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PROGRAMA DE PÓS-GRADUAÇÃO EM BIODIVERSIDADE E CONSERVAÇÃO

Alexandre Villela Vieira Ribeiro

VARIAÇÃO ESPAÇO-TEMPORAL DO ICTIOPLÂNCTON NA ÁREA DE INFLUÊNCIA DA USINA HIDROELÉTRICA (UHE) BELO MONTE, AMAZÔNIA BRASILEIRA

Orientador: Prof. Dr. Tommaso Giarrizzo

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Dissertação apresentada à Universidade Federal do Pará, como parte das exigências do Programa de Pós-graduação em Biodiversidade e Conservação para obtenção do título de Mestre em Biodiversidade e Conservação.

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Dedicatória

À minha família, pelo apoio e incentivo constantes a seguir esse caminho e pela compreensão ainda maior pela ausência em suas vidas por esses dois anos.

Saibam que independente do tempo e distância, sempre estiveram presentes em meus pensamentos e decisões.

Agradecimentos

À Universidade Federal do Pará (UFPA), ao Programa de Pós-Graduação em Biodiversidade e Conservação (PPGBC) e Laboratório de Ictiologia de Altamira (LIA) por possibilitar minha formação enquanto cientista.

À Fundação de Amparo e Desenvolvimento da Pesquisa (FADESP) em conjunto a Norte Energia S.A. pelo financiamento do projeto de pesquisa de mestrado (Programa de Conservação da Ictiofauna da Área de Influência da UHE Belo Monte – Código 4276).

À equipe do Laboratório de Ecologia do Ictioplâncton e Pesca em Águas Interiores (LEIPAI-UFOPA), com a liderança do Prof. Dr. Diego Zacardi, pelo excelente trabalho de triagem e identificação do material biológico.

Agradeço a Sérgio Messias, Jerry Max Corrêa, Ruineris Cajado, Fernando Guido, Paulo Bezerra, Lucas Peres e Cláudia Chaves pela dedicação diária nas coletas de material biológico. E à Anne Macedo, Jéssica Gabriela, Samilly Costa, Maria Aparecida Suzuki, Matuzalém Nascimento e Kaylane Rodrigues pelo apoio técnico nas coletas e triagens.

Aos meus orientadores Dr. Tommaso Giarrizzo e Dr. Friedrich W. Keppeler pelas orientações e apoio durante todo o processo do mestrado. Obrigado pela amizade e todos os ensinamentos, motivações e construção da minha carreira como cientista. Agradeço especialmente aos novos aprendizados na escrita e análises de dados, que foram essenciais para o meu crescimento e desse trabalho. E a possibilidade de participação em outros projetos que permitiram conhecer o rio Xingu e toda excepcional equipe envolvida.

Agradeço aos membros da banca da disciplina de seminários, qualificação e dissertação pelas correções e contribuições durante todo o percurso desse projeto.

À minha companheira, Aline Vitoriano, por ser meu porto-seguro nesses dois anos em um lugar totalmente novo para mim. Por me fortalecer, motivar e ajudar a enxergar que podemos construir algo quando realmente nos dedicamos a ele. Por ser a pessoa que fez todo esse processo ainda melhor.

Agradeço pelas risadas, companheirismo e ajuda aos amigos que consegui em Altamira, especialmente a Lucas Peres, Cláudia Chaves, Isaac Cabral, Fabrício Otavio e Maria do Céu de Lima.

Obrigado a todos!

