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Environmental influence on the reproductive strategy of *Helogenes marmoratus* (Siluriformes: Cetopsidae) in the Amazonian streams

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The reproductive strategy of a species must be adjusted to variations in environmental conditions to guarantee population balance. Hydrological fluctuations in Amazonian streams of *terra firme* (non-flooded) are controlled primarily by local rainfall. Fish assemblages are composed predominantly of species of small size. We investigated the reproductive strategy of the cryptic catfish *Helogenes marmoratus* and assessed the influence of environmental variables (*e.g.*, rainfall, conductivity, habitat descriptors) on its reproductive activity in a catchment of the Guamá River in the eastern Brazilian Amazon. Through monthly collections between March 2019 and March 2020, we identified an extended reproductive period between July 2019 and March 2020. Males mature at smaller sizes than females (♂ = 27.41 mm; ♀ = 31.36 mm). We confirmed batch spawning, low fecundity (59.55 ± 22.76 stage IV oocytes), and large oocytes (1.24 ± 0.15 mm). Our results indicated that *H. marmoratus* strategy occupies an intermediate place between opportunistic and equilibrium gradient. Multiple regressions showed that thalweg depth, electrical conductivity, leaf litter, and rainfall are important drivers of reproductive activity of females of *H. marmoratus*, explaining 32% of the variation of the GSI. Our study provides evidence of differentiated reproductive response between the sexes to environmental variables.

Keywords: Environmental variables, Life History, Rainfall, Reproductive strategy, Reproductive traits.

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La estrategia reproductiva de una especie debe ajustarse a las variaciones de las condiciones ambientales para garantizar el equilibrio poblacional. En los riachos amazónicos de tierra firme las fluctuaciones hidrológicas están controladas principalmente por las lluvias locales, predominando especies de peces de pequeño porte. Investigamos la estrategia reproductiva de *Helogenes marmoratus* y la influencia de variables ambientales (*e.g.*, lluvia, conductividad, descriptores del hábitat) en su actividad reproductiva. Colectamos mensualmente entre marzo de 2019 y marzo de 2020 en una microcuenca del río Guamá, en la Amazonia oriental brasileña. Identificamos un período reproductivo prolongado entre julio de 2019 y marzo de 2020. Los machos comienzan a reproducirse con un menor tamaño (♂ = 27.41; ♀ = 31.36 mm). Confirmamos desove parcial, baja fecundidad (59.55 ± 22.76 ovócitos) y ovócitos grandes (1.24 ± 0.15 mm). La estrategia reproductiva de *H. marmoratus* ocupa un lugar intermedio entre el gradiente oportunista y de equilibrio. Regresiones múltiples destacan la importancia de la profundidad, la conductividad eléctrica, los bancos de hojas y la lluvia como reguladores de la actividad reproductiva de las hembras, explicando 32% de la variación del IGS. Nuestro estudio proporciona evidencia de una respuesta reproductiva diferenciada entre los sexos a las variables ambientales.

Palabras clave: Características reproductivas, Estrategia reproductiva, Historia de vida, Lluvia, Variables ambientales.

INTRODUCTION

The combination of traits and behaviors adopted by an organism to guarantee its reproductive success, and how environmental factors constrain these traits, is a central issue of Life History Theory (Stearns, 1992). To maintain a viable population of a species over the long term, it needs an adequate reproductive strategy composed of a set of reproductive tactics that vary systematically in response to environmental fluctuations (Wootton, 1989). In fish, variable reproductive tactics may include body size, body length at first maturity, fecundity, the type and frequency of spawning, and reproductive behavior (Potts, Wootton, 1984).

The analysis of reproductive strategies in fishes by Winemiller, Rose (1992) resulted in the proposal of the "opportunistic–equilibrium–periodic" triangular continuum model. In this model, the life-history strategies of fish reflect the trade-offs between the basic demographic parameters of fecundity, survival, and the onset and duration of reproduction. Based on these parameters, the strategies can be classified as (i) the Equilibrium strategy, when the species has well-developed parental care, an extended breeding season, repeated reproduction, large eggs, and small to medium body size; (ii) the Opportunistic strategy, when the species is small in size, has little or no parental care, a extend breeding season, repeated bouts of reproduction, relatively small clutches, and small eggs; and (iii) the Periodic strategy, observed in medium to large species with very little or no parental care, a short breeding season, few bouts of reproduction, intermediate to high fecundity, and small eggs.

Although this model is widely used to classify the life histories of freshwater fishes (Mims, Olden, 2012; Logez *et al*., 2015), it has been applied predominantly to species that inhabit the floodplains of major rivers systems. In these environments, the flood pulse is the principal driver of the structure of aquatic communities and the life history strategies of resident fishes (Junk *et al*., 1989). In these systems the reproductive activity of most fish is related directly to the annual flood pulse, in particular, the species that undertake lateral and longitudinal migrations in search of food and microhabitats for reproduction which become more abundant as the floodplain is inundated (Vazzoler, 1996; Agostinho *et al*., 2004; Bailly *et al*., 2008).

Conversely, in *terra firme* (non-flooded) streams, fluctuations in water level are controlled primarily by local rainfall (Espírito-Santo *et al*., 2013), resulting in a long-term pattern of short and frequent pulses in discharge (Tomasella *et al*., 2008). In these ecosystems, fish assemblages are composed predominantly of small-sized species with a limited migratory capacity (Castro, 1999). Studies of typical *terra firme* stream-dwelling species have demonstrated a predominance of reproductive characteristics, such as a more extended breeding season, more diverse reproductive timing, and multiple spawning (Kramer, 1978; Schwassmann, 1978).

Even if the three endpoints of life-history strategies are fairly distinctive, intermediate strategies are recognized near the center and along the boundaries of a trilateral gradient (Winemiller, Rose, 1992; DeBoer *et al*., 2015). These intermediate strategies had been corroborated in recent studies which show how some small-sized fish occupy intermediate positions within opportunistic-periodic gradient (Alkins-Koo, 2000; Fagundes *et al*., 2020) and the intermediate multivariate space between the endpoints (Espírito-Santo *et al*., 2013).

