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VARIAÇÃO DAS CARACTERISTICAS DE HISTÓRIA DE VIDA DOS PEIXES DE RIACHOS DA AMAZÔNIA ORIENTAL E A INFLUÊNCIA AMBIENTAL NAS ESTRATÉGIAS REPRODUTIVAS

Belém

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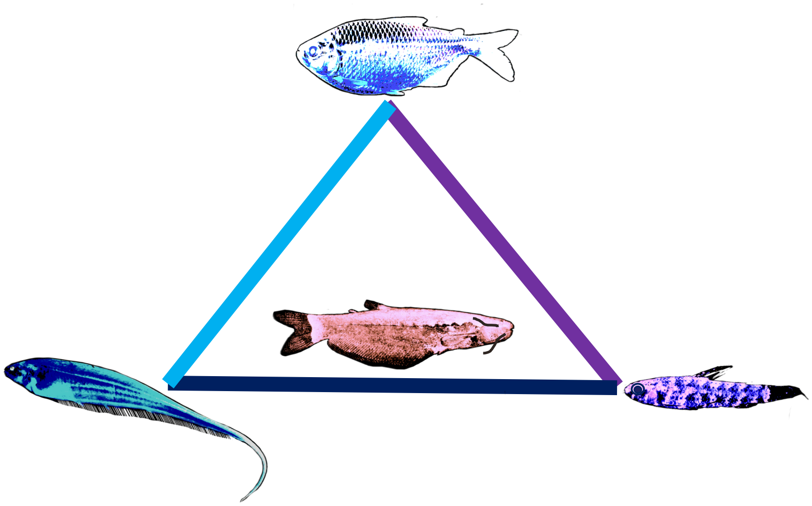

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Orientador: Prof. Dr. Luciano F. A. Montag
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Aprovada em: 27 de janeiro de 2023.

Defesa remota: https://meet.google.com/ugo-rpgc-soi

Пухачу Сергію Васильовичу
Для тебе.

Мій найкращий друг,
моя справжня любов.
Найхоробріший воїн з
найблагороднішою душею.

Слава україні!

A Serhii Vasylovich Puhach
Para ti e por ti.
Meu melhor amigo,
meu amor verdadeiro.
O guerreiro mais corajoso
com a alma mais nobre.

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Variação das características de história de vida dos peixes de riachos da Amazônia oriental e influência ambiental nas estratégias reprodutivas

RESUMO

O conjunto de características que compõem a estratégia de história de vida de um organismo, descreve a forma em que este aloca recursos para seu crescimento, desenvolvimento, sobrevivência e reprodução. Como resposta as diferentes forças evolutivas, os organismos precisam fazer ajustes nessas características da sua estratégia para ter sucesso reprodutivo. Para muitas das espécies de peixes de pequeno porte que habitam os riachos amazônicos as suas características de história de vida ainda não foram descritas, e os seus ambientes estão sendo a cada vez mais ameaçados pela destruição dos habitats, poluição e introdução de espécies. Por esse motivo identificar o tipo de estratégias reprodutivas que representam a estes grupos de espécies, permitiria predizer as respostas reprodutivas em face as mudanças ambientais. Neste contexto, na primeira sessão foram estimadas oito características reprodutivas de 17 espécies de peixes: proporção sexual, tamanho a primeira maturação, índice gonadossomático, duração do período reprodutivo, fecundidade, diâmetro do ovócito, tipo de desova e cuidado parental. Posteriormente, as características foram analisadas por meio de uma ordenação, para verificar se as estratégias resultantes se encaixam no modelo contínuo de história de vida. Se evidenciou que algumas espécies ocupam os pontos finais das três estratégias do modelo: Oportunista (*Microcharacidium weitzmani* e *Hemigrammus guyanensis*), Equilibrio (*Eigenmannia pavulagem, Gymnorhamphichthys rondoni* e *Aequidens tetramerus*) e periódico (*Astyanax bimaculatus* e *Moenkhausia oligolepis*), as outras espécies ocupam um espaço nos gradientes oportunista – periódico (*Moenkhausia collettii* e *Bryconops melanurus*) e uma grande maioria no gradiente oportunista – equilíbrio (*Hyphessobrycon heterorhabdus, Hypopygus lepturus, Helogenes marmoratus, Copella arnoldi, Pyrrhulina capim, Iguanodectes rachovii, Anablepsoides urophthalmus e Apistogramma* gr *regani*). O tamanho corporal e a fecundidade foram as características que mais contribuíram na segregação das espécies, destacando a estratégia intermediária entre o gradiente oportunista e de equilíbrio como a mais representativa para as espécies analisadas. Na Sessão II, foram avaliadas as características reprodutivas de *Eigenmannia pavulagem, Gymnorhamphichthys rondoni* e *Hypopygus lepturus* com o fim de detectar se as espécies mais emparentadas (*G. rondoni* e *H. lepturus*) manifestariam o mesmo conjunto de características, e se variáveis ambientais locais teriam alguma influência na variação mensal do índice gonadossomático. Os resultados não agruparam as espécies com base nos atributos reprodutivos, mas se observou que a chuva, a condutividade elétrica e descritores do habitat (tipo de substrato velocidade da correnteza e profundidade) foram fatores importantes para explicar a variação do índice gonadossomático das fêmeas. Na Sessão III, a avaliação das características reprodutivas de *H. marmoratus* o posicionam em um ponto intermediário entre as estratégias oportunista – equilíbrio. Evidenciou-se o efeito significativo de um conjunto de variáveis que incluíram a profundidade, a condutividade elétrica, os bancos de folhas e a chuva, como os principais responsáveis pela variação mensal do índice gonadossomático das fêmeas.

PALAVRAS-CHAVE: características reprodutivas**,** estratégia reprodutiva, *terra firme*, variáveis ambientais.

Life-history traits variation of fishes from eastern Amazonian streams and environmental influence on reproductive strategies

ABSTRACT

The set of characteristics that compound an organism's life history strategy describes how it allocates resources for its growth, development, survival, and reproduction. In response to different evolutionary forces, organisms need to adjust these features of their strategy for reproductive success. For many of the small fish species that inhabit Amazonian streams, their life history characteristics still need to be described, and their environments are being increasingly threatened by habitat destruction, pollution, and species introduction. For this reason, identifying the reproductive strategies of these species would allow for predicting their reproductive responses in the face of environmental changes. In this context, in the first chapter of this work, eight reproductive characteristics of 17 fish species were estimated: sex ratio, size at first maturation, gonadosomatic index, length of the reproductive period, fecundity, oocyte diameter, type of spawning, and parental care. Later, the characteristics were analyzed by ordination to verify if the resulting strategies fit the continuous life-history model. It was evidenced that some species occupy the endpoints of the three strategies of the model: Opportunistic (*Microcharacidium weitzmani* and *Hemigrammus guyanensis*), Equilibrio (*Eigenmannia pavulagem*, *Gymnorhamphichthys rondoni*, and *Aequidens tetramerus*) and periodic (*Astyanax bimaculatus* and *Moenkhausia oligolepis*), the other species occupy a space in the opportunistic – periodic gradients (*Moenkhausia collettii* and *Bryconops melanurus*) and a large majority in the opportunistic – equilibrium gradient (*Hyphessobrycon heterorhabdus*, Hypopygus *lepturus*, *Helogenes marmoratus*, *Copella arnoldi*, *Pyrrhulina capim*, *Iguanodectes rachovii*, *Anablepsoides urophthalmus* and *Apistogramma* gr. *regani*). Body size and fecundity were the characteristics that most contributed to species segregation, highlighting the intermediate strategy between the opportunistic and equilibrium gradient as the most representative for the analyzed species. In Session II, the reproductive characteristics of *Eigenmannia pavulagem*, *Gymnorhamphichthys rondoni*, and *Hypopygus lepturus* were evaluated in order to detect whether the more closely related species (*G. rondoni* and *H. lepturus*) would manifest the same set of characteristics and whether local environmental variables would have some influence on the monthly variation of the gonadosomatic index. The results did not group the species based on reproductive attributes. However, rainfall, electrical conductivity, and habitat descriptors (type of substrate, current velocity, and depth) were important factors in explaining the variation in the gonadosomatic index of females. In Session III, the evaluation of the reproductive characteristics of *H. marmoratus* positioned it at an intermediate point between the opportunistic – equilibrium gradient. There was evidence of the significant effect of a set of variables that included depth, electrical conductivity, leaf banks, and rainfall as the main factors responsible for the monthly variation of the female gonadosomatic index.

KEYWORDS: reproductive traits, reproductive strategy, terra firme, environmental variables.

SUMÁRIO

1. APRESENTAÇÃO

As diversas estratégias de história de vida adotadas pelos peixes, são o resultado de uma combinação de características que evoluem de forma coordenada e determinam como eles se reproduzem ao longo da vida (Roff, 1992; Stearns, 1992). Desta forma, cada organismo deve manifestar uma estratégia bem-sucedida que permita manter as populações viáveis ao longo prazo, sendo este um aspecto fundamental da Teoria da História de Vida (Stearns, 1992) pois fornece importantes informações sobre à adaptação dos mesmos ao ambiente e também sobre a sua evolução (Vazzoler, 1996).

A pesar de que os peixes de pequeno porte, com um comprimento padrão de até 15 cm nos adultos (Castro, 1999; Castro et al., 2005) representam 70% da riqueza de peixes de água doce na região Neotropical (Reis et al., 2003), estimada em mais de 6.200 espécies (Albert et al., 2020), muitos aspectos sobre a sua história de vida têm sido pouco explorados ou documentados quando comparados com os estudos reprodutivos de peixes da calha principal dos grandes rios (Camargo et al., 2015; Caramaschi & Brito, 2021).

Um número considerável desses peixes de pequeno porte ocorre exclusivamente em cursos de água menores (Oliveira et al., 2009; Benone et al., 2018; Silva et al., 2019), os quais estão sometidos a impactos de origem antrópico (Figueiredo et al., 2010; Juen et al., 2016; Leal et al., 2016), fator relevante para integrar o estudo das estratégias de historia vida com a resposta reprodutiva que algumas espécies poderiam expressar como mecanismo de resistência as certas pressões ambientais (Duarte et al., 2011).

Considerando que possuímos o mais diverso conjunto regional de peixes de água doce do mundo na bacia Amazônica, com 2.716 espécies válidas (Dagosta & Pinna, 2019), a grande quantidade de pequenos riachos, sua maior vulnerabilidade a impactos antrópicos e as enormes lacunas no conhecimento autoecológico de muitas das espécies de pequeno porte (Castro & Polaz, 2020), esta tese em História Natural dos peixes de riachos pretende: i) Dar visibilidade às espécies que habitam esses sistemas; ii) Detectar os padrões reprodutivos e associar os atributos reprodutivos à estrutura conceitual das estratégias reprodutivas; e iii) Avaliar a influência de variáveis ambientais locais na dinâmica reprodutiva das espécies de peixes de riachos.

Este tipo de enfoque permitirá estudos comparativos com abordagem evolutiva e ao mesmo tempo representa uma ferramenta para a avaliação da qualidade ambiental (Caramaschi & Brito, 2021), contribuindo para o gerenciamento e conservação das espécies uma vez que as características reprodutivas podem ser componentes nestas análises que incluem novas medidas de biodiversidade (Cianciaruso et al., 2009).

Deste modo, esta tese apresenta informações inéditas sobre a biologia reprodutiva de 17 espécies representativas da Amazonia Oriental Brasileira, coletadas mensalmente em oito riachos de 1ª a 3ª ordem, em uma micro-bacia do rio Guamá, entre março de 2019 e março de 2020. Na primeira sessão titulada "**Decoding the reproductive strategies of Amazonia stream fish**" foram avaliadas oito características reprodutivas para 17 espécies, as quais foram ordenadas, e os grupos formados foram analisados com base no modelo continuo de história de vida proposta por Winemiller (1989) e Winemiller e Rose (1992). A contribuição de cada característica foi calculada, se destacando a grande amplitude da fecundidade e do comprimento total, para influenciar a segregação dos grupos. Nove espécies (53%) se posicionaram no gradiente oportunista – equilíbrio indicando que a estratégia intermediária é relevante ao momento de caracterizar os padrões reprodutivos para esta assembleia. Na segunda sessão "**Comparative analysis of the life-history traits of small gymnotiformes from the Eastern Amazon"** detectou-se que espécies mais aparentadas filogeneticamente, não exibem necessariamente as mesmas táticas reprodutivas quando se encontram no mesmo habitat, e respostas diferenciadas são evidenciadas entre as espécies e entre os sexos à influência de variáveis ambientais locais na dinâmica reprodutiva. E por fim, na terceira sessão: "**Environmental influence on the reproductive strategy of *Helogenes marmoratus* (Siluriformes: Cetopsidae) in the Amazonian streams**" foi verificado que o conjunto de características reprodutivas de *H. marmoratus* o posicionam em um ponto intermediário entre o gradiente oportunista – equilíbrio, sendo importante o tamanho dos ovócitos maduros, para a definição da estratégia. Na avaliação da possível influência do ambiente sobre a atividade reprodutiva, se evidenciou o efeito significativo de um conjunto de variáveis que incluíram a profundidade, a condutividade elétrica, os bancos de folhas e a chuva, como os principais responsáveis pela variação mensal do índice gonadossomático das fêmeas.

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2. INTRODUÇÃO GERAL

2.1. Os riachos amazônicos de terra firme

A bacia Amazônica apresenta em toda a sua extensão uma complexa e densa rede de pequenos riachos, denominados regionalmente como igarapés (Junk, 1983). Ao longo destes riachos podem ser encontradas três zonas ecológicas distintas: (1) a zona de inundação ou curso inferior, (2) a zona intermediária ou curso médio que pode ser alcançada pela inundação em época de grandes cheias e (3) a zona superior ou de *terra firme* (Fittkau, 1967), que ao contrário da zona de inundação, não sofre a influência da enchente sazonal dos grandes rios, apresentando alterações no nível de suas águas em função do regime de chuva local (Franken & Leopoldo, 1984; Espírito-Santo et al., 2013).

A zona de *terra firme*, engloba riachos de 1ª, 2ª e 3ª ordens (Vannote, 1980). Um riacho de 1ª ordem é aquele que não possui tributários, sendo a ordem do riacho aumentada pela junção de dois riachos de mesma ordem. Assim, a união de dois riachos de 1ª ordem forma um riacho de 2ª ordem, dois de 2ª ordem formam um de 3ª ordem e assim por diante (escala de Horton, modificada por Strahler (Petts, 1994)).

Dependendo da sua complexidade estrutural, os segmentos dos riachos de *terra firme* podem ser classificados em três ambientes típicos: (1) corredeiras, com alta velocidade da correnteza, baixa profundidade e substrato composto basicamente de areia, seixo e raízes, (2) água corrente, com velocidade da correnteza e profundidade médias e (3) seções empoçadas, com baixa velocidade da correnteza, alta profundidade e substrato composto por bancos de liteira (Zuanon et al., 2015).

Os cursos dos riachos de *terra firme* estão cobertos pelo dossel das árvores adjacentes, o que dificulta a penetração de luz tornando estes ambientes pobres em nutrientes e a sua fauna dependente da entrada de material alóctone do sistema terrestre circundante (Goulding, 1980; Walker, 1991; Lowe-McConnell, 1999). No entanto, durante os períodos de fortes chuvas, o aumento abrupto no nível d'água ultrapassa o limite das margens, permitindo assim novas áreas de exploração, alimentação e refúgio para os peixes (Anjos et al., 2005; Espírito-Santo et al., 2009).

Muitas das espécies que habitam os riachos de *terra firme,* sincronizam seus tempos reprodutivos com os períodos chuvosos, estação mais favorável do ano para o crescimento da prole (Alkins-Koo, 2000; Espírito-Santo et al., 2013; Waddell et al., 2019; Winemiller, 1993). A apesar de que estes sistemas exibam uma menor amplitude de inundação (< 0,5 m) em comparação com os sistemas de rio-várzea (até 16 m) (Junk, 1997), as inundações intermitentes e rasas nos riachos de *terra firme* de ordens menores desempenham um papel importante visto que, a dinâmica das comunidades de peixes estaria ligada a uma expansão e contração sazonal do habitat (Waddell et al., 2019).

2.2. Os riachos da Bacia do rio Guamá

O presente trabalho foi realizado numa micro-bacia do rio Capitão Poço, que drena à margem esquerda do rio Guamá, com uma área de aproximadamente 1,240 hectares, pertencente inteiramente ao município de Capitão Poço, mesorregião do Nordeste Paraense, microrregião do Guamá, Pará, Brasil (**Figura 1**). A vegetação da micro-bacia estudada enquadra-se na região fitoecológica denominada de Floresta Equatorial Subperenifolia (IBGE, 1992). Contudo, a atual paisagem da micro-bacia é predominantemente composta por áreas de agricultura e pecuária (Pacheco & Bastos, 2001), com pequenos remanescentes de vegetação secundária (capoeiras) (Silva et al*,* 1999) e faixas estreitas de vegetação no entorno de seus cursos d'águas, denominada Áreas de Preservação Permanente (APP) segundo o art. 30 do Código Florestal Brasileiro, Lei nº12.651/12.

A região possui um clima do tipo tropical úmido que se enquadra no subtipo *Af* de acordo com a classificação de Köppen, adaptada por Peel et al*.,* (2007). A temperatura média anual na região é de 26,9º C, com precipitação anual média de 2.370 mm, com maiores níveis de precipitação entre os meses de janeiro a maio, e menores níveis entre agosto e novembro (Pacheco & Bastos, 2001) (**Figura 2**).

Figura1. Localização da micro bacia do rio Guamá (Amazônia Oriental Brasileira). Os círculos vermelhos indicam os riachos que foram amostrados desde março de 2019 até março de 2020.

As espécies de peixes foram coletadas em oito riachos com estruturas físicas semelhantes. De acordo à classificação hierárquica de ordens de riachos proposto por Stralher (1957), os pontos 2, 5, 6 e 8 são classificados como riachos de 1ª ordem, os pontos 1, 4 e 3 são classificados como riachos de 2ª ordem; e o 7, o único riacho de 3ª ordem (o mais ocidental do mapa) resulta de um grande número de nascentes próximas (**Figura 1**).

Os oito pontos compreendem riachos encaixados suscetíveis de alagamento lateral devido a fortes chuvas, com vegetação arbórea nas suas margens, com exceção do ponto 1 que a possui somente em uma das margens e que por conta de uma maior largura e por conseguinte maior abertura de dossel, apresenta abundância de macrófitas na margem desprovida deste tipo de vegetação (**Figura 3**).

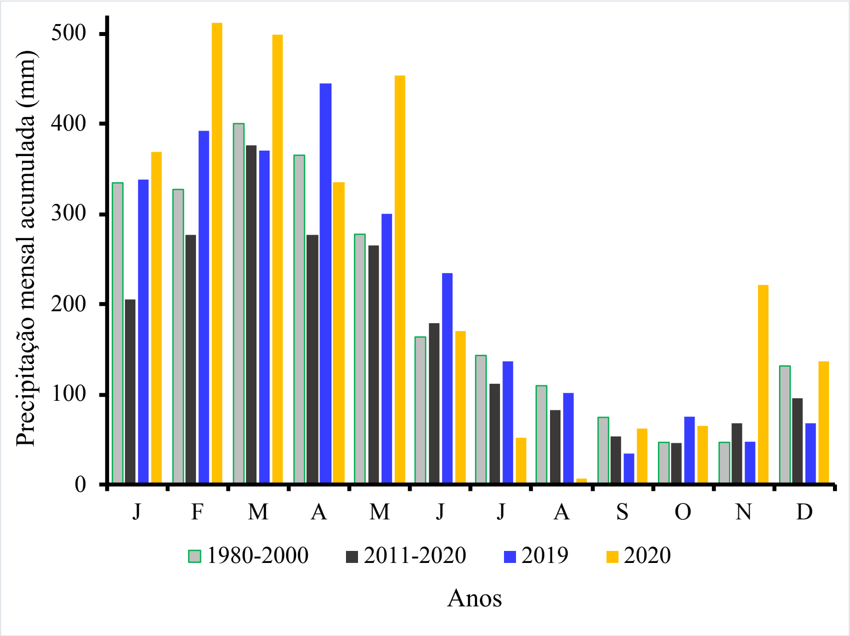

Figura 2. Registros históricos de precipitação média mensal acumulada no município de Capitão Poço entre 1980 a 2000 (Pacheco & Bastos, 2001), entre 2011 a 2020 (INMET), e a precipitação mensal acumulada registrada em 2019 e em 2020.

2.3. Mensuração das variáveis ambientais

Os riachos foram amostrados a cada mês entre março de 2019 e março de 2020 em um trecho de 50 m, dividido em cinco seções longitudinais de 10 m por seis seções transversais. Antes da coleta dos peixes, foram medidas quatro características físico-químicas d'água em cada riacho: Oxigênio Dissolvido (OD; %), Condutividade Elétrica (CE; µS/cm^{-1}), pH e Temperatura (T; ºC), utilizando um aparelho multiparâmetro Horiba U-50.

Foram avaliados seis descritores estruturais de habitat, seguindo um protocolo simplificado e eficiente para amostragem em riachos de 1ª a 3ª ordem (Mendonça et al., 2005). Nas seis seções transversais de cada riacho, mensuramos a largura molhada (LM – m), a profundidade do talvegue (PT – cm), o tipo de substrato (*e.g.* banco de folhas, areia, raízes, galhos, madeira, cascalho grosso e fino – S; %) e a cobertura do dossel (DOS;%).

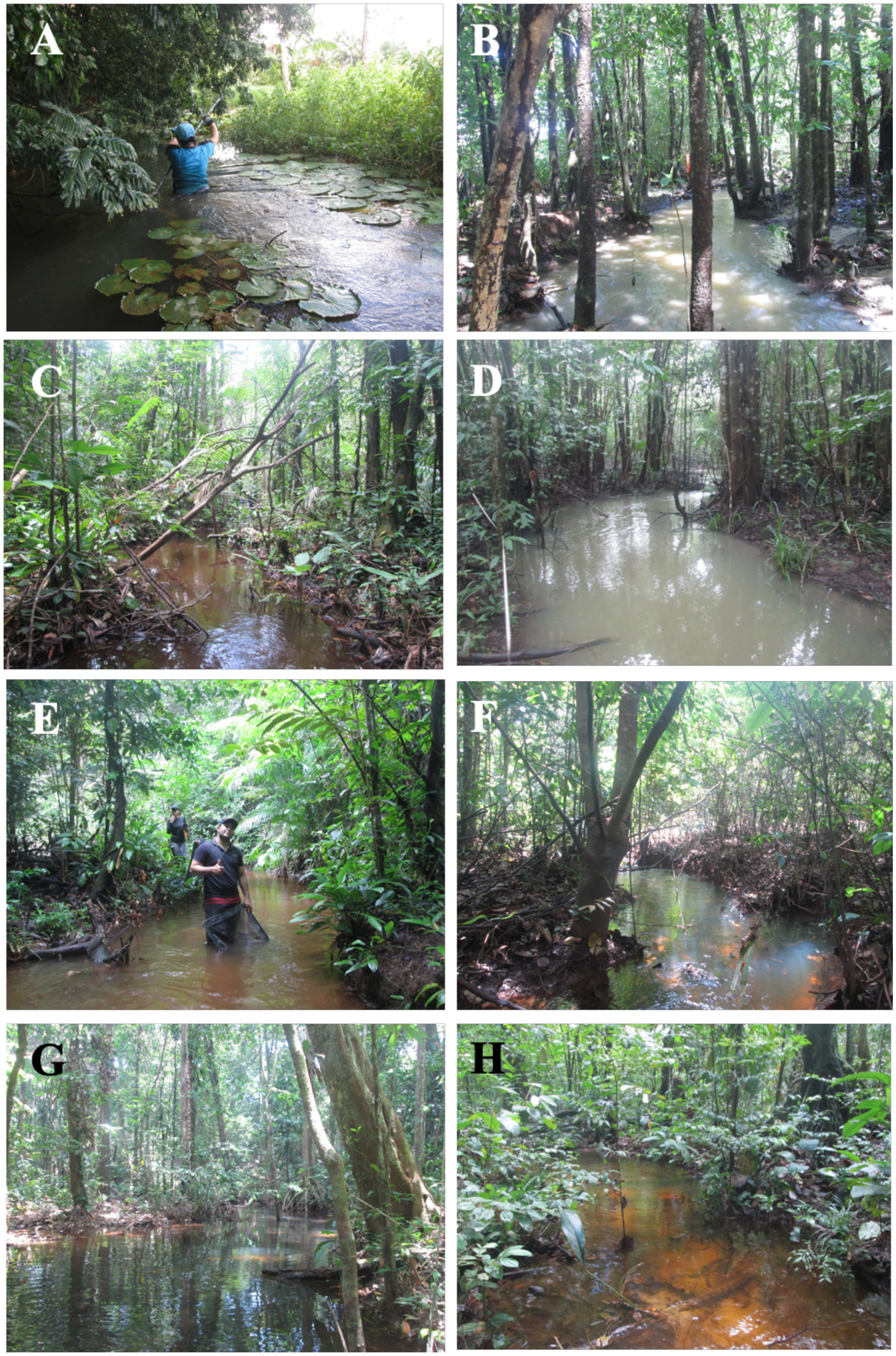

Figura 3. Riachos de 1º a 3ª ordem amostrados entre março de 2019 a março de 2020, em uma micro bacia do Rio Guamá (Amazônia Oriental). A. 1 (janeiro 2020), B. 2 (julho 2019), C. 3 (outubro 2019), D. 4 (fevereiro 2020), E. 5 (julho 2019), F. 6 (fevereiro 2020), G. 7 (setembro 2019) e H. 8 (abril 2019).

A largura molhada foi definida como a distância transversal entre as margens inundadas do riacho, e foi medida usando um cano graduado, o mesmo elemento se utilizou para medir a profundidade em cinco pontos equidistantes dentro de cada seção transversal, onde registrou-se visualmente o tipo de substrato. A cobertura do dossel foi calculada com fotografias digitais em três pontos dentro de cada seção transversal (no meio do canal e em cada margem), que foram convertidas em uma escala preto e branco para calcular a porcentagem de cobertura (pixels pretos) usando o software Image J®

A velocidade da correnteza (VM – m/s) foi calculada com base na média do tempo em que um objeto flutuante leva para percorrer uma distância conhecida em três pontos equidistantes ao longo do canal. A vazão (VZM – m^3/s) foi calculada pela fórmula $Q = A * Vm$ onde Q = vazão; Vm = velocidade média do fluxo superficial; A = área média na secção transversal do curso de água. A área média da secção, foi determinada para cada um dos seis segmentos, pela fórmula: $At = \Sigma^n {}_i A_n$ onde At = área da transecção, dada pela somatória de $[(Z_1+Z_2)/2].l + [(Z_2+Z_3)/2].l + \ldots [(Z_n+Z_n+1)/2].l$ onde, Zn = profundidade medida em cada segmento; l = largura de cada segmento.

Os dados pluviométricos foram obtidos da estação meteorológica do Instituto Nacional de Meteorologia (INMET – Estação A248 https://portal.inmet.gov.br/), localizada no município de Capitão Poço (**Figura 2**).

Durante o período de estudo, a maior temperatura média mensal do ar foi registrada em novembro (27,5 ° C) e a menor em janeiro e fevereiro (24,8 ° C), com uma temperatura média anual de 25,8°C. A precipitação acumulada entre março de 2019 e março de 2020 foi de 1500,4 mm, sendo o maior volume em fevereiro (511,6 mm) e o menor em agosto (34 mm). A dinâmica das chuvas não diferiu do padrão histórico de precipitação do município, com a maior intensidade ocorrendo entre janeiro e maio (**Figura 2**).

Os oito riachos que drenam a micro-bacia, apresentam canais principais com grande complexidade estrutural, com substrato predominantemente arenoso e bancos de folha acumulando-se nas margens. As raízes de matas ciliares, troncos submersos e pequenas cavernas compõem importantes unidades de habitat, sendo em grande parte os responsáveis pela complexidade estrutural do canal. Em seis dos oito riachos amostrados a presencia de poças temporárias foi outro dos microambientes mais frequentes ao longo do período de estudo.

Nos ambientes amostrados o oxigênio dissolvido teve a maior variação ao longo do período de estudo com uma média de 63,94% (± 30,42), apresentando o valor médio mais baixo em agosto de 2019 (21%) e o maior em janeiro de 2020 (102,11%), por sua vez a temperatura d'água e o pH tiveram a menor variação com valores médios de 26,59ºC±1,12 e 5,88 ± 0,74 respetivamente (**Figura 4**).

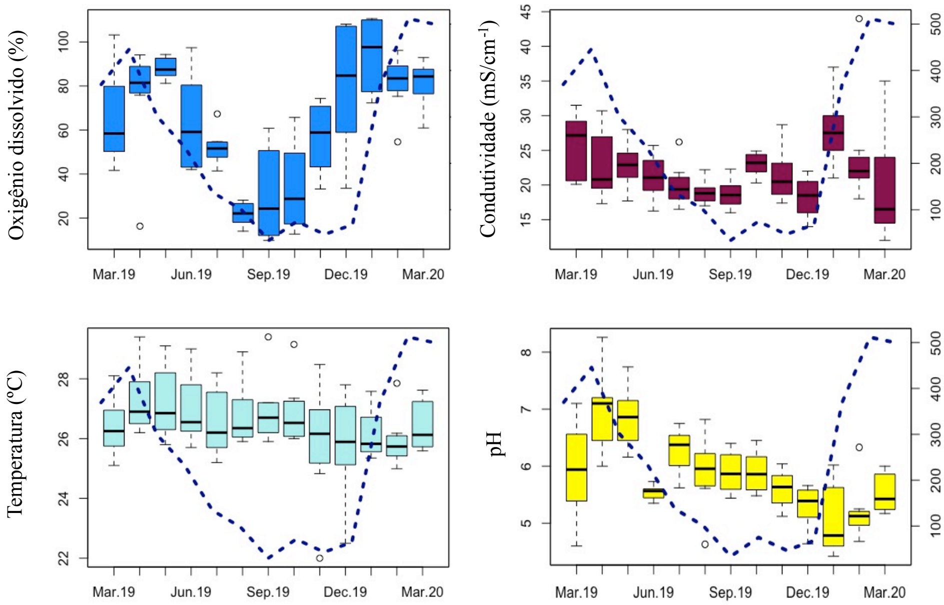

Figura 4. Variação mensal de quatro variáveis físico-químicos d'água registrados em oito riachos de uma micro bacia do rio Guamá (Amazônia Oriental) entre março de 2019 e março de 2020. A linha tracejada representa a precipitação mensal acumulada.

