al., 2021). Therefore, fish living in floodplain environments experience alternating periods of flood and drought with periodic hydrological variations, and these environmental characteristics may determine the optimal trade-off strategy for maintaining their populations (Tondato et al., 2018; Rauber et al., 2021).

Knowledge of life history strategies in small species has increased over the past decades, but remains limited in the Neotropical region. For the knifefish *Eigenmannia desantanaei*, information on life history traits is particularly scarce (Muniz et al., 2017; Tondato et al., 2018). This species was previously recorded as *Eigenmannia trilineata* in the Paraguay River basin and was recognized as a distinct species (*E. desantanaei*) by Peixoto et al. (2015). Available studies focus primarily on trophic ecology, conducted by Santos et al. (2009), Corrêa et al. (2011), Ximenes et al. (2011), and Gouveia et al. (2022).

Among Gymnotiformes, seasonal environmental changes such as increased rainfall and the resulting rise in water levels have been widely recognized as key drivers of reproductive activity (Giora et al. 2014; Waddell et al. 2019; López-Rodríguez et al. 2025). In the study by López-Rodríguez et al. (2025), three sympatric Gymnotiformes species from the

Eastern Amazon exhibited distinct reproductive responses under the same environmental conditions, underscoring the role of phenotypic plasticity in traits such as fecundity, reproductive period duration, and oocyte development. Therefore, we hypothesize that although the equilibrium strategy is maintained among Gymnotiformes, life history traits display plasticity and intraspecific variation shaped by local environmental factors. In the context of the Pantanal, the historical water level of the Paraguay River is expected to serve as an important predictor of reproductive activity, influencing both the timing and intensity of reproductive effort across the hydrological cycle.

Based on this framework, the objective of this study was to evaluate the life history traits of *E. desantanaei* by (i) characterizing the population based on length, sex ratio, and length-weight relationship; (ii) determining the reproductive period, considering gonadal development stages and the Gonadosomatic Index (GSI); (iii) assessing the influence of environmental factors on the reproductive periods of males and females; (iv) estimating the size at first maturation (L_{50} and L_{100}); and (v) determining fecundity and spawning type.

2. Material and Methods

2.1. Study area

The study was conducted in the southern portion of the Pantanal, in the municipality of Porto Murtinho, Mato Grosso do Sul, Brazil (Figure 1), encompassing two distinct environments: the Paraguay River, the main river of the Upper Paraguay Basin (gray circles), with an average width of approximately 300 meters and a flow of $0.81 \text{ m}\cdot\text{s}^{-1}$ ($\pm 0.36 \text{ SD}$); and the Amonguijá River, a smaller tributary (green circles), with an average width of approximately 40 meters and a slower flow of $0.20 \text{ m}\cdot\text{s}^{-1}$ ($\pm 0.23 \text{ SD}$). The riverbanks are characterized by abundant stands of aquatic macrophytes, including *Eichhornia azurea*, *E. crassipes*, *Polygonum ferrugineum*, and *Urochloa subquadrifera*. The region is part of an extensive seasonally flooded plain, characterized by a monomodal and asynchronous hydrological regime. While in the northern Pantanal flooding occurs synchronously with the period of highest rainfall (November to March), in the southern Pantanal river flooding is delayed by 3 to 6 months relative to peak precipitation, resulting in a temporally asynchronous flood pulse (Hamilton et al., 1996). The hydrological cycle in this region is divided into dry (Dec-Jan), rising waters (Feb-May), flood (Jun-Aug), and receding season (Sept-Nov). The strong seasonality, combined with environmental heterogeneity provided