Small-sized species account for 50% of the fish diversity of the Amazon basin (Carvalho *et al*., 2007). However, little is known of their life-history traits. In this context, the understanding of the influence of environmental factors on the reproductive strategies of most Amazonian stream fishes is still incipient (Castro, Polaz, 2020).

The whale catfish *Helogenes marmoratus* Günther, 1863 is one of the few species of the family Cetopsidae found in Amazonian streams (Reis *et al*., 2003), and is known for its cryptic behavior (Sazima *et al*., 2006). This species typically uses leaf banks and gravel in the bottoms of shallow forested streams with gentle currents (Le Bail *et al*., 2000). It is also considered an important bioindicator of the ecological integrity of Amazonian streams (Montag *et al*., 2008; Ferreira *et al*., 2018; Prudente *et al*., 2018). Its relationship with a specific type of microhabitat in Amazon streams makes *H. marmoratus* a valuable model for evaluating the impacts of environmental fluctuations on the reproductive strategies of stream fish.

Given the selective pressure that the local rainfall exerts on the physical and chemical variables of the water and the physical habitat of Amazonian streams, and their influence on the reproductive strategy of the local fish species (Kramer, 1978; Schwassmann, 1978; Carvalho *et al*., 2007; Waddell *et al*., 2019; Waddell, Crampton, 2020), the present study aimed: (i) characterize the reproductive strategy of *H. marmoratus* in terms of the triangular continuum model of Winemiller, Rose (1992), based on size at first maturity, type of spawning, fecundity, oocyte size, and the length of the reproductive period; and (ii) identify the environmental variables associated with the reproductive activity of *H. marmoratus*. Considering the small size of the species and its cryptic behavior associated with leaf litter, *H. marmoratus* will exhibit an extended reproductive period and batch spawning, characteristics shared by opportunistic and equilibrium strategies but not compatible with the periodic strategy. We hypothesized that the species would have reproductive traits corresponding to an intermediate strategy in the triangular continuum model (Winemiller, Rose, 1992). We predicted that mature individuals of *H. marmoratus* to be more frequent during the rainy months, when the local rainfall influences variations in the water level and the physical characteristics of the stream habitat, which would be associated with the reproductive activity of this species.

MATERIAL AND METHODS

Study area. The study was conducted in a left margin catchment of the Guamá River, which has an area of approximately 12.4 km^2, in the municipality of Capitão Poço, Pará State, in eastern Brazilian Amazon (Fig. 1). The local vegetation is classified as equatorial sub-perennial forest (IBGE, 1992). However, the catchment landscape is currently dominated by farmland and cattle pasture (Pacheco, Bastos, 2001), with small remnants of secondary (Silva *et al.*, 1999) and riparian forests, considered areas of permanent preservation under article 30 of the Brazilian Forest Code, federal law number 12,651/12.

The region has a humid tropical climate, subtype *Af* in the Köppen classification adapted by Peel *et al.* (2007). The mean annual temperature is 26.9 °C, which varies

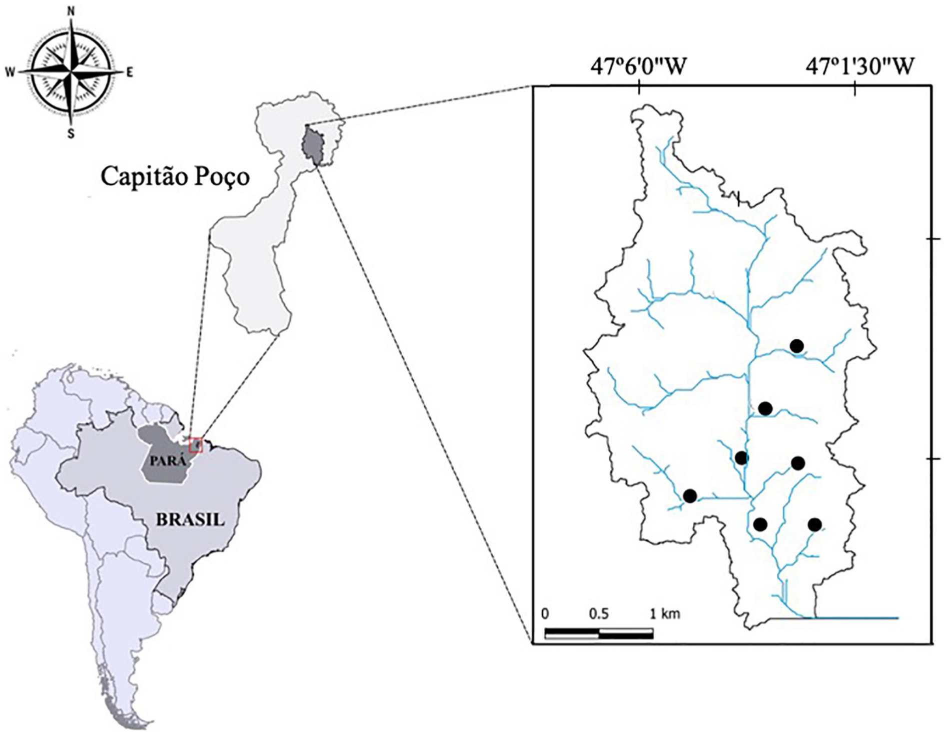

FIGURE 1 | Study streams (black dots) in a catchment of the Guamá River in the municipality of Capitão Poço, Pará State, Brazil.

only slightly over the year. The mean annual rainfall is 2370 mm, with a rainy season between January and May, and a dry season between August and November (Pacheco, Bastos, 2001).

We choose seven low-order streams (1st to 3rd order *sensu* Strahler, 1957) with similar physical structures, being that the only third-order stream (the westernmost on the map) results from a large number of proximate headwater sources. All stream reaches were characterized based on their riparian zone, proportion of litter leaf in the stream bottom [we included this substrate because it is associated with the cryptic behavior of *H. marmoratus* (Sazima *et al*., 2006)], depth, width and water current velocity. These environmental variables dataset is appropriate for describing instream habitat conditions (Benone *et al*., 2017; Prudente *et al*., 2018; Santos *et al*., 2019; Cruz, Pompeu, 2020). Despite the different orders, the overall characterization of stream reaches was comparable.