A largura molhada, a velocidade da correnteza e a cobertura do dossel, foram os descritores do habitat que sofreram expressivas mudanças ao longo do ciclo hidrológico, os valores da largura molhada variaram entre 1,70 a 11,79 m (3,83 ± 2,06) e a a profundidade máxima média de 5,6 a 110,8 cm (35,35 ± 18,02). A velocidade da correnteza variou entre 0,02 a 0,54 m/s (0,20 ± 0,1), a vazão média oscilou de 0,01 a 2,38 m/s (0,35 ± 0,42). a cobertura do dossel variou entre 63,32 a 100 % (76,82 ± 5,91) A maior parte de seus leitos foram cobertos predominantemente por bancos de folha (29,96% ±17,88), areia (24,47% ± 20,11) e raízes (22,80% ± 13,08).

2.4. Espécies estudadas

Foram coletados 16.634 exemplares pertencentes a 64 espécies, seis ordens e 27 famílias (Tabela 1). A família Characidae foi a mais abundante com 16 espécies (26,15%), seguida por Cichlidae (n=7, 10,77%). Em relação às espécies, as mais representativas em abundância foram *Hyphessobrycon heterorhabdus* (n=4263, 25,47%), *Microcharacidium weitzmani* (n=1721, 10,28%), *Apistogramma* gr. *regani* (n=1521, 9,09%), *Pyrrhulina capim* (n=1417, 8,46%), *Copella arnoldi* (n=1410, 8,42%) e *Hemigrammus guyanensis* (n= 1052, 6,29%) que, juntas, representaram 68,01% da abundância total. Seis espécies tiveram ocorrência única: *Apteronotus albifrons*, *Hypselecara temporais*, *Tatia* sp., *Hemiodontichthys* sp., *Poecilia* sp. e *Jupiaba anteroides*

Tabela 1. Abundância mensal das espécies coletadas em uma micro-bacia do rio Guamá (Amazônia Oriental) entre março de 2019 e março de 2020.

					2019							**2020**		
Táxon/Autoridade	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**total**
BELONIFORMES														
Belonidae														
Potamorrhaphis sp.			3			1	1		1	3				9
CHARACIFORMES														
Acestrorhynchidae														
Acestrorhynchus sp.	1	1						1			1			4
Characidae														
Astyanax bimaculatus (Linnaeus 1758)	6	2	4	3	3	4	4	2	2		4	4		38
Charax sp.				1										1
Hemigrammus bellottii (Steindachner 1882)			8	13		12	2	6		18	2			61
Hemigrammus guyanensi Géry 1959	3	44	142	150	133	117	98	77	104	85	54	31	14	1052
Hemigrammus rodwayi Durbin 1909	35	17	17	18	18	12	7	6	11	1	3	35	4	184
Hyphessobrycon heterorhabdus (Ulrey 1894)	367	369	355	265	415	429	304	295	325	281	342	245	271	4263
Jupiaba anterior (Eigenmann 1908)				1				1	1		1			4
Jupiaba anteroides (Géry 1965)	1													1
Knodus sp.	1			2		2		1	2	1	1		1	11

Microschemobrycon sp.			5	10		3		2		2	5		2	29
Moenkhausia aff. *mikia* Marinho & Langeani 2010		16		1	1									18
Moenkhausia collettii (Steindachner 1882)	2	25	66	35	49	54	13	20	14	14	9	55	16	372
Moenkhausia comma Eigenmann 1908		1		1		1				1	1	3	1	9
Moenkhausia oligolepis (Günther 1864)	6		5	1	11	2	17	7	5	6	4	1	1	66
Phenacogaster sp.					1	5		1		3		7		17
Poptella brevispina Reis 1989	7	2	2										8	19
Chilodontidae														
Chilodus punctatus Müller & Troschel 1844						1	4		1	1		3		10
Crenuchidae														
Characidium etheostoma Cope 1872				2		3	2	5	1	2	1			16
Microcharacidium weitzmani Buckup 1993	56	52	35	145	98	156	170	193	240	196	174	134	72	1721
Erythrinidae														
Erythrinus erythrinus (Bloch & Schneider 1801)	6	1		1	3	1	1				4	1	4	22
Hoplerythrinus unitaeniatus (Spix & Agassiz 1829)			1								1	2		4
Hoplias malabaricus (Bloch 1794)	10	11		5	5	4	5	4	12	11	5	5	7	84
Gasteropelecidae														
Carnegiella strigata (Günther 1864)								1		4				5
Iguanodectidae														
Bryconops aff. *melanurus*	14	2	81	69	21	13	18	1	1	15	12	41	138	426
Iguanodectes rachovii Regan 1912	18	16	19	7	9	7	29	11	26	13	15	1	21	192
Lebiasinidae														
Copella arnoldi (Regan 1912)	61	28	56	52	108	122	156	276	156	149	82	106	58	1410
Pyrrhulina capim Vieira & Netto-Ferreira 2019	46	44	44	106	102	136	138	112	188	163	136	119	83	1417
CICHLIFORMES														
Cichlidae														
Acaronia nassa (Heckel 1840)	3	5	5	4	1		7	5	8	9	7	2	2	58
Aequidens tetramerus (Heckel 1840)	27	28	15	16	2	14	10	24	11	34	28	23	5	237
Apistogramma gr. *regani* Kullander 1980	73	68	59	87	91	212	125	175	162	158	129	82	100	1521
Crenicichla saxatilis (Linnaeus 1758)	6	1	6	10	5	9	7	5	14	4	3	2		72
Heros sp.					1	1			1	1	1		1	6
Hypselecara temporalis (Günther 1862)							1							1
Satanoperca jurupari (Heckel 1840)		1	5		2	7				1		1	3	20
CYPRINODONTIFORMES														

Poecilidae													
Poecilia sp.										1			1
Rivulidae													
Anablepsoides urophthalmus (Günther 1866)	61	29	7	69	78	126	157	154	159	102	178	59	42	1219
GYMNOTIFORMES														
Apteronotidae														
Apteronotus albifrons (Linnaeus 1766)											1			1
Gymnotidae														
Gymnotus carapo Linnaeus 1758			1	4	4	12	1	1	2					25
Gymnotus coropinae Hoedeman 1962							3	1	4	2				10
Hypopomidae														
Brachyhypopomus sp	8	40	4	22	22	26	10	20	45	36	27	23	9	292
Microsternarchus sp	7	4	1	1	11	7	7	18	19	7	7	8	3	100
Rhamphichthyidae														
Gymnorhamphichthys rondoni (Miranda Ribeiro 1920)	19	11	10	18	10	13	16	23	18	25	9	11	9	192
Hypopygus lepturus Hoedeman 1962	10	2	12	20	16	61	53	77	70	67	105	24	13	530
Steatogenys duidae (LaMonte 1929)						5		1	3	2	3			14
Sternopygidae														
Eigenmannia pavulagem Peixoto, Dutra & Wosiacki 2015	1	3	30	21	22	29	26	20	24	11	8	8	24	227
Sternopygus macrurus (Bloch & Schneider 1801)											1		1	2
SILURIFORMES														
Auchenipteridae														
Tatia sp.										1				1
Callichthyidae														
Hoplosternum sp.	1	1		1					1		1		3	8
Hoplosternum thoracatum (Valenciennes 1840)	1	2		3	2	2	1		1	2			1	15
Cetopsidae														
Denticetopsis epa Vari, Ferraris & de Pinna 2005	2			1	1									4
Helogenes marmoratus Günther 1863	13	26	15	22	9	14	17	20	22	7	16	16	19	216
Doradidae														
Acanthodoras cataphractus (Linnaeus 1758)		1	2											3
Heptapteridae														

Mastiglanis asopos Bockmann 1994					1				12	3				16
Pimelodella sp.		1	1	2	1	4	3	2		1	2			17
Rhamdia muelleri (Günther 1864)		1		1	1		1		1			2	27	34
Loricariidae														
Ancistrus sp.					1						1		1	3
Hemiodontichthys sp.						1								1
Rineloricaria hasemani Isbrücker & Nijssen 1979	10	18	8	13	7	7	10	5	5	1	5	2	3	94
Pseudopimelodidae														
Batrochoglanis raninus (Valenciennes 1840)										5		1		6
Trichomycteridae														
Ituglanis amazonicus (Steindachner 1882*)*	3	5	3	8	4	7	7	11	4	11	9	5	2	79
Potamoglanis hasemani (Eigenmann 1914)	7	2	1	8	15	13	14	10	17	9	16	10	2	124
SYNBRANCHIFORMES														
Synbranchidae														
Synbranchus marmoratus Bloch 1795	1			1	1	5		2		3	1	3	3	20

O critério de seleção das espécies, foi apresentar um número de indivíduos relativamente constante com uma frequência suficiente ao longo dos meses do período de estudo para poder realizar as análises de seus aspectos populacionais e reprodutivos. A ictiofauna selecionada é representada principalmente por peixes de pequeno porte (n = 5763; Comprimento Total= 38,66 ± 26,41 mm) de cinco ordens. A continuação será apresentada uma breve descrição das espécies estudas.

Characiformes

Família Characidae

Astyanax bimaculatus (Figura 5A) ocorre ao longo de quase todas as drenagens na América do Sul, representando um dos morfotipos mais abundantes (Lucena & Soares, 2016). A sua plasticidade adaptativa lhe permitiu reproduzir e sobreviver nos mais variados habitats como lagos, represas, riachos, pântanos e rios (Mereles et al., 2017; Normando et al., 2013), adotando diversas estratégias reprodutivas como resposta à variação do habitat, principalmente associadas com a duração do período reprodutivo e o tipo de desova (Cordeiro et al., 2019)

Moenkhausia oligolepis (Figura 5B) ou "*glass tetra*" está amplamente distribuída nas bacias Amazônica, do rio Paraguai, Orinoco e drenagens costeiras da Guiana, Suriname e Mearim (Reia, 2018). Ocorre predominantemente em locais de águas claras com fundos cobertos por folhiço e habita principalmente o curso médio dos igarapés e raramente o curso inferior. Os machos se diferenciam por apresentar pequenos ganchos nas nadadeiras pélvicas e anal.

Hemigrammus guyanensis (Figura 5C) se distribui em tributários da Guiana francesa e Surinam, prefere as zonas de contracorrente e zonas de inundação de riachos onde o substrato é coberto com folhas e depósitos aluviais (Planquette, Keith & Le Bail, 1996).

Hyphessobrycon heterorhabdus (Figura 5D) se distribui desde as bacias costeiras do baixo Amazonas nos estados do Maranhão e Pará, passando pelas bacias dos rios Tocantins, Tapajós, e Curuá-Uma até a bacia do rio Madeira nos estados do Amazonas e Rondônia (Faria, 2020). É uma espécie extremamente abundante em riachos de pequeno porte, de águas claras, substrato arenoso ou com presença de bancos de folhas e de uma faixa, mesmo que estreita, de vegetação ripária (Prudente et al*.,* 2017, Ferreira et al*.,* 2018, Santos et al*.,* 2019). Se classifica como nectônica e ocupa principalmente áreas de remanso próximas às margens, onde se alimenta tanto de itens suspensos na coluna d'agua como associados ao substrato, podendo formar cardumes de 5 a 30 indivíduos (Brejão et al*.,* 2013).

Moenkhausia collettii (Figura 5E) se distribui por Brasil, Colômbia, Guiana Francesa, Guiana, Venezuela, Suriname e Peru (Lima et al., 2003; Reis et al., 2016), é abundante na bacia Amazônica, onde é popularmente conhecida como lambari ou piaba. Quanto à reprodução, estudos com espécies congenéricas sugerem uma estratégia sazonal, considerando a dinâmica de rios (Lourenço et al., 2008; Hernandes, 2015), e oportunista em reservatórios e riachos amazônicos (Casimiro et al., 2011; Sousa et al., 2018).

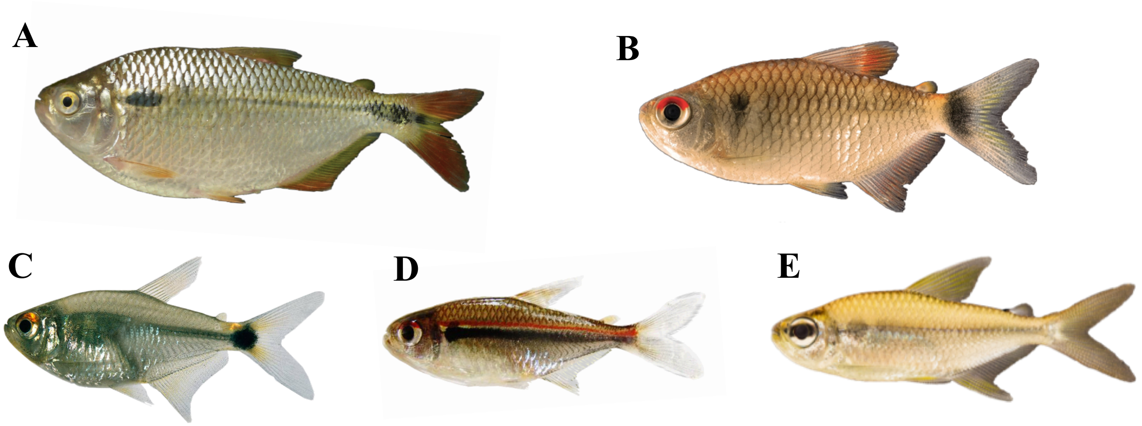

Figura 5. Exemplares da família Characidae: **A.** *Astyanax bimaculatus* (Imagem: Tiago P. Carvalho), **B.** *Moenkhausia oligolepis* (Imagem: Silva-Oliveira C, Canto ALC, Ribeiro FRV), **C.** *Hemigrammus guyanensis,* **D.** *Hyphessobrycon heterorhabdus* (Imagem: Ricardo Britzke) e **E.** *Moenkhausia collettii* (Imagem: Gilberto Salvador).

Família Crenuchidae

Microcharacidium weitzmani (Figura 6) ocorre nas bacias do rio Amazonas e o rio Orinoco e está associado a poças temporárias, sendo pouco tolerante à hipóxia e dependendo das maiores taxas de troca de água com o canal (Couto et al., 2018). Seu comportamento de forrageio, consiste em ações de tocaia e espreita, fazendo uso dos itens estruturais presentes nos riachos (Breijão et al., 2013; Pérez-Mayorga, 2015).

Figura 6. Exemplar de *Microcharacidium weitzmani.*

Família Iguanodectidae

Bryconops melanurus (Figura 7A) conhecido como "*Lizard bite tetra*", se distribui nos riachos costeiros do Escudo das Guianas, ocorre em igarapés de água preta ou mista em locais com fundo de folhiço onde habita o curso alto, médio e baixo, sendo capturado principalmente na água livre, nadando próximo a superfície (Hercos, Queiroz, & Almeida, 2009). A espécie é encontrada ao longo do ano inteiro, porém em baixa abundância. Vive em grupos e se alimenta de insetos (Nobile et al., 2017).

Iguanodectes rachovii (Figura 7B) distribui-se no Brasil, no rio Amazonas de Manaus a Belém, e rios costeiros próximos a Belém, norte e sul da foz do Rio Amazonas, incluindo o Rio Capim (Moreira, 2003). A espécie é observada muito próxima às margens em condições de fluxo variáveis, em grupos de 3-30 indivíduos (Brejão, 2013).

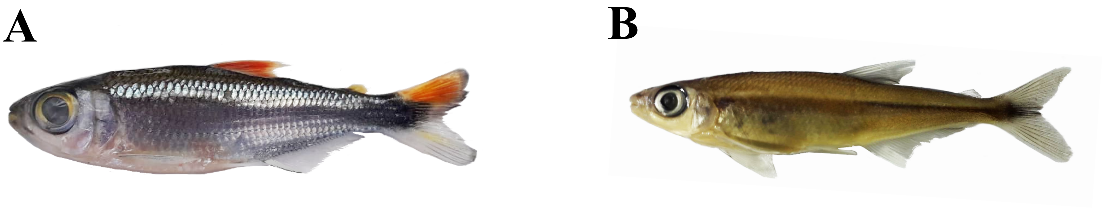

Figura 7. Exemplares de **A.** *Bryconops melanurus* e **B.** *Iguanodectes rachovii.*

Família Lebiasinidae

Copella arnoldi (Figura 8A) pode ser encontrada na bacia amazônica, no Pará e Amapá, nas Guianas (Guiana Francesa, Guiana e Suriname) e Venezuela, na foz do rio Orinoco e nas drenagens costeiras de Sucre e Monagas (Marinho & Menezes, 2017). No momento da reprodução a fêmea coloca os ovos na parte inferior das folhas da vegetação adjacente e o macho os fertiliza com seu esperma (Krekorian & Dunham, 1972; Nelson & Krekorian, 1976; Marinho & Menezes, 2017). A função do macho será a de manter húmidos e oxigenados aos embriões em desenvolvimento até a eclosão, quando as larvas caem na água (Nelson & Krekorian, 1976; Mol, 2012).

A espécie ***Pyrrhulina capim*** (Figura 8B) se distribui ao longo da Amazônia Oriental, mais especificamente nas bacias dos rios Anapu, Capim, Guamá, Xingu, além de drenagens costeiras do estuário da Amazônia no estado do Pará, destaca-se por ser constantemente encontrada em riachos com águas claras e com substratos arenoso e vegetação submersa, e (Vieira & Ferreira, 2019).

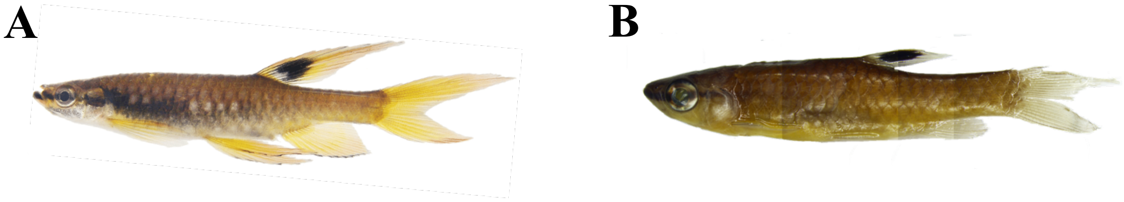

Figura 8. Exemplares de **A.** *Copella arnoldi* (Imagem: Marinho & Menezes, 2017) e **B.** *Pyrrhulina capim*.

Cichliformes

Família Cichlidae

Aequidens tetramerus (Figura 9A) apresenta uma ampla distribuição geográfica incluindo os rios da bacia Amazônica na Bolivia, Brasil, Colombia Peru e Equador, assim como em rios da Guiana Francesa, Guyana e Suriname (Queiroz et al., 2013). Destaca-se sua marcada coloração durante o período reprodutivo e por exibir um intenso comportamento territorial e forte cuidado parental (Reis, Kullander & Ferraris Jr., 2003).

Apistogramma* gr. *regani (Figura 9B) se distribui na bacia do rio Amazonas e na bacia do baixo rio Negro. Dentro do gênero se observa um forte comportamento territorial por parte do macho, principalmente se for polígamo, pois precisa defender vários territórios, pois cada fêmeas do harem depositará os ovos em alguma cavidade ou caverna onde tomará conta da prole. Se o macho estiver vinculado somente a uma fêmea, ambos os sexos compartilham igualmente todas as tarefas, incluindo o cuidado direto da prole (Richter, 1988; Koslowski, 2002; Römer, 2006).

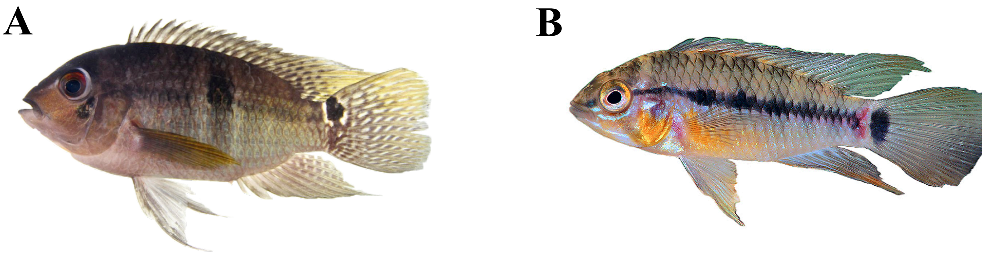

Figura 9. Exemplares de A. *Aequidens tetramerus* (Imagem: Clinton & Charles Robertson) e B. *Apistogramma* gr. *regani* (Imagem: Frank Schäfer).

Cyprinodontiformes

Família Rivulidae

Anablepsoides urophthalmus ocorre na bacia do rio Amazônas no Brasil. É uma espécie de comportamento bentopelágico e não migrador (Lazara, 2000). Não existem informações sobre a biologia reprodutiva no ambiente natural, mas em condições controladas reportam que as fêmeas liberam diariamente entre cinco e 15 ovos, e tomariam entre quatro e cinco meses em atingir a maturidade sexual, com um tempo de vida estimado 3 anos (Vermeulen, 2022).

Figura 10. Exemplar de *Anablepsoides urophtalmus.*

Gymnotiformes

Família Rhamphichthydae

Gymnorhamphichthys rondoni (Figura 11A) se distribui nas bacias dos rios Amazonas, Alto Paraná e Orinoco e rios costeiros das Guianas, ocorrendo em igarapés rasos com fundo de areia onde fica enterrado no substrato durante o dia e emerge à noite para forragear, interagir socialmente e se reproduzir (Schwassmann, 1976, Zuanon et al. 2006).

Hypopygus lepturus (Figura 11C) se distribui nas bacias do rio Orinoco e do rios Amazonas e em rios costeiros de Guiana tendo preferencia por riachos rasos de fundo arenoso apresenta um padrão de coloração que o assemelha a uma folha, e que pode ser diferente nos flancos de um mesmo indivíduo e varia de um indivíduo pro outro em função da origem geográfica (Planquette, Keith & Le Bail, 1996).

Família Sternopygidae

Eigenmannia pavulagem (Figura 11B) (‘*electric glass knifefish*’) se distribui em pequenos tributários das bacias do rio Capim e do rio Guamá no nordeste do Pará (Peixoto et al., 2015).

Figura 11. Exemplares de A. *Gymnorhamphychtys rondoni*, B. *Eigenmannia pavulagem* e C. *Hypopygus lepturus*.

Siluriformes

Família Cetopsidae

O bagre-baleia ***Helogenes marmoratus*** (Figura 12) é uma das poucas espécies da família Cetopsidae encontrada em riachos amazônicos (Reis et al., 2003) e é conhecido por seu comportamento críptico (Sazima et al., 2006) e ocupar bancos de folhas e cascalho no fundo de riachos florestais rasos com correntes suaves (Le Bail et al., 2000). Também é considerado um importante bioindicador da integridade ecológica dos riachos amazônicos (Ferreira et al., 2018; Prudente et al., 2018).

Figura 12. Exemplar de *Helogenes marmoratus* (Imagem: Mark Sabaj Perez/ANS).

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3. SESSÃO I

Decoding reproductive strategies in Amazonian stream fishes

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Decoding reproductive strategies in Amazonian stream fishes

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3.1. ABSTRACT

For the small fishes that inhabit streams, continuous reproduction characterized by early maturation, low batch fecundity compensated by multiple spawning is their formula for success in maintaining viable populations. However, how much differentiation of reproductive traits does this assemblage allow? To understand how some species regulate their reproductive dynamics, we estimated and analyzed eight reproductive traits: sex ratio, body size, length at first maturity, breeding period, gonadosomatic index, fecundity, oocyte size, spawning type, and parental care for 17 species of fish from Amazon streams belonging to five different orders of teleost fish. The aim was to identify their reproductive strategies and verify if the Triangular life history Continuum model characterizes the reproductive patterns of these stream fishes. We monthly sampled eight streams in a micro-basin of the Guamá, Eastern Amazonian, Pará, Brazil, between March 2019 and March 2020. After the ordination to the traits matrix and a dissimilarity analysis, we identified the three reproductive strategies of the Continuum model; however, nine species did not fit in the endpoints of the model remaining in the opportunistic – equilibrium gradient. The traits that contributed more to segregating the species were fecundity and total length. Intermediate strategy should be considered in approaches.

Key words**:** Fecundity, Life-history, reproductive strategy, small-size fish, *terra firme*

3.2. INTRODUCTION

The variety of ways organisms allocate resources for growth, development, reproduction, and survival determines their life history pattern (Begon et al., 1987). Within the components of life history, the reproductive strategy summarizes the different phenotypic expressions of reproductive traits, such as fecundity, egg size, size and age at first maturation, type and spawning frequency, and reproductive behavior, among others (Potts & Wootton, 1984).

This set of traits evolves coordinately and is expressed by an individual, determining how it reproduces throughout its life (Stearns, 1992); thus, to maintain viable populations over the long term, each organism must manifest a successful strategy (Roff, 1992, 2001; Stearns, 1992). Life history theory (Pianka, 1970; Stearns, 1992) predict that environments favor specific sets of traits, resulting in the evolution of life history strategies that allow a species to deal with various ecological problems.

Within a species, some individuals exhibit remarkably divergent life history traits within a given habitat, probably because of the need to adjust their traits in response to particular environmental conditions (or limitations) or specific environmental situations. This change means an alteration in the traits combination and the variation in any of them (Wootton, 1984).

Therefore, the reproductive strategy of a species is the overall pattern of reproduction common to individuals within a species. In contrast, reproductive tactics are those variations in reproductive traits that change an organism's typical reproductive strategy as a response to environmental fluctuations (Wootton, 1989; Roff, 1992) and that are allowed by phenotypic plasticity (Stearns, 1989).

The reproductive tactics are fundamental parameters for population dynamics models because they describe the trade-offs between the populations and the species (Pianka, 1970; Stearns, 1989). Besides that, these life-history traits provide a common language to compare the functioning of populations of different species and various biological groups (Roff, 1984; Stearns & Koella, 1986; Charnov, 1995). Because a wide diversity of life-history strategies reflects a combination of phylogenetic constraints and selection pressures, the life-history traits can be used as indicators of similarity in the operation of certain kinds of selection, even among groups of organisms that are very different.

The "habitat temple" theory (Southwood, 1977; Townsend & Hildrew, 1994) suggest that spatial and temporal characteristics of the habitat are the main determinants of observed species traits. The species in unstable environments (such as streams), which seldom approach equilibrium, manifest the ability to reproduce rapidly (r selection); its strategy would aim to maximize the production of offspring so they can reach sexual maturity and high productivity. In opposition to the above, organisms in environments considered more stable and dominated by density-dependent regulation mechanisms show adaptations promoting survival or persistence as parental care and smaller litters (K-selection) (Pianka, 1970).

Because of the greater variation in life history traits shown by fish, this group has presented various classification models based on reproductive tactics. Although Kawasaki (1980) had already developed a model of life history strategies for Pacific marine fish, the best known is the trilateral continuum model initially proposed by Winemiller (1989) for Venezuelan freshwater tropical fish and then expanded by Winemiller & Rose (1992) for North American marine and freshwater fish.

This model explains the adaptive response of reproductive traits to environmental variation in predictability and generation times. Therefore, species are generally classified depending on their set of tactics and relationships to their habitat as periodic, opportunists (r selection), or equilibrium (k selection) strategists. 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), specially within opportunistic-periodic gradient (Alkins-Koo, 2000; Espírito-Santo et al., 2013; Fagundes et al., 2020).

Small forest stream fishes may have prolonged breeding periods and spawn multiple times (Schwassmann 1978; Winemiller 1989), exhibiting peaks of reproductive activity in relatively predictable periods (Helfman et al., 2007). The streams conditions tend to favor opportunistic species, characterized by the small size, short life span, high growth rate, early sexual maturation, and long reproductive period.

Due to the great biodiversity that the Amazon region houses, and the importance of streams for the structuring of communities of small fish species, identify the kind of reproductive strategies that characterizing those species and produce basic knowledge about their biology, will allow to understand better the ecological process that are carried out there and how much differentiation is necessary to allow the coexistence of these species. In an attempt to answer this question, we estimated eight reproductive traits of 17 species of fish from Amazonian streams to determine, in the first instance, their reproductive strategy and analyze them in the context of the continuous model of life history proposed by Winemiller (1989) and Winemiller & Rose (1992). Second, synthesize the direction and magnitude of interspecific variations of multiple life history traits for the assessed assemblage. We expect a variation, particularly in fecundity and reproduction period, which allows for considering the alternative strategy as the main pattern in the Amazonian streams.

3.3. MATERIAL AND METHODS

3.3.1. Study area

We conducted the study in a left margin catchment of the Guamá River, which has an area of 12.4 km^2, in the Capitão Poço municipality (State of Pará), in eastern Brazilian Amazonia (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). Over the year, the mean annual temperature is 26.9ºC. 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).