SUMÁRIO

RESUMO GERAL

A construção de barragens também pode alterar a reprodução de peixes adultos e a deriva natural de ovos e larvas, aumentando as falhas de recrutamento. Entretanto, pouco se sabe sobre o efeito de grandes usinas hidrelétricas na distribuição espaço-temporal do ictioplâncton em rios tropicais altamente diversificados. Aqui, investigou-se a dinâmica da ocorrência, riqueza e composição do ictioplâncton nos setores fluviais influenciados por Belo Monte no rio Xingu, o maior projeto hidrelétrico da Amazônia. O ictioplâncton foi investigado com amostragens diários durante um ciclo de pulso de cheia, de meados de novembro 2020 a abril de 2021. Foram realizados três setores distintos: à montante do reservatório principal, o reservatório principal e o setor de vazão reduzida, localizado à jusante da barragem. Foi analisada a influência do nível do rio, período do dia e outras covariáveis ambientais sobre ictioplâncton. Um total de 10.147 ovos e 27.442 larvas de peixe de 30 famílias foram amostradas. Os setores mais próximos à barragem (reservatório e setor de vazão reduzida) tinham uma maior abundância e riqueza de ictioplâncton do que o setor a montante. A desova foi fracionada em setores mais próximos à barragem, seguindo a variação menos previsível do nível da água causada pela barragem. Além disso, a atividade reprodutiva dos peixes estava fortemente ligada ao nível do rio com associações negativas no setor a montante, mas positivas nos setores do reservatório e de vazão reduzida. Os resultados indicaram que os setores mais próximos da barragem ainda são relevantes para a reprodução de peixes na região. Entretanto, os padrões podem estar ligados a processos indesejáveis, tais como retenção de larvas e ovos no reservatório e a interrupção da migração de peixes reprodutores para montante. A falta de sincronia entre os setores fluviais e a reprodução fracionada em locais mais próximos da barragem também pode ter consequências deletérias a longo prazo, tais como maiores taxas de predação no ictioplâncton. Os resultados corroboram estudos anteriores sobre a forte influência das barragens na dinâmica do ictioplâncton e fornecem informações fundamentais para criar melhores diretrizes para o estabelecimento de barragens mais sustentáveis. O monitoramento contínuo é aconselhado para avaliar melhor a magnitude das mudanças ecológicas causadas pela operação da Usina Hidroelétrica Belo Monte e para orientar futuros projetos hidrológicos em bacias tropicais.

Palavras-chave: Barragens de Belo Monte; Ovos de peixe; Larvas de peixe; Reprodução de peixes; Rio Xingu.

INTRODUÇÃO GERAL

A construção de barragens e seus respectivos reservatórios para produção de energia e abastecimento de água é considerada uma das principais ameaças aos ambientes de água doce (Liermann *et al*., 2012; Wu *et al.*, 2019). Atualmente, existem mais de 58.000 barragens construídas que afetam direta ou indiretamente mais de 60% dos rios do planeta (Grill *et al.*, 2019). As barragens alteram vários aspectos de um rio, como aconversão de um ambiente lótico em lêntico na região do reservatório (Pelicice, Pompeu & Agostinho, 2015; Loures & Pompeu, 2019), a redução do fluxo e da temperatura da água para trechos a jusante da barragem (Cheng *et al.*, 2015; Keppeler et al, 2022), fragmentação e diminuição da conectividade dos organismos entre montante e jusante da barragem (Kitanishi *et al.*, 2012; David *et al.*, 2022), aumento da retenção de sedimentos e nutrientes (Palinkas *et al.*, 2019), e homogeneização da dinâmica natural dos rios entre as estações do ano (Poff *et al.*, 2007). A este respeito, o recente *boom* de projetos e construções em bacias tropicais mega-diversas, como a Amazônia, tem sido um ponto de intenso debate e preocupação (por exemplo, Winemiller *et al.*, 2016).

Grandes bacias hidrográficas tropicais são caracterizadas por pulsos de cheia sazonais, que modificam ciclicamente o fluxo do rio, juntamente com parâmetros físico-químicos como pH, temperatura, oxigênio dissolvido, condutividade e nutrientes dissolvidos, principalmente de fontes alóctones (Ngor *et al.*, 2018; Drake *et al.*, 2021). Esta flutuação sazonal está fortemente ligada à biologia dos organismos aquáticos, que através de sua história evolutiva desenvolveram estratégias para maximizar o sucesso reprodutivo (Varpe, 2017; Oliveira *et al.*, 2020). Espera-se que a modificação da dinâmica natural de um rio com a construção de uma barragem afete diretamente as populações de peixes, bem como outros organismos aquáticos e consequentemente, os processos ecológicos (Wu *et al.*, 2019; Sousa *et al.*, 2021).