The streams were sampled each month between March 2019 and March 2020, within 50 m reach of each stream divided into five 10 m longitudinal sections by six cross-sections. Before the fish collection, we measured four physicochemical characteristics of the water at each stream: Dissolved Oxygen (%), Electrical Conductivity ($\mu S/cm^{-1}$), pH, and Temperature (°C), using a Horiba U–50 multiparameter device.

We assessed six structural habitat descriptors, following a simplified and efficient protocol for sampling in 1st to 3rd order streams (Mendonça *et al*., 2005). In the six cross-sections established at each stream, we calculated the wetted width (WW - m), the thalweg depth (TD – cm), the leaf litter (LL – %), and the canopy cover (CC – %). We determined the WW (transversal distance between stream flooded margins) and the TD using a ruled pole. We measure the TD at five equidistant points within each cross-section, where we also visually registered the LL presence (%). We measure the CC at three points within each cross-section (at the mid-channel and each margin) through digital photography converted to a black and white scale to calculate the cover percentage (black pixels) using the Image J. software.

We registered the flow speed (FS – m/s) at three equidistant points along the channel, by measuring the time taken by a floating object to move a known distance. The discharge (D – m^3/s) was calculated using the formula $Q = A^{\star}Vm$, where Q = the discharge, Vm = mean surface flow speed, and A = mean transect area. The mean transect area was calculated by $A = \Sigma^{n}{}_{i}A_{n}$ where A = area of the transect, which is given by the sum of $[(Z_1 + Z_2) / 2]^{\star}w + [(Z_2 + Z_3) / 2]^{\star}w + \ldots [(Z_n + Z_{n+1}) / 2]^{\star}w$, where, Z_n = the measured depth of each segment, and w = the width of each segment.

We used the average monthly values of the environmental variables obtained for each stream for the statistical analysis. Rainfall data were provided by the meteorological station of the Instituto Nacional de Meteorologia (INMET 2021 – Station A248), located in the municipality of Capitão Poço (Fig. **S1**).

The specimens of *H. marmoratus* were collected from each 10-m longitudinal section for 12 min by three people using rectangular sieves (80 cm x 60 cm) with a 2 mm mesh. The individuals captured were euthanized with an overdose of Eugenol (6 ml / 3 L of water) and fixed in a 4% formalin solution in the field and preserved in 70% ethanol solution under vouchers number MPEG 35954, MPEG 35955, and MPEG 35956 (Ichthyological Collection, Museu Paraense Emílio Goeldi, Belém, PA, Brazil).

In the laboratory, the specimens were weighed (total weight in g – TW), measured (total length in mm – TL), and eviscerated for the removal of the gonads, which were also weighed (weight in g – GW). The gonads were assessed macro and microscopically to define the sex of the individual and its gonadal maturation stage, following Vazzoler (1996) and Nuñez, Duponchelle (2009), respectively. For the microscopic analysis, we adopted the histological routine for optical microscopy described by Prophet *et al*., (1995). The females were classified into five gonadal stages: immature, maturing, mature, spawned, and resting; and males into four stages: immature, maturing, mature, and spent.

Reproductive traits. Six reproductive traits were estimated for *H. marmoratus*: sex ratio, length at first maturity, egg size, spawning type, fecundity, and the duration of the reproductive period. The sex ratio was calculated for each month based on the relative frequency of males and females in the samples, with significant deviations from a 1:1 ratio identified using Chi-square (χ^2), as proposed by Sokal, Rohlf (1995).

The mean length at first sexual maturity (L_{50}), when 50% of the individuals examined were able to reproduce, was estimated separately for the females and males, based on the frequency of adults (all gonadal maturation stages except immature), considering total length intervals of 10 mm. The L_{50} was calculated based on the logistic equation $P=A(1+e^{-r(TL-L50)})^{-1}$ where P = the proportion of reproductive individuals, A = the asymptote of the curve, r = the rate of change between non-reproductive and reproductive status, TL = total length, and L_{50} = the average length of sexual maturity. To detect recruitment periods, we organized the total length values of all the individuals in monthly histograms. We assumed that recruitment occurred in the months with a high frequency of individuals smaller than L_{50}.

The spawning type was determined by the visual inspection of the frequency distribution of oocyte diameters and the histological analysis of the development of the oocytes. We photographed all oocytes from 11 mature females chosen randomly under a Leica M125 stereomicroscope equipped with a DMC 2900 camera, using the measured diameter of one oocyte as a reference for the measurement of the others. In the Image J software we determine the area of all the oocytes visible in the processed photographs, using the formula $\sqrt{((a*4)/\pi)}$, where a = the area of each oocyte. Here, we apply the term "total spawning" to a unimodal distribution and "batch spawning" for a multimodal distribution (Vazzoler, 1996).

Fecundity, defined as the number of mature-sized yolked eggs produced in both ovaries (Alkins-Koo, 2000), was estimated based on the same 11 mature females by counting the stage IV oocytes (Nuñez, Duponchelle, 2009) under a stereoscope after manual dissociation. We measured the diameter of 198 stage IV oocytes (~20 from each mature female) using the Leica Application Suite (LAS) microscope software. We applied an index between the oocyte size (diameter) and body size (total length) for comparison with the data available on small-bodied siluriform species to verify whether *H. marmoratus* produces relatively large or small oocytes (Fig. **S1**).

The duration of the reproductive period was estimated based on both the gonadosomatic index (GSI) considering just adult individuals (all gonadal maturation stages except the immature) expressed by the equation $GSI = (GW/TW)*100$, and the relative frequency of the gonadal maturation stages per month. The variation in the monthly GSI values was assessed using the nonparametric Kruskal-Wallis analysis of variance, followed by Wilcoxon's post hoc multiple comparison test. These analyzes were applied separately to the females and males.

After identifying reproductive traits of *H. marmoratus*, we evaluated them in the context of the triangular continuum model of Winemiller, Rose (1992) to determine whether the species presents a single reproductive strategy or an intermediate position in the continuum.