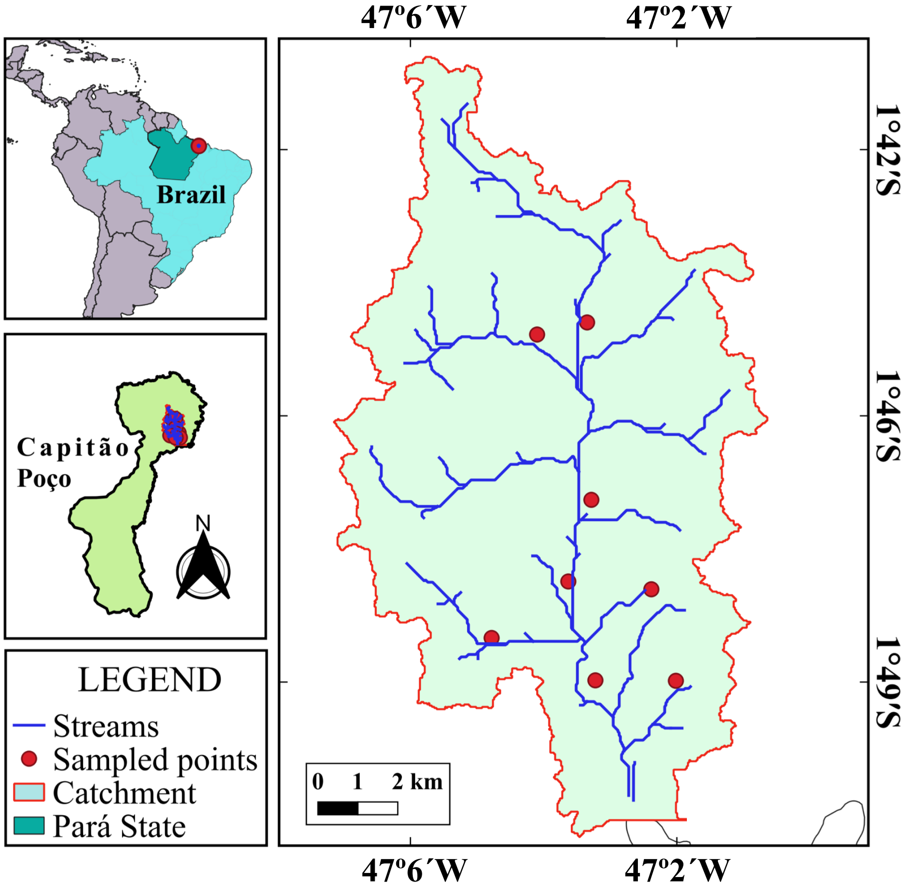


Figure 1. Sampled streams (red dots) in a catchment of the Guamá River (Eastern Brazilian Amazon).

We choose eight low-order streams (1st to 3rd order; *sensu* Strahler, 1957) with similar physical structures. The eight points comprise streams susceptible to lateral flooding due to heavy rains, main channels with great structural complexity, and tree vegetation on their banks. The stream's bottom mainly comprises banks of leaves, sand, and submerged roots

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. Rainfall data were provided by the meteorological station of The Brazilian National Institute of Meteorology (INMET – Station A248), located in the municipality of Capitão Poço.

3.3.2. Fish collection

The specimens were collected from each 10-m longitudinal section for 12 minutes 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/3l of water) and fixed in a 4% formalin solution in the field and preserved in 70% ethanol solution. The specimen collections were authorized by license 63603-3, issued by the federal Chico Mendes Institute for Biodiversity Conservation - ICMBio, through the Biodiversity Authorization and Information System – SISBIO. The Animal Ethics Committee of the Federal Rural University of Amazon (UFRA) approved the study, through process number 054/2018. Specimens will be deposited in Natural History Collection of the Museology Course (RTM) of the Universidade Federal do Pará, Belém (Brazil).

3.3.3. Selected species and biometry procedures

We analyzed 17 species that presented a constant number and sufficient frequency of individuals each month (APÊNDICE A) to compare the reproductive activity and assess some reproductive traits over the study period. For species with a very high abundance (more than 400 specimens collected), we separated the largest and smallest individuals each month and randomly selected 30 individuals from all streams.

We measured specimens with a digital caliper (0,01 mm) from the tip of the snout to the tip of the distal extremity of the caudal fin or until the end of the caudal filament for specimens belonging to Gymnotiforms order (Total length). They were weighed on a precision scale (0.0001 g) after removing excess alcohol with a paper towel to determine their total mass/weight. Gonads were removed, weighed (0.00001 g), and fixed in 70% ethanol. Sex was determined through a macroscopic analysis of the presence or absence of oocytes. The gonadal maturation stage was determined according to macroscopic characteristics such as shape, weight, and size of the gonads in the abdominal cavity; for females, the size and stage of development of oocytes were also considered Vazzoler (1996). Subsequently, gonads of *Helogenes marmoratus, Gymnorhamphichtys rondoni*, *Eigenmannia pavulagem*, *Hypopygus lepturus*, *Hyphessobrycon heterorhabdus*, *Moenkhausia colletti,* and *Pyrrhulina capim* followed a histological routine to corroborate the previous classification.

The other species had some stages confirmed by histological slides, but their classification was determined to a greater extent at the macroscopic level. Specimens in which it was not possible to distinguish sex through macroscopic assessment of gonads were classified as juveniles. Then, we defined five stages for females and four for males: immature, maturing, mature, spawned or spent, and resting (just for females) (Vazzoler, 1996; Azevedo et al., 2000; Nuñez & Duponchelle, 2009).

3.3.4. Reproductive traits

We estimated eight reproductive traits: sex ratio, body size (total length), gonadosomatic index, the duration of the reproductive period, length at first maturity, fecundity, egg size, spawning type, and parental care. 1. Sex ratio: A chi-square test was applied to verify the existence of significant differences between the number of males and females for the entire study period (Sokal & Rohlf, 1995). 2. Body size: Differences in total length between the sexes for each species including all individuals were tested with the Wilcoxon-Mann Whitney test. We elaborated a histogram of monthly length frequencies for each species to detect changes in the population structure over the months. 3. 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 individuals classified as adults and immatures, considering total length intervals according to Sturges rule. The L_{50} was calculated based on the logistic equation $P = A\left(1 + e^{-r(TL - L_{50}))}\right)^{-1}$ 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.

For *Astyanax bimaculatus* and *Moenkhausia oligolepis* we estimated this parameter separately for sexes as the average total length, between the smaller mature specimen and the larger juvenile, due to insufficient juveniles frequency. 4. Fecundity, defined as the total number of mature oocytes prior to spawning produced in both ovaries (Alkins-Koo, 2000; Bagenal & Braun, 1978), was estimated by direct counting of mature oocytes under a stereoscope after manual dissociation (Absolute Fecundity) based on available mature females with the highest GSI values for the 17 species.

For species with high fecundity as *A. bimaculatus*, *M. oligolepis,* and *Bryconops melanurus* (APÊNDICE C) we counted the mature oocytes present in three subsamples of the same lobule, previously weighted. Afterward, we calculate the fecundity based on the total gonad weight (gravimetric method - Hunter et al., 1985). 5. Oocyte diameter: For this measure we considered just the mature/vitellogenic oocytes that were used to calculate fecundity; for species with high fecundity *A. bimaculatus*, *M. oligolepis, B. melanurus*, and *A. tetramerus* we randomly measured 100 oocytes of each sub sample totaling 300 per female. We used the same equipment and software which is described below. 6. The spawning type were determined by the visual inspection of the frequency distribution of all oocyte diameters contained in mature ovaries (including those described in point 4). We did this measure using a Leica M125 stereomicroscope equipped with a DMC 2900 camera using the Leica Application Suite (LAS) microscope software. Here, we apply the term “total spawning” to a unimodal distribution and “batch spawning” for a multimodal distribution (Vazzoler, 1996) (APÊNDICE D e E). We have histological confirmation of spawning type for *H. marmoratus, G. rondoni*, *E. pavulagem*, *H. lepturus*, *H. heterorhabdus*, *M. colletti,* and *P. capim.* 7. The duration of the reproductive period (months) 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, without considering the immature stage for both sexes and resting stage just for females. Thus, we considered reproductive activity the months in which more than 50% of the population were maturing, mature, spawned or spent stages.

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. We estimated the recruitment period based on two aspects, first on the months with a high frequency of individuals classified as immature (see *Selected species and biometry procedures*). Second, we took as reference the lowest value of the length at first maturity (of males or females as the case) calculated for each species over the plot of size frequency histogram described in point 2. 8. The manifestation of parental care at any level was verified according to records in the literature for the species or genus. We classified *Aequidens tetramerus* (Keenleyside, 1979; Reis, Kullander & Ferraris Jr., 2003), *Apistogramma* gr. *regani* (Koslowski, 2002, Richter, 1988, Römer, 2006), *Copella arnoldi* (Krekorian & Dunham, 1972; Marinho & Menezes, 2017; Nelson & Krekorian, 1976) and *Eigenmannia pavulagem* (Kirschbaum & Schugardt, 2002) as species with parental care.

3.3.5. Comparison of reproductive traits

We performed a principal coordinate analysis (PCoA) of the set of reproductive traits using the 17 species as groups using the "Gower" coefficient. We used the individual values for total length (mm), gonadosomatic index (%), fecundity and oocyte diameter (mm) from the females chosen for estimate fecundity. We assigned the same value to each group of females for traits estimated for the species as length at first maturity (mm) reproductive period length (months), spawning type (Batch or Total) and parental care (Present or Absent). We applied a Permanova analysis by the Gower coefficient to the matrix of reproductive traits to verify if existed differences between species. Finally, a Simper analysis (similarity between percentages) was performed to identify the attributes most responsible for the dissimilarity between species. All statistical tests were run in the R 4.2.1 (2022-06-23) software (R Development Core Team, 2022), using significance at the 5% level, and the packages *ggplot2* (Wickham, 2016), *MASS* (Venable & Ripley, 2002) and *vegan* (Oksanen et al., 2020).

3.4. RESULTS

We analyzed 5763 individuals belonging to five orders, nine families, and 17 species (APÊNDICE B). After random selection for the species with the high abundances (more than 400 specimens), we dissected 778 for *Hyphessobrycon heterorhabdus*, 552 for *Microcharacidium weitzmani*, 491 for *P. capim*, 471 for *C. arnoldi*, 459 for *Hemigrammus guyanensis*, 458 for *Anablepsoides urophthalmus*, 420 for *A.* gr. *regani*, 384 for *H. lepturus*, and 217 for *B. melanurus.* For the rest of the species, we evaluated all the individuals collected during the 13 campaigns (APÊNDICE A).

3.4.1. Sex Ratio

The expected proportion between females and males (1:1), considering the entire study period was recorder for *A. urophthalmus*, *A.* gr. *regani*, *A. bimaculatus*, *G. rondoni*, *H. marmoratus*, *H.*

guyanensis, *H. lepturus*, *Iguanodectes rachovii*, *M. weitzmani*, *M. oligolepis*, and, *P. capim.* The chi-squared test (χ^2, p <0.05, degrees of freedom = 1) showed a significant difference in the sex ratio for the entire study period, with a predominance of females for *B. melanurus* (96♀ : ♂67; χ^2=5.1595) and *M. collettii* (186♀ : ♂100; χ^2=25.68), and more males than females for *A. tetramerus* (51♀: ♂88; χ^2=9.8489), *C. arnoldi* (193♀ : ♂271; χ^2=13.112), *E. pavulagem* (82♀: ♂129; χ^2=10.469), *H. heterorhabdus* (303♀ : ♂378; χ^2=10.469).

3.4.2. Body size

The body size (Total length) ranged from 9.36 mm of *M. weitzmani* to 194.35 mm of *E. pavulagem* (mean = 38.66 mm ± standard deviation= 26.41 mm) (Figure 2). The most/greatest variation was observed in Characiforms where a female of *B. melanurus* (Iguanodectidae) registered the maximum total length (131.01 mm) of the species assessed for this group, although the average length for the species was 45.71 mm (± 22.42). *A. bimaculatus* size, ranged between 41.43 to 119.99 mm of TL (80.82 ± 19.93 mm) and *M. oligolepis* from 46.72 to 88.96 mm (67.85 ± 8.55) (Figure 2 and Table S2). We did not capture juvenile forms for these species along the study period. The smallest body sizes are found in the families Chrenuchidae, Rivulidae and Characidae (*H. heterorhabdus* and *H. guyanensis*) ranging between 9.36 mm to 44.6 mm (24.97 ± 6.01). Lebisanids species length varied from 11.03 mm to 75.98 mm (30.48 ± 12.17), being larger *P. capim.* Similar maximum total length were detected in *H. marmoratus* (65.21 mm), *A.* gr. *regani* (64.16 mm), *I. rachovii* (60.23 mm) and *M. collettii* (59.21 mm) (Figure 2 and Table S2). Gymnotiforms as group presented the highest adult sizes ranged between 50. 76 mm of TL (male of *H. lepturus*) to 194.35 mm (male of *E. pavulagem*) (Figure 2 and APÊNDICE B).

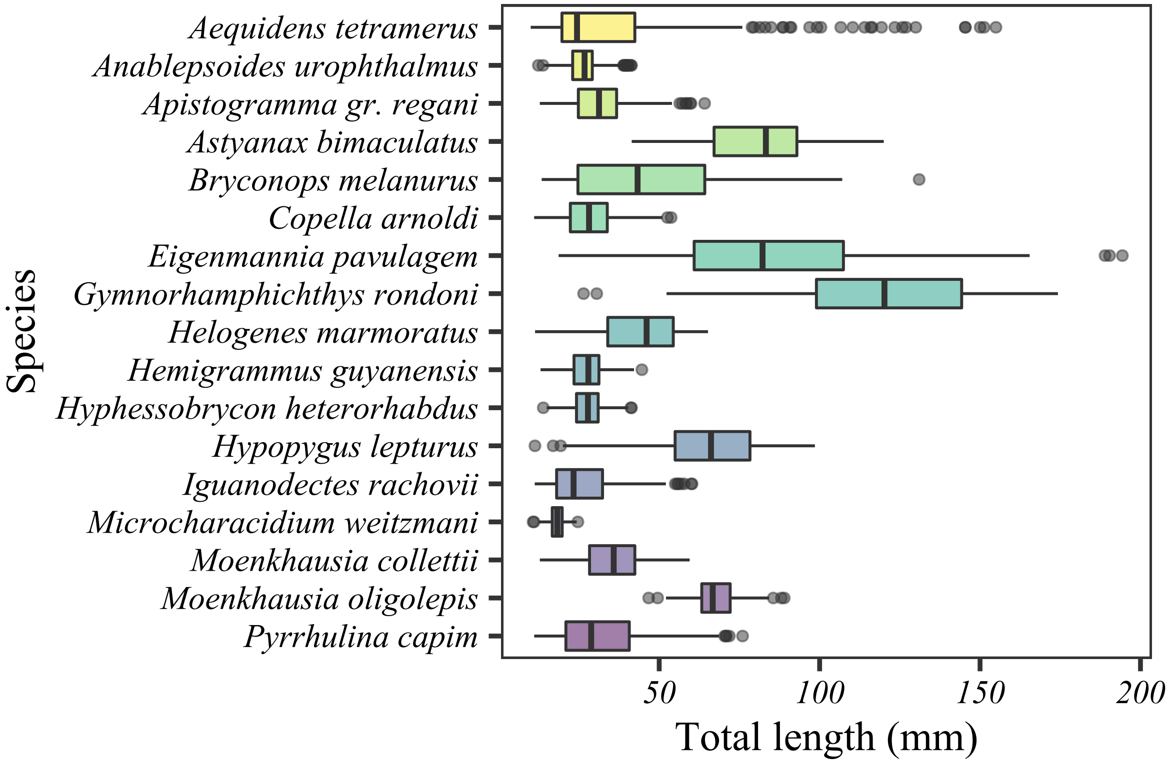


Figure 2. Total length (mm) of the 17 species sampled between March 2019 and March 2020 in a catchment of the Guamá River (Eastern Brazilian Amazon).

We found body size differences between sexes for *A. gr. regani* (U=17891; df=427; p <0.001), *H. lepturus* (U=12008; df=367; p <0.001), and *C. arnoldi* (U=13750, df=376, p <0.001) in which males were larger than females. In the other hand for *A. tetramerus* (U=2908.5, df=137, p < 0.01), *H. marmoratus* (U=6239,5, df=202, p<0.05), *H. guyanensis* (t=5.1838; df=446; p <0.001), *H. heterorhabdus* (U=86634, df=680, p <0.001), *M. weitzmani* (t=4.9103; 547; p <0.001), *M. collettii* (U=7353, df=241, p<0.05), and, *M. oligolepis* (t=3.6851, df=64, p <0.001) females were larger than males (Table S2).

3.4.3. Size at first maturity

The length in which the assessed species reached the maturity represented approximately half their body size (total length). For females this proportion ranged between 30.28 to 63.11% (50.11 ± 8.77%). In the case of males, this proportion varied from 29.93 to 66.56% (50.39 ± 9.85%). *M. weitzmani* and *M. oligolepis* for both females and males, were the species that took the longest to reach maturity with more to the 60% of their total length. On the other hand, females of *A. tetramerus* (36.84%) and *B.*

melanurus (30.28%) were considered the earlies species to start to reproduce; for males the precocity was represented for *A. regani* (29.93 %) and *P. capim* (33.64 %) (Table 1).

3.4.4. Breeding and recruitment periods

A. bimaculatus, and *M. oligolepis,* presented the lowest abundances (Table S1). *A. bimaculatus* recorded less than 50 mm specimens in June and July 2019; for *M. oligolepis,* we observed smaller specimens, no less than 40 mm only in March 2019. (Figure 3). The juveniles of *B. melanurus* were constant throughout the year, with the exception of the driest months (October and November) where two specimens were captured. The highest frequency of young individuals is observed in rainy months (March and April 2019 and March 2020). Regarding *I. rachovi*, we detected smaller individuals during all months, with the higher frequency in April 2019; they had higher monthly frequencies compared to individuals larger than 25 mm in total length.

Pyrrhulina capim presented the highest frequency of juvenile individuals throughout the year; C. *arnoldi* had a higher frequency of juveniles during the first semester (March and October 2019) and a more discreet one between November 2019 and March 2020. For *H. heterorhabdus* and *A.* gr. *regani*, the frequencies of young specimens were not so high but were constant throughout the months. Few large individuals were captured for *A. tetramerus*, only in May, June, September and November we observed sizes larger than 100 mm; the monthly mode was around 50 mm, with juveniles of less than 30 mm between August and October and between December and April. The highest frequency of *A. urophthalmus* juveniles, with TL less than 17 mm, occurred in June and September 2019 (Figure 3). Although we captured some juveniles of the gymnotiforms species, the highest frequencies were represented by adult individuals. For *E. pavulagem,* we recorded juveniles in April, May, and March 2020. *G. rondoni* had some juveniles during the first semester, especially in May. For *H. lepturus*, juveniles were recorded during the period of least rainfall (June to November), highlighting their absence in the months in which the largest sizes and highest rainy values were recorded (March 2019 and February and March 2020) (Figure 3).

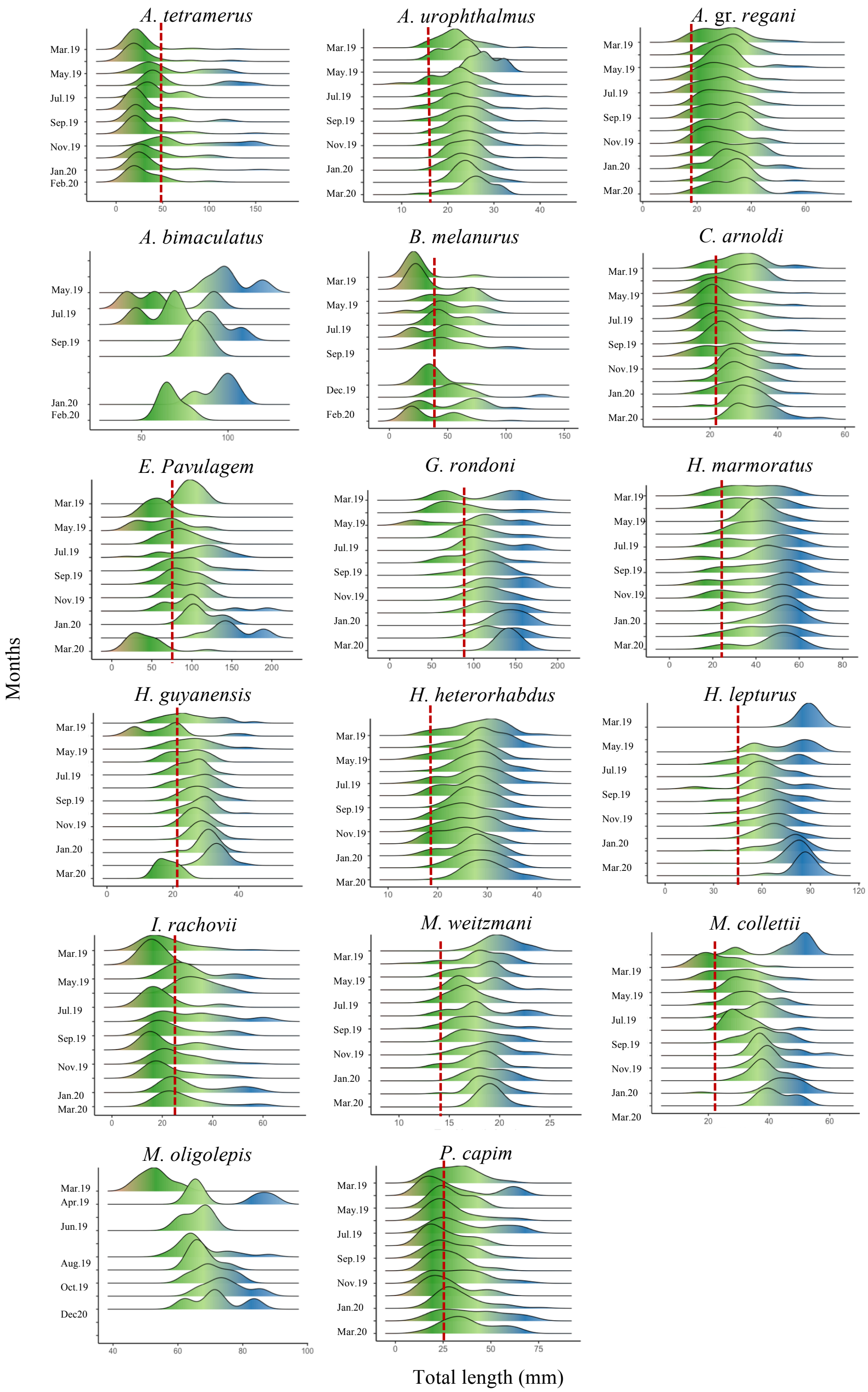
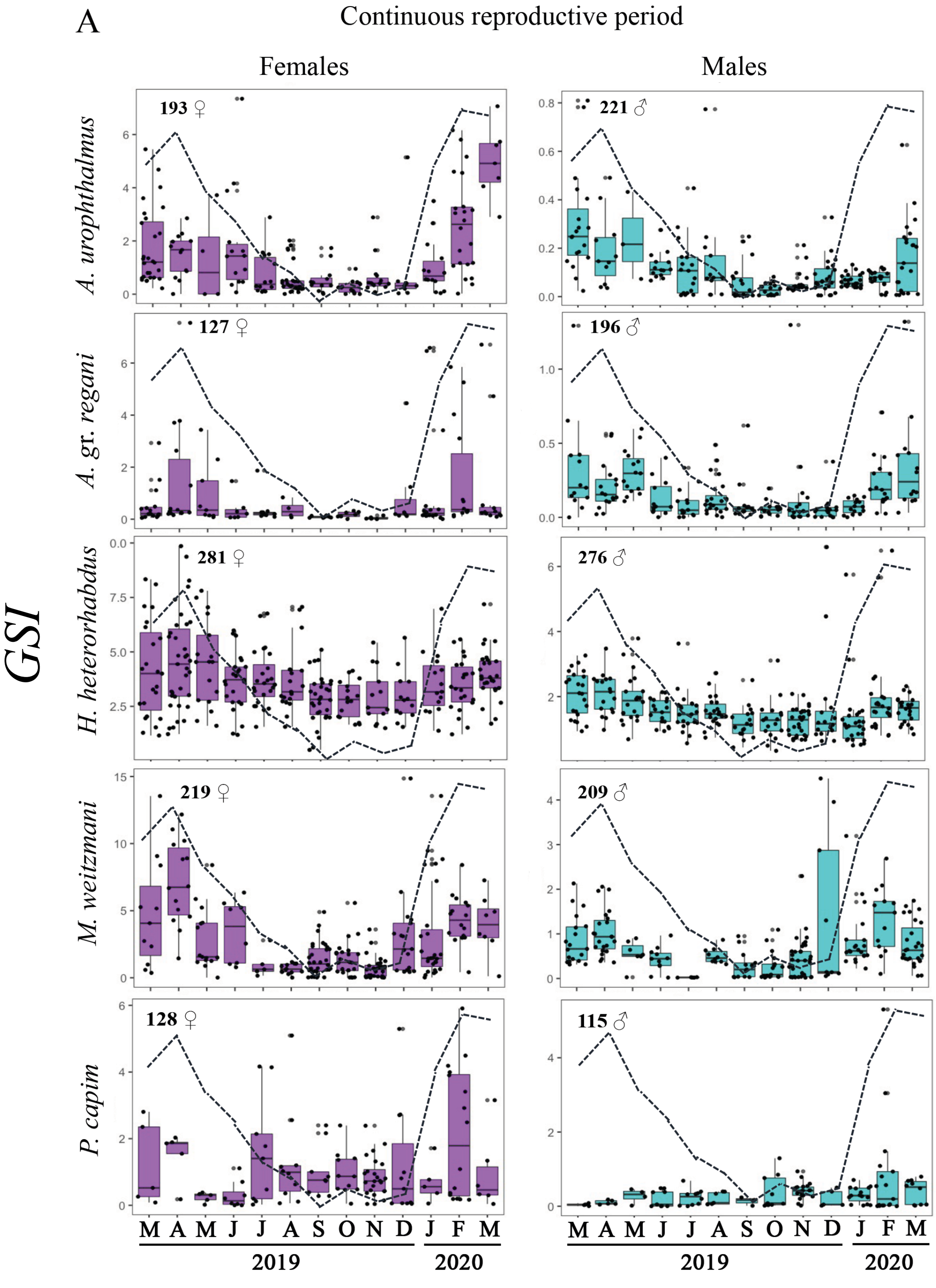


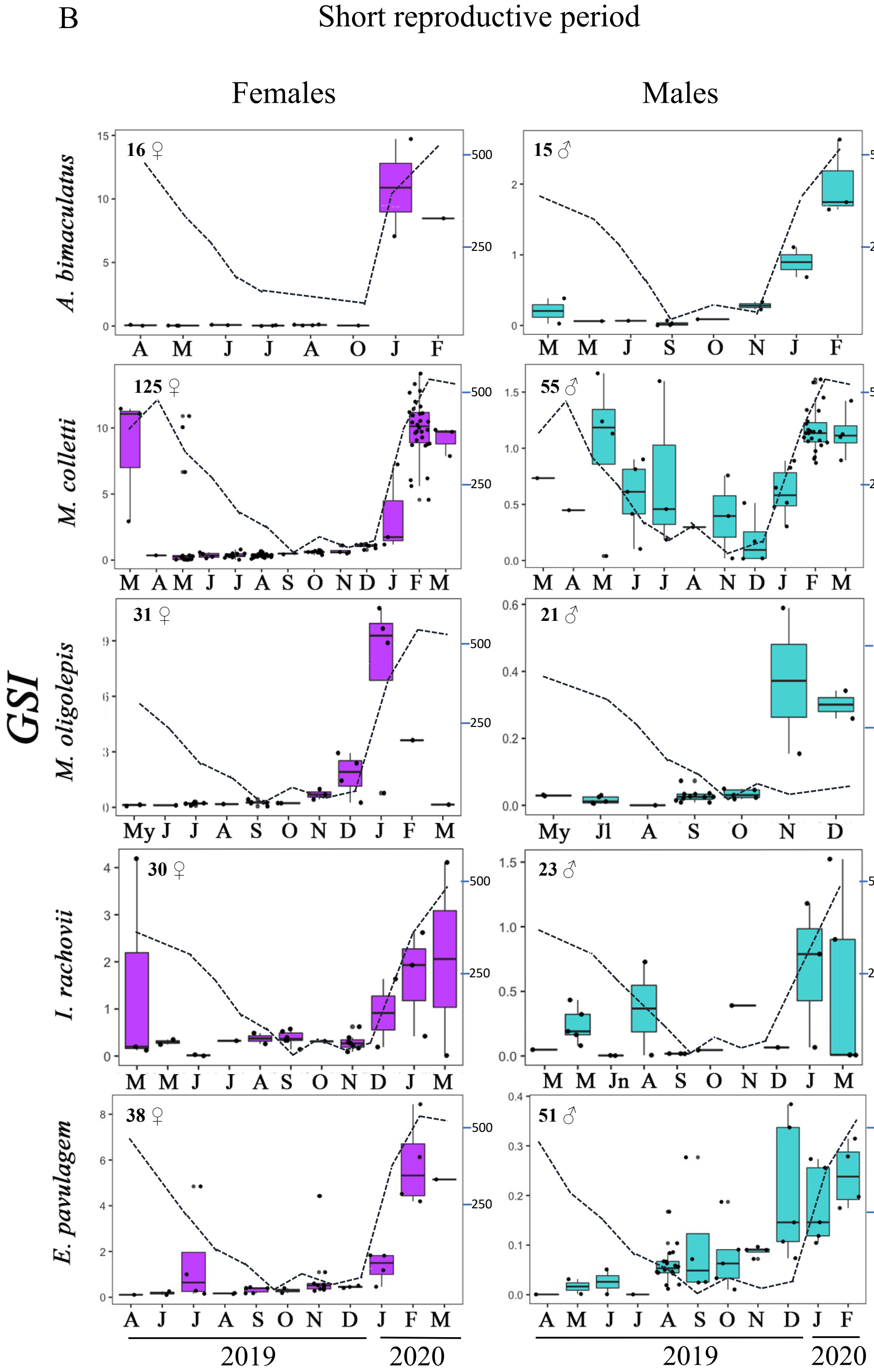
Figure 3. Multi-histogram with monthly total length variation of 17 species sampled between march 2019 to march 2020 in a catchment of the Guamá River (Eastern Brazilian Amazon). The red dash lines indicate the length at first maturity estimated for each species.