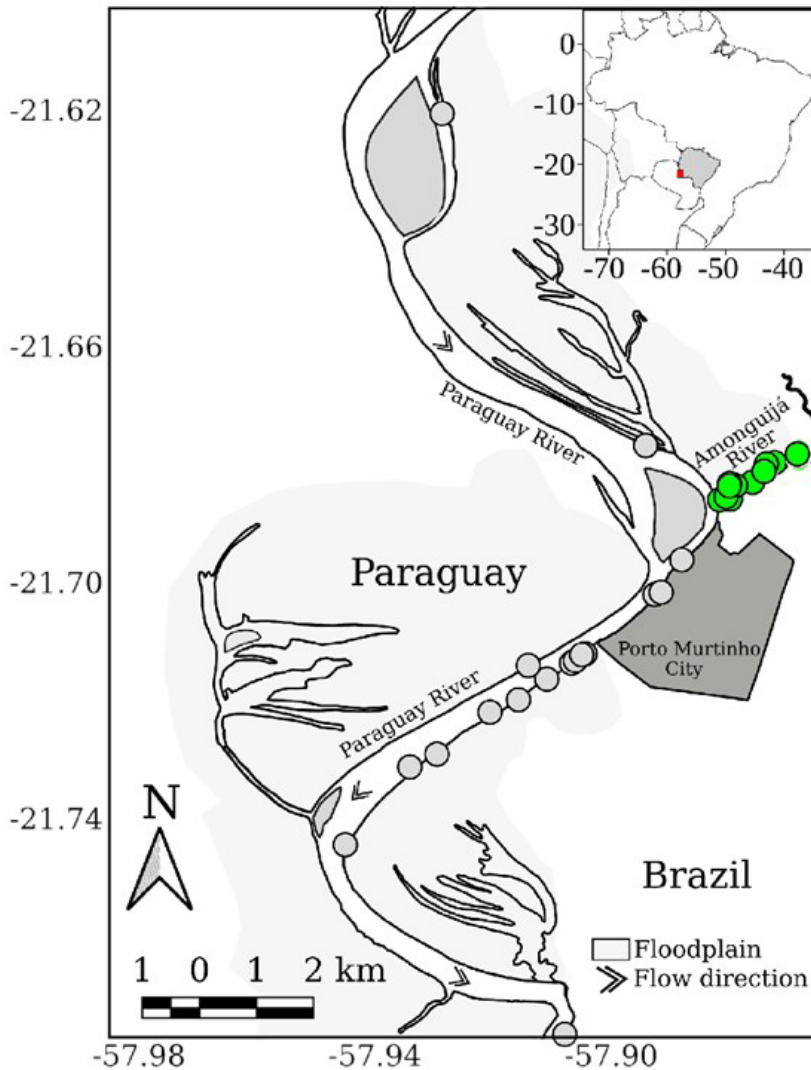


Figure 1. Location of sampling points along the Amonguijá (green circles) and Paraguay (gray circles) rivers in the southern Pantanal, Porto Murtinho, MS, Brazil.

by macrophyte diversity, shapes the life-history traits of fish species in these aquatic ecosystems.

2.2. Data collection

Sampling occurred monthly between February 2009 and January 2011 (Authorization – SISBIO 1345801), along littoral zones and marginal lakes of the Paraguay River, southern Pantanal. In addition, the distance between sampling sites is small, not exceeding 25 km between the most distant points. There are no physical barriers or physicochemical differences between the sites. Moreover, flooding homogenizes the fish distribution, so the population is considered a single unit.

Fish were collected beneath stands of aquatic macrophytes using seine nets (1.5 x 5 m) and rectangular sieves (0.8 x 1.2 m), both with a

mesh size of 2 mm. Sampling effort was not standardized. The specimens were anesthetized with eugenol, placed in plastic bags, and fixed in 10% formaldehyde. In the laboratory, the fish were preserved in 70% ethanol, and identification was performed with the aid of the study by Peixoto et al. (2015). Voucher specimens were deposited in the Coleção Zoológica da Universidade Federal de Mato Grosso do Sul - ZUFMS (ZUFMS 8683, 8684). Subsequently, approximately 30 fish per month were analyzed, but it was not possible to capture 30 individuals every month over the 24-month period, resulting in a reduced sample size. To ensure a more temporally representative dataset, we grouped data from equivalent months across the two years. We followed the data grouping procedure used in other studies conducted in floodplain

environments, based on evidence that the consistent seasonal hydrological pattern, which repeats over time, creates a predictable environment and does not substantially alter the temporal reproductive pattern (Tondato et al., 2018; Pereira et al., 2021; Tondato-Carvalho et al., 2025). Therefore, we assume that the analyzed parameters (Gonadosomatic Index and frequency of gonadal maturation stages) do not exhibit significant interannual variation.

Biometric measurements were taken, including total weight (TW in g), standard length (SL in mm), and total length (TL in mm). The fish were then eviscerated for sex identification, gonad weight, and gonadal maturation stage, which was determined based on macroscopic characters (immature, maturing, mature, and semi-spent) according to Vazzoler (1996).

During sampling, water temperature was recorded at each site. River level data were obtained from the base of the Marinha do Brasil station in 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 were supplied by the Instituto Nacional de Meteorologia (INMET).

2.3. Data analysis

The distribution of standard length and total weight was visually inspected for both males and females. Afterwards, the Kolmogorov-Smirnov test was applied to assess differences between sexes.

A Chi-Square (X^2) test was used to evaluate whether the sex ratio significantly differed from the expected (1:1) across the study period and between months. The length-weight relationship was obtained for each sex using the equation $\log W = a + b \log L$, where W is weight (g), L is standard length (mm), " a " is the intercept, and " b " is the slope coefficient, estimated via nonlinear regression (Froese, 2006).

The reproductive period was determined by analyzing the monthly frequency distribution of gonadal maturation stages and variation in the Gonadosomatic Index (GSI), calculated using the equation $GSI = \frac{GW}{TW} \times 100$, where " GW " is equivalent to Gonad Weight and " TW " is Total Weight (Vazzoler, 1996). The Kruskal-Wallis test was conducted to test for significant differences in the GSI of females and males between sampling months.

To assess the effect of environmental factors (precipitation, temperature, average river level, historical average river level, and photoperiod) on reproductive activity (GSI) of males and females, a Generalized Linear Model (GLM) with a Gamma

distribution and stepwise selection procedure was applied to select the best model based on the Akaike Information Criterion (AIC) (Zuur et al., 2009). The model with the lowest AIC was chosen. The analyses were performed using R software (R Development Core Team, 2021), employing the "glm" function.