Para espécies de peixes migratórios, a barreira imposta pelas barragens interrompe os movimentos a montante e a jusante, reduzindo o número de reprodutores que podem alcançar as áreas de desova (Antonio *et al.*, 2007). Outro impacto é a regulação do fluxo do rio pela barragem que pode alterar o período reprodutivo, modificando os estímulos necessários (por exemplo, pico de fluxo do rio) para migração, maturação gonadal e desova (Humphries *et al.*, 2013; Duponchelle *et al.*, 2021). Portanto, isto altera a sincronia e fraciona o período reprodutivo natural e consequentemente diminui o sucesso reprodutivo (Duponchelle *et al.*, 2021). Por outro lado, muitas espécies sedentárias e oportunistas não dependem diretamente das variações sazonais dos rios para a reprodução. As evidências sugerem que em alguns casos estas espécies são até favorecidas pela mudança causada pela construção do reservatório (Agostinho *et al.*, 2016).

Os estágios iniciais do ciclo de vida dos peixes, como ovos e larvas (i.e., ictioplâncton), são particularmente sensíveis às mudanças ambientais causadas pelas barragens (Vasconcelos *et al.*, 2021; Zacardi *et al.*, 2021). Por exemplo, o maior tempo de residência associado aos reservatórios pode fazer com que o ictioplâncton decante e não complete seu desenvolvimento, uma vez que requer um período de deriva na coluna de água (Lechner, Keckeis & Humphries, 2016). Além disso, as larvas podem ser danificadas ou mesmo perecer ao passar por turbinas, vertedouros ou escadas de peixes (Alves *et al.*, 2019). A jusante da barragem, a intensidade das cheias naturais é reduzida, levando a mudanças na área inundada e reduzindo a quantidade de contribuição alóctone (por exemplo, matéria orgânica no solo e frutos das matas ciliares e inundadas) das margens do rio e a conectividade lateral com os ambientes adjacentes. Estes ambientes, tais como lagos e florestas inundadas, servem como berçários para larvas e juvenis de peixes (Valdez *et al.*, 2019; Lopes & Zaniboni-Filho, 2019). Eles conferem maior proteção e fontes de alimento adequadas para o crescimento de larvas de peixe e posterior recrutamento biológico (Zacardi, Bittencourt & Queiroz, 2020; Hermann *et al.*, 2021). Entretanto, a modificação da dinâmica do rio pode aumentar a taxa de mortalidade do ictioplâncton e em última instância, reduzir o recrutamento de populações de peixes.

A redução no recrutamento de peixes muda automaticamente a dinâmica da pesca. Na bacia amazônica, cerca de 93% de todos os desembarques de peixes consistem em Siluriformes e Characiformes migratórios, que proporcionam receitas de mais de US$ 400 milhões por ano e empregam centenas de milhares de pessoas (Duponchelle *et al.*, 2021). As reduções na população de peixes são particularmente preocupantes para a população ribeirinha e indígenas que dependem do pescado como sua principal fonte de renda e proteína (Loring *et al.*, 2019; Tregidgo *et al.*, 2020).

A Usina Hidroelétrica Belo Monte (BM Complexo) é a maior hidrelétrica da Amazônia e a terceira maior do planeta, com capacidade instalada de até 11.233,1 MW (Norte Energia, 2021). Sua operação começou em 2016, mas a região tem sido alvo do governo brasileiro desde 1975 para fomentar o desenvolvimento econômico do país (Fearnside, 2017). A concepção do BM Complexo passou por várias mudanças em função dos intensos debates sobre a viabilidade econômica e os impactos socioambientais do projeto, o que resultou na liberação da licença de instalação somente em 2011 (Sabaj

Perez, 2015; Fearnside, 2017). O BM Complexo foi construído como um sistema de fio-d'água (*run-of-the-river*), que foi apresentado como uma alternativa mais sustentável para a produção de energia (Kuriqi *et al.*, 2021). A sustentabilidade do projeto sempre foi um ponto de grande interesse porque esta região tem altas taxas de diversidade e endemismo de peixes, especialmente para peixes reófilos na Volta Grande do Xingu (~450 espécies; Camargo, Giarrizzo & Isaac, 2004; Fitzgerald *et al.*, 2018). Por ser um desenvolvimento relativamente recente, ainda há poucas informações publicadas sobre o efeito do BM Complexo na ictiofauna adulta (Mendes *et al.*, 2021; Keppeler *et al.*, 2022) e nenhuma sobre sua atividade reprodutiva. Isto é preocupante dado que a informação sobre a atividade reprodutiva é um elemento crucial para o manejo da pesca e o acesso à saúde da população de peixes e comunidades ribeirinhas e indígenas (Zacardi *et al.,* 2020).