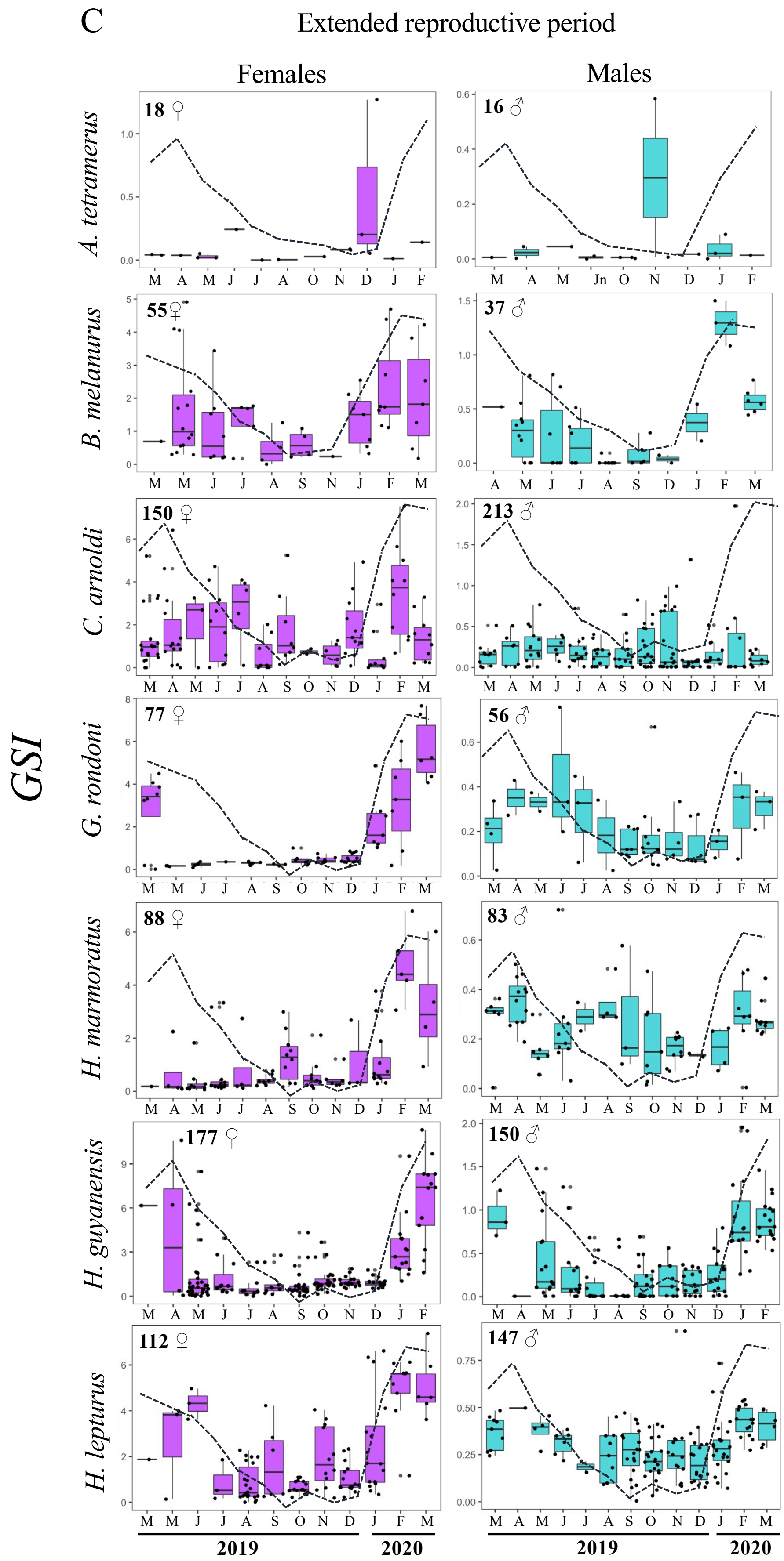
According to *GSI* monthly variation and the gonadal development stages, females and males of the 17 species presented a significant variation in the mean *GSI* among months except for *G. rondoni* males ($H_{(12,\ 38)}$= 14,99; p >0.05). We detected two significant aspects of assessing the reproductive period: the first is that there was a differentiated reproductive activity between sexes, being the males more active along the studied period (Figure 4. A – C). The second aspect is that regardless of the duration of the reproductive period, the highest frequency of mature individuals and the highest gonadosomatic indices were associated with the increase of the rain or in the months where rainfall was more intense/recorded the highest values (Figure 4. A – C).

Three reproductive periods could be distinguished: 1. Continuous reproduction throughout the year: *A. urophthalmus*, *A.*gr. *regani*, *H. heterorhabdus*, *M. weitzmani*, and, *P. capim* (Figure 4-A). 2. A short period of reproduction coinciding with the increase in rainfall or the rainiest months (December – March): *A. bimaculatus*, *E. pavulagem*, *M. collettii*, *M. oligolepis*, *I. rachovii* (Figure 4-B), and 3. A prolonged/extended period of reproduction associated with high rainfall: *A. tetramerus*, *B. melanurus*, *C. arnoldi*, *G. rondoni*, *H. marmoratus*, *H. guyanensis*, and, *H. lepturus* (Figure 4-C).

A. tetramerus presented the lowest GSI among the evaluated species (1.27%) and low GSI values over the months, which could be explained by the high frequency of spawned females and spent males. For *G. rondoni* females, the histological analysis allowed us to verify that low *GSI* values between April and August were because females were "resting." In the driest period (between October to December), females were maturing because the period of reproductive activity was extended (Figure 4-C). The length of the breeding period and maximum *GSI* values are detailed in Table 5.


A
Continuous reproductive period
Females
Males
GSI
A. urophthalmus
193 ♀
221 ♂
A. gr. regani
127 ♀
196 ♂
H. heterorhabdus
281 ♀
276 ♂
M. weitzmani
219 ♀
209 ♂
P. capim
128 ♀
115 ♂
M A M J J A S O N D J F M
2019
2020
M A M J J A S O N D J F M
2019
2020


B
Short reproductive period
Females
Males
GSI
A. bimaculatus
16 ♀
15 ♂
M. colletti
125 ♀
55 ♂
M. oligolepis
31 ♀
21 ♂
I. rachovii
30 ♀
23 ♂
E. pavulagem
38 ♀
51 ♂
A M J J A O J F
M M J S O N J F
M A M J J A S O N D J F M
M A M J J A N D J F M
My J J A S O N D J F M
My Jl A S O N D
M M J J A S O N D J M
M M Jn A S O N D J M
A J J A S O N D J F M
A M J J A S O N D J F
2019
2020
500
250



C
Extended reproductive period
Females
Males
GSI
A. tetramerus
18 ♀
16 ♂
M A M J J A O N D J F
M A M Jn O N D J F
B. melanurus
55♀
37 ♂
M M J J A S N J F M
A M J J A S D J F M
C. arnoldi
150 ♀
213 ♂
M A M J J A S O N D J F M
G. rondoni
77 ♀
56 ♂
M M J J A S O N D J F M
M A M J J A S O N D J F M
H. marmoratus
88 ♀
83 ♂
M A M J J A S O N D J F M
M A M J J A S O N D J F M
H. guyanensis
177 ♀
150 ♂
M A M J J A S O N D J F
H. lepturus
112 ♀
147 ♂
M M J J A S O N D J F M
M A M J J A S O N D J F M
2019
2020

Figure 4. Gonadosomatic index of females and males of 17 species sampled in streams of a catchment of the Guamá River (Eastern Brazilian Amazon) between March 2019 to March 2020. Species were grouped by length of the breeding period: A. Continuous reproductive period, B. Short breeding period and C. Extended breeding period. The dash dark line represent the cumulate monthly rainfall.

3.4.5. Fecundity, Oocyte size and Spawning type

The mature stage of ovarian development in all species is easily identified by the large size of the ovary and the presence of stage IV oocytes (APÊNDICE D and APÊNDICE E) The number of mature oocytes varied from 3 (*A. urophthalmus*) to 22851 (*A. bimaculatus*). The family Characidae presented the highest average fecundities, even with differences among the species. After *A. bimaculatus*, the genera *Moenkhausia* showed a high fecundity, but with a significant advantage of *M. oligolepis* with 2725 (± 1327) to *M. collettii* with 617 (±110). For *H. guyanensis* were counted 363 (± 130) and for *H. heterorhabdus* 197 (± 104). The representatives of Iguanodectidae family presented very different values, *B. melanurus* with 841 (± 165), between the Moenkhausia's fecundity, and *I. rachovii* with 104 (± 39) after *H. heterorhabdus*. Although within the gymnotiforms species, the average fecundity values were divergent, to considered the set of assessed species, we could group *E. pavulagem* (103 ± 33) and *H. lepturus* (47 ± 22) as low fecundity species together with *I. rahovii*, *H. marmoratus* (60 ± 23), *A.* gr. *regani* (61 ± 27) and the leabiasinids, *P. capim* (69 ± 36) and *C. arnoldi* (50 ± 21). Within that spectrum, the average lowest fecundities were detected in *M. weitzmani* with 26 (± 9), *G. rondoni* with 36 (± 12) oocytes and *A. urophthalmus* (Table 1).

The average mature oocyte diameter varied from 0.412 mm (± 0.1) of *H. heterorhabdus* to 1.36 mm (± 0.11) of *A. urophthalmus.* The highest average diameters were observed in Cichliforms: *A.* gr. *regani* (1.33 mm ± 0.18) and *A. tetramerus* (0.994 ± 0.08 mm), the gymnotiforms: *H. lepturus* (1.16 ± 0.2 mm), *E. pavulagem* (1.32 ± 0.16 mm) and in *G. rondoni* (1.39 ± 0.22 mm) and the only representative of the catfishes, *H. marmoratus* (1.24 ± 0.15 mm). Among Characiforms species, just the

Iguanodectidae family presented the higher values: *B. melanurus* (0.77 ± 0.09 mm) and *I. rachovii* (0.679 ± 0.1), followed by the characins *M. oligolepis* (0.66 ± 0.041), *M.collettii* (0.666 ± 0.07), *A. bimaculatus* (0.658 ± 0.04) and the leabisinid *C. arnoldi* (0.658 ± 0.05). The smallest average diameters were detected in *H. guyanensis* (0.595 ± 0.05), *M. weitzmani* (0.567 ± 0.061), *P. capim* (0.534 ± 0.01) and *H. heterorhabdus* (0.412 ± 0.1) (Table 1).

Analyzing the frequency distribution of all oocyte diameters of *H. marmoratus*, *G. rondoni*, *E. pavulagem*, *H. lepturus*, *H. guyanenis, H. heterorhabdus, P. capim, C. arnoldi,* and *I. rachovii* we can observe the presence of reserve oocytes at all stages of maturation (Figure 2 – Supplementary material), with two or more modes, and in the mature stage, a wide range of diameter sizes. These modes represent the batches of oocytes that will be spawned throughout the breeding season. Through histological analysis, it was possible to prove this fact, since in addition to mature oocytes, can be observed oocytes in different stages of development and the presence of empty follicles (post-ovulatory). The histological sections of the spawning-capable and mature females for *H. marmoratus*, *G. rondoni*, *E. pavulagem, H. lepturus*, *P. capim, C. arnoldi, and H. heterorhabdus* revealed oocytes at all stages of development, indicating the continuous release of oocytes as they reach full maturity, consistent with batch spawning in these species (Figure 2 – Supplementary material). These characteristics analyzed together, confirm that those species present a batch spawning.

The macroscopic analyze of mature ovaries of *A. bimaculatus, B. melanurus M. oligolepis*, and *M. collettii* suggest that spawning would be total, since the most of oocyte (90%) were mature and very numerous in relation to other development oocytes stages (APÊNDICE C and APÊNDICE E). Also, the population reproductively active for both species tend to focus on a single period (a single reproductive type). The all assessed reproductive traits were summarized in Table 1.

We observed for *M. colletti* a development synchronous in a group (APÊNDICE E), the oocytes mature concomitantly, being eliminated only once during the spawning period. For *A. urophthalmus, A.* gr. *regani*, *E. pavulagem, H. guyanensis*, and *M. weitzmani,* the oocyte development described the synchronic in two groups mechanism, in which at each reproduction period, two batches are evidenced: the stock oocytes and the oocytes that will mature synchronously and be eliminated during the spawning period (APÊNDICE D).

The oocyte diameter distribution of *G. rondoni* and *H. lepturus* looks similar to synchronic in more than two groups (APÊNDICE D). Next to the batch of stock oocytes, there are batches of oocytes in different phases of development, being that each batch develops synchronically, and the most developed batch (which reaches maturity) will be released. We did not observe batches for *H. marmoratus*, *H. heterorhabdus*, and *Pyrrhulina capim* (APÊNDICE D), but oocytes are present in all stages of development, suggesting that their elimination occurs as they reach full maturation.

Table 1. Summary of the eight reproductive traits, assessed in 17 species sampled in eight Amazonian streams in a catchment of the Guamá River (Eastern Brazilian Amazon) between March 2019 and March

2020. The sex ratio was calculated for the entire study period. L50 (%) corresponds to the proportion representing the size at first maturity concerning the maximum total length measured for females and males for each species. >IGS corresponds to the maximum gonadosomatic index found within mature females of each species. Fecundity refers to the average number of vitellogenic oocytes counted in selected mature females. Oocyte diameter, refers to the diameter of only vitellogenic oocytes. Exten – Extended period.

Taxon	**Sex ratio ♀:♂**	**Maximum Total Length (mm) ♀/♂**	**L50 (mm) ♀/♂**	**L50 (%) ♀/♂**	**Length of the reproductive period (months)**	**> IGS**	**Average Fecundity**	**Oocyte diameter (mm)**	**Spawning type**	**Parental care**
A. tetramerus	1 : 1.7	131.01 / 83.72	48.27 / 40.12	36.8 / 47.9	Exten (9) Oct-Jun	1.27	646	0.994 ± 0.08	Batch	Present
A. urophthalmus	1 : 1.2	41.34 / 41.21	18.45 / 17.93	44.6 / 43.5	Long (12) Jan-Dec	7.35	5 ± 2	1.36 ± 0.11	Batch	Unknow
A gr. regani	1 : 1.1	42.93 / 64.16	24.3 / 19.2	56.6 / 29.9	Long (12) Jan-Mac	7.54	61 ± 27	1.334 ± 0.14	Batch	Present
A. bimaculatus	1 : 1.1	107.9 / 119.99	62.19 / 53.45	57.6 / 44.6	Short (2) Jan/Feb	14.71	13219 ± 7987	0.658 ± 0.04	Total	Absent
B. melanurus	1 : 1.4	131.01 / 83.72	39.67 / 43.15	30.3 / 51.5	Exten (7) *Jan-Aug	4.81	841 ± 165	0.770 ± 0.09	Total	Unknow
C. arnoldi	1 : 1.4	38.80 / 57.72	23.26 / 30.84	59.9 / 53.4	Exten (8) Dec-Jul	7.52	50 ± 21	0.658 ± 0.05	Batch	Present
E. pavulagem	1 : 1.6	149.23 / 194.35	83.01 / 88.15	55.6 / 45.4	Short (3) Jan-Mar	8.44	103 ± 33	1.32 ± 0.16	Batch	Present
G. rondoni	1 : 1.1	167.63 / 174.27	89.33 / 103.62	53.3 / 59.5	Exten (6) Oct-Mar	7.67	36 ± 12	1.39 ± 0.22	Batch	Unknow
H. marmoratus	1.1 : 1	65.21 / 59.89	31.33 / 27.41	48.1 / 45.8	Exten (9) Jul-Mar	6.78	60 ± 23	1.24 ± 0.15	Batch	Unknow
H. guyanensis	1 : 1	42.16 / 38.05	23.71 / 24.14	56.2 / 63.4	Exten (7) ★Int	11.32	363 ± 130	0.595 ± 0.05	Fract	Absent
H. heterorhabdus	1 : 1.3	41.34 / 35.42	19.3 / 18	46.7 / 50.8	Long (12) Jan-Dec	9.86	197 ± 104	0.412 ± 0.10	Batch	Absent
H. lepturus	1 : 1.1	95.09 / 98.53	50.11 / 58.12	52.7 / 58.9	Exten (7) Dec-Jul	7.38	47 ± 22	1.158 ± 0.20	Batch	Unknow
I. rachovii	1.2 : 1	57.81 / 60.23	25.98 / 29.27	44.9 / 48.6	Short (3) Dec-Mar	4.19	104 ± 39	0.679 ± 0.1	Batch	Unknow
M. weitzmani	1 : 1.1	24.65 / 22.97	15.85 / 15.91	64.2 / 69.3	Long (11)†Jan-Dec	13.55	26 ± 8.5	0.567 ± 0.06	Batch	Unknow
M. collettii	1.9 : 1	59.49 / 50.27	25.12 / 24.24	42.2 / 48.2	Short (3) Jan-Mar	14.12	617 ± 110	0.666 ± 0.07	Total	Absent
M. oligolepis	1 : 1	88.96 / 84.26	56.14 / 56.08	63.1 / 66.6	Short (3) Nov-Jan	10.76	2878 ± 1285	0.66 ± 0.04	Total	Absent
P. capim	1.2 : 1	65.53 / 75.98	28.06 / 25.56	42.8 / 33.6	Long (10) Jul-Apr	5.91	69 ± 36	0.534 ± 0.01	Batch	Unknow

*Except April.

★Intermittent: peaks in Jun/Jul, Sep/Oct, and between Jan to Mar.

†Activity during all months except in July.

3.4.6. Comparison of reproductive traits

The first two axes of PCoA explained 77.42% of the variation of reproductive traits. The first axis explained 44.88% and was influenced positively by the length of the breeding period fecundity and negatively by the body size, the length at first maturity and the spawning type. The second explained 32.54% and was influenced positively by relative fecundity and the gonadosomatic index, and negatively by the oocyte diameter, and the parental care. Species with large total length (> 120 mm), large length at first maturity and batch fecundity were placed in the left side in the first axis, species with long breeding period (up to 11 months) were placed at the right. In the second axis, species with high mean relative fecundity (> 400 mature oocytes per gram of body weight), had positive values, while species with bigger oocyte diameter (> 1.0 mm), and some degree/level of parental care were placed in the bottom of second axis (Figure 5).

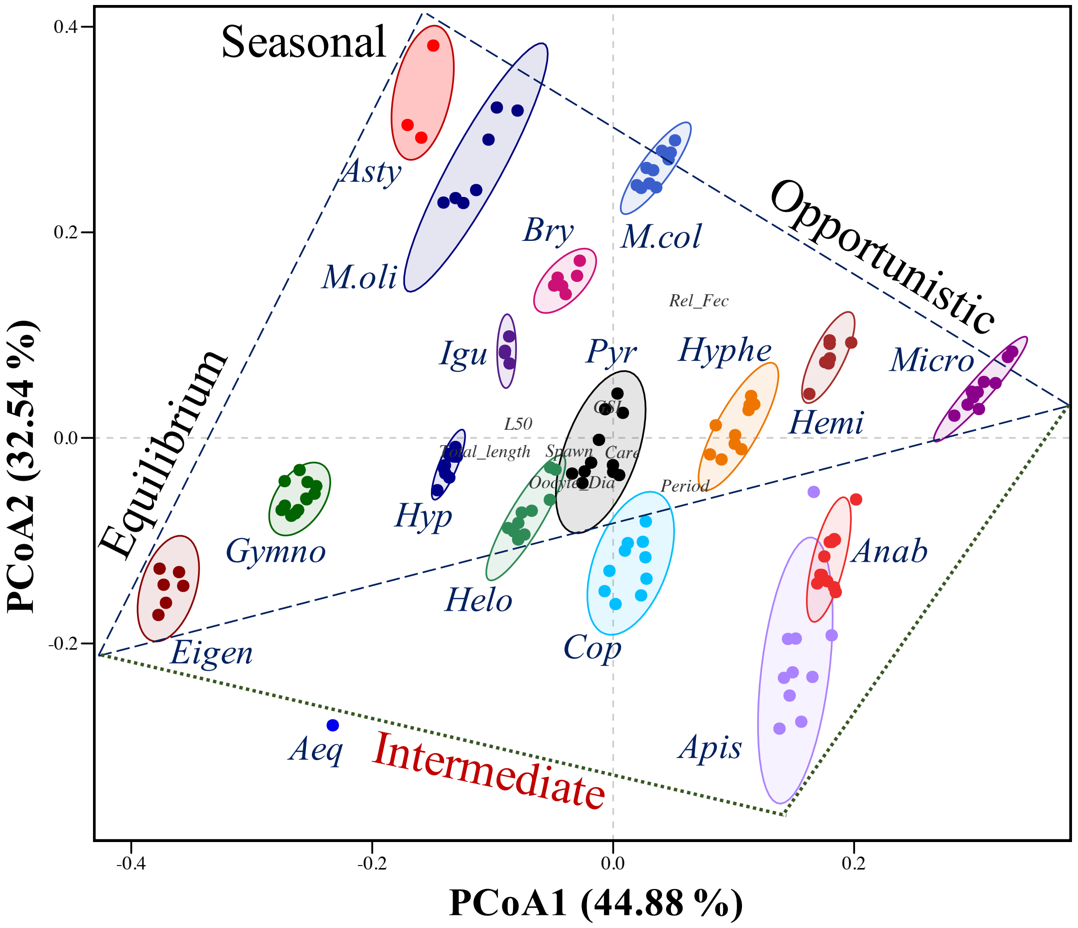


Figure 5. PCoA plot using Gower distance of eight reproductive characteristics from 17 fish species sampled in Amazonian streams between March 2019 to March 2020. The first axis was more influenced by the fecundity, separating *A. bimaculatus* and *M. oligolepis* from the rest of species. The second axis was more influenced by body size, separating *E. pavulagem* from *M. weitzmani.* The dashed line indicates the endpoints of the Triangular Continuum model of Life History. The dotted line illustrates an intermediate strategy between the Equilibrium – Opportunistic gradient, where the majority of species

analyzed are positioned. Each circle represents a female. *Aeq – Aequidens tetramerus, Anab – Anablepsoides urophthalmus*, *Apis – Apistogramma* gr. *regani*, *Asty – Astyanax bimaculatus*, *Bry – Bryconops melanurus, Cop – Copella arnoldi*, *Eigen –Eigenmannia pavulagem*, *Gym – Gymnorhamphichthys rondoni*, *Helo – Helogenes marmoratus*, *Hemi – Hemigrammus guyanensis*, *Hyphe – Hyphessobrycon heterorhabdus*, *Hyp – Hypopygus lepturus, Igu – Iguanodectes rachovii*, *Micro – Microcharacidium weitzmani*, *M.col– Moenkhausia collettii*, *M.oli – Moenkhausia oligolepis*, *Pyr – Pyrrhulina capim*.

A plot of species by their scores on the first two principal coordinates revealed a triangle with apices corresponding to the three strategies of the Continuum Model of Life-history. On the top, from the Characidae family, *A. bimaculatus* and *M. oligolepis*, with the highest relative fecundity, represented the periodic strategy. To the left on the y-axis, with the larger body size *E. pavulagem* and *G. rondoni*, and *A. tetramerus* represented the equilibrium strategy. To the right over the same axis, *M. weitzmani*, and *H. guyanensis* with small body sizes, longer breeding period and fractional spawning represented the opportunistic strategy (Figure 5). *M. collettii,* and *B. melanurus*, were located in the gradient periodic – opportunistic, and eight species occupied the equilibrium – opportunistic gradient. The reproductive strategy manifested by these last species that cannot fit in the endpoints of the continuum model, and occupies a "multivariate space" along the gradient, is known as "Intermediate". Based on the results of Permanova analysis (Table 2) and the Simper analysis, the traits that most contributed to dissimilarity among the species were relative fecundity and total length (Table 3 and 4).

Table 2. Permutational multivariate analysis of variance (PERMANOVA) results based on Gower dissimilarity distance, using eight reproductive traits of the fish assemble compounds of 17 species sampled in eight streams of a catchment of the Guamá River (Eastern Brazilian Amazon)

	Df	**SS**	**R^2**	**Pseudo-F**	**p-value**
Species	16	8.812	0.977	324.23	0.001
Residual	122	0.207	0.023		
Total	138	9.019	1.00		

Df – degrees of freedom; SS – sum of squares; R^2 – the effect size; Pseudo-F – value by permutation. Statistical significance with $p < 0.05$ based on 999 permutations.

Table 3. SIMPER analysis (percent dissimilarity) with comparative contribution greater than 90% of the fecundity between the species.

Species	**Average**	**Contribution (%)**
A. bimaculatus_H. lepturus	0.949	99.5
A. bimaculatus_B. melanurus	0.780	99.4
M. oligolepis_B. melanurus	0.640	99.1
A. bimaculatus_A. regani	0.964	99.1
A. bimaculatus_A. urophthalmus	0.979	99
A. bimaculatus_I. rachovii	0.941	99
A. bimaculatus_E. pavulagem	0.925	99
A. bimaculatus_H. marmoratus	0.948	99
A. bimaculatus_M.collettii	0.826	98.9
M. oligolepis_H. lepturus	0.858	98.9
A. bimaculatus_P. capim	0.948	98.9
A. bimaculatus_G. rondoni	0.938	98.7
M. oligolepis_I. rachovii	0.907	98.7
A. bimaculatus_H. guyanensis	0.882	98.7
M. oligolepis_A. urophthalmus	0.969	98.6
A. bimaculatus_C. arnoldi	0.956	98.6
A. bimaculatus_H. heterorhabdus	0.921	98.5
A. bimaculatus_M. weitzmani	0.965	98.3
M. oligolepis_C. arnoldi	0.934	98.1
M. oligolepis_H. marmoratus	0.856	97.7
M. oligolepis_I. rachovii	0.835	97.6
M. oligolepis_M. weitzmani	0.947	97.6
M. oligolepis_P. capim	0.856	97.4
B. melanurus_H. lepturus	0.678	97.2
M. collettii_I. rachovii	0.566	96.9
M. oligolepis_C. arnoldi	0.553	96.6
M. oligolepis_M. collettii	0.878	96.4
H. guyanensis_C. arnoldi	0.535	96.3
M. oligolepis_H. guyanensis	0.683	96.2
M. oligolepis_E. pavulagem	0.796	96.1
M. oligolepis_H. heterorhabdus	0.781	95.9
B. melanurus_H. marmoratus	0.672	95.8
M. collettii_P. capim	0.625	95.4
M. oligolepis_G. rondoni	0.831	95.3

Table 4. SIMPER analysis (percent dissimilarity) with comparative contribution greater than 30% of the body size between the species.

Species	**Average**	**Contribution (%)**
G. rondoni_M. weitzmani	0.343	55.9
G. rondoni_H. lepturus	0.140	50
H. lepturus_M. weitzmani	0.221	49.2
G. rondoni_H. marmoratus	0.196	48.5
G. rondoni_P. capim	0.206	47.4
H. lepturus_A. regani	0.146	43.7
G. rondoni_A. urophthalmus	0.290	43.5
E. pavulagem_M. weitzmani	0.275	42.2
E. pavulagem_I. rachovii	0.149	41.9
G. rondoni_C. arnoldi	0.234	41.8
G. rondoni_A. regani	0.231	41.6
H. lepturus_A. urophthalmus	0.203	41.5
E. pavulagem_ A. gr. *regani*	0.151	41.4
E. pavulagem_P.capim	0.159	40.2
G. rondoni_I. rachovii	0.191	39.9
H. marmoratus_M. weitzmani	0.150	37.9
E. pavulagem_H. heterorhabdus	0.167	37.4
E. pavulagem_A. regani	0.184	37
P. capim_M. weitzmani	0.138	36.7
E. pavulagem_C. arnoldi	0.186	35.5
E. pavulagem_H. lepturus	0.101	34
G. rondoni_H. heterorhabdus	0.207	33.6
E. pavulagem_A. urophthalmus	0.229	33.6

3.5. DISCUSSION

A wide diversity of life-history strategies was verified for this assemblage. The dissimilarity analysis among the eight traits attributed to fecundity as the main character in differentiating the species and in second place the body size, which we did not contemplate as a relevant trait in the segregation of the species.

Otherwise, after the estimation and ordination of the eight life-history traits for 17 stream fish species of eastern Brazilian Amazonian, we identify the three reproductive strategies proposed by Winemiller (1989) and Winemiller and Rose (1992), with nine species located in the equilibrium – opportunistic gradient, confirming our hypotheses of the relevance of the intermediate strategy for stream fishes (see Figure 5).

For the species set, *A. bimaculatus* was the most influenced the segregation presented high fecundity, seasonal reproduction, small oocyte diameter, and no parental care standing at the edge of the relatively periodic type strategy (Winemiller, 1996). The composition of two groups clustered near the extremes of Figure 5 is associated to some degree with phylogeny. The gradient periodic – opportunistic is dominated by Characiformes order, the two species associate with periodic strategy (*A. bimaculatus* and *M. oligolepis*) are Characidae; *M. weitzmani* associated with opportunistic strategy, small-bodied species, fractional spawner, capable of rapid colonization belongs to Chrenuchidae family, and in the middle, *M. colletti* and *H. guyanensis* from Characidae and *B. melanurus* from Iguanodectidae family.

On the other hand, *E. pavulagem* and *G. rondoni* associated with equilibrium strategy, are gymnotiformes. In the gradient equilibrium – opportunistic, we can see members of the most diverse order and size, *C. arnoldi,* and *P. capim* (Lebiasinidae), *H. marmoratus* (Cetopsidae), *A.* gr. *regani* and *A. tetramerus* (Cichlidae), *H. lepturus* (Rhamphychtidae), *I. rachovii* (Iguanodectidae), and *H. heterorhabdus* (Characidae).

3.5.1. Body size and length at first maturity

The set of assessed species are considered as small-sized, with up to 15 cm of standard length (Castro, 1999; Castro et al., 2005). This trait presented a great amplitude among the species . Therefore, an approach that considers subcategories of body size would be helpful to understand the dynamics of these communities better since body size acts as a proxy for many life-history characteristics.

The estimated shortest length at first maturation (between males and females of each species) was a practical parameter to help identify recruitment periods and use the percentage in relation to the maximum recorder size allowed to compare the different species, considering the high variation in the body size.

We observed differences in the size to reach maturity for both sexes. It is expected that males reach maturity with smaller sizes since the energy allocation for ovarian development is 15 to 20% greater than for the tests (Wooton, 1998), but *A. tetramerus* and *B. melanurus* were the exception, both species with higher body sizes. For *A. tetramerus*, this small length to reach maturity is not atypical since smaller sizes (18 mm for the females and 20 mm for the males) have already been reported for populations of streams of Rondônia (Southwestern Amazon, Brazil) (Costa et al., 2019

For females of *Apistograma* gr. *regani* the length at first maturity was less than the males (♀=19.2 mm ♂= 24.3 mm of TL), but looking at the ratio between L_{50} and *TL*, for males, this relationship is higher because they reached the maximum largest sizes (Table S2). We found slight differences in this parameter when compared with *Apistogramma agassizii* (♀=19.85 mm ♂= 21.38 mm of *SL*) and *A. bitaeniata* (♀=20.04 mm ♂= 20.06 mm of *SL*) in a lake from the Reserva de Desenvolvimento Sustentável Mamirauá (RDSM) in Amazonas State (Brazil) (Oliveira & Queiroz, 2017).