The length at first maturity where 50% (L_{50}) and 100% (L_{100}) of the population (females and males) reaches sexual maturity were estimated using logistic regression. Immature individuals were considered non-reproductive (0), while fish with gonads in maturation, mature, and spent stages were classified as sexually active (1). Standard length was used as the exploratory variable and the frequency of mature individuals as the response variable (Roa et al., 1999; Alves et al., 2020).

To estimate absolute fecundity, 20 females with mature gonads the highest GSI values were selected. The total number of oocytes was counted. Relative fecundity was determined by the number of oocytes counted per milligram of total female weight (Suzuki et al., 2000; Arantes et al., 2013). The possible relations between relative fecundity and standard length (mm), total weight (g) and gonad weight (g) were determined using Spearman's correlation.

For determining spawning type, a random gonad subsample was obtained from 11 mature females for analysis. For each female, 101 oocytes were randomly selected from the gonads, photographed using a Leica photomicroscope (M205C/DFC420), and measured for in terms of diameter using ImageJ software. Frequency distribution of oocyte diameters was then performed for visual inspection of the spawning type.

3. Results

A total of 484 individuals of *E. desantanae* were analyzed, consisting of 351 females, 113 males, and 20 individuals of indeterminate sex. Females predominated in the population with a sex ratio of 3.1:1 (Female: Male) ($X^2 = 121.60$; $p < 0.001$), and were significantly more numerous throughout all sampled months ($X^2 = 31.9$; $p < 0.001$) (Figure 2).

The total weight of females ranged from 0.13 g to 8.14 g, and from 0.04 to 6.51 g in males. Standard length ranged from 44 to 174.00 mm for females and 31 to 175.85 mm for males. Nevertheless, no significant difference was observed in total weight ($p = 0.14$) and standard-length distribution ($p = 0.17$) between sexes (Figure 3).

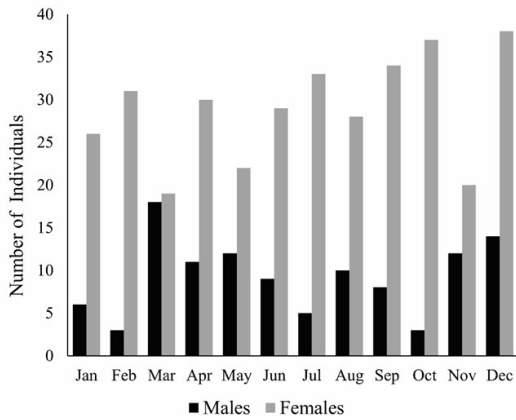


Figure 2. Temporal variation in the number of females and males of *Eigenmannia desantanai* from February 2009 to January 2011 in the southern Pantanal, Brazil.

The average slope coefficient for the length-weight relationship in females was 2.77 ($R^2 = 0.83$), with a minimum value of 2.64 and a maximum of 2.90. For males, the average was 2.69 ($R^2 = 0.86$), ranging from 2.48 to 2.90. This result indicates a negative allometric growth for both sexes of *E. desantanai*, showing a greater increase in length compared to weight (Figure 4).

Regarding the Gonadosomatic Index (GSI), significant variation was observed across months for females ($H = 50.06$; $p < 0.001$) and males ($H = 23.34$; $p < 0.01$). Females exhibited two periods with elevated GSI values were observed: the first from January to April, and the second comprising June, August, and September (Figure 5). For males, a peak

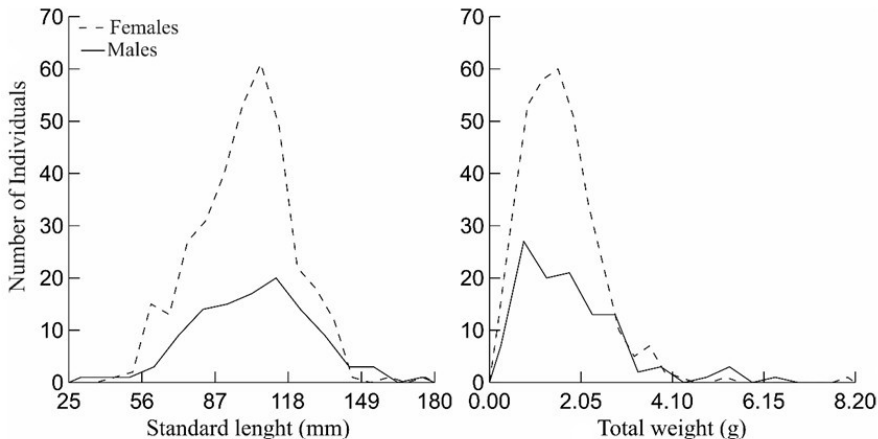


Figure 3. Density plot of standard length (mm) (A) and total weight (g) (B) for females (dashed line) and males (solid line) of *Eigenmannia desantanai* collected from February 2009 to January 2011 in the southern Pantanal, Brazil.