Effects of environment variables. Before being associated with the reproductive activity of *H. marmoratus*, we pre-selected the physicochemical water characteristics, and habitat descriptors (except for monthly rainfall). We excluded variables with a low coefficient of variation (≤ 10%) among the sampling months. The retained variables were then compared using Spearman's correlation coefficient to identify multicollinearity. In the case of the redundant variables ($r_S > |0.60|$, $p < 0.05$), those known to have potential predictive importance for tropical stream fish were retained based on published data. The monthly variation in these retained variables is presented in the Fig. **S2**.

We ran a Principal Components Analysis (PCA) based on the matrix of the monthly mean values of the environmental variables retained after this procedure to determine temporal variation in the physicochemical characteristics of the water and the habitat descriptors of the streams (Legendre, Legendre, 2012). The two first axes of the ordination were interpreted considering the environmental variables with loadings equal to or greater than of 0.6.

The relationship between reproductive activity, indicated by the GSI variation (response variable), and the environmental variables retained for analysis, including monthly rainfall (predictor variables), was assessed using a multiple linear regression analysis (MLR). The MLR considered both sexes together and females and males separately. The GSI was log-transformed to standardize non-linear trends.

We selected the best model based on the Akaike Information Criterion (AIC; Zuur *et al*., 2009). Although the residuals of all the models were homoscedastic, only the female's dataset was normal-distributed. We adopted a significance level of 5% for all analyzes. All statistical tests were run in the R 4.0.3 software (R Development Core Team, 2020) using the packages *MuMIn* (Bartoń, 2020), *MASS* (Venables, Ripley, 2002), *car* (Fox, Weisberg, 2019), and *vegan* (Oksanen *et al*., 2020).

RESULTS

Reproductive traits. We collected 204 specimens (107 females and 97 males) between March 2019 and March 2020. The female:male ratio was 1.1:1, with a significant difference being recorded only in January 2020 ($\chi^2 = 4$; df = 1; $p < 0.05$), when 12 females and four males were collected (Fig. 2).

Female specimens ranged from 18.35 to 65.21 mm (mean = 46.15; standard deviation = ± 10.11 mm), and males ranged from 16.4 to 59.89 mm (43.13 ± 12.39 mm). Males reached the length of first gonadal maturation at 27.41 mm ($R^2 = 0.811$) (Fig. 3A), approximately 10% shorter than females (31.33 mm; $R^2 = 0.733$) (Fig. 3B). Mean size at sexual maturity (L_{50}) represents 48% and 46% of the maximum length reached by females and males, respectively.

The monthly distribution of the total length (Fig. 3C) indicates juveniles in the population throughout the studied period, except in May 2019 and January 2020. We detected two recruitment periods, between March and April 2019 and between October and November 2019.

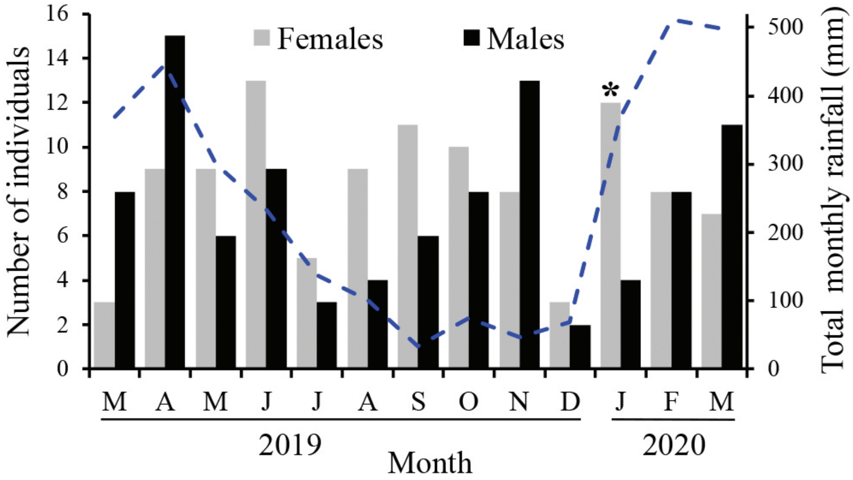

FIGURE 2 | The number of females and males *Helogenes marmoratus* collected in a catchment of the Guamá River in Capitão Poço, Pará State, Brazil, each month between March 2019 and March 2020. The dashed blue line represents the total monthly rainfall. * Indicates a significant difference in the sex ratio in that month.

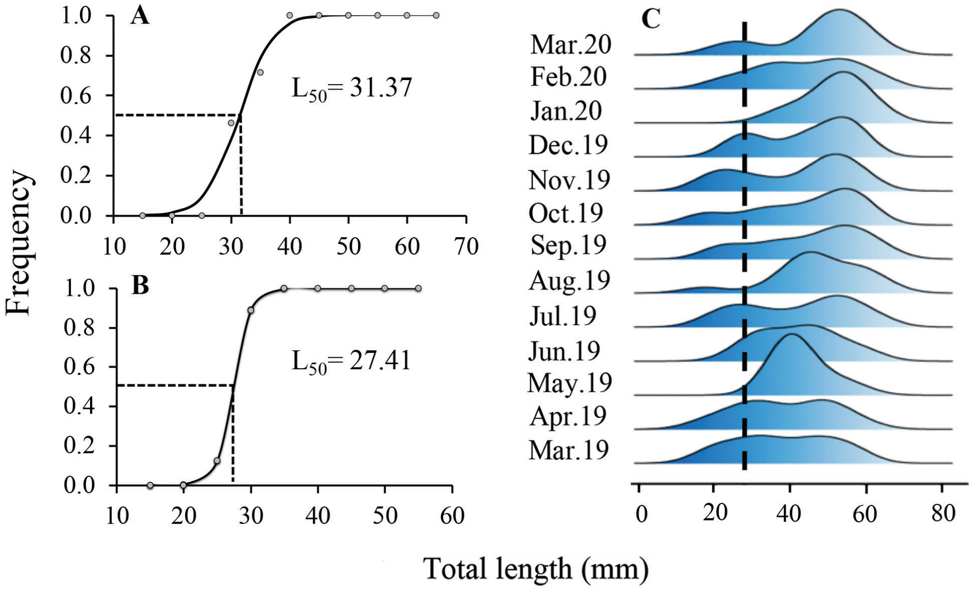

FIGURE 3 | Length at first sexual maturation (L_{50}) in **A.** Females and **B.** Males *Helogenes marmoratus*; and **C.** The monthly frequency histogram of the variation in total length recorded in a catchment of the Guamá River in Capitão Poço, between March 2019 and March 2020. The black dashed line indicates the lowest L_{50}, which separates adults from juveniles.