Aqui, investigou-se a variação espaço-temporal do ictioplâncton no trecho do rio sob a influência das barragens de Belo Monte. Esta área foi represada em 2015 pela barragem de Pimental, formando o reservatório principal. Parte do fluxo que chega é desviado para o reservatório intermediário e para a barragem de Belo Monte, onde a maior parte da energia é produzida. Devido ao desvio para a barragem de Belo Monte, o fluxo de água na Volta Grande do Xingu foi reduzido (Keppeler *et al.*, 2022) e agora é referido como o trecho de vazão reduzida. Imaginamos que (i) o trecho de vazão reduzido apresentaria uma menor ocorrência de ovos de peixe e menor ocorrência e riqueza de larvas de peixe do que as áreas não reguladas localizadas à montante do reservatório; (ii) o período de desova no reservatório e no trecho de vazão reduzida seriam mais fracionados do que o setor à montante; e (iii) a abundância de ictioplâncton de peixes migratórios (e.g., Prochilodontidae) e grupos dependentes de inundação (e.g., Auchenipteridae) seria baixa, especialmente em setores próximos à barragem (i.e., reservatório e no trecho de vazão reduzida).

Este capítulo está formatado nas normas da revista Freshwater Biology, disponível em: https://onlinelibrary.wiley.com/page/journal/13652427/homepage/forauthors.html

Ichthyoplankton distribution during the main reproductive season at the largest Amazonian hydropower project

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Funding information - This research was funded by Norte Energia S.A.

Aqui inicia o seu capítulo padronizado de acordo com as normas da Freshwater Biology.

ABSTRACT

1. Artificial changes in river flow caused by dam regulation are likely to affect the reproductive biology of fishes. Dam construction may also block the natural drift of eggs and larvae, increasing recruitment failure. However, little is known about the effect of large hydropower plants on the spatiotemporal distribution of ichthyoplankton in highly diverse tropical rivers. Here, we investigated the dynamics of ichthyoplankton occurrence, richness, and composition in the river sectors influenced by Belo Monte in the Xingu River, the largest hydroelectric project in the Amazon.

2. The ichthyoplankton was investigated with daily surveys during a flood pulse cycle, from mid-November to April (167 consecutive days). Surveys were carried out in eight sampling stations from three distinct river sectors: upstream of the main reservoir, the main reservoir, and the reduced flow sector located downstream of the Pimental dam. The influence of river level, period of the day, and other environmental co-variables on the fish eggs and larvae were analyzed.

3. A total of 10,147 fish eggs and 27,442 fish larvae from 30 different families were sampled. There were profound spatiotemporal variations in fish reproductive activity in the area impacted by the Belo Monte operation. The sectors closer to the dam (reservoir and reduced flow sector) had a higher abundance and richness of ichthyoplankton than the upstream sector. Spawning was parceled in sectors closer to the dam, following the less predictable variation in water level caused by the regulation of the Pimental dam. In addition, fish reproductive activity was strongly connected with river level with negative associations in the upstream sector, but positive in the reservoir and reduced flow sectors.

4. The results indicated that sectors closer to the dam are still relevant for fish reproduction in the region. However, we caution that the patterns may be linked with undesired processes, such as larvae and egg retention in the reservoir, due to low water velocities and the upstream interruption of reproductive fish migration. The lack of synchrony between river sectors and parceling reproduction in sites closer to the dam may also have deleterious consequences in the long term, such as higher predation rates on the ichthyoplankton.

5. The results corroborate previous studies regarding the strong influence of dams on the dynamic of ichthyoplankton and provide pivotal information to create better guidelines for the establishment of more sustainable dams. Continue monitoring is advised to better assess the

magnitude of the ecological changes caused by the Belo Monte operation and to guide future hydrological projects in tropical basins.

Keywords: Belo Monte dams; Fish eggs; Fish larvae; Fish reproduction; Xingu River

1 INTRODUCTION

The construction of dams and their respective reservoirs for energy production and water supply is considered one of the main threats to freshwater environments and their associated fauna (Liermann *et al.*, 2012; Wu *et al.*, 2019). Currently, there