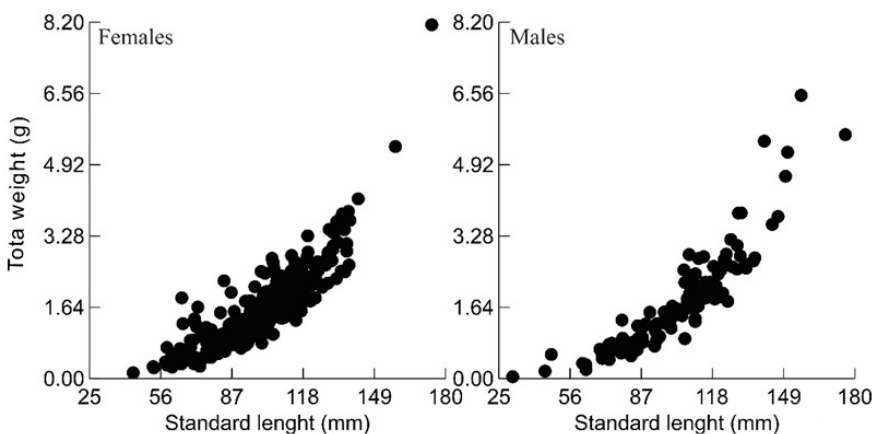


Figure 4. Weight-length relationship for females and males of *Eigenmannia desantanai* collected from February 2009 to January 2011 in the southern Pantanal, Brazil.

in GSI was observed in June, with elevated values throughout almost the entire year (Figure 5).

In terms of gonadal development, females showed pronounced peaks in reproductive activity (mature stage) during January and August, but mature females were present throughout the year (except May). Additionally, the spent stage was frequently observed across most of the year, with notable occurrences in December and September. Immature females were not recorded in January and June (Figure 6). For males, a similar pattern to females was observed, with individuals being reproductively active throughout the year. Moreover, 50% of males collected each month were classified

as mature (Figure 6). Thus, the reproductive period observed through the temporal variation in gonadal maturation stages was confirmed by GSI variation, with reproductive activity occurring throughout the year, specifically with two peaks of higher reproductive intensity for females, from January to April and from August to September.

According to the GLM, the environmental variables retained in the best-fitting model (lowest AIC) that had a negative effect on female reproductive activity (GSI) were river level from 2009-2011 (Estimate = -0,43; $t = -2.87$; $p = 0.018$) and average water temperature ($^{\circ}\text{C}$) (Estimate = -0,04; $t = -2.31$; $p = 0.04$), explaining 55.5% of the deviance (pseudo- $R^2 = 0.55$). Figure 7

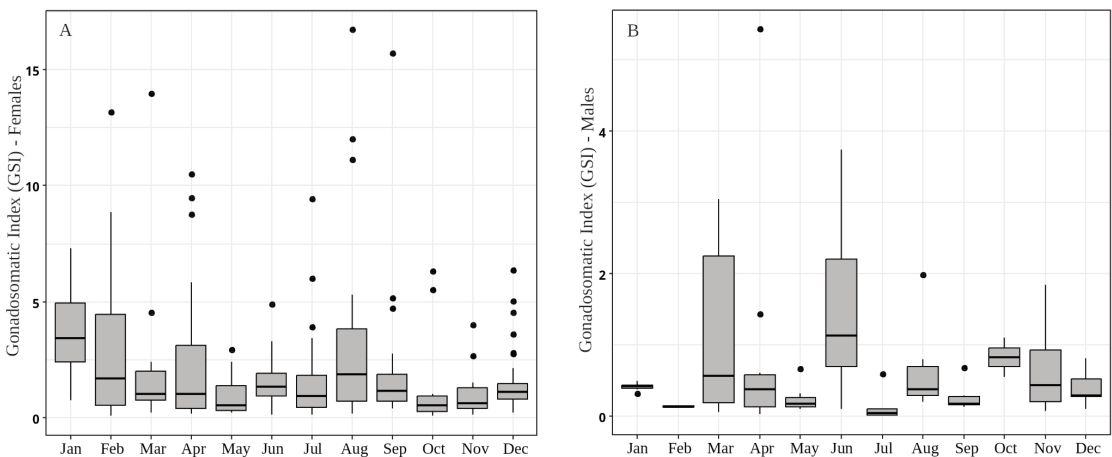


Figure 5. Monthly frequency distribution of mean Gonadosomatic Index values (Median $\pm$ Interquartile) for females (A) and males (B) of *Eigenmannia desantanai* from February 2009 to January 2011 in the southern Pantanal, Brazil. The points represent outliers.