The total length of mature females varied between 53.36 mm and 64.48 mm (58.50 ± 3.89; n = 11), and the total number of oocytes per female varied from 84 to 236 (data from mature females in Tab. S3). The diameter of all types of oocytes ranged from 0.11 mm to 1.77 mm, with a bimodal frequency that indicates two oocyte batches at different stages of development, that is, asynchronous development (Fig. 4A).

The histological sections of the spawning-capable and mature females revealed oocytes at all stages of development, indicating the continuous release of oocytes as they reach full maturity, consistent with batch spawning in this species (Fig. 4B). The mature stage of ovarian development in *H. marmoratus* is easily identified by the large size of the ovary and the presence of stage IV oocytes (Fig. 4C). Fecundity (the number of stage IV oocytes) observed in the 11 *H. marmoratus* females ranged from 18 to 90 (59.55 ± 22.76), and the diameter of these oocytes ranged from 0.83 mm to 1.77 mm (1.24 ± 0.15; n = 198).

Females presented a significant variation in the mean GSI among months (Fig. 5A: $H_{12,78} = 38.98$, $p < 0.01$) with a greater reproductive activity in September (GSI = 1.29), and between December 2019 and March 2020, with a peak in February 2020 (GSI = 4.74). The monthly variation in the GSI of the males also varied significantly among months (Fig. 5B: $H_{12,72} = 33.48$, $p < 0.01$), with three peaks of reproductive activity, the first in March (GSI = 0.27) and April 2019 (GSI = 0.35), the second in July (GSI = 0.29), August (GSI = 0.34), and September (GSI = 0.27), and the last in February (GSI = 0.30) and March (GSI = 0.28) 2020.

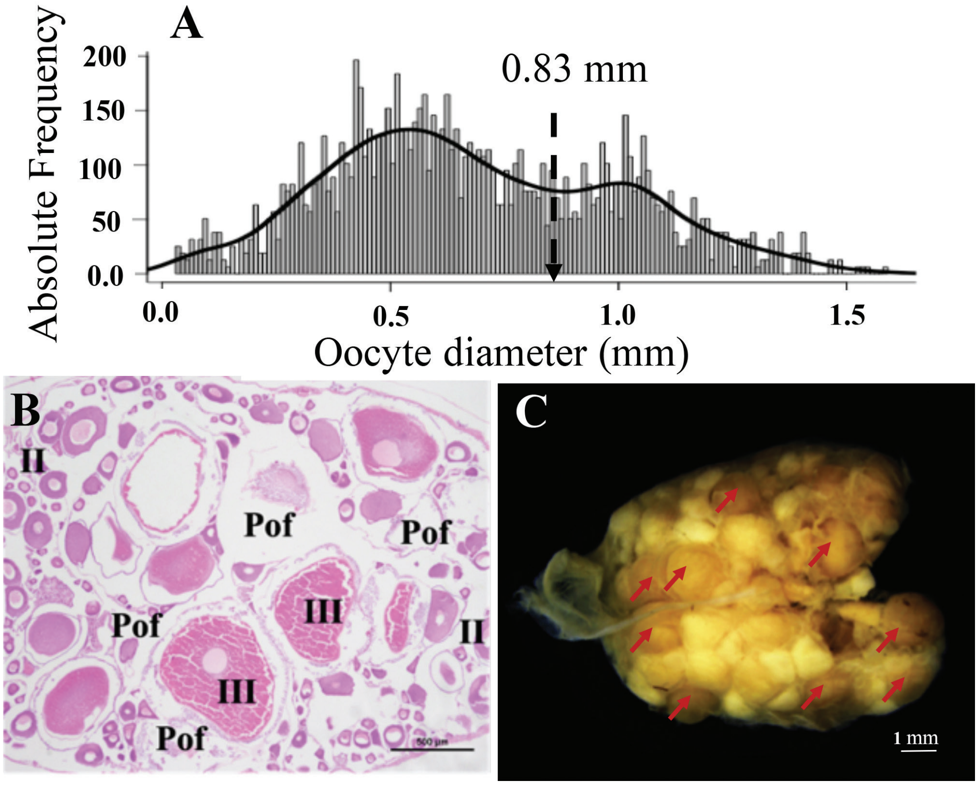

FIGURE 4 | **A.** Variation in the diameter of the oocytes collected from 11 mature *Helogenes marmoratus* females collected from a catchment of River Guamá in Capitão Poço, Pará State, Brazil. The dashed black arrow indicates the minimum diameter of the mature oocytes. **B.** Photomicrograph of spawned female with oocytes in different stages of maturation: II, stage II oocyte; III, stage III oocyte; Pof: Post-ovulatory follicle. **C.** Ovary with mature oocytes (red arrows).

The monthly frequencies of the different gonadal phases in both genders also indicated reproduction activity throughout the study period (Figs. 5C–D). The abundance of immature females increased in the rainy months, in particular in March and April 2019. Maturing females predominated between May 2019 and January 2020, representing 33.65% of the gonadal phases. Mature females were detected between June 2019 and March 2020, except for August, when we recorded the highest frequency of spawned females (Fig. 5C).

We also observed a more significant proportion of immature males in September 2019, the driest month. Spent males were predominant overall and represented 44.44% of all the gonadal phases recorded during the present study (Fig. 5D). The variation in the monthly mean GSI values and the distribution of the gonadal phases recorded in the female and male *H. marmoratus* for the study period were consistent with an extended reproductive period between July 2019 and March 2020.