Length at first maturity is a fundamental life history variable, as it represents the size (or age) at which resources are no longer channeled exclusively to growth, maintenance and storage, but also to reproduction. Both variables can have a powerful influence on fitness and are considered sensitive to selection (Stearns, 1992). Age and size at maturity tend to have opposite effects on fitness. A reduction in the age of maturity reduces the duration of the generation and reduces the probability of the individual dying before reproducing, the point is that a smaller size in females implies a lower fecundity.

This last aspect depends on the species in question (Barneche et al., 2018), because for the small-sized females assessed, there was no correlation between their length and fecundity, at least for batch spawners (see Table 1). In addition and particularly for the species of the Cichlidae family that, despite having a large body size in the case of *A. tetramerus* and some big females of *A*. gr. *regani* apparently with a large abdominal capacity; their mature gonads occupied less than 50% of that cavity, observing an empty space, whence predictions about reproductive capacity based on body size alone should be made with caution, especially for small-sized fish.

In the case of males, small length at first maturity it may be associated with a limited ability to compete for a territory or nest site and to exclude rivals during mating (Wooton & Smith, 2016). In many species, the size or age of the females generally alters the reproductive capacity at different levels, which may affect the initiation, duration or frequency of spawning and the fertility and quality of the eggs produced (Macchi et al., 2004; Marteinsdottir & Begg, 2002)

3.5.2. Spawning type

More than half of the species evaluated in this assembly presented batch spawning (APÊNDICE D), this spawning type may also be necessitated by physiological constraints associated with small body size (Wootton, 1992), and in small fishes batch spawning might allow them to increase their reproductive output compared to total spawning. The best-known advantage of the batch spawning type is the possibility of releasing batches of eggs in different spawning sites, decreasing competition between adults both for resources and by spawning sites and between larvae for food (McEvoy & McEvoy, 1992). Even if the classification for the type spawning was just total or batch, the oocyte development mechanisms exhibited by the species encompassed all the classifications (Wallace & Sellman, 1981). This breadth in this trait could be a key in optimizing the times to reproduce and the management of space and available resources, it would facilitate the coexistence of these species and the maintenance of fish populations in the streams.

Winemiller (1989) highlights that spawning is one of the reproductive characteristics modulated by the environment that determine the survival of the population, then identify the variable or set of variables that can modulate or regulate the way in which the oocytes shoul be released would be of paramount importance for the stability and survival of fish populations. Fishes can carry out the transition of total and batch spawning depending on the environmental and physiological changes that are submitted to a specific population (Carvalho et al., 2009). Among the assessed species, *A. bimaculatus* has the widest geographic distribution and its adaptive plasticity that allowed to reproduce and survival in most varied habitats such as lakes, dams, streams, swamps and rivers (Mereles et al., 2017; Normando et al., 2013) being the clear example of the effect of the environment in reproductive traits, since depending on the environmental conditions it can show batch or total spawning (Gennari Filho & Braga, 1996).

Although the advantages of presenting a batch spawning are clear, for species that have partial spawning, the conceptus of fecundity is complicated, there are species with determined and indeterminate fecundity or with intervals of just one day or several days, for them o term 'Batch Fecundity' would be the most appropriate since it represents the number of eggs produced in each spawning episode and can be approximately equal to the number of eggs produced by a total spawning (Wootton & Smith, 2016).

An important aspect regarding this characteristic is that changes in fecundity would work as a mechanism to regulate populations depending on densities (Bagenal, 1978). In this background, the number of reserve oocytes and atresia could help predict the reproductive potential for assessed species in streams because we can estimate how many mature oocytes will be released, however, we need more certainty about the survival of the future larva or if the next batch of oocytes will be liberated or reabsorbed.

Variation in egg size reflects a maternal investment in each oocyte and can be used to estimate parental care among bony fish (Sargent et al., 1987; Iglesias-Rios et al., 2021). Although producing large eggs provides a trade-off between egg size – fecundity, egg size – survival, and egg size – hatchling size (Stearns, 1992), the costs could be reflected in the extension of parental care since a larger egg will take more time to develop, which implies a higher risk of being predated (Sargent et al., 1987) and also more care. Therefore, the extent of parental care will be directly related to the incubation period, which means that long incubation periods are often associated with parental care (Wootton and Smith, 2016).

Suppose selection favors a larger egg or embryo size, in that case. It will necessarily be a decline in litter size (reduced fecundity). A. *urophthalmus* presented the lowest fecundity and the second large average size after *G. rondoni*. After the examination, we can detect that the mature oocytes of *A. urophthalmus* are not filled with yolk but have a wide perivitelinic space that probably has protective functions. The group of killifish, to which *A. urophthalmus* belongs, tends to bury their eggs to protect them in the dry season, as well as rains coming back in the wet season months they hatch. In this case, an increase in the oocyte size would be more associated with a response to environmental constraints to protect the embryo.

Larger eggs (up to 1.2 mm) were also observed in gymnotiformes, *H. marmoratus*, and *A*. gr. *regani*. Even if fecundity among gymnotiformes varied from 36 to 103, it would be more correlated to the period in which spawning occurs than to the oocyte diameter (because they are very similar) or body size. Parental care is relatively rare in teleosts (Clutton-Brock, 1991), but when it does occur, it is often associated with more extended developmental periods and larger-sized eggs (Sargent et al., 1987; Smith & Wootton, 1995).

Gymnotiforms are usually linked to the equilibrium strategy, mainly by their large-sized eggs. Considering all 17 species, we can classify them as “big oocytes.” Bringing up the second trade-off, egg size, and mortality, a way to guarantee the survival of the gymnotiforms larvae would be explained with the substrate used. Gymnotiforms species and *H. marmoratus* are nocturnal and tend to camouflage themselves in litter and sandbanks during the day (Garcia, 2019; Sazima et al., 2006) then they will have less risk of predation and greater foraging ability (Bagenal, 1969).

Most cichlids have biparental care, but some species, such as dwarf cichlids (*Apistogramma* spp.), have maternal care (Winemiller, 1995). The genus *Aequidens* exhibits intense territorial behavior and strong parental care (Reis; Kullander; Ferraris Jr.,2003), with a great portion of the species, performing oral incubation (Keenleyside, 1979).

3.5.3. Reproductive traits variation

Often, for stream fishes, a continuous reproduction and low fecundity compensated by batch spawning, can explain (in part) the reproductive dynamic in these environments. However, inside the big picture, we can identify a wide range of possible phenotypic expressions for some traits, which measure a trait's phenotypic plasticity. To objectively assign species to strategies, it is often necessary to partition the possible range of expressions for each trait into categorical, mutually exclusive states or modalities (Poff et al., 2006; Vieira et al., 2006).

Although most of the studied fish species do not fully fit in one of the trilateral continuum's three endpoints (equilibrium, opportunistic or seasonal), they may occupy intermediate multivariate space between the endpoints (Espírito-Santo et al., 2013), observation that was already pointed out by Winemiller (1989) in the periodic–opportunistic gradient. Another aspect reported by Espírito-Santo et al., (2013) in 1st and 2nd order streams in central Amazon, was the lack of representative species in the periodic strategy, attributing three possible causes: the limited stream dimensions to benefit large size, the low productivity of Amazonian headwater streams, and the absence of some potential environmental triggers to fish migration.

Even though, we agree that exist a limitation imposed by the physical conditions of smaller-order *terra firme* streams, the intermittent floods caused by local rainfall, would be linked to a seasonal expansion and contraction of the habitat (Waddell et al., 2019) which could provoke a stimuli to reproduce and migrate. In fact, *A bimaculatus*, *M. oligolepis*, *E. pavulagem*, and *B. melanurus* just disappeared in different moments; all of them would have swimming capacities according to their sizes, which may suggest that they carry out small migrations for unknown purposes. In addition, the low abundance and lack of juvenile forms of *A. bimaculatus* and *M. oligolepis* suggested that they could explore other places during their cycle. We discarded a mechanical effect during collection because we used a mesh with a narrow separation between nodes (2 mm).

Regarding these species, both fit in the periodic strategy: they produce a large amount of eggs, their eggs are small when compared with the egg size of other assessed species, and reproduced in a short period that coincides with the rainy season, despite of the periodic strategy is more associated with larger body sizes. Even knowing that it is difficult for a given set of species to adjust to any particular strategy, the measurement of trait breadth, to identify those slight particularities of reproduction could better understand, at least in the reproductive sphere, how species deal with these ecological problems to ensure the production of offspring, and determine the reproductive potential of these populations.

The above could be interpreted as the creation of an own scale that serves as a reference and allows us to make a more accurate or precise comparison of what it means to be small in the case of size or low in the case of fecundity. Thereupon, a review of the species' biology would be required to link species distributions to habitat suitability and understand how trait breadth or plasticity enables fish populations to persist in the face of dynamic lotic environments (Frimpong & Angermeier, 2009).

Species traits provide a promising means to establish general rules in community ecology (Frimpong & Angermeier, 2009). Trait-based approaches that quantify the relative magnitude of interspecific variability on fish life-history traits will be essential to understanding the ecological relationships of a community (Vazzoler, 1996), and predicting the responses of stream fish communities to their environment (Goldstein & Meador, 2004; Lamouroux et al., 2002). This approach is relevant in climate change, processes of species extinction, species invasion, and assemblage homogenization.

The variation of traits observed in this work reinforces the idea that basic biological information becomes a significant source for unraveling how to function and maintain the fish populations. Knowing the life history characteristics that fish populations display in their natural environment allows for predicting their responses to the threats of anthropogenic origin to which these environments are being subjected (Cassatti et al., 2006; . The life-history traits approach should be integrated into studies or research about stream ecology, which will better understand the structuring of these communities and, subsequently, their protection.

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4. SESSÃO II

Comparative analysis of the reproductive life-history traits of small gymnotiformes from the Eastern Amazon streams

A segunda sessão desta tese foi formatada conforme as normas da publicação científica *Environmental Fish Biology*, disponível em: https://www.springer.com/journal/

Comparative analysis of the reproductive life-history traits of small gymnotiformes from the eastern Amazon streams

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4.1. ABSTRACT

Usually, differences in reproductive life-history traits are associated with environmental pressures; for fish species living in the same habitats, we expected those differences to be related to phylogeny. In this study, we assessed and compared the variation of seven reproductive traits and the influence of some local environmental variables in the monthly variation of the gonadosomatic index for *Gymnorhamphichthys rondoni*, *Eigenmannia pavulagem,* and *Hypopygus lepturus* in Northeast Amazonian streams, intending to detect if their life-history traits are the reflection of their phylogenetic proximity or consequence of the environmental influence. Samplings were performed monthly from March 2019 to March 2020, using dip nets at eight streams located in Eastern Brazilian Amazon. We detected the reproductive and recruitment periods through monthly variations of the Gonadosomatic Index and the frequency of gonadal development stages. Half of the three populations reached sexual maturity with less than 50% of their maximum total length. The sex ratio was biased for males just for *E. pavulagem*. The three species presented batch spawning, batch fecundity with different oocyte development mechanisms, and larger oocyte size. However, differences in the breadth of fecundity and body size segregate the tree species with no evidence of an effect of phylogenetic proximity in the life-history traits. The monthly variation of the gonadosomatic index was more associated with the influence of local variables, including rainfall, electrical conductivity, and substrate type. Studies, including other reproductive traits and more species, could elucidate the effect of phylogeny on the life-history traits in this group.

Keywords: *Gymnorhamphichthys rondoni*, *Eigenmannia pavulagem*, environmental influence *Hypopygus lepturus*, reproduction.

4.2. INTRODUCTION

The life-history strategy is a complex pattern of co-evolved life-history traits resulting of both the evolutionary history from the species and its adaptation to the environmental conditions where it lives. The plasticity of reproductive traits as the size at birth, the sex ratio, the spawning habitat, the spawning season, fecundity, among others (Helfman et al. 1997), allow populations to face environmental variability (Rochet 2000).

This plasticity also allows that individuals of the same species distributed in a wide latitudinal range display different reproductive tactics under different environmental conditions (Munro1990; Mazzoni and Iglesias-Rios 2002; Becker et al. 2008). Although different species can exhibit distinctive reproductive strategies, notable differences can exist within closely related groups and even within individuals of the same species inhabiting different locations (e.g. the genus *Cichla*, Gomiero and Braga 2004; Vieira et al. 2009).

Agostinho et al. (2009) consider that the reproductive strategy of a species is the most conservative in its life history. Regarding the similar patterns in the size at maturation of *Hyphessobrycon eques* founded by Santana et al. (2017), they suggested a stronger effect of evolution aspects even in different environmental conditions. On the other hand, rapid changes in age and size at sexual maturity of *Oreochromis niloticus* at the intra and inter-population level suggest that the observed variations may be explained by differences in environmental variables (phenotypic plasticity) rather than by genetic differences (Duponchelle and Panfili 1998).

According to the above, and depending on the species, some traits are fixed (are resistant to change) and others are highly plastic (Berven and Gill 1983). So which reproductive traits are most likely to respond to environmental influence and which are retained by species due to strong genetic influence? For species that occur in the same habitat type, we may expect similar tactics in phylogenetically distant species (Olden and Kennard 2010), but what about those phylogenetically close that inhabit the same place?

The order Gymnotiformes comprises the fish popularly known as "*electric fish*" because they can generate an electrical current, which allows navigating, foraging, and orienting themselves in waters of poor visibility. These discharges also determine habitat selection (Crampton 1998), predatory (Crampton 1998; Westby 1988), and reproductive behaviors (Kramer 1983). This group occurs in streams, small channels, flooded areas in the rainy season, and, mainly, at the bottom of the main channels of large rivers, where they find abundant food throughout the year (Albert and Crampton, 2003). Currently, the order consists of 240 species distributed in 35 genera (Ferraris et al. 2017) and five families: Gymnotidae as a basal group, Rhamphichthyidae as a sister of Hypopomidae, and Sternopygidae as a sister of Apteronotidae (Albert 2001; Albert and Crampton 2005; Tagliacollo et al. 2015).

Regarding gymnotiforms reproduction, it is known that low conductivity and increased rainfall would be potent spawning triggers (Hopkins 1974; Kirschbaum and Schugard 2002; Giora and Fialho 2009). In Brazil, at higher latitudes, the reproductive cycle is related to an increase in temperature (Quintana et al. 2004; Schaan et al. 2009), photoperiod (Giora and Fialho 2009; Giora et al. 2014), or these two factors simultaneously (Silva et al. 2002, Cognato and Fialho 2006). At lower latitudes (Ilha de Marajo – Rio Goiapí), the diversity of reproductive tactics would be related to the moment the gonads develop (which does not always coincide with the rainy season) and with the movement within the habitat (Schwassmann 1976). A reproductive aspect that characterize the Gymnotiformes species is release more than one oocyte batch during one reproductive period (fractional spawning) *Brachyhypopomus* (Giora and Fialho 2009; Waddell et al., 2019), *Gymnotus carapo* (Barbieri and Barbieri 1985; Cognato and Fialho 2006), *Gymnorhmphichthys rondoni* (Garcia 2019).

Gymnotiform species from different genera and even families in the same region show identical patterns of the reproductive period establishment, suggesting that environmental conditions influence reproductive period determination in gymnotiformes more strongly than the degree of relationship between the taxa, being an adaptive condition, instead of an inherited character (Giora, Tarasconi and Fialho 2014).

Considering that the ecology and life history of most gymnotiforms species in the Amazon basin remain practically unknown, being one of the regions where this group reaches its highest degree of diversity (Crampton, 1996) and the environmental influence in the life-history traits, we characterized the life-history traits of three species of small electric fish. From the Rhamphichthyidae family (‘Sand knife fishes’): *Gymnorhamphichthys rondoni* (Miranda Ribeiro, 1920) and *Hypopygus lepturus* Hoedeman, 1962, both widespread within Amazon, Orinoco, and coastal drainages in Guiana basins and coastal rivers of Guyana, *G. rondoni* also in upper Paraná River and *H. lepturus* is found just in a few tributaries of the upper portion of the Paraguay River basin in west central Brazil (Ferraris, 2003; Santana and Crampton 2011). The two species occur in shallow streams with a sandy bottom. It is documented that *G. rondoni* is buried in the substrate during the day and emerges at night to forage, interact socially and reproduce (Schwassmann 1976; Zuanon et al. 2006). Additionally, from the family Sternopygidae ('electric glass knifefish'), *Eigenmannia pavula*gem distributes in small tributaries of the River Capim and River Guamá basins in northeastern Pará State in Brazil (Peixoto et al., 2015).

We proposed two main objectives to elucidate aspects of the life-history of these three species: 1. Compare the reproductive biology of the three species by analyzing seven reproductive characteristics: breeding period, variation of gonadosomatic index, sex ratio, size at first maturity, fecundity, egg size, spawning type, and parental care, and discuss the reproductive characteristics in a phylogenetic context, and 2. Evaluate possible environmental influence on the reproductive cycle of the three species. We expect batch spawning for the three species but similar reproductive traits between *G. rondoni* and *H. lepturus* because of phylogenetic proximity. We expect that electric conductivity and rainfall influence the variation of the monthly gonadosomatic index for the three species.

4.2. MATERIAL AND METHOD

4.2.1. Study área

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 and 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.

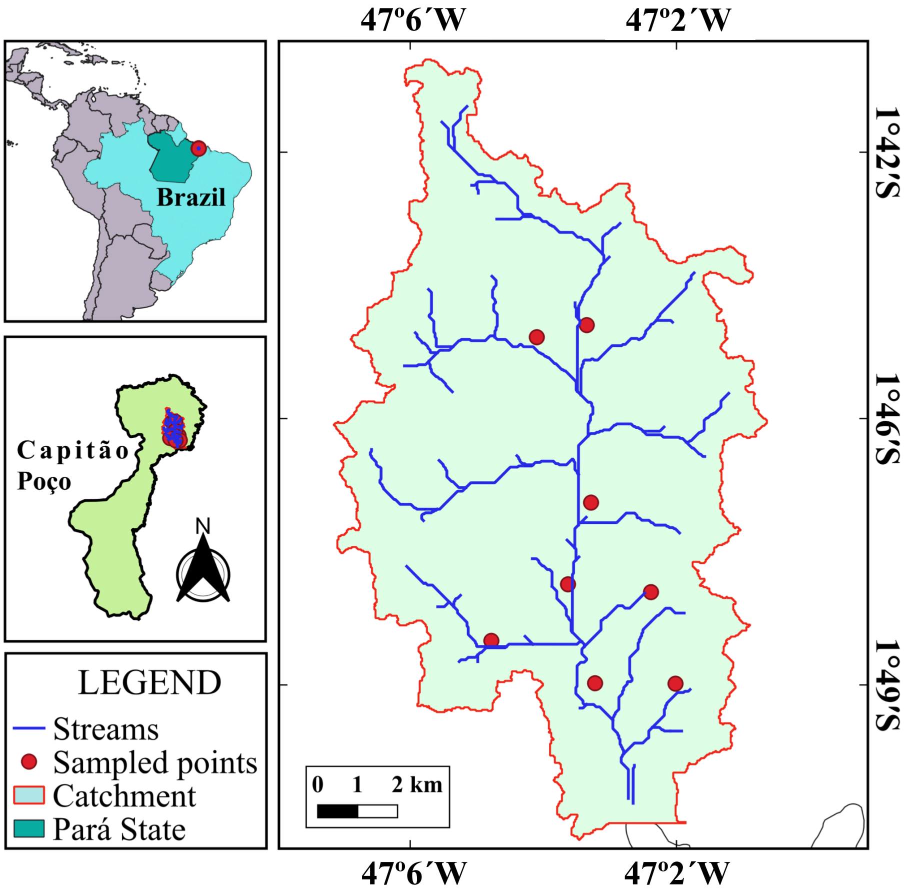

Fig. 1. Sampled streams (red dots) in a catchment of the Guamá River (Eastern Brazilian Amazon).

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 ºC, which varies 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 and Bastos 2001). We registered 1500.4 mm of accumulated rainfall during the study period (since March 2019 to March 2020), the highest value in February (511.6 mm) and the lowest in August (34 mm). The rainfall dynamics did not differ from the municipality's historical rainfall pattern, with the highest intensity occurring between January and May.

We monthly sampled eight low-order streams (1st to 3rd order *sensu* Strahler, 1957). We choose 50 m reach of each stream based on their riparian zone, substrate type in the stream bottom, depth, width and water current velocity. We divided each stream 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 (µS/cm^{-1}), pH, and Temperature (ºC), 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 reach, we calculated the wetted width (WW - m) considering the transversal distance between stream flooded margins with a ruled pole. The thalweg depth (TD - cm) was registered at five equidistant points, where we also visually registered the substrate type (SB %). We measure the Canopy Cover (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 calculated 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*Vm, where *Q* = the discharge, *Vm* = mean surface flow speed, and *A* = mean transect area. The mean transect area was calculated by $A=\sum_{in}A_n$ where *A* = area of the transect, which is given by the sum of $Z_1+Z_2/2*w+Z_2+Z_3/2*w+\ldots Z_n+Z_n+1/2*w$, where, Z_n = the measured depth of each segment, and w = the width of each segment.

We used the 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 (Figure 2, General Introduction).

The specimens of *G. rondoni, E. pavulagem* and *H. lepturus* 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. We sampled all available microhabitats for fish: areas with sandy sediment, leaf banks, marginal crevices, main channel, puddles remaining from rain and banks with riparian vegetation or macrophytes. 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. The specimen collections were authorized by license 63603-3, issued by the federal Chico Mendes Institute for Biodiversity Conservation - ICMBio, through the Biodiversity Authorization and Information System – SISBIO. The Animal Ethics Committee of the Federal Rural University of Amazon (UFRA) approved the study, through process number 054/2018. Specimens will be deposited in Natural History Collection of the Museology Course (RTM) of the Universidade Federal do Pará, Belém (Brazil).

In the laboratory, the specimens were weighed (total weight in g - *TW*), measured from the snout to the end of the caudal filament (total length in mm - *TL*) and from the snout to the last ray of anal fin (standard length in mm – *SL*), 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: 1) immature: contained oogonia and numerous type I oocytes (primary growth) and a few Type II oocytes, clustered together in the ovuligera lamellae. No atresia, thin ovarian wall and little space between oocytes; 2) maturing: presence of type I, II oocytes, and numerous type III oocytes. No evidence of postovulatory follicle complex or type IV oocytes; 3) mature: presence of high number of type IV oocytes (vitellogenic), previtellogenic, and store oocytes along with some oogonia; atresia of vitellogenic oocytes may be present; 4) spawned: showed a high occurrence of post-ovulatory follicles, store oocytes, and atretic follicles; 5) resting: presence of primary oocytes (type I) and the ovigerous lamellae distended; differs from immature stage by having a more open lumen and reticular arrangement of the oocytes. Males were classified into four stages: 1) immature: had seminiferous tubules filled with spermatogonia, the only type of cell present in this stage, 2) maturing: the tubules increased in size, and were observed spermatogenic lineages at various stages of development: spermatogonia, spermatocytes and spermatids 3) mature: tubules were filled with spermatozoa, although some spermatids and spermatocytes could still be observed 4) spent: residual spermatozoids present in lumen of lobules and in sperm ducts. Widely scattered spermatocysts near periphery containing secondary spermatocyte, spermatid and spermatozoa. Spermatogonial proliferation and regeneration of germinal epithelium common in periphery of testes.

4.2.2. Reproductive traits

The sex ratio was calculated monthly and for the whole period 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 and Rohlf (1995). Differences in total length between the sexes for each species were tested with the Wilcoxon-Mann Whitney test.

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 $P = A\left(1 + e^{-r(TL - L_{50})}\right)^{-1}$= 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 used this parameter to detect recruitment periods, by the occurrence of in the months with a high frequency of individuals smaller than L_{50}.

Batch fecundity (F_B), defined as the number of mature oocytes produced in both ovaries (Alkins-Koo 2000), was estimated by direct counting of mature oocytes under a stereoscope after manual dissociation, based on available mature females with the highest GSI values for the three species. We measured the diameter of all type IV oocytes (mature oocytes diameter) that were intact (after manual dissociation) for each species using the Leica Application Suite (LAS) microscope software.

The spawning type was determined by the visual inspection of the frequency distribution of all oocyte diameters and the histological analysis of the development of the oocytes. We photographed all oocytes (except type IV, which were measured previously in the process to estimate the batch fecundity) from the same ten mature females selected for fecundity estimation, 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, and converted to diameter using the formula $\sqrt{((a * 4)/\pi)}$, where a = the area of each oocyte. Afterward we collect all the oocytes diameters to plot the histogram. We apply the term “total spawning” to a unimodal distribution and “batch spawning” for a multimodal distribution (Vazzoler, 1996).

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.

To evaluate the seven reproductive traits, a principal coordinate analysis (PCoA) was performed. Parental care was classified according to records in the literature for the species, genus or family

(Kirschbaum and Schugardt 2002; Crampton and Hopkins 2005), and the "gower" coefficient was used. Finally, a Simper analysis (similarity between percentages) was performed to identify the attributes most responsible for the dissimilarity between species.

4.2.3. *Effects of environment variables*

We pre-selected the physicochemical water characteristics, and habitat descriptors (except for monthly rainfall). We excluded water temperature and canopy open for presenting 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 relationship between reproductive activity, indicated by the *GSI* variation (response variable) for each species, 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 transformed ($\sqrt{}^2$) 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 normal-distributed, only the *G. rondoni* females dataset was heteroscedastic. 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 and Ripley 2002), *car* (Fox and Weisberg 2019), and *vegan* (Oksanen et al. 2007).

4.3. RESULTS

4.3.1. *The environments*

The eight streams that drain the micro-basin presented main channels with structural complexity, overflowing during the wettest period and flooding the adjacent forest zone. Regarding the water parameters, the dissolved oxygen had the highest variation over the study period with an average of 66.9% (±3 0.42), with the lowest average value in August 2019 (21.95 ± 5.13%) and the highest in January 2020 (92.11 ± 15.27%). The water temperature and pH had the slightest variation with average values of 26.59 ºC ± 1.12 and 5.88 ± 0.79, respectively. Electrical conductivity ranged between 12 and 44 mS/cm^{-1} (21 ± 5.01). Average current velocities in the main channel measured between 0.02 and 0.54 m/s (0.2 ± 0.1). Wetted width values ranged from 1.70 to 11.79 m (3.83 ± 2 .06), and the average thalweg depth of 15.83 to 119.23 cm (52.55 ± 22.21). The predominant substrates in the sampled environments were leaf banks (29.47 ± 20.11 %) accumulating on the margins, sand (24.96 ± 17.88 %), and roots of riparian forests (22.8 % (± 13.1).

4.3.2. Abundance, sex ratio, and total length

We analyzed 91 females, 99 males, and two juveniles of *G. rondoni* (n=192), 82 females, 129 males, and eight juveniles of *E. pavulagem* (n=219), and 177 females, 196 males, and 11 juveniles of *H. lepturus* (n=384) (Fig2). Males registered the maximum total length (*TL*) for the three species, but we found differences in the *TL* between sex sizes only for *H. lepturus* (Table 1).

Table 1. Minimum, Maximum and Mean of Total length (±SD) of females, males and juveniles of *Gymnorhamphichthys rondoni*, *Eigenmannia pavulagem* and *Hypopygus lepturus.* Results of the Man-Whitney test and Kruskall-Wallis/Anova test.

Species	Sex	n	Min - Max *TL* (mm)	Mean ± SD	Man Whitney	Kruskall-Wallis/Anova
G. rondoni	Females	91	52.29 - 167.63	119.85 ± 31.94	W = 4315, df=188, p>0.05	$H_{7,25}$= 22.691; p< 0.05
	Males	99	31.94 - 174.27	128.77 ± 28.08		$H_{12, 38}$= 14.99; p>0.05
	Juveniles	2	26.43 - 30.53	28.48 ± 2.05		
E. pavulagem	Females	82	36.68 - 149.23	86.8 ± 24.26	W = 5194.5, df=209, p>0.05	$H_{10,27}$ = 25.068, p < 0.01
	Males	129	21.96 - 194.35	89.99 ± 36.45		$H_{10,40}$ = 31.452, p < 0.01
	Juveniles	8	18.65 - 30.47	24.62 ± 3.85		
H. lepturus	Females	177	19.3 - 95.09	66.27 ± 14.38	W = 12080, dl=368, p<0.01	$H_{11,106}$ = 51.437, p < 0.01
	Males	196	29.65 - 98.53	73.45 ± 13.35		$F_{12,133}$ = 3,891 p < 0.01
	Juveniles	11	53.35 - 11.27	32.40 ± 13.92		

We detected differences in monthly sex ratio for *G. rondoni* in April 2019 (χ^2= 4.4545; p < 0.05), where we found more males than females (4.5:1) (**Fig. 2**). For *E. pavulagem* we found more males in August (3.8:1) (χ^2= 9.9655, p< 0.01). We observed differences for *H. lepturus* in August when were more females (2.25:1) (χ^2=7.6923, p < 0.01) and in March 2019 when there were more males (9:1) (χ^2= 6.4, p < 0.01) (**Fig. 2**). When considering the whole period, just *E. pavulagem* presented differences between sexes, with more males than females (χ^2= 10.469, p < 0.01) **(Fig. 2**).