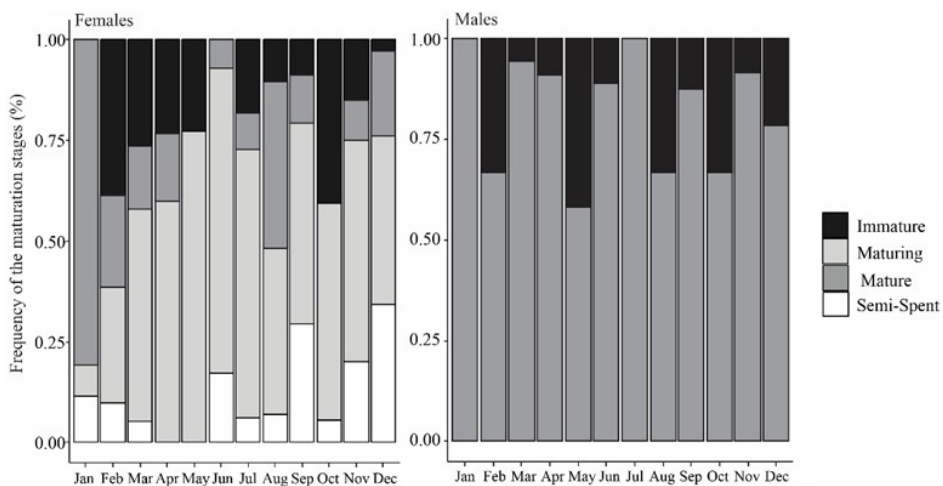


Figure 6. Monthly frequency of maturation stages for females and males of *Eigenmannia desantanai* collected from February 2009 to January 2011 in the southern Pantanal, Brazil.

shows that higher reproductive intensity (elevated GSI) occurred at higher river levels and with higher temperatures. For males, precipitation was the only variable retained in the best-fitting model (lowest AIC); however, it did not have a significant influence on male reproductive activity (Estimate = 0.006; $t = 0.8$; $p = 0.43$; pseudo- $R^2 = 0.06$).

The estimated standard length at first sexual maturity (L_{50}) was 63.06 mm (CI = 52.67 - 73.44) for females and 59.58 mm (CI = 38.91 - 80.25) for males. While 100% of the female population began reproduction at around 153.84 mm (CI = 131.95 - 175.74) and males at approximately 159.13 mm (CI = 117.29 - 200.98) (Figure 8).

Absolute fecundity ranged from 133 to 460 oocytes (with standard lengths varying between 65.1 and 136.1 mm), with an estimated average of 305.3 oocytes (SD = 97). The average relative fecundity was 0.17 oocytes per milligram of female total weight. Absolute fecundity values were not significantly related to total weight ($r^2 = 0.32$; $p = 0.152$) and standard length ($r^2 = 0.08$; $p = 0.723$); however, a positive correlation with gonad weight was detected ($r^2 = 0.46$; $p = 0.039$).

The oocyte diameter ranged from 0.107 mm to 0.616 mm, with a mean of 0.289 mm (SD = 0.10). The frequency distribution of oocyte diameters indicated three groups, or batches of developing

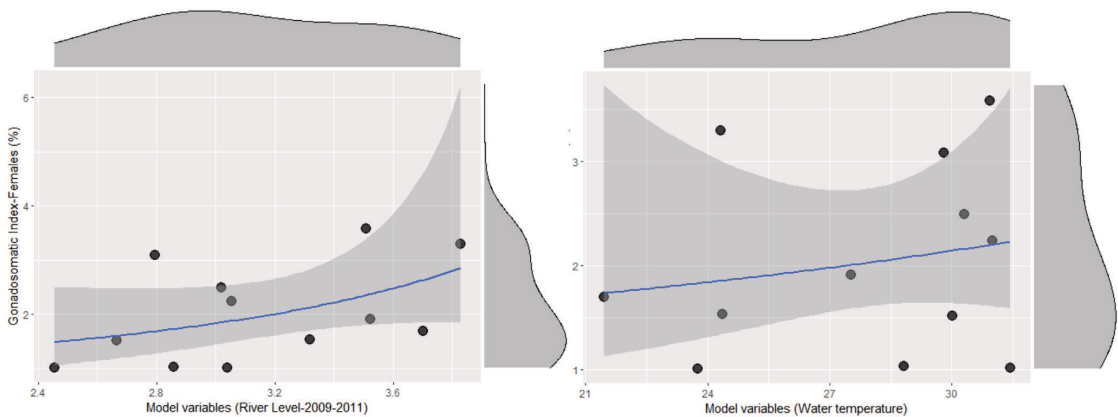


Figure 7. Relationship between the Gonadosomatic Index (%) of female *Eigenmannia desantanai* and the Paraguay River level and water temperature from February 2009 to January 2011 in the southern Pantanal, Brazil. The blue line represents the fitted model. Light gray areas surrounding the line indicate the 95% confidence interval of the model. Gray distributions along the top and side margins show data densities: at the top, for the predictor variables (river level and water temperature), and along the side, for GSI values, highlighting regions with higher data concentration.