Environmental effects on reproductive activity. The studied streams shared similar water physicochemical characteristics. The annual mean of the water temperature was 26.58 °C (± 1.12), and the annual pH mean was 5.84 (± 0.74), with more acidic water being recorded in January and February 2020. Well-oxygenated water was recorded between March and June 2019 and January and March 2020, coinciding with the highest monthly rainfall levels (Tab. **S3**). The mean electrical conductivity was 21.94 µS/cm^{-1} (± 4.97), peaking in January 2020 and March 2019, and reaching its low point in September, coinciding with the lowest rainfall (Tab. **S3**).

The stream habitat descriptors varied mainly in terms of wetted width and thalweg depth. Based on the preselection of the environmental variables, we excluded the water temperature and pH because they presented low coefficients of variation (4.05% and

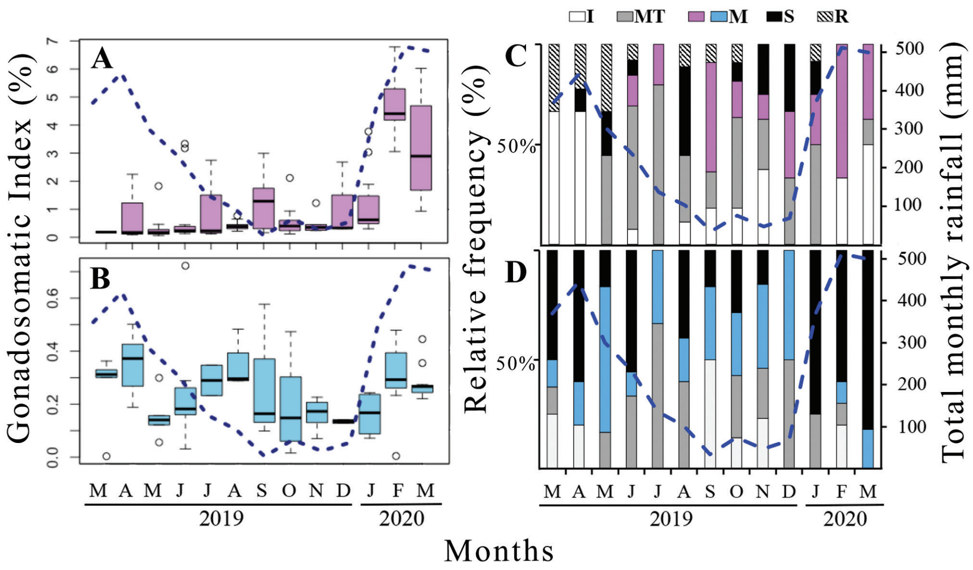

FIGURE 5 | Mean monthly Gonadosomatic Index (GSI) of (**A**) the females and (**B**) the males *Helogenes marmoratus* compared with the relative frequency of the different gonadal development phases: I: immature, MT: maturing, M: mature, S: spawned/spent, R: repousing of (**C**) the females and (**D**) the males collected in a catchment of Guamá River in Capitão Poço, Pará State, Brazil, between March 2019 and March 2020. The dashed blue line represents the total monthly rainfall.

8.08%, respectively). Significant correlations were also observed between discharge and mean flow speed ($r_S = 0.96$), mean thalweg depth ($r_S = 0.92$), and mean wetted width ($r_S = 0.80$). Mean flow speed was also correlated significantly with mean wetted width ($r_S = 0.80$), while canopy cover was correlated with dissolved oxygen ($r_S = 0.84$), and mean wetted width correlated with the maximum mean depth ($r_S = 0.72$). Given this, only dissolved oxygen, thalweg depth, electrical conductivity, and leaf litter were retained for the subsequent analyzes (Tab. **S3**).

The first two axes of the Principal Components Analysis (PCA) from the four retained environmental variables explained 70.77% of the total variation (Fig. 6). The first PCA axis explained 39.95% of the variation in the data (Tab. 1), and was influenced negatively by dissolved oxygen (%) and electrical conductivity (µS/cm^{-1}), with the rainy months being assigned to the left side of the plot. The second axis represented 37.33% of the variation (Tab. 1), and was influenced positively by maximum depth (cm) and negatively by the leaf litter (%).

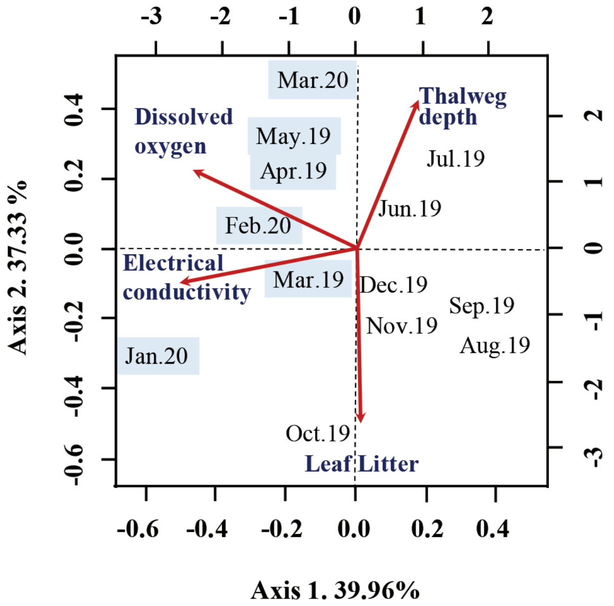

FIGURE 6 | Ordination of the 13 monthly samples collected in a catchment of the Guamá River, in the municipality of Capitão Poço, Pará State, Brazil, between March 2019 and March 2020. The months with a blue background represent the rainy season.

TABLE 1 | Loadings of the first two PCA axes with the environmental variables recorded in the seven streams of a catchment of the Guamá River in Capitão Poço, Pará State, Brazil.

Variables	Axis.1	Axis.2
Thalweg Depth (cm)	0.23	**0.60**
Dissolved Oxygen (%)	**-0.66**	0.34
Electrical conductivity (µS/cm^{-1})	**-0.71**	-0.14
Leaf Litter (%)		**-0.71**
Explaining	39.96	37.33
Eigenvalues	1.60	1.49

TABLE 2 | Results of multiple regressions between the GSI of the females and males *Helogenes marmoratus* and the environmental variables recorded in seven streams of a catchment of the Guamá River in Capitão Poço, Pará State, Brazil.