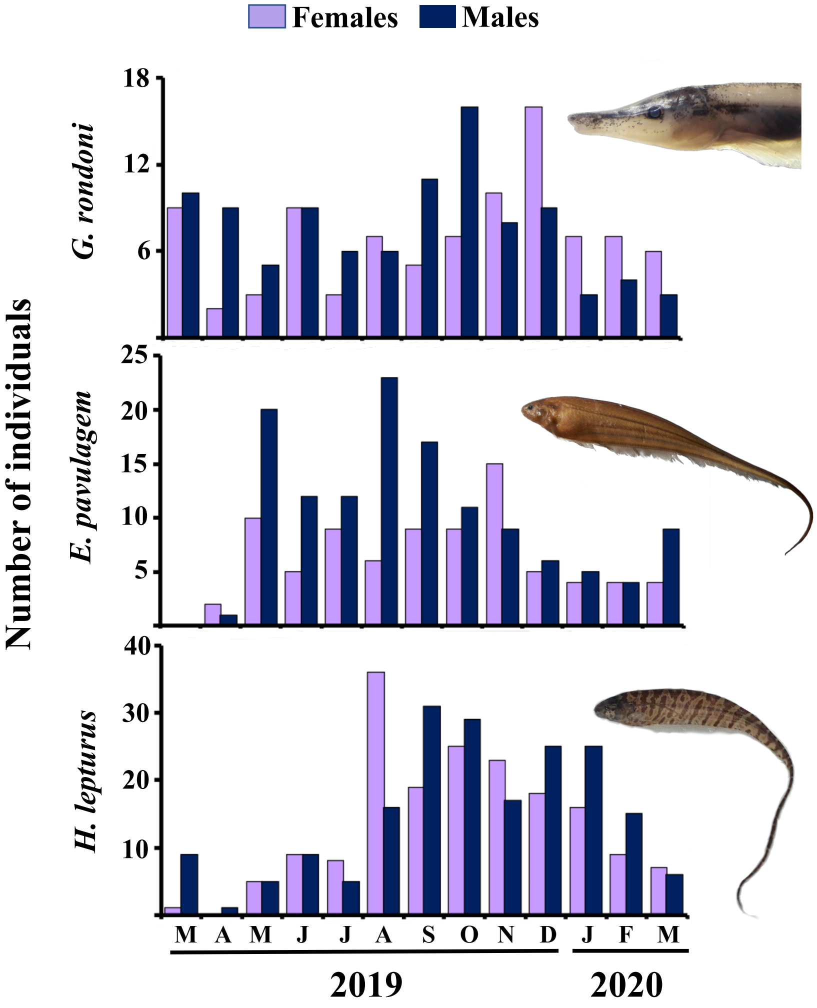

Fig2. Montly abundance of females and males of *Gymnorhamphichthys rondoni*, *Eigenmannia pavulagem* and *Hypopygus lepturus* collected in Eastern Amazon streams, Pará State, Brazil, between March 2019 and March 2020.

4.3.3. *Macroscopic characterization and gonadal development*

Macroscopically, it was possible to identify the females of the three species by presenting oocytes in different stages of gonadal development, especially in the mature stage, exhibiting large ovaries occupying a large part of the abdominal cavity with big yellowish mature oocytes (Fig3A-C). Gonads in maturing stage are smaller appeared rigid and compact, with translucent oocytes (Type III), and spawned females presented ovaries with a more flaccid consistency and type II, III, and IV oocytes.

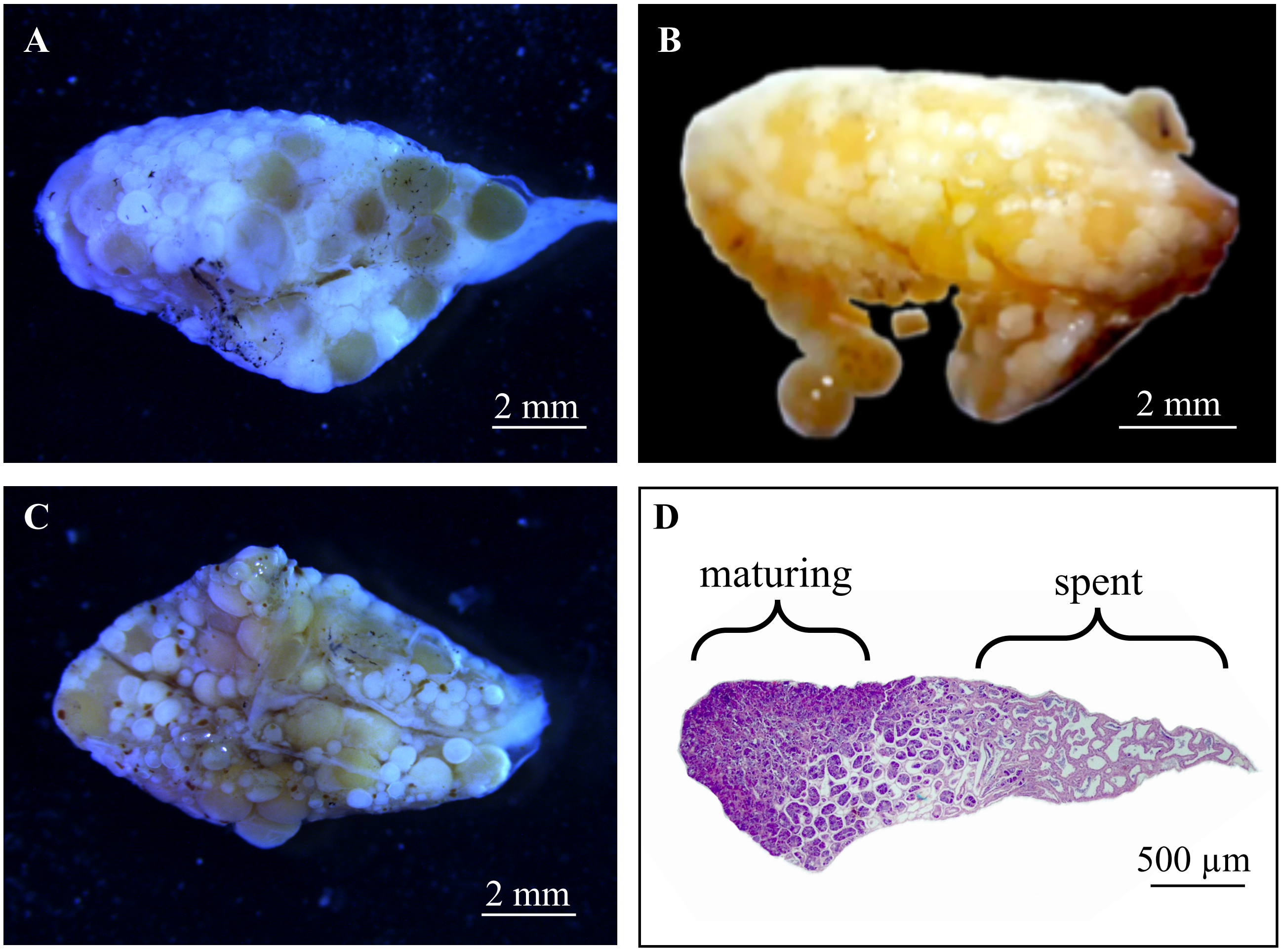

Fig 3. Mature oocytes are easily recognized by their larger size and yellowish color in mature ovaries of A. *Gymnorhamphichthys rondoni*, B. *Eigenmannia pavulagem,* C. *Hypopygus lepturus.* D. Testis of *Gymnorhamphichthys rondoni* at different stages of development: maturing in the caudal side to spent in the cranial side of the testis.

We did not detect differences in the oocyte development stage between the two lobules of the same female. However, we found three stages of germinal differentiation in the same testis: maturing, mature, and spent (Fig 3D).

The reproduction activity of females of *G. rondoni* and *E. pavulagem* showed clear seasonality regarding ovarian maturation. For *G. rondoni*, we observed more than 60% of females in maturing stage from October 2019 to January 2020, with some spawned females. Immature and resting females were common between March and September 2019, on the other hand, the proportion of mature females increased in the rainiest months (from January to March) with a peak in March 2020 (Fig4 and Fig5).

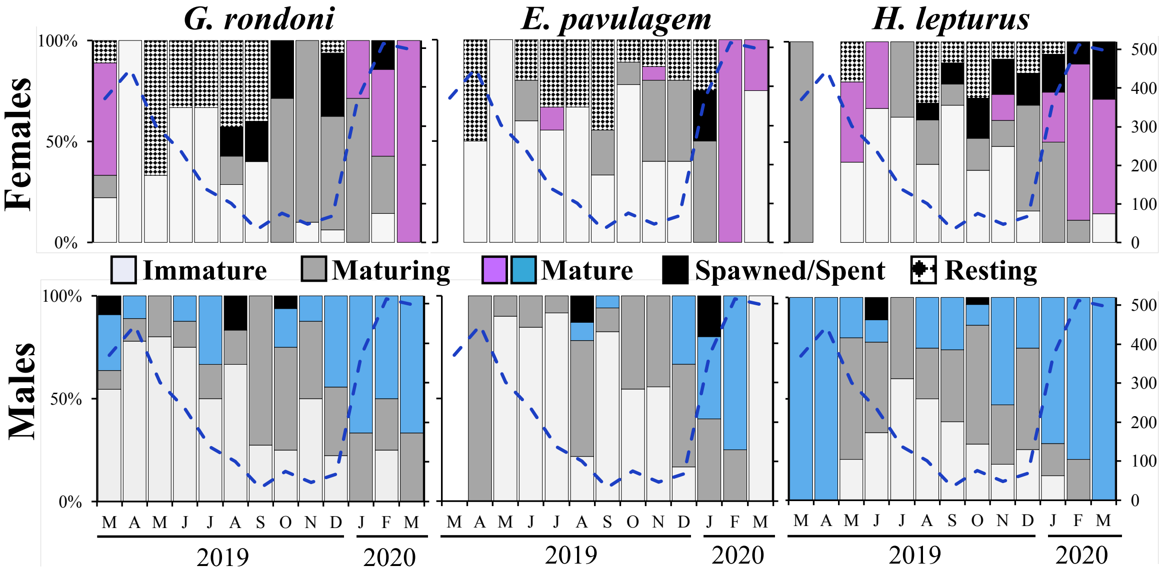

Fig 4. Relative frequency of five gonadal development stages described for the females and four for the males of *Gymnorhamphichthys rondoni*, *Eigenmannia pavulagem* and *Hypopygus lepturus* collected in a catchment of Guamá River (Eastern Brazilian Amazon), between March 2019 and March 2020. The dashed blue line represents the cumulated monthly rainfall.

The frequencies of the stages of gonadal development for both sexes of *G. rondoni* and *E. pavulagem* and the females of *H. lepturus* indicate a seasonal reproductive cycle with spawning occurring mainly during the second period (October 2019 – March 2020). Immature specimens were frequent during the 13 campaigns, mainly between March – August 2019, except for *H. lepturus* in which we did not register immature males in the rainiest months. It is noteworthy the frequency of resting females of *G. rondoni* during the first period.

4.3.4. *GSI monthly variation*

The mean *GSI* values differed over the sampled months for *G. rondoni* females, and both sexes of *E. pavulagem* and *H. lepturus* (Table 1; Fig5). We observed peaks of reproductive activity for *G. rondoni* females in March 2019 (3.75%), February (3.72%), and March 2020 (5.62%). On the contrary, the mean males *GSI* values were not different over the months (Table 2), displaying a continuous reproductive activity with greater intensity between April and July 2019 (Fig5).

We detected a higher frequency of mature individuals in the second half of the study period for females and males of *E. pavulagem*, with the highest mean value of the *GSI* in February 2020 for both sexes (female = 5.82%; male = 0.24%). Mature females of *H. lepturus* were registered in May and June 2019, and between January and March 2020, and the mature males were observed throughout the study (except in July). *H. lepturus* showed the greatest values of *GSI* for both sexes among the three species: females in March 2020 (7.38%), and males in January 2020 (0.73%).

4.3.5. *Reproductive time and Recruitment period*

According to the stages of gonadal development and *GSI* monthly variation, the highest frequency of mature females and males for the three species coincided with the rainy months (Fig4 and Fig5). We observed a more intense reproductive activity in the second half of the study period, specifically for *G. rondoni* and *E. pavulagem,* despite capturing mature males of *G. rondoni* in most months and the presence of maturing males of *E. pavulagem* since April 2019. Unlike these species, *H. lepturus* showed a more continuous reproductive activity (Fig4 and Fig5). Regarding the recruitment period, we detected a high frequency of immature specimens during the first semester (between March and September for *G. rondoni* and between April and November for *E. pavulagem*). For *H. lepturus*, the frequency of immature individuals was concentrated between July and September. We estimated the reproductive period for *G. rondoni* from October to March (six months); for *E. pavulagem*, concentrated in two months: January and February and for *H. lepturus* from October to June (nine months).

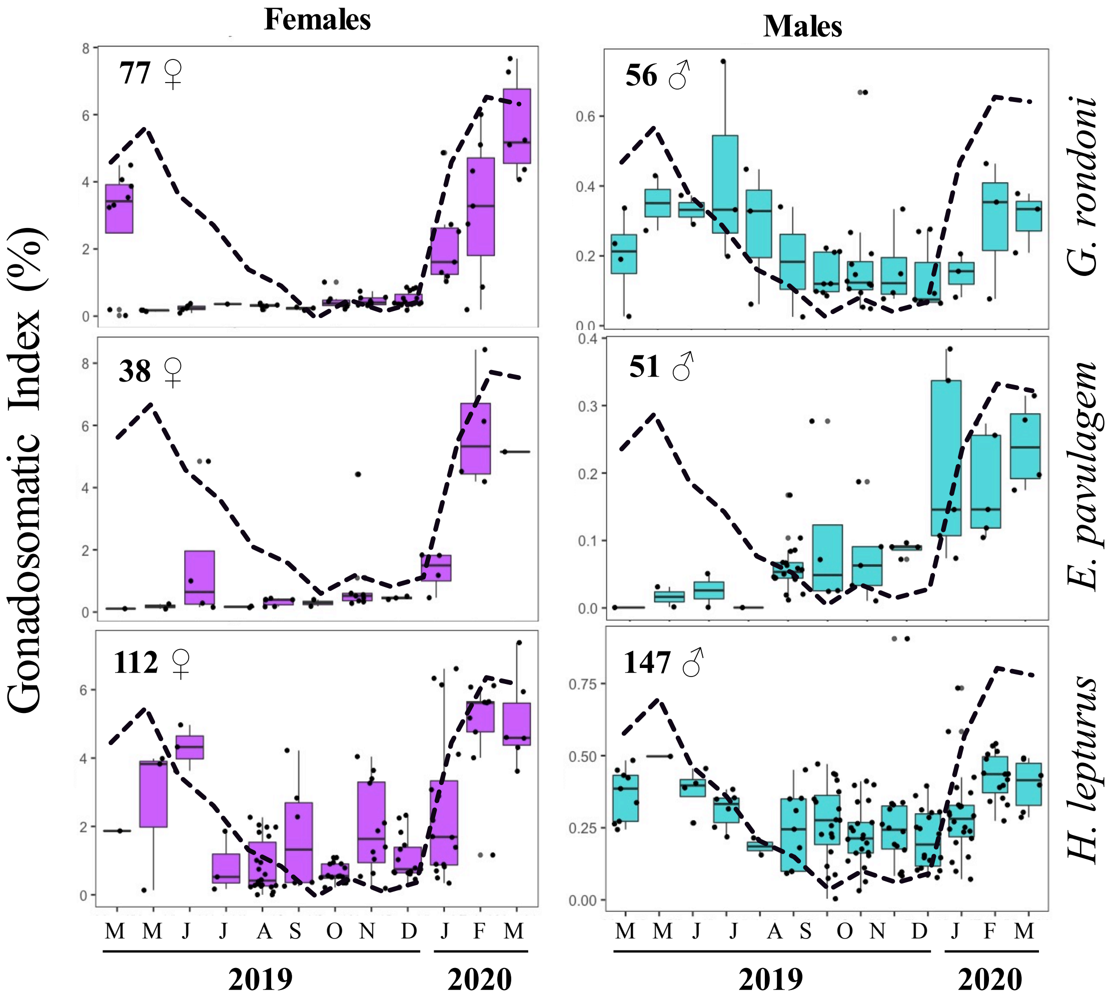

Fig 5. Mean monthly Gonadosomatic Index (*GSI*) of the females and the males of *Gymnorhamphichthys rondoni*, *Eigenmannia pavulagem* and *Hypopygus lepturus* collected in a catchment of Guamá River (Eastern Brazilian Amazon), between March 2019 and March 2020. The dashed blue line represents the cumulated monthly rainfall.

4.3.6. *Length at first maturity* (*L_{50}*)

The size at which 50% of females of *G. rondoni* reached sexual maturity was estimated to be 89.33 mm, representing 53.29 % of the total length. The males reach sexual maturity with 103.63 mm, representing 59.47% of the total length. For *E. pavulagem* females, the length was estimated at 83.01 mm (55.63 % of *TL*) and 88.15 mm for males (45.36% of *TL*). In the case of *H. lepturus*, half of the female population can reproduce when they get 50.11 mm (52.7% of *TL*) and 58.12 mm (59% of *TL*) for males.

4.3.7. *Fecundity, oocyte diameter and spawning type*

The plot of oocyte diameters from mature or spawning capable females of the three species, exhibited a wide range of sizes, indicating different oocyte stages of development. Mature oocytes (yellowish under stereomicroscopic observation) are part of a heterogeneous group of less-developed oocytes (Fig 6). In spawning capable ovaries, oocytes at all stages of development were recorded (Fig 3 and Fig 6), indicating asynchronous oocyte development.

Oogenesis in the three species seems to be a continuous process, as proved by the occurrence of small oocytes in fully mature or spawning capable females and the presence of oogenic areas. The oocyte size-frequency showed two (*E. pavulagem*), three (*G. rondon*i) and four modal oocytes size groups for and *H. lepturus* revealing asynchronic oocyte development, patterns consistent with a batch spawning in

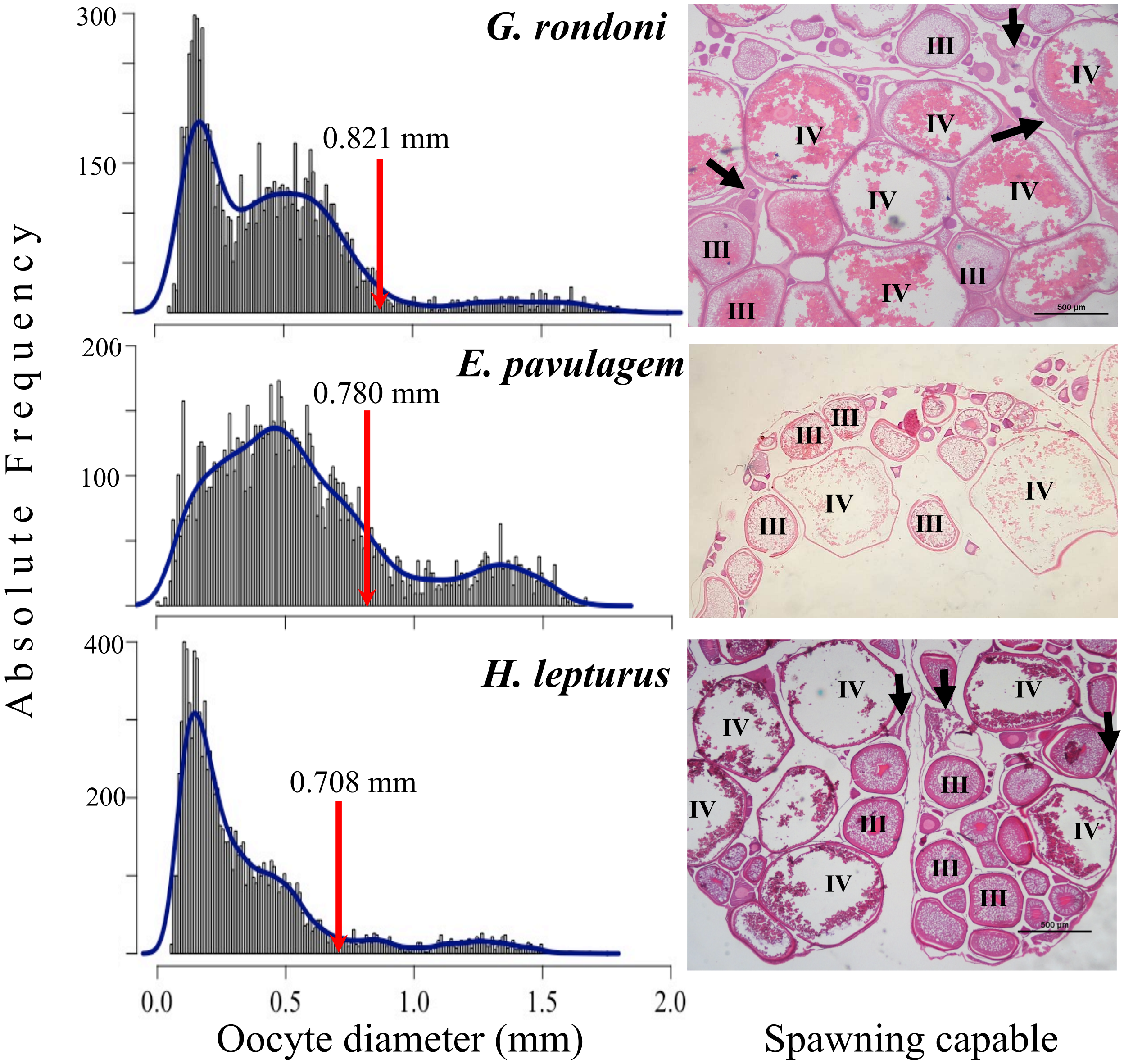

Fig 6. Left: Distribution of the frequency of the diameter of the oocytes of mature ovaries from females of the three species collected from a catchment of Guamá River (Eastern Brazilian Amazon); red arrows indicate the minor mature oocyte diameter. Right: Photomicrograph of spawned capable females of *Gymnorhamphichthys rondoni*, *Eigenmannia pavulagem* and *Hypopygus lepturus* with oocytes in different stages of maturation: III, stage III oocyte; IV, vitelogenic oocytes; black arrows indicate Post-ovulatory follicles.

which oocytes mature continuously and are released in successive batches separated by recovery periods. The definition of a batch spawning for *G. rondoni*, *E. pavulagem,* and *H. lepturus* was also confirmed by gonadal histological observation (Fig 8).

The batch fecundity (mature oocytes) estimated for *G. rondoni* ranged from 15 to 56 (36 ± 12; n=12), from females since 130.57 to 163.87 mm of *TL* (147.31 ± 9.21 mm); *E. pavulagem* ranged from 43 to 154 type IV oocytes (103 ± 33, n=6) from females since 119.79 to 149.23 mm of *TL* (129.47± 12.06 mm) and for *H. lepturus* between 15 to 80 type IV oocytes (47 ± 22 n=12) from females since 67.1 to 88.2 mm of *TL* (81.76 ± 5.36 mm). The relationship between batch fecundity and size of females was correlated positively just for *H. lepturus* (R^2=0.4912). We observed differences in the total number of oocytes (stage I, II, III, and IV oocytes) among the species, *G. rondoni* 209 ± 58 (n=12); *E. pavulagem* 726 ± 126 (n=6), and *H. lepturus* 495 ± 219 (n=12).

The average of mature oocyte diameter was similar for the three species: 1.38 mm (±0.22) for *G. rondoni*, 1.32 mm (±0.15) for *E. pavulagem*, and 1.16 mm (±0.20) for *H. lepturus*

4.3.8. *Relationship between life-history traits*

Ordering the species based on seven reproductive characteristics did not generate groupings. There were two main explanatory axes of variation, the first explained 69.68% of the variation, showing negative scores in traits related to size: total length and length at first maturity and positive scores for the gonadosomatic index and breeding period. The second axis explained 24.33% with batch fecundity and Parental care positioned in negative scores and positive values for oocyte diameter. (Fig 7). *Eigenmannia pavulagem* presented the highest batch fecundity, *Gymnorhamphichthys rondoni* the larger body size and oocyte diameter, and *Hypopygus lepturus* the longer breeding period.

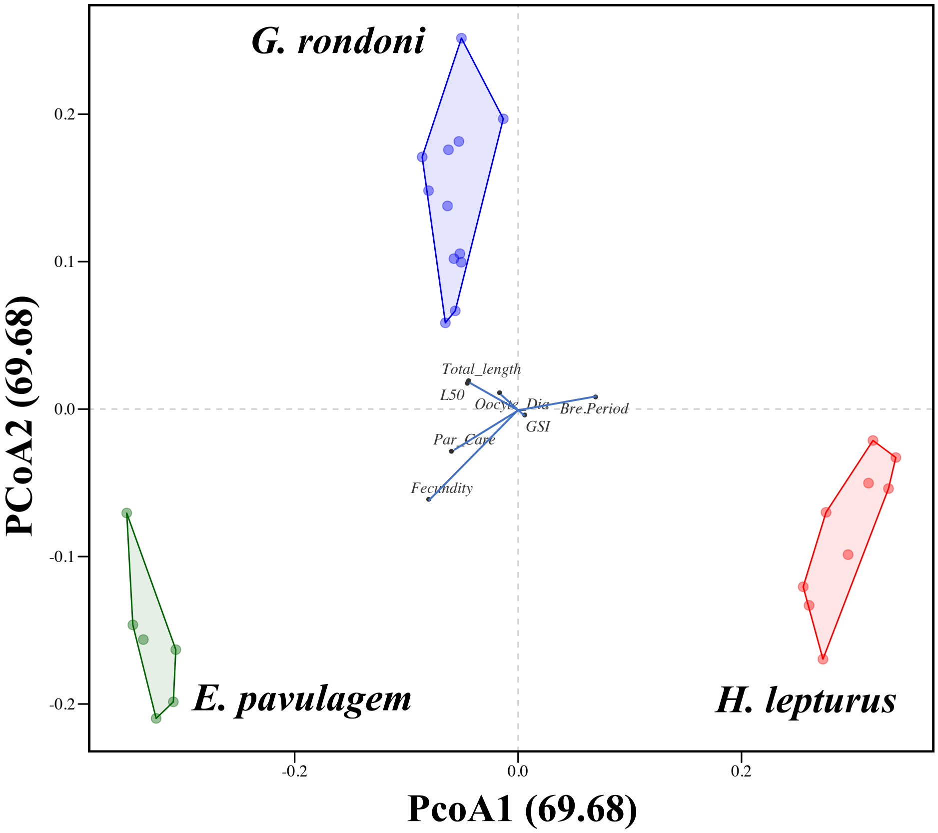

Fig 7. Principal coordinate analysis (PCoA) between the values of reproductive attributes of each species. Each point represents a female. Batch Fecundity (number of mature oocytes), Total length, Average diameter of mature oocytes (Oocyte_Dia), and Gonadossomatic Index (GSI), were calculated for each female in the matrix; Parental Care (Par_Care), Length at first maturity (L50), and Duration of breeding period (Bre_Period) were estimated for each species.

High dissimilarity was observed between the values of the seven reproductive attributes among the three species (PERMANOVA, $R^2 = 0.9054$, $p< 0.05$). According to Simper's analysis, the batch fecundity (68.3%) was the characteristic that most contributed to separating *E. pavulagem* from *G. rondoni* and *H. lepturus* and the total length (50.7%) contributed to the dissimilarity between *G. rondoni* and *H. lepturus.*

After the analyses, we did not observe grouped species, and despite the three species presenting the same spawning type and similar egg sizes, the results pointed out that with these traits set, the phylogenetical proximity between *G. rondoni* and *H. lepturus* did not influence the species.

Table 2. Simper analysis (percent similarity) using seven reproductive attributes 12 females of *Gymnorhamphichthys rondoni*, six of *Eigenmannia pavulagem* and 12 of *Hypopygus lepturus*. *L_{50}*: Length at first maturity; *GSI*: Gonadosmatic index

Species	**Traits**	**Average**	**Dissimilarity ratio**	**Contribution (%)**	**p-value**	
E.pavulagem _G.rondoni	**Batch Fecundity**	**0.105**	1.978	**69.4**	**0.001**	***
	Total length	0.027	1.575	17.6	1	
	L_{50}	0.010	18.02	6.8	1	
	Breeding period	0.005	18.02	3.2	0.015	*.
	GSI	0.003	1.056	1.7	0.827	
	Parental Care	0.002	18.02	1.1	0.000	***
	Oocyte diameter	0.000	1.283	0.2	0.992	
H. G.rondoni _ lepturus	**Total length**	**0.137**	**5.834**	**50.5**	**0.000**	***
	L_{50}	**0.082**	**16.31**	**30.3**	**0.000**	***
	Batch Fecundity	0.044	1.472	16.2	0.999	
	Breeding period	0.004	16.31	1.5	0.098	
	GSI	0.003	1.508	1.3	0.117	
	Oocyte diameter	0.000	1.773	0.2	0.000	***
	Parental Care	0.000	NaN	0	1	
H. E.pavulagem _ lepturus	**Batch Fecundity**	**0.11831**	**1.8**	**40.1**	**0.000**	***
	Total length	**0.0985**	**4.336**	**33.4**	**0.004**	**
	L_{50}	0.06343	12.902	21.5	0.000	***
	Breeding period	0.00964	12.902	0.33	0.000	***
	GSI	0.00285	1.276	0.01	0.659	
	Parental Care	0.00193	12.902	0.01	0.000	***
	Oocyte diameter	0.00038	1.433	0.00	0.571	

4.3.9. *Environmental effects on reproductive activity*

Rainfall was a common factor among the set of variables in explaining the monthly reproductive activity variation for the three species of gymnotiforms, except for the males of *E. pavulagem,* for which the chemical parameters of water were more significant in explaining the variation in their reproductive dynamic. The models explained between 40 and 65% of the *GSI* monthly variation of the females; electric conductivity was a common variable for *G. rondoni* and *E. pavulagem* females. For the males, the models explained between 16 to 47% of the *GSI* monthly variation, highlighting the type of substrate as a component in the set of chosen variables; sand for *G. rondoni* and roots for *E. pavulagem* and *H. lepturus* (Table 4).

4.4. DISCUSSION

The *terra firme* streams are not subject to flood pulses, periods of rain and drought are well defined for the eastern region of the Brazilian Amazon and an increase in the water level produced by sudden rains would modify the water conditions as well as the structure of their habitat and could trigger reproduction. The breeding pattern in those environments is characterized by an extended reproductive period, batch spawning with low fecundity and a certain precocity.

Gymnorhamphichthys rondoni, *E. pavulagem* and *H. lepturus* presented differentiated reproductive dynamic between sexes, interspecific variations in the reproductive traits mainly associated with the batch fecundity, body size and the during of the breeding period, and some environmental factors in common that regulates or influence the reproductive activity as rainfall and electric conductivity.

4.4.1. *Body size*

In this study, males were longer than females just for *Hypopygus* lepturus. This can be explained partly in terms of the expenditure of energy on sexual development, because that the development of the testes is related more to the size of the male fish than to the annual reproductive cycle, whereas in the females, the amount of energy spent on egg formation handicaps their general growth, resulting in smaller asymptotic lengths (Lowe-McConnell 1969; Chellapa et al. 2003).

Table 4. Linear multiple regressions models for the effect of environmental variables on gonadosomatic index of females and males of three species of gymnotiforms: *Gymnorhamphichthys rondoni*, *Eigenmannia pavulagem* and *Hypopygus lepturus* from eight streams of a catchment of Guamá River (Eastern Brazilian Amazon).

Response variable (*GSI*)	Multiple regression	Catchment variables	ß	SE of ß	t	p
G. rondoni females	$R^2=0.6475$; $F_{(3,73)} = 47.53$, p = < 2.2e-16*	Electric conductivity	-4.3002	0.7896	-5.446	< 0.001
		Rainfall	1.4751	0.1323	11.149	< 0.001
		Wetted width	-3.9612	0.5806	-6.823	< 0.001
G. rondoni males	$R^2=0.2112$; $F_{(3,52)} = 5.909$, p = 0.001508	Sand	-0.0281042	0.0117255	-2.397	0.02017
		Flow speed	0.2980324	0.1095945	2.719	0.00887
		Rainfall	0.0002462	0.0001299	1.895	0.06366
E. pavulagem females	$R^2=0.4024$; $F_{(3,34)} = 9.304$, p = 0.0001239	Rainfall	0.65981	0.19737	3.343	0.00203
		Roots	-0.1044	0.05024	-2.078	0.04531
		Electric conductivity	1.49493	0.76882	1.944	0.06015
E. pavulagem males	$R^2=0.4797$; $F_{(3,47)} = 16.36$, p = 2.034e-07	Dissolved Oxygen	0.006312	0.00207	3.049	0.00376
		pH	-0.285172	0.093483	-3.051	0.00375
		Roots	-0.036889	0.008429	-4.376	< 0.001
H. lepturus females	$R^2=0.4172$; $F_{(3,108)} = 27.48$, p = 2.762e-13	Flow speed	-1.1492792	0.5924218	-1.94	0.055
		Rainfall	0.0025421	0.0002999	8.477	< 0.001
		Thalweg Depth	0.0070957	0.0024875	2.853	0.0052
H. lepturus males	$R^2=0.1592$; $F_{(3,142)} = 10.15$, p = 4.235e-06	Electric conductivity	-0.02575	0.11614	-0.222	0.8249
		Rainfall	0.15191	0.03331	4.561	< 0.001
		Roots	-0.01431	0.00835	-1.713	0.0889

*χ^2= 22.528, p < 0.001

The maximum size of *G. rondoni* in eastern Amazonian streams was 174.27 mm *TL* (121.28 mm of standard length – *SL*, to facilitate the comparisons), shorter when compared with other regions: Ramos (2010) registered in Museum specimens over Brazil a *TL* of 184.7 mm, Garcia (2019) measured individuals with more of 181 mm of *SL* Central Amazonian, and Soares et al. (2017) and Lima (2021), registered 215 mm of *TL* and 169.8 mm of *SL* respectively in the Saracá-Taquera National Forest (Pará State). Schwassmann (1976) registered also higher sizes for *G. hypostomus* in Manaus (263 mm), Rondônia (192 mm) e Belém (188 mm). In contrast, Machado et al. (2020) reported smaller sizes for *G. rondoni*

(110.19 mm *SL*) and *H. lepturus* (56.86 mm *SL*) in the Capim River basin (Pará State). We recorder 194.35 mm as the maximum *TL* for *E. pavulagem,* for south (*E. trilineata*) and central (*E. vicentespelaea*) congeners the length was larger: 247.79 and 210.7 mm respectively (Gioria and Fialho 2009; Bichuette and Trajano 2017).

A full development at reduced sizes may be associated with the absence of natural predators in the ecosystem and the great abundance of food (Gomiero et al. 2009). We discard the first, due to the presence of carnivorous species such as *Crenicichla* gr. *saxatilis* and *Hoplias malabaricus,* but in view of the integrity of the caudal filaments of the three species throughout the campaigns, this could suggests that nocturnal habits and shelters (such as small caves and underwater roots) provided by the sampled streams would be effective to avoid attacks by potential predators. Then the minor sizes for *G. rondoni* could be associated to the physical conditions of these low order streams, specifically the sand deposits on the bottom providing a relatively secure resting place for the fish during the day, and also a main source of food, given the sand-burrowing habit and a snout greatly modified for suctorial feeding on a limited range of insect larvae (Schwassmann 1976)

4.4.2. *Sex ratio and parental care*

Although the sex ratio may vary according to the life cycle, growth, mortality, behavior and possible environmental instabilities (Vazzoler 1996), in this study *G. rondoni* and *H. lepturus* had a sex ratio that did not differ from 1: 1 along the hydrological cycle. The results obtained here were similar to those observed in other genera of Gymnotiformes (Cognato and Fialho 2006; Schaan et al. 2009; Giora and Fialho 2009; Giora et al. 2012).

Just for *E. pavulagem* the sex ratio showed a clear predominance of males; this probably is associated with the parental care exhibited by some species of gymnotiforms. For *Gymnotus* species in the Amazon basin (Crampton and Hopkins 2005), *E. trilineata* (Gioria and Fialho 2009) and, *Brachyhypopomus gauderio* (Giora et al. 2014) the presence of an adult male with larval agglomeration under the vegetation during the breeding period suggest a kind of protection. We detected juveniles agglomeration accompanied by an adult female of *E. pavulagem* without captures of males in March 2020. Probably females guard the eggs and larvae while males patrol the territory and repel all possible predators (Barlow 1974). Then, males could increase their chances of being caught during the reproductive period, owing to their aggressive territorial defense and protection of their offspring from invaders (Jepsen et al. 1997).

4.4.3. *Breeding period*

The reproductive activity of *G. rondoni* in the sampled streams takes place during the rainy season. Mature females followed the female's tendency in Central Amazon, a high frequency between December and March corresponding with the more intense rains in the region (Garcia 2019). The results obtained here differ from those found by Lima (2021) in Saracá-Taquera National Forest (Pará State), who despite observed maximum *GSI* values during rainy season, did not find significant difference between rainy and dry periods. Contrary to detected in females of *G. rondoni*, the continuous reproductive activity of the males throughout the year, could explained by the simultaneous stages of development (maturation, mature and spent) of several testis after histological verification.

Eigenmannia pavulagem exhibited a very short time for reproducing; even if we found one mature female in July and in November, most of them were immature or resting, so we did not consider those months as reproductive periods. Mature males were registered between December and February, peaking in the last one corresponding to the rainiest month. Following this, the egg-releasing process and larvae hatching seems to occur in March, matching with the numerous larvae we found just in march 2020. For this species, such a short period is suspicious if we compare the five months breeding period of *E. trilineata* in higher latitudes where species depend on photoperiod and water temperature to reproduce (Giora and Fialho 2009; Giora et al. 2014).

Looking closely at the abundance (Table 1), the absence of adult individuals during March and April 2019 and March 2020 (rainy periods) could indicate that they are probably not faithful to the site. The connectivity due to the increase in the water level allows them to look for better places to spawn. Schwassmann reported that some species of *Eigenmannia* also disappeared and seemed to undertake a migration toward yet unknown areas for spawning; being that they did not longer find in the river bed in Marajó island (Pará State). The bigger individuals with greater swimming capacity can probably explore other places to keep their fry safe. Perhaps, for this reason, the average body size found in these streams for the species was relatively small (Table 2).

Hypopygus lepturus displayed a better synchronicity between mean females and males *GSI* with an extended reproductive period, following the typical pattern in small-sized species (Mazzoni et al. 2002, 2005; Hojo et al. 2004). We also detected low abundance in the rainy months (March and April 2019 and in February and March 2020), but different from *E. pavulagem* we just found mature specimens, probably due to the expansion of the habitats and the new available environments as nurseries and sites of growth for the juveniles (Junk et al. 1989).

Some authors have referred to the semelparity of some species of gymnotiforms (Garcia 2019; Waddel et al. 2019). Studies in *Gymnorhamphichthys* sp., estimated one year to reach maturity, and after many successive bouts for three to four months, it seems likely that the spawners die (Schwassmann 1992). The disappearance of adult individuals after the breeding period is also reported by Garcia (2019) in *G. rondoni*, indicating three possible causes: population depletion, migration or semelparity.

In the samples streams, *G. rondoni* was the more constant species without sudden changes in its abundance. In contrast*, H. lepturus and E. pavulagem* had an increase in abundance from the onset of the dry period to the beginning of the rainy period (August 2019 to January 2020) (Fig1).

4.4.4. Length at first maturity (L_{50})

The age or size at first maturity is a reproductive trait very unstable, intimately related to growth and genotype-environment interaction (Wootton 1992; Vazzoler et al. 1997). Contrary to expectations, the females length at first maturity was smaller than males for all species. For Central Amazonian population, Garcia (2019) found the same pattern for *G. rondoni*, she estimated the L_{50} in 105.5 mm for females and 117.3 mm for males. For *E. trilineata* in south Brazil (Gioria and Fialho 2009), the size at first maturity for females was similar to we found (80.5 vs 83.01 mm respectively), but the L_{50} that we estimated for males was longer (63.5 vs 88.15 mm). The first gonadal maturation size for *Brachyhypopomus. gauderio* males as 108.0 mm and for females as 104.5 mm male and female from the smallest length classes were collected. According to Nikolsky (1969), fecundity is related to length at first maturity, this trait is adapted to the conditions of life cycle and shows a lower intraspecific than interspecific variation in fish species (Blanck and Lamoroux, 2007).

4.4.5. Fecundity and spawning type

The type of spawning is one of the reproductive traits molded by the environment, which determines the survival of the populations (Winemiller 1989). As a rule, gymnotiforms are considered batch spawners (Barbieri and Barbieri 1982; (Kirschbaum 1979; Kirschbaum and Schugardt 2002; Gioria and Fialho 2009). The presence of four distinct size classes of oocytes in the ovaries before the onset of spawning activity supports batch spawning and indicates successive spawning bouts.

The batch fecundity registered for three species in this micro-basin was very low compared to other genders of *Gymnorhamphichthys*, *Eigenmannia*, and Brachyhypopomus (Garcia 2019; Gioria and Fialho 2009; Waddell et al. 2019). Among the three studied species, the lowest fecundity was of *G. rondoni* (36 ± 12 oocytes). For populations of *G. rondoni* in Central Amazon were reported 254 ± 15 oocytes (Garcia 2019), and for another one in Saracá-Taquera, Pará, State, 234 ± 62 oocytes, ranging between 138 to 331(Lima 2021). The congener *G. hypostomus* also presented low fecundity of 63 oocytes, ranging from 53 to 97.

We estimated mature oocyte diameter average of 1.4 mm for *G. rondoni,* ranging from 0.89 to 1.87 mm, considering 231 mature oocytes from 12 females. The maximum mature oocyte diameter for the population of Saracá-Taquera was 2.06 mm (Lima 2021), and 2 mm for the population of Central Amazon (Garcia 2019). For *G. hypostomus*, the mature oocyte diameter ranges between 1.7 to 2.2 mm (Schwassmann 1976). Thus, we can conclude that in addition to the low fecundity, the oocytes of *G. rondoni* in the Eastern Amazon are also small.

When comparing to other species of gymnotiforms the average batch fecundity was very low for the three assessed species. For *Brachyhypopomus bombilla* the absolute fecundity was calculated in 587 oocytes (369 – 773) and for *B. guaderio* 589 oocytes (299 – 799) 2), with the absolute frequency distribution of oocyte diameter corresponded to development synchronic in more than two groups (Giora et al. 2014). For *H. lepturus* there is not available data to compare it.

4.4.6. *Relationship between life-history traits and environment influence*

Although the gymnotiforms are usually classified as equilibrium strategists (*sensu* Winemiller 1989), the analysis of the reproductive traits of *Gymnorhamphichthys rondoni*, *E. pavulagem*, and *H. lepturus* indicates different reproductive investments inside the reproductive strategy. The results of SIMPER test indicated that batch fecundity and body size were the traits that most contributed to separating the species. Even if they all release few eggs, interspecific variation in the number of eggs, the body size, the duration of breeding period, and the care involved in the offspring are remarkable. A short breeding period, a greater number of oocytes, and a possible parental care degree would fit *E. pavulagem* in an equilibrium–periodic gradient. Although *H. lepturus* and *G. rondoni*, with a more extended reproductive period and low fecundity, would fit in an opportunistic – equilibrium gradient, the ordination did not display grouping, which means that those small differences in reproductive traits are important.

A similar pattern was observed when ordering the life-history attributes of *Microsternachus bilineatus*, *Gymnotus carapo* and *G. rondoni* collected in the Saracá-Taquera National Forest also in Eastern Amazonian, resulting in the separation of the three gymnotiforms species that formed three groups corresponding to the model proposed by Winemiller (1989) (Lima 2021).

According to the author, the only trait that showed more remarkable similarity for species more phylogenetically close was the gonadal morphology and location in the coelomic cavity de *G.rondoni* and *M. bilineatus*, which suggests a possible phylogenetic sign of this characteristic. Lima (2021) pointed out that the use of different microhabitats among species did not result in notable differences in the reproductive attributes of the species, which also suggests a possible degree of conservatism in their reproductive strategy. It is essential to include another reproductive traits and habitat use, as well as more species in this kind of studies to elucidate the factors that could support whether a trait is conserved or not.

The variables selected by the models explained to a greater extent the variation in the reproductive activity of females (between 40 and 65 %), rainfall being one of the factors that modulated this reproductive response, as expected for stream fishes. For males, it was not a determining factor, explaining less than 20% of that variation for *G. rondoni* and *H. lepturus*, because the males of these species have a relatively continuous reproductive activity that does not seem to be controlled by these specific environmental changes.

The effect of electric conductivity in gonadal development was verify for females of *G. rondoni* and *E. pavulagem*, in which the onset of rainy period and drop in the electric conductivity stimulated the gonadal maturation. Probably this was not determinant for *H. lepturus* females due to their extended reproductive period. there are few works that aim to explain which are the probable factors that influence the species to occupy different spaces. The difficulty in specifying environmental factors that might be involved in synchronizing gonadal ripening and spawning is due to the differences in the spawning time among species that are closely related and live together in the same aquatic habitat (Schwassmann, 1992).

Despite the three species share attributes, as batch spawning and large oocytes-size, for the assessed population differences in reproduction time, parental care and habitat use would be determining factors to allow the coexistence, and explore deeper the differences among their life-history traits (i.e. oocyte development mechanisms), permit us to understand better how they deal with environmental restrictions. This is extremely important for *G. rondoni*, which exhibits high degree of substrate specificity (Schwassmann, 1976; Ferraris, 2003; Zuanon et al. 2006; Virgilio et al. 2019), worth noting, in these sampled environments the physical conditions seem to be advantageous for maintaining longer breeding seasons.

In contrasts, the abundance and longer breeding season of *H. lepturus* suggests a higher rate of population growth, and the migratory capacity of *E. pavulagem* could indicate the flexibility to explore other sites to reproduce presumably. The differences in reproductive traits and response to the environmental factors, suggest that for these species the interspecific reproductive plasticity due to environmental conditions influence more the reproductive traits, than phylogenetic proximity.

The preference of some fish species for occupying microhabitats or biotopes (as *G. rondoni)* could be a limiting factor because if the species do not adapt sufficiently to the environmental changes, which is a constant threat for streams systems due to anthropogenic activities, which would have as a consequence the homogenization of the physical structure of the streams, compromising the survival of species highly dependent on these microhabitats or substrates.

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5. SESSÃO III

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

A terceira sessão desta tese foi publicada na revista *Neotropical Ichthiology* disponível em: https://www.scielo.br/j/ni/a/bmxg74GpdFQLxGgnQPsfmfM/

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

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5.1. ABSTRACT

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

5. 2. 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.

5.3. MATERIAL AND METHODS

5.3.1. *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 Capitão Poço municipality (State of Pará), in eastern Brazilian Amazonia (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.

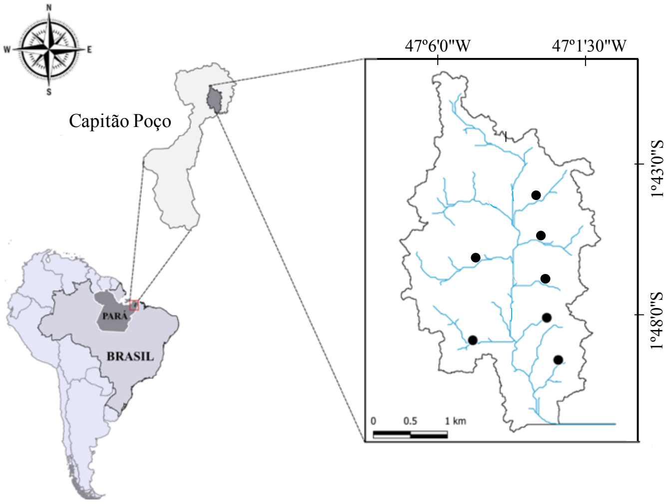

Fig. 1. Study streams (black dots) in a catchment of the Guamá River in the municipality of Capitão Poço, Pará state, Brazil.

The region has a humid tropical climate, subtype *Af* in the Köppen classification adapted by Peel *et al.* (2007). The mean annual temperature is 26.9ºC, which varies 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 watercurrent velocity. These environmental variables dataset is_appropriate for describing instream habitat conditions (Prudente *et al*. 2018; Benone *et al*. 2017; 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 (μS/cm^{-1}), pH, and Temperature (ºC), 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 $Q = A*Vm$, where Q = the discharge, Vm = mean surface flow speed, and A = mean transect area. The mean transect area was calculated by $A = \mathbf{\Sigma}^{n}{}_{i}A_{n}$ where A = area of the transect, which is given by the sum of $[(Z_1+ Z_2) / 2]*w + [(Z_2 + Z_3) / 2]*w + ... [(Z_n + Z_{n+1}) / 2]*w$, 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 Brazilian National Institute of Meteorology (INMET – Station A248), located in the municipality of Capitão Poço (See **S1** in supplementary material).

The specimens of *H. marmoratus* were collected from each 10-m longitudinal section for 12 minutes 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). The specimen collections were authorized by license 63603-3, issued by the federal Chico Mendes Institute for Biodiversity Conservation - ICMBio, through the Biodiversity Authorization and

Information System – SISBIO. The study was approved by the Animal Ethics Committee of the Federal Rural University of Amazon (UFRA), through process number 054/2018.

In the laboratory, the specimens were weighed (total weight in grams – TW), measured (total length in millimeters – TL), and eviscerated for the removal of the gonads, which were also weighed (weight in grams – 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.

5.3.2. ***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 $P = A\left(1 + e^{-r(TL-L_{50}))}\right)^{-1}$ 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 (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.

5.3.3. *Effects of environment variables*

Before being associated with the reproductive activity of *H. marmoratus*, we preselected 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 supplementary material (S4).

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 Core Team, 2020) using the packages *MuMIn* **(**Bartoń, 2020), *MASS* (Venables, Ripley, 2002), *car* (Fox, Weisberg, 2019), and *vegan* (Oksanen *et al.* 2020).

5.4. RESULTS

5.4.1. *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).

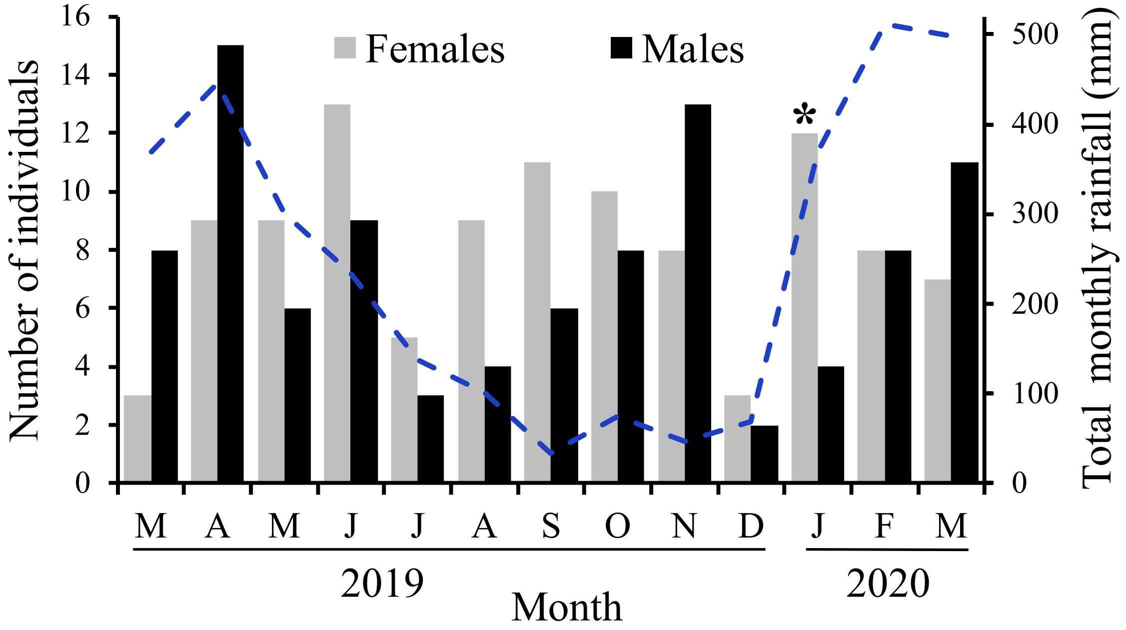

Fig.2. The number of females and males *Helogenes marmoratus* collected in a catchment of the Guamá River in Capitão Poço, Pará state (Brazil) each month between March 2019 and March 2020. The dashed blue line represents the total monthly rainfall. * indicates a significant difference in the sex ratio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

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.

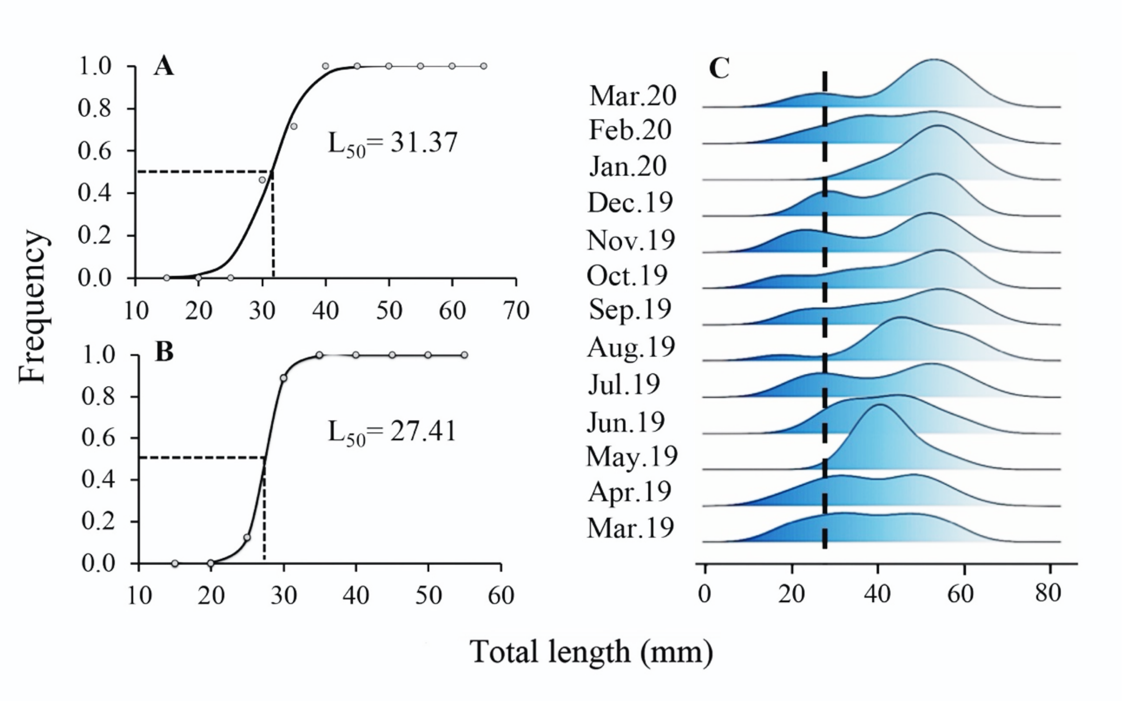

Fig. 3. Length at first sexual maturation (*L_{50}*) in A females and B males *Helogenes marmoratus*, and C the monthly frequency histogram of the variation in total length recorded in a catchment of the Guamá River in Capitão Poço, between March 2019 and March 2020. The black dashed line indicates the 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 is in supplementary material **S2**). 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).

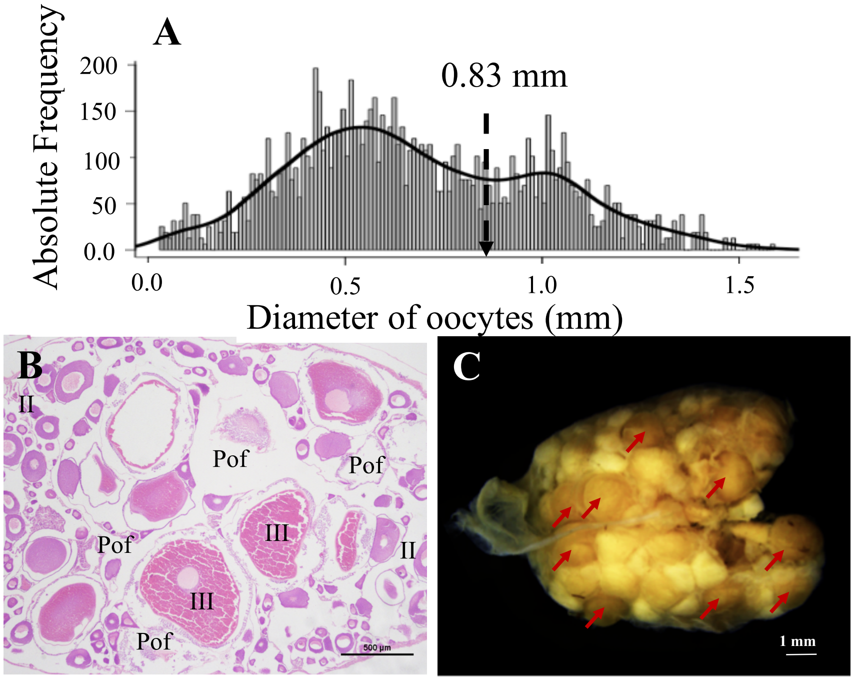

Fig. 4. A. Variation in the diameter of the oocytes collected from 11 mature *Helogenes marmoratus* females collected from a catchment of River Guamá in Capitão Poço, Pará (Brazil). The dashed black arrow indicates the minimum diameter of the mature oocytes. B. Photomicrograph of spawned female with 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).

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.

The monthly frequencies of the different gonadal phases in both genders also indicated reproduction activity throughout the study period (Fig. 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.

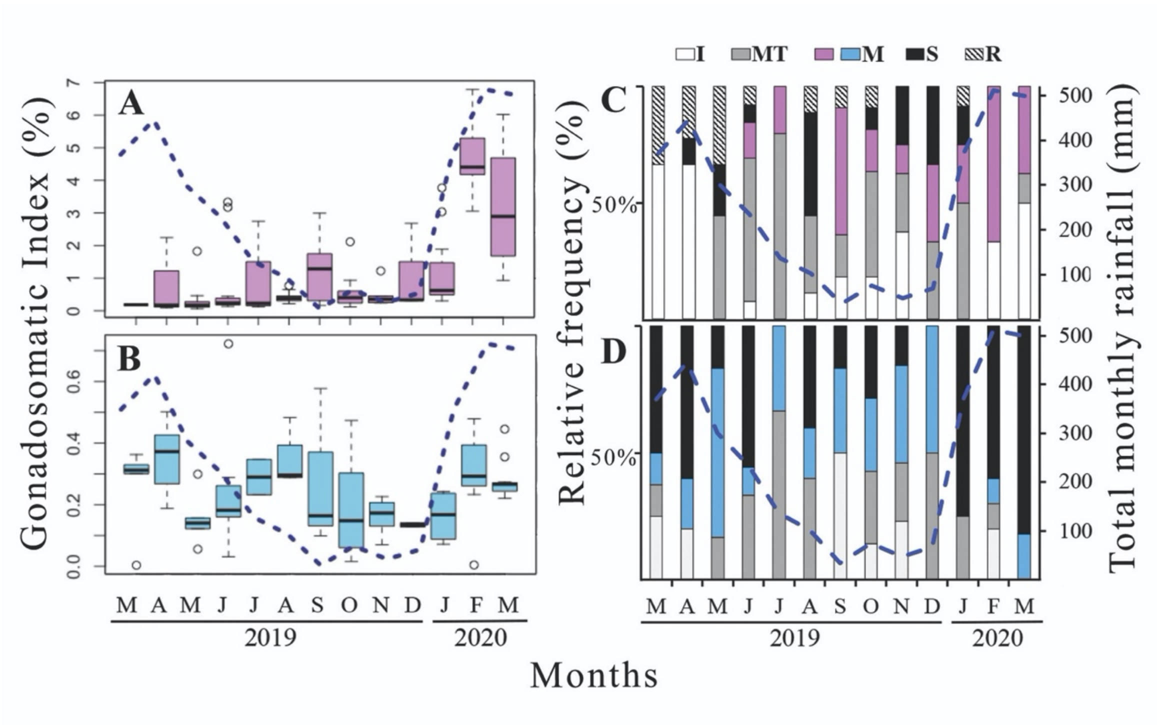

Fig. 5. Mean monthly Gonadosomatic Index (GSI) of **A** the females and **B** the males *Helogenes marmoratus* compared with the relative frequency of the different gonadal development phases: I: immature, MT: maturing, M: mature, S: spawned/spent, R: repousing of **C** the females and **D** the males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

5.4.2. *Environmental effects on reproductive activity*

The studied streams shared similar water physicochemical characteristics. The annual mean of the water temperature was 26.58ºC (± 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 (S2). 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 (S2).

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 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 (S2).

The first two axes of the Principal Components Analysis (PCA) from the four retained environmental variables explained 70.77% of the total variation (Fig.7). 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 (%).

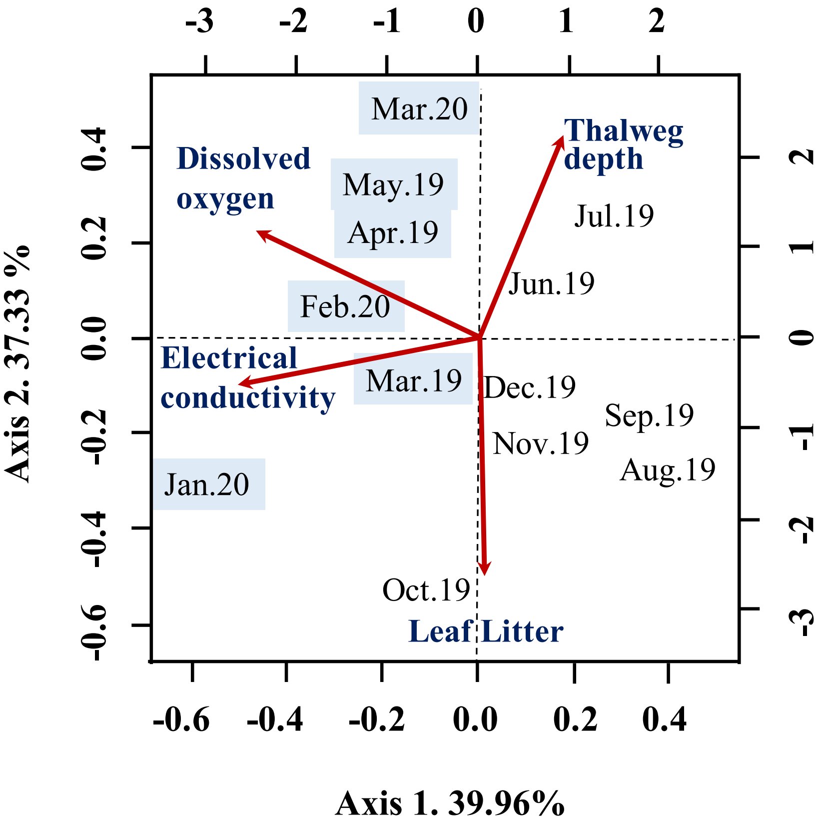

Fig. 6. Ordination of the 13 monthly samples collected in a catchment of the Guamá River, in the municipality of Capitão Poço (Pará, Brazil), between March 2019 and March 2020. The months with a blue background represent the rainy season.

Tab 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, 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

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).

Tab 2. Results of multiple regressions between the GSI of the female and male *Helogenes marmoratus* and the environmental variables recorded in seven streams of a catchment of the Guamá River in Capitão Poço, Pará, 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
		Rain	0.000631	0.000257	2.451	0.0164

5.5. 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 (TL = 65.21 mm) exceeded the length registered by Rosa *et al.* (2016) in the Saracá-Taquera National Forest (TL= 52 mm) 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 (standard length = 79 mm**).**

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. o 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.* 1995; 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* 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; Rondinelli *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 1.7mm to 6.0mm (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; Rondinelli *et al.* 2011), and in the callichthyds is about 2mm (Winemiller, 1989) (Supplementary Material S3).

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 (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 Fig. 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* and *Astyanax altiparanae* was related to conductivity, turbidity, depth, and precipitation, while the increase in gonadosomatic index in *Piabina argentea* 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 requires 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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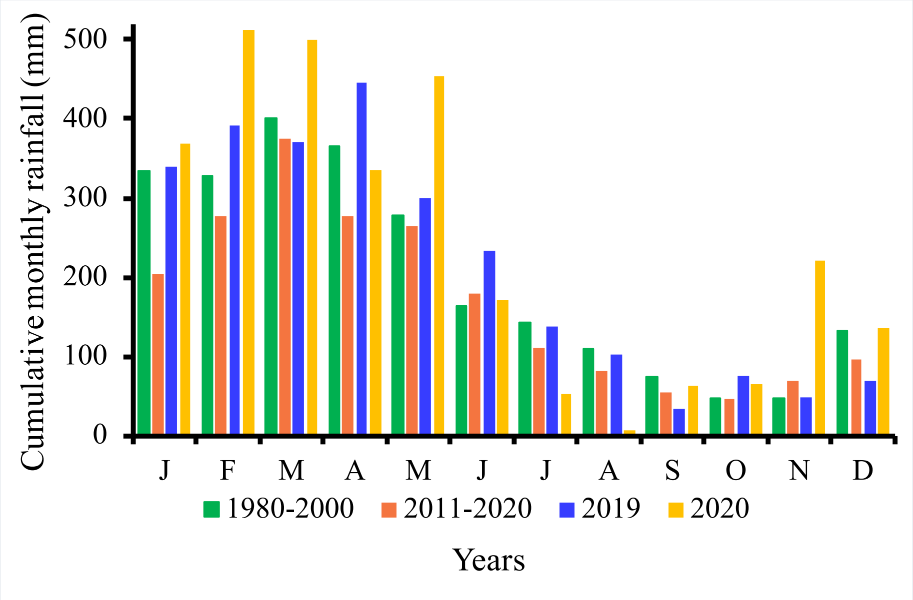
SUPPLEMENTARY MATERIAL



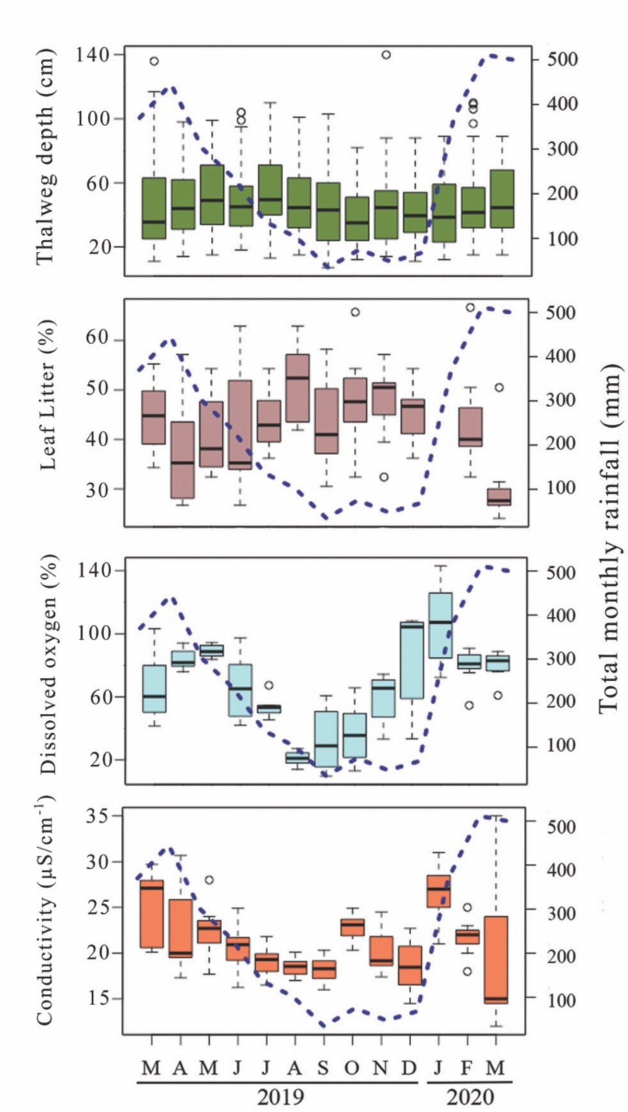
S1. A. Historical monthly average rainfall records in the municipality of Capitão Poço between 1980 to 2000 (Pacheco, Bastos, 2001), between 2011 to 2020 (INMET), and cumulative monthly rainfall values registered for 2019 and 2020. B. Cumulative monthly rainfall between 2011 and 2020 in Capitão Poço, Pará State, Brazil (INMET).

S2. Data on the total length, the month of collection, number of oocytes, and number of type IV oocytes from 11 mature females of *Helogenes marmoratus* collected in a catchment of the Guamá River in Capitão Poço, Pará State (Brazil) between March 2019 and March 2020.

ID	Month	TL	Nº Oocytes	Nº IV Type oocytes
Hm73	Jul.19	64.48	189	59
Hm100	Sep.19	54.59	103	42
Hm108	Sep.19	61.19	106	52
Hm117	Oct.19	55.44	84	18
Hm158	Nov.19	55.81	190	64
Hm166	Jan.20	56.06	200	34
Hm167	Jan.20	64.44	236	92
Hm174	Jan.20	53.36	206	82
Hm190	Jan.20	62.59	143	46
Hm178	Feb.20	56.04	161	90
Hm206	Mar.20	59.45	159	76

S3. Comparison of total length (TL–mm), fecundity, and oocyte size (Diameter–mm) , and the oocyte:body size ratio in selected small-sized species of the order Siluriformes.

Family	Species	Total Length (TL - mm)	Fecundity	Egg Diameter (ED - mm)	ED/TL	References
Callichthydae	*Hoplosternum littorale*	218	2684	2.00	0.01	Winemiller, 1989
Cetopsidae	***Helogenes marmoratus***	**65**	**60**	**1.24**	**0.02**	
Cetopsidae	*Helogenes marmoratus*	84	224	1.59	0.02	Cardoso, 2012
Heptapteridae	*Rhamdia quelen*	229	29757	1.20	0.01	Gomiero *et al*. 2007
Heptapteridae	*Rhamdia quelen*	245	26305	0.96	0.00	Olaya-Nieto *et al*. 2010
Heptapteridae	*Taunayia bifasciata*	120	319	1.53	0.01	Rondinelli *et al*. 2011
Loricariidae	*Ancistrus sp.*	68	48	4.00	0.06	Winemiller, 1989
Loricariidae	*Hypostomus argus*	190	289	3.20	0.02	Winemiller, 1989
Loricariidae	*Hypostomus auroguttatus*	268	411	6.00	0.02	Gomes *et al*. 2015
Loricariidae	*Hypostomus francicsi*	330	585	3.40	0.01	Sales *et al*. 2016
Loricariidae	*Loricarichthys typus*	224	421	3.10	0.01	Winemiller, 1989
Loricariidae	*Panaqolus tankei*	98.3	37	2.87	0.03	Mendes *et al*. 2018
Loricariidae	*Pterygoplichthys multirad*	233	763	3.50	0.02	Winemiller, 1989
Loricariidae	*Rineloricaria caracasensi*	113	255	1.70	0.02	Winemiller, 1989



S4. Monthly variation in chemical water variables and habitat descriptors in a catchment of the Guamá River, in the Brazilian municipality of Capitão Poço, between March 2019 and March 2020. The dashed blue line represents the total monthly rainfall.

CONSIDERAÇÕES FINAIS

Os resultados obtidos neste trabalho, representam uma grande contribuição para o conhecimento sobre a reprodução de peixes de pequeno porte que habitam os riachos amazônicos. As informacões sobre aspectos da história de vida destas espécies, poderiam complementar estudos sobre diversidade funcional e compreender melhor os padrões de biodiversidade local e regional.

Com relação ao estudo das características reprodutivas, a avaliação do potencial reprodutivo das populações que inclua estimações da fecundidade, a frequência e duração da desova e o tamanho dos ovos forneceriam um conjunto de informações mais robusto para identificar o tipo de estratégias. Uma forma de categorizar melhor as estratégias reprodutivas que representam as espécies de pequeno porte que habitam os riachos, seria por médio da criação de parâmetros de referência para estas espécies, e uma padronização na forma de avaliar tanto as características reprodutivas como o efeito das variáveis ambientais na dinâmica reprodutiva.

Outro aspecto se relaciona com as variáveis ambientais que poderiam estar influenciando no só a variação do índice gonadossomático senão alguma característica em particular. Ainda que foi possível verificar que a precipitação é um fator que modula a atividade reprodutiva, muitas das espécies que ocorrem nos riachos apresentam uma reprodução contínua que não estaria explicada pela dinâmica das chuvas e sim por fatores que ainda não tem sido considerados.

Desta forma uma abordagem por características poderia dilucidar a direção e magnitude da variação desses atributos. Estudos que foquem em avaliar a variação das características reprodutivas entre as espécies, mais do que entre populações, permitiriam definir melhor a relevância de características no nível de espécie, para tentar prever as respostas das diversas assembleias de peixes as mudanças do seu ambiente, considerando principalmente os distúrbios provocados pelos humanos.

O último aspecto que gostaria de ressaltar é a importância da estrutura física dos riachos, o substrato os micro habitats e a mata riparia dos quais dependem muitas espécies e que garantem certas condições para que se desenvolvam os processos vitais nesses ambientes, a pesar da vulnerabilidade dos riachos de ordens menores.

APÊNDICE

APÊNDICE A. MONTHLY ABUNDANCE OF 17 SPECIES ANALYZED BETWEEN MARCH 2019 AND MARCH 2020 IN A MICRO-BASIN OF THE GUAMÁ RIVER IN EASTERN BRAZILIAN AMAZON.

		2019										2020			
		Months													
Species	Author	M	A	M	J	J	A	S	O	N	D	J	F	M	Total
CHARACIFORMES															
Characidae															
Astyanax bimaculatus	(Linnaeus 1758)	2	2	4	4	3	4	4	3	3	0	5	4	0	38
Hemigrammus guyanensis	Géry 1959	3	30	79	35	30	34	55	39	41	36	32	30	15	459
Hyphessobrycon heterorhabdus	(Ulrey, 1894)	60	60	60	59	60	60	60	60	60	59	60	60	60	778
Moenkhausia collettii	(Steindachner, 1882)	2	25	66	35	49	54	13	20	14	14	9	55	16	372
Moenkhausia oligolepis	(Günther 1864)	6	0	5	1	11	2	17	7	5	6	4	1	1	66
Crenuchidae															
Microcharacidium weitzmani	Buckup 1993	31	49	32	32	29	32	71	58	71	33	49	30	35	552
Iguanodectidae															
Bryconops melanurus	(Bloch, 1794)	12	19	31	20	20	17	18	1	1	15	11	17	35	217
Iguanodectes rachovii	Regan 1912	18	16	19	7	9	7	29	11	26	13	15	1	25	196
Lebiasinidae															
Copella arnoldi	(Regan, 1912)	36	28	35	52	46	27	51	40	41	35	34	23	23	471
Pyrrhulina capim	(Vieira & Ferreira 2019)	21	34	27	47	38	36	32	35	76	35	43	42	25	491
SILURIFORMES															
Cetopsidae															
Helogenes marmoratus	Günter 1863	13	26	15	22	9	14	17	20	22	7	16	16	19	216
GYMNOTIFORMES															
Ramphicthydae															
Gymnorhamphichthys rondoni	(Miranda Ribeiro, 1920)	19	11	10	18	10	13	16	23	18	25	9	11	9	192
Hypopygus lepturus	Hoedeman 1962	14	2	10	20	14	57	51	55	40	43	41	24	13	384
Sternopygidae															
Eigenmannia pavulagem	Peixoto, Dutra & Wosiacki, 2015	1	3	30	21	22	29	26	20	24	11	8	8	24	227
CYPRINODONTIFORMES															
Rivulidae															
Anablepsoides urophthalmus	(Günther, 1866)	58	30	7	31	31	54	32	30	33	30	39	49	34	458
CICHLIFORMES															

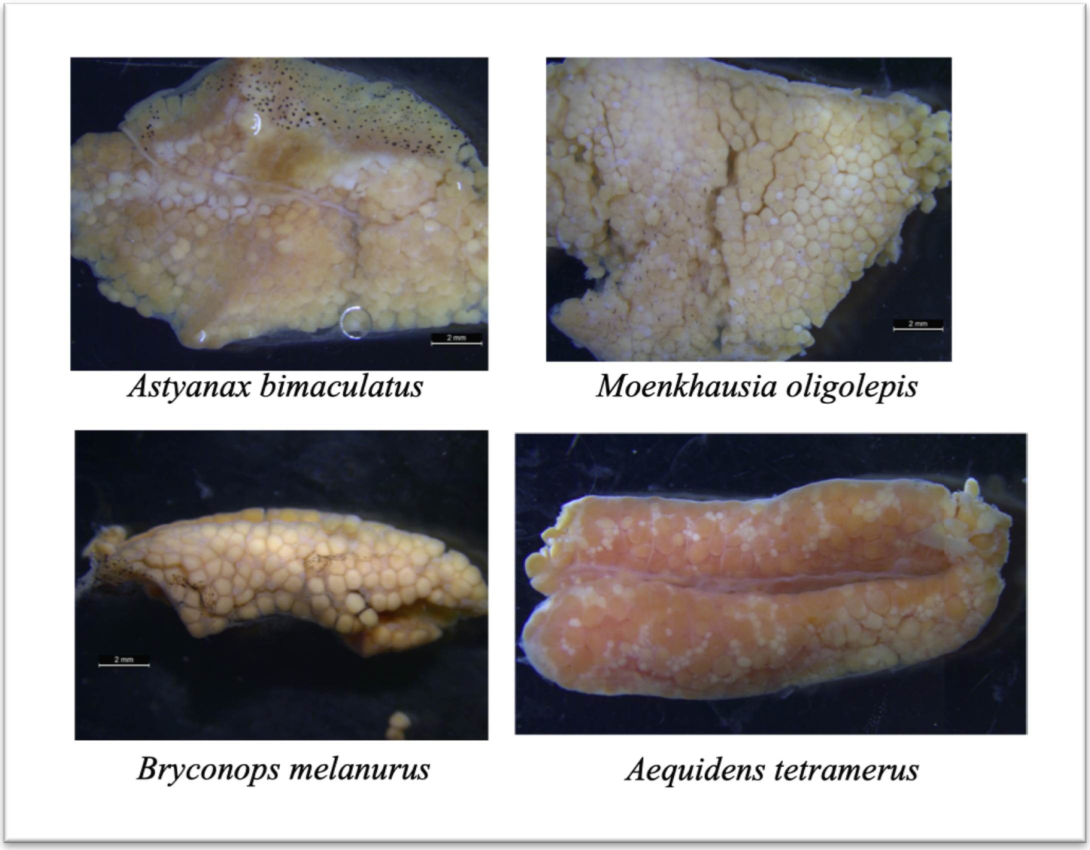
Cichlidae														
Aequidens tetramerus	(Heckel 1840)	27	28	15	16	2	14	10	24	11	34	28	23	5	237
Apistogramma gr. *regani*	Kullander 1980	35	31	30	31	33	30	34	31	35	31	33	33	33	420

APÊNDICE B. TOTAL LENGTH (MM) WITH MINIMAL AND MAXIMUM VALUES (MEAN AND STANDARD DEVIATION) AND TOTAL WEIGHT (G) WITH MINIMAL AND MAXIMUM VALUES (MEAN AND STANDARD DEVIATION, FOR FEMALES, MALES, AND JUVENILES OF EACH ASSESSED SPECIES. F – FEMALES, M – MALES, J – JUVENILES.

Species	Sex	n	Total length	Mean ± SD	Total weigth	Mean ± SD
Aequidens tetramerus	F	51	15.55 - 129.96	50.91 ± 30.34	0.0616 - 46.36	6.01 ± 10.92
	M	88	17.89 - 154.95	40.61 ± 31.17	0.0575 - 77.96	5.09 ± 14.5
	J	54	9.95 - 21.5	17.40 ± 2.42	0.012 - 0.1277	0.0615 ± 0.0256
Anablepsoides urophthalmus	F	212	12.33 - 41.34	26.12 ± 4.52	0.0127 - 0.68	0.1594 ± 0.0975
	M	249	13.76 - 41.21	26.42 ± 5.01	0.0139 - 0.593	0.1618 ± 0.098
Apistogramma gr. *regani*	F	203	15.19 - 42.93	29.38 ± 6.72	0.0337 - 1.3061	0.4172 ± 0.2681
	M	226	12.79 - 64.16	33.47 ± 10.05	0.0294 - 3.8334	0.6887 ± 0.6341
Astyanax bimaculatus	F	18	46.81 - 107.9	83.74 ± 17.28	0.8453 - 18.08	8.77 ± 5.56
	M	16	41.43 - 119.99	77.54 ± 18.09	0.8119 - 22.91	6.68 ± 5.85
Bryconops melanurus	F	96	19.39 - 131.01	55.74 ± 21.69	0.0421 - 22.8989	2.0458 ± 3.1
	M	67	19.1 - 83.72	51.43 ± 15.67	0.0361 - 4.9959	1.2353 ± 1.07
	J	57	13.37 - 32.26	20.22 ± 3.62	0.0106 - 0.0664	0.0367 ± 0.0175
Copella arnoldi	F	193	11.03 - 38.08	25.82 ± 6.32	0.0163 - 0.3602	0.1137 ± 0.0717
	M	271	11.27 - 53.72	28.66 ± 8.55	0.0076 - 0.8247	0.1608 ± 0.1242
	J	9	10.54 - 16.44	13.11 ± 2.16	0.066 - 0.0251	0.0148 ± 0.0062
Eigenmannia pavulagem	F	82	35.68 - 149.23	86.8 ± 24.26	0.0700 - 3.820	1.0090 ± 0.7964
	M	126	21.96 - 194.35	91.27 ± 36.16	0.0286 - 8.506	1.3420 ± 1.4243
	J	14	18.65 - 46.22	27.11 ± 8.67	0.0207 - 0.1658	0.0593 ± 0.0507
Gymnorhamphich-thys rondoni	F	89	55.56 - 167.63	120.54 ± 27.71	0.1096 - 2.705	1.0302 ±0.6144
	M	94	52.29 - 174.27	123.40 ± 31.75	0.1000 - 2.6209	1.0657 ± 0.6664
Helogenes marmoratus	F	107	18.35 - 65.21	46.15 ± 10.11	0.0404 - 2.09	0.819 ± 0.580
	M	97	16.4 - 59.89	43.13 ± 12.39	0.028 - 1.531	0.582 ± 0.25
Hemigrammus guyanensis	F	219	15.09 - 42.16	28.89 ± 5.41	0.0124 - 0.6983	0.2081 ± 0.1294
	M	228	14.16 - 38.05	26.36 ± 5.08	0.0203 - 0.4943	0.1532 ± 0.0950
	J	5	13.02 - 16.79	14.58 ± 1.23	0.0106 - 0.0294	0.0191 ± 0.0065

Hyphessobrycon heterorhabdus	F	303	15.75 - 41.34	30.71 ± 4.29	0.0226 - 0.6963	0.3030 ± 0.1245
	M	379	14.94 - 35.42	26.83 ± 3.74	0.0271 - 0.5195	0.1838 ± 0.0757
	J	71	13.87 - 24.36	19.46 ± 2.10	0.0203 - 0.1611	0.0668 ± 0.0244
Hypopygus lepturus	F	166	19.3 - 95.09	67.30 ± 14.74	0.0465 - 1.0981	0.4096 ± 0.2316
	M	176	29.65 - 98.53	73.86 ± 13.40	0.0287 - 1.0445	0.5073 ± 0.2333
	J	11	11.27 - 53.35	32.40 ± 13.92	0.062 - 0.424	0.1899 ± 0.1225
Iguanodectes rachovii	F	64	14.29 - 57.81	31.18 ± 10.37	0.0157 - 0.9729	0.2231 ± 0.2234
	M	55	14.71 - 60.23	31.82 ± 12.35	0.0172 - 1.4806	0.2575 ± 0.3206
	J	34	11.21 - 23.41	15.15 ± 2.20	0.0020 - 0.0658	0.0177 ± 0.0130
Microcharacidium weitzmani	F	273	10.98 - 24.65	18.87 ± 2.46	0.0069 - 0.1186	0.0390 ± 0.0196
	M	279	10.7 - 22.97	17.82 ± 2.13	0.0010 - 0.0923	0.0315 ± 0.0139
Moenkhausia collettii	F	168	16.87 - 59.49	40.22 ± 8.42	0.0478 - 2.373	0.8182 ± 0.524
	M	75	21.26 - 50.27	37.99 ± 5.60	0.1018 - 1.6154	0.5904 ± 0.2588
	J	117	12.8 - 40.28	26.79 ± 6.65	0.0203 - 0.6282	0.2192 ± 0.153
Moenkhausia oligolepis	F	33	52.12 - 88.96	71.43 ± 8.50	1.7781 - 14.7143	5.8415 ± 3.049
	M	33	46.72 - 84.26	64.28 ± 6.96	1.3776 - 9.9492	3.9186 ± 1.6014
Pyrrhulina capim	F	251	12.15 - 65.53	32.20 ± 12.88	0.0151 - 2.6186	0.3842 ± 0.4804
	M	217	11.82 - 75.98	33.73 ± 15.74	.0104 - 2.9204	0.4628 ± 0.6226
	J	23	11.04 - 47.05	21.15 ± 10.58	0.0083 - 0.7556	0.1186 ± 0.198

APÊNDICE C. MATURE OVARIES FROM FEMALES OF *ASTYANAX BIMACULATUS*, *MOENKHAUSIA OLIGOLEPIS*, *BRYCONOPS MELANURUS* AND *AEQUIDENS TETRAMER*US.



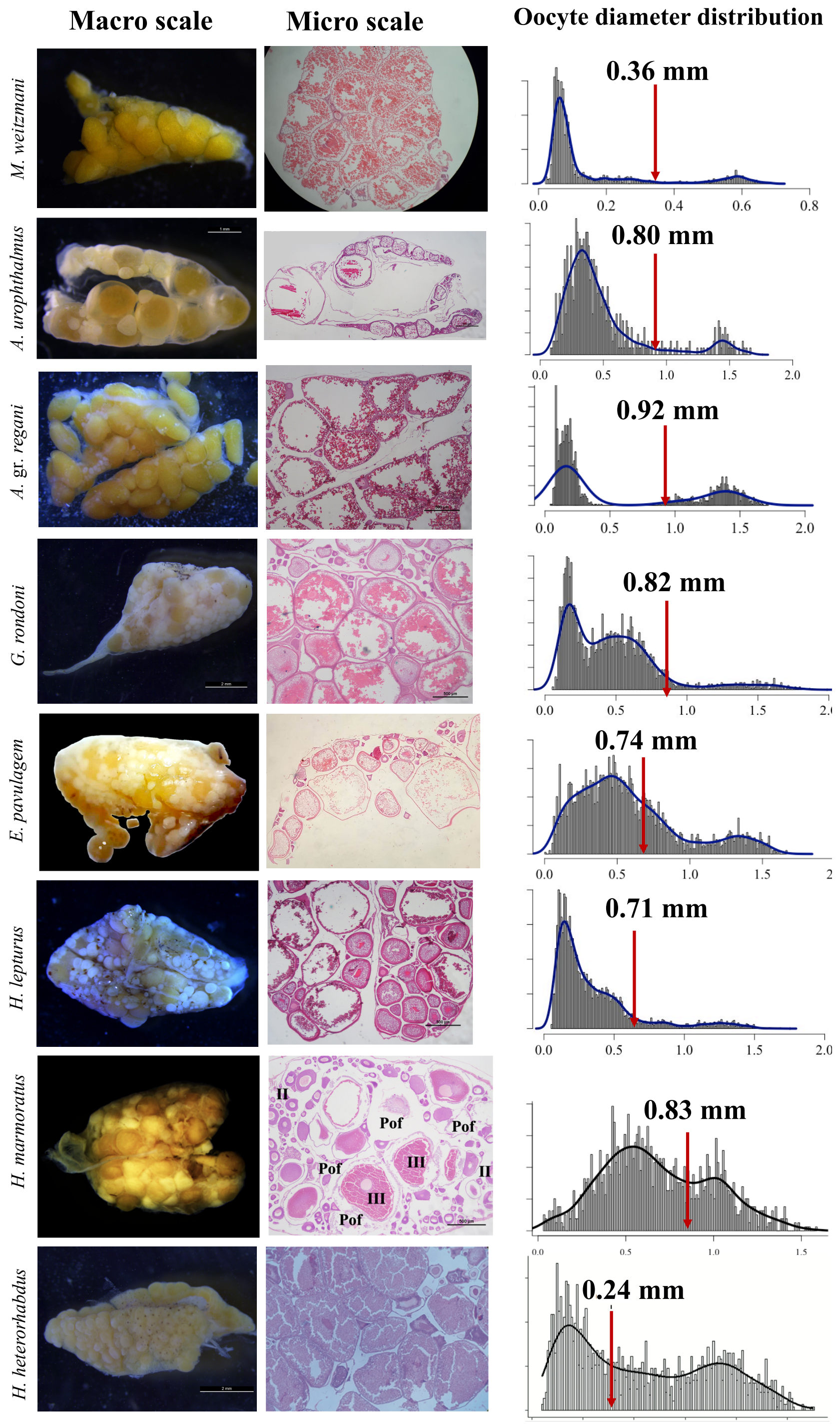
Astyanax bimaculatus

Moenkhausia oligolepis

Bryconops melanurus

Aequidens tetramerus

APÊNDICE D. PHOTOGRAPHIES (FIRST COLUMN), MICROPHOTOGRAPHIES OF HISTOLOGICAL SLIDES (SECOND COLUMN), AND OOCYTE DIAMETER DISTRIBUTION (THIRD COLUMN) OF SPAWNING CAPABLE FEMALES OF EIGHT SPECIES IN A CATCHMENT OF THE GUAMÁ RIVER (EASTERN BRAZILIAN AMAZON). THE RED ARROW INDICATES THE MINIMUM DIAMETER IN WHICH MATURE OOCYTES WERE OBSERVED.



APÊNDICE E. DIFFERENCES IN MACRO AND MICRO SCALES OF SPAWNING TYPE OF *MOENKHAUSIA COLLETTII* (TOTAL SPAWNER) FROM *AEQUIDENS TETRAMERUS* AND *IGUANODECTES RACHOVII* (BATCHER SPAWNERS). THE RED ARROW INDICATES THE MINIMUM DIAMETER IN WHICH MATURE OOCYTES WERE OBSERVED.