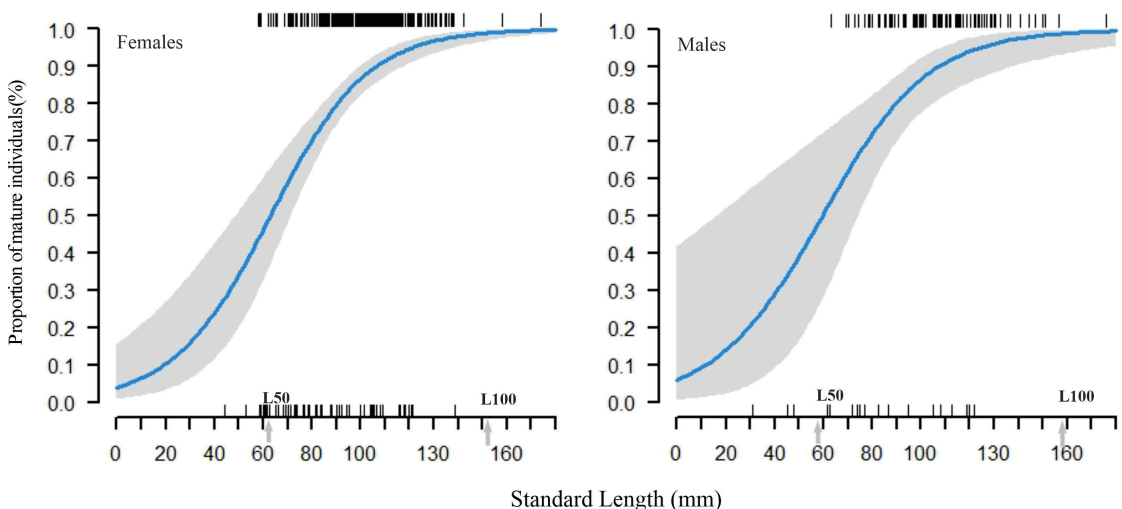


Figure 8. Proportion of sexually mature females and males of *Eigenmannia desantanai* as a function of standard length (mm) collected from February 2009 to January 2011 in the southern Pantanal, Brazil.

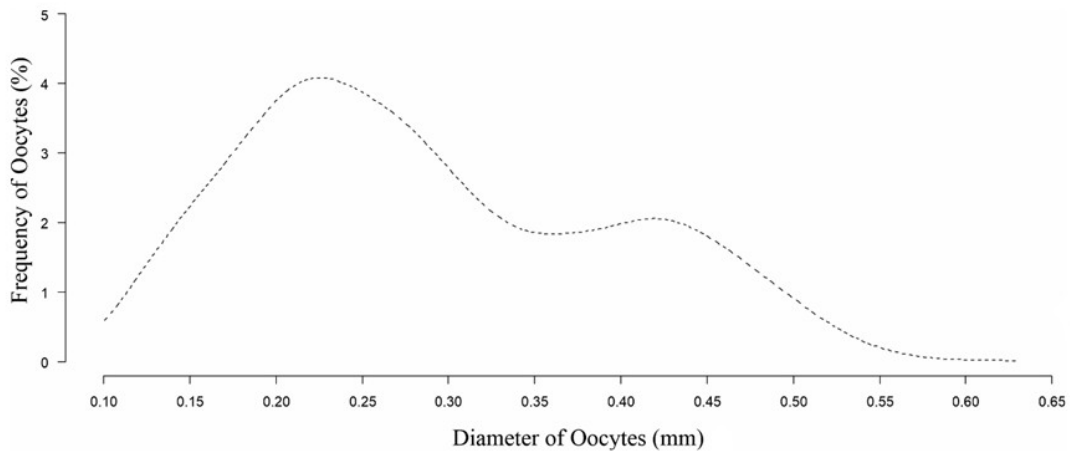


Figure 9. Relative frequency distribution of oocyte diameter for *Eigenmannia desantanai* sampled from February 2009 to January 2011 in the southern Pantanal, Brazil.

oocytes, suggesting a batch spawning pattern for female *E. desantanai* (Figure 9).

4. Discussion

The sex ratio of *E. desantanai* showed a predominance of females (3:1 female: male), which contrasts with the expected patterns for natural fish populations (Nikolskii, 1969; Vazzoler, 1996) and studies on Gymnotiformes (Mendes-Junior et al., 2016; Vanin et al., 2017), including *E. trilineata* in the subtropical region of Brazil (Giora & Fialho, 2009). This characteristic may reflect an adaptive reproductive strategy aimed at maintaining population parameter stability, such as increasing recruitment rates, accounting for sex-specific differences in mortality rates, and mediating ecological interactions (Rodd & Reznick, 1997; Ribolli et al., 2023).

In *E. trilineata* (= *E. desantanai*), no sexual dimorphism in length or weight was observed, but variation in the maximum female size was recorded, with individuals in the northern Pantanal reaching 159 mm (Muniz et al., 2017) and those in the present study reaching up to 174 mm, possibly due to spatial differences in growth rates among populations (Tondato et al., 2018).

Previous studies on Gymnotiformes species have reported similar growth patterns, although the *b* coefficient value varies among species and regions, potentially indicating isometric, positive or negative allometric growth (Kirschbaum & Schugardt, 2002; Hernández-Serna et al., 2014; Mendonça et al., 2015; Freitas et al., 2017; Silva et al., 2019; Machado et al., 2020). *Eigenmannia desantanai*

exhibited negative allometric growth, characterized by a higher investment of energy in growth relative to weight. This initially suggests that high growth rates are aimed at reducing predation pressure, as smaller individuals are more susceptible to being captured as bait in the Pantanal. Furthermore, the greater investment in growth observed may lead to early sexual maturity, suggesting that *E. desantanai* uses this strategy to increase recruitment, recolonize, and maintain viable populations.