Response Variable	Multiple regression	Catchment variables	*ß*	SE of *ß*	*t*	*p*
Females GSI + Males GSI	R^2=0.0858; $F_{(4,167)}$= 3.921, p = < 0.05	Electrical conductivity	-0.091276	0.026285	-3.473	<0.001
		Thalweg depth	-0.025575	0.009928	-2.576	0.0109
		Leaf litter	0.023869	0.010614	2.249	0.0258
		Rainfall	0.0016	0.000426	3.756	<0.001
Females GSI	R^2=0.3196; $F_{(4,85)}$ = 9.982, p = < 0.001	Electrical conductivity	-0.156757	0.03171	-4.943	<0.001
		Thalweg depth	-0.055637	0.011464	-4.853	<0.001
		Leaf litter	0.026987	0.012742	2.118	0.0371
		Rainfall	0.003093	0.00053	5.836	<0.001
Males GSI	R^2=0.08778; $F_{(2,79)}$ = 3.801 p = 0.027	Electrical conductivity	-0.044833	0.021602	-2.075	0.0412
		Rainfall	0.000631	0.000257	2.451	0.0164

Although the multiple linear regression models were significant ($p < 0.05$), they evidenced a weak influence of the environmental variables on reproductive activity when we analyzed either pooled sexes or separately. However, the selected model did explain a third of the variation in the female GSI (Tab. 2). The model described the environmental effects of all variables on both sexes together (AIC = 248.4; w = 0.539) and females only (AIC = 108.2; w = 0.248), except for dissolved oxygen. For males, the AIC also eliminated the leaf litter and the thalweg depth, in addition to dissolved oxygen (AIC = 80.9; w = 0.248). The models explained only 8.8% of the variation in the GSI in the males and 8.6% when we included both sexes (Tab. 2). The multiple regressions indicated that thalweg depth, electrical conductivity, leaf litter, and monthly rainfall are important drivers of the reproductive activity of the female *H. marmoratus*, explaining 32% of the GSI variation over the studied period (Tab. 2).

DISCUSSION

We found that *H. marmoratus* has an extended reproductive period associated with the rainfall dynamics and low fecundity compensated by batch spawning, as expected for stream small-sized fishes. Small body size and early maturation place *H. marmoratus* in the opportunistic strategy, whereas its relatively large oocytes place the species in the equilibrium strategy, which leads us to attribute an intermediate position to it along this gradient.

The constant abundance of *H. marmoratus*, including juveniles observed throughout the study period, allows us to conclude that these environments present minimal conditions necessary to sustain fish reproduction. The protection offered by riparian vegetation in these streams would favor food input and maintains their general physical characteristics (*e.g.*, water temperature), making spawning sites available and providing resources to support the early stages of life.

The species presented a balanced sex ratio, a tendency exhibited by teleosts (Kraak, Pen, 2002), accentuated during the reproductive period (Vazoller, 1996; Pavlov, Emel'yanova, 2016). Differences in sex ratios may be related to differentiated growth and mortality rates (Vicentini, Araujo, 2003; Fagundes *et al*., 2020), predation rates or spatial segregation (Cetra *et al*., 2011; Tondato *et al*., 2012), and the influence of the selectivity of fishing gear (Vazoller, 1996; Gurgel, 2004). A possible explanation for the predominance of females in January could be that the males were more likely to predation due to their smaller size this month (♂ = 42.98 ± 7.1 *vs.* ♀ = 54.88 ± 4.98 mm) and their vulnerability after releasing the gametes.

The largest body size recorded in the present study (65.21 mm TL) exceeded the length registered by Rosa *et al*. (2016) in the Floresta Nacional de Saracá-Taquera (52 mm TL) also in Pará State, but is much smaller than the values recorded for *H. marmoratus* by Cardoso (2012) in Central Amazon (84.36 mm), and by Allard *et al.,* (2015) in Guyana (79 mm SL).

We believe that smaller body size can also result in reduced mean size at first maturity. However no references concerning the reproductive strategy of *Helogenes* species were found to allow comparisons. Although this is the first study to present the size at first sexual maturation of *H. marmoratus*, some studies with small-sized fishes reveal that an early maturity would represent about 50% of the maximum standard length that a species could reach (Mazzoni *et al*., 2005; Oliveira, Queiroz, 2017; Fagundes *et al*., 2020). This pattern has also been recorded for *H. marmoratus*, reflecting possible effects of predation pressure (*e.g*., *Hoplias malabaricus* (Bloch, 1794) and *Crenicichla* spp. presence) or competition (Bruce, 1990). The latter author concluded that a decrease in the age at maturation represents an evolved response to reduced life expectancy, which selects for early maturation.

Batch spawning and low fecundity are features of species with parental care or territoriality (Lowe-McConnel, 1975), although it is unclear if this applies to *H. marmoratus*, given the lack of behavioral data on this species. In fact, batch spawning may also be influenced by the fish size (Nikolsky, 1963; Alkins-Koo, 2000). Even if this spawning type is confirmed for *H. marmoratus*, it is uncertain whether the next batch of oocytes will be released or re-absorbed, depending on the prevailing environmental conditions.

In the present study, we recorded very low fecundity (60 oocytes) for *H. marmoratus* compared to a single female from Central Amazon (224 oocytes; Cardoso, 2012), and with other small-bodied Neotropical siluriforms, such as loricariids (37–736 oocytes, Winemiller, 1989; Gomes *et al*., 2015; Mendes *et al*., 2018), heptapterids (317–29757 oocytes, Gomiero *et al*., 2007; Olaya-Nieto *et al*., 2010; Rondineli *et al*., 2011), and callichthyds (2684 oocytes, Winemiller, 1989). The mean diameter of the stage IV oocyte herein recorded for *H. marmoratus* was 1.24 mm, representing 0.02% of its total length, a relatively large size compared to other species ranging from 0.004 to 0.06. For instance, for loricariids, which are known to have large eggs and parental care, the diameter of the stage IV oocytes varies from 1.7 mm to 6.0 mm (Winemiller, 1989; Gomes *et al*., 2015; Mendes *et al*., 2018), while in the heptapterids range from 0.96 to 1.53 (Gomiero *et al*., 2007; Olaya-Nieto *et al*., 2010; Rondineli *et al*., 2011), and in the callichthyds is about 2 mm (Winemiller, 1989) (Tab. **S4**).