The analysis of the gonadosomatic index (GSI) confirmed a pattern of prolonged reproduction with peaks of intensity over time in females. In contrast, males exhibited elevated GSI values throughout most of the year, indicating a continuous reproductive pattern with flexible, opportunistic characteristics. These findings were corroborated by gonadal development data, which revealed mature females in nearly all months, except May, and a high frequency of the semi-spent stage, suggesting multiple reproductive events. Approximately 50% of males captured monthly were classified as mature. This may indicate phenotypic plasticity in the species. This flexibility may allow *E. desantanai* to maximize its reproductive success under varying environmental conditions, favoring recruitment during different periods and potentially reducing intraspecific competition during early life stages.

Variation in the reproductive traits of *E. desantanai* may be associated with adaptive strategies shaped by both intrinsic (physiological) and extrinsic (environmental) factors, such as temperature, water level, and resource availability (Junk et al., 1989; Mims et al., 2010; Vazzoler,

1996). Although the results of the model presented here indicate a negative relationship between river level, temperature (2009–2011), and the mean gonadosomatic index (GSI) in females, these values may not fully capture the complexity of the relationship between environmental factors and reproductive activity.

The reproductive pattern is prolonged, with peaks coinciding with favorable environmental events: the first (January to April) associated with rising temperatures and the onset of flooding, and the second (August) with the flood peak, when temperature increases again. Such conditions may enhance juvenile survival by increasing the availability of shelter and food (Tondato et al., 2018). There are also spatial variations between populations in the northern and southern Pantanal, likely due to differences in the hydrological regime (Muniz et al., 2017; Tondato et al., 2018). Studies on closely related species, such as *E. trilineata* (Giora & Fialho, 2009), and other representatives of the Gymnotiformes order (Vanin et al., 2017; Waddell et al., 2019) indicate that this pattern, characterized by two reproductive peaks and an extended reproductive period, is a common trait within the order.

The Paraguay River level and temperature (2009 to 2011) were the primary factors influencing female reproductive activity, while no significant relationship with environmental variables was observed for males. Temperature is a predictive factor that affects gonadal development, triggering the maturation processes (Vazzoler, 1996; Suzuki et al., 2004). For some Gymnotiformes species, such as *Brachyhyopomus pinnicaudatus* (Hopkins, Comfort, Bastian & Bass 1990) and *Gymnotus carapo* Linnaeus 1758, presence of sexually mature males and females was observed during periods of high temperatures (Silva et al., 2003), while others are more closely related to increased photoperiod (Giora et al., 2012; Giora et al., 2014). Thus, *E. desantanaei* experienced a sudden temperature increase in August, coinciding with the flood peak, which also resulted in a peak of reproductive activity, that is, triggering final gonadal development. Despite its prolonged reproduction period, the plasticity of the analyzed species is evident, as it synchronizes its major investment during periods considered more favorable for offspring survival, as highlighted by King (1995).

Mainly, in the southern Pantanal, the flood peak (June to August) occurs asynchronously with temperature and rainfall (October to March), leading to a prolonged reproductive period for small species

that benefit from the favorable flood conditions and also from the high temperatures associated with rainfall (Tondato et al., 2014; Pereira & Suárez, 2018; Santana et al., 2018; Santos et al., 2019).

Furthermore, Tondato et al. (2018), in evaluating fish recruitment patterns of species in the Northern and Southern Pantanal, found that recruitment of *E. trilineata* (= *E. desantanaei*) was correlated with historical river levels under a synchronous regime (Northern Pantanal), but not in the asynchronous regime (Southern Pantanal). Therefore, the results suggest that *E. desantanaei* responds to immediate environmental conditions and highlights maximum reproductive investment, with a prolonged reproductive period, the first peak (January/February - rising water) related to high temperatures and flood, and the second peak (August-flood) associated with a sharp rise in temperature and higher Paraguay River levels. This differentiated reproductive strategy may represent an adaptation to optimize reproductive success in the Southern Pantanal, reflecting life-history traits of the species.

The estimated length at first sexual maturity (L50) for *E. desantanaei* females and males was similar to the values reported for females (67.9 mm) and males (85.6 mm) of the congeneric species *E. trilineata* (Bichuette & Trajano, 2017), although L50 was not calculated in that study. However, the observed L50 values were lower than those reported for other species within the same genus (Giora & Fialho, 2009), such as, for example, *E. pavulagem*, whose females and males matured at 83.01 mm and 88.15 mm, respectively (López-Rodríguez et al., 2025).

Additionally, mature gonads of *E. trilineata* (= *E. desantanaei*) were recorded from 39 mm in Baía Caiçara, Paraguay River (Muniz et al., 2017), whereas in this study, they were observed from 58 mm, demonstrating spatial variation in populations of the same species. This result suggests that *E. desantanaei*, compared to closely related species, reaches a reproductive maturity at a smaller size as an adaptive response to local environmental conditions, including its adaptive and recolonizing capacities, in an effort to maintain populations despite mortality due to exploitation (e.g., bait fishing). Moreover, fishes in this region, including *Eigenmannia desantanaei*, benefit from a wide variety of food sources, such as insects, crustaceans, and smaller fish, which enhance their energy reserves and support reproductive processes.