Larger females usually produce more oocytes, implying higher fecundity (Tsoukali *et al*., 2016) which may explain the higher fecundity observed by Cardoso (2012) for *H. marmoratus*. For our population of *H. marmoratus* it may be more advantageous to start reproduction early and invest in large oocytes than in larger females; this would reduce the cost of growth during earlier life stages and does not affect future expected fecundity (Stearns, 1992). Although the observation of Cardoso (2012) was based on a single individual, which can provide valuable insights, it is necessary to assess a broader scenario. It means to include more individuals over a more extended period to detect better the variation in reproductive traits associated with fluctuations in environmental variables.

During the breeding season (September to March), the highest GSI values of females were recorded when the greatest amount of rain was observed (February). We did not find an equivalent pattern in March and April 2019. However, the highest frequency of immature females indicated a recruitment period that coincided with the first peak of the rainfall. The male maturation curve revealed a more extended period, probably because they must be ready to reproduce when the first mature females become available. Indeed, an early maturation of males than females is for longer, a condition facilitated by the reduced energetic cost of producing spermatozoa compared to oocytes (Chaves, 1991). It may also explain why males usually reached first sexual maturation at a smaller size than females, a pattern found for most teleosts (Helfman *et al*., 1997).

Kramer (1978) pointed out that a prolonged spawning season tends to occur in relatively stable environments. During the studied period, dissolved oxygen, electrical conductivity, and leaf litter varied in response to rainfall dynamics (Tab. **S4**). For the most part, these environmental variables explained the variation between the streams sampled in this study (Fig. 6). However, the hydrological cycle did not reflect any marked response in the reproductive activity of the *H. marmoratus* males and explained only a third of the female GSI variation. Probably intra or interspecific interactions, as well as food availability could potentially be meaningful in explaining variation in these reproductive traits.

In tropical streams with slight variation in altitude, there is typically an association between the fluctuations in water level and the reproductive behavior of the local fish (Winemiller *et al*., 2008). Although the increase in rainfall influenced the frequency of mature individuals of both sexes in the present study (see Figs. 5A–B), it is interesting to note that the lower rainfall intensity did not interrupt reproduction. Conversely, peaks of reproductive activity were observed in the dry period for both sexes.

Our results provide important insights into the influence of local rainfall on the water parameters dynamics in the streams and habitat descriptors, and the role of these set of environmental variables in the reproductive activity of *H. marmoratus*. The changes in the stream water level in the streams provoked by local rainfall may trigger fish spawning. This observation is commonly described for species that inhabit floodplain systems, where electrical conductivity is considered the principal factor influencing spawning (Vazzoler, 1996; Baumgartner *et al*., 2008).

For some small fishes in south-eastern Brazil streams, the conductivity also appears to be a relevant factor for initiating gonadal maturation when associated with other variables (Lourenço *et al*., 2015). The maturation time in *Geophagus brasiliensis* (Quoy & Gaimard, 1824) and *Astyanax altiparanae* Garutti & Britski, 2000 (= *A. lacustris* (Lütken, 1875)) was related to conductivity, turbidity, depth, and precipitation, while the increase in gonadosomatic index in *Piabina argentea* Reinhardt, 1867 was related only to conductivity and dissolved oxygen. These variables are similar as we found for *H. marmoratus* in *terra* *firme* streams and denote that each species seems to require a unique combination of environmental factors to initiate oocyte development (Lourenço *et al*., 2015).

In the cryptic *H. marmoratus*, the leaf litter brought into the canal by the runoff of the rains may favor the species by providing shelter and food in the form of the invertebrates associated with the litter (Carvalho *et al*., 2013). The current challenge is determining which specific factors associated with local rainfall levels influence the spawning and the cycle of gonadal maturation and recrudescence in Amazonian stream fishes. This is supported by given the marked differences in the environmental heterogeneity of the streams located within different basins (Benone *et al*., 2017), and the paucity of data on the history life of stream fish.

The persistent knowledge gaps on the reproductive biology and ecology of the species that inhabit Amazonian forested streams (Castro, Polaz, 2020) hinder the classification of their reproductive patterns. Although identifying endpoints of the continuum is easy, understanding the trade-offs between life- history traits of the "intermediate points" may lead to differential life-history expression among species or even among populations experiencing the same ecological conditions (DeBoer *et al*., 2015). Further studies of the reproductive traits of the small-body species would permit a more reliable definition of parameters such as fecundity, egg size, and the timing of the first maturity and related them to environmental factors.

Helogenes marmoratus occupies an intermediate position between the opportunistic and equilibrium extremes of the life-history gradient. While local rainfall appears to be a factor determining the reproductive patterns of this fish, it only explained a third of the variation in the GSI of the females, together with thalweg depth, electrical conductivity, and leaf litter, in the present study. Thus, the analysis of life-history traits between sexes is indispensable for understanding intraspecific variations in reproductive behavior and population dynamics (Tondato *et al*., 2012).

Our knowledge shortfall on how genders differ in their reproductive patterns in response to environmental regulation hinders us from predicting how populations may respond in terms of their phenotypical response to typical environmental variation or their evolutionary response to climate change (Ball, Ketterson, 2007). Finally, we encourage researching fish life history, especially how the reproductive strategy is being adjusted in the environments and which environmental factors drive the stream fish reproduction. We also highlight if a new model for classifying the small size fish by assessing the variation of their reproductive traits should be proposed.

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ETHICAL STATEMENT

The specimen collections were authorized by license 63603–3, issued by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), through the Sistema de Autorização e Informação em Biodiversidade (SISBIO). The study was approved by the Animal Ethics Committee of the Universidade Federal Rural da Amazônia (UFRA), through process number 054/2018.

COMPETING INTERESTS

The authors declare no competing interests.

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