The absolute fecundities observed in the analyzed individuals were lower than Gymnotiformes species

(Giora & Fialho 2009; Barbieri & Barbieri, 1982). However, the relative fecundity observed was similar to *Brachyhypopomus draco* (0.17) (Schaan et al., 2009) and comparable to other Gymnotiformes, such as *Brachyhypopomus bombilla* Loureiro & Silva 2006 (0.21) (Giora et al., 2012), *Brachyhypopomus gauderio* Giora & Fialho 2009 (0.20) (Giora et al., 2014), and *Gymnotus aff. carapo* (0.20) (Cognato & Fialho, 2006), following the observed pattern in the group. Conversely, *E. pavulagem* exhibited a relative fecundity of 0.033 oocytes/mg, with a mean diameter of mature oocytes of 1.32 mm (range: 0.774–1.558 mm) (López-Rodríguez et al., 2025).

In contrast, *E. desantanai* presented a strategy based on the production of a larger number of smaller oocytes, differing from *E. pavulagem*. These findings suggest that, although absolute fecundity may vary according to environmental and phylogenetic contexts, Gymnotiformes tend to maintain low relative fecundity, with variation in oocyte size reflecting different reproductive investments, possibly associated with the duration of the reproductive period, environmental characteristics, or life-history strategy plasticity.

The absence of a correlation between fecundity and weight and length may be explained by the distinct body structure of Gymnotiformes compared to other fish orders, as they have a small coelomic cavity located strictly in the anterior part of the body (Cognato & Fialho, 2006). Other factors, such as parental care and spawning strategy, may also affect fish fecundity (Vazzoler & Menezes, 1992), with possible parental care indicated for the congeneric species *E. trilineata* (Giora & Fialho, 2009).

We observed the release of three batches of vitellogenic oocytes, suggesting that *E. desantanai* exhibits batch spawning. Although the presence of multiple oocyte peaks strongly suggests batch spawning, histological analysis would provide further confirmation of the spawning behavior. This tactic is common among tropical fish species (Lowe-McConnell, 1975; Santana et al., 2018), as seen in all Gymnotiformes analyzed so far, such as *E. trilineata* (Giora & Fialho, 2009), *Eigenmannia virescens* (Valenciennes 1836) (Kirschbaum, 1979), five species of *Brachyhypopomus* (Waddell et al., 2019) and *E. pavulagem* (López-Rodríguez et al., 2025). *Eigenmannia desantanai* revealed a multimodal distribution of oocyte diameters, indicating a pattern of continuous oocyte recruitment. This result indicates that batch spawning may enhance fecundity and, consequently, reproductive investment, as these

species possess a reduced coelomic cavity, leading to the fragmented development of their oocytes.

Thus, based on the life-history traits analyzed in this study, such as low fecundity, batch spawning, prolonged reproductive period, and parameters reported in other studies, such as potential parental care (Giora & Fialho, 2009), low growth rate, reduced mortality, and high longevity (Tondato et al., 2018), *E. desantanai* can be classified as an equilibrium strategist. This classification aligns with the triangular life-history model proposed by Winemiller & Rose (1992), which defines opportunistic, periodic, and equilibrium strategists. According to the authors, equilibrium strategists are characterized by low fecundity with large oocytes, parental care investment, delayed maturity, an extended reproductive period, and high juvenile survival, traits that are well adapted to stable environments with intense competition. This occurs in the Pantanal, where the flooding regime, with periods of rising and peak water levels, increases resource availability, in contrast to receding and dry seasons, which expose species to greater competition and predation. It is important to note that this strategy also implies greater sensitivity to environmental or anthropogenic disturbances, such as overexploitation, since population recovery is slower due to the low immediate reproductive potential.

Based on the data presented in this study, we recommend the adoption of management measures aimed at the conservation of *Eigenmannia desantanai*. Information such as the identification of periods of highest reproductive activity and the determination of the length at first maturity ($L_{50} = 60$ mm) provide important support for establishing temporal fishing closures and regulating minimum catch size. These measures aim to ensure the sustainability of populations of this species, which holds significant ecological importance and economic potential. Furthermore, we emphasize the importance of maintaining the natural flood pulse in the Pantanal, which plays a fundamental role in providing habitats favorable for reproduction and feeding. The preservation of these natural hydrological cycles, especially the flood pulse, should be considered in the formulation of public policies aimed at fishing management and the conservation of *Eigenmannia desantanai*, to ensure the species' sustainability in the face of threats posed by climate change and alterations in land use and water resources. As pointed out by Pelicice et al. (2017), detailed biological knowledge of species is essential for the proper management of natural resource use and the implementation of public policies aimed at

conservation, thereby supporting effective strategies for sustainable management.

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Data availability

The entire dataset supporting the results of this study has been published in the article itself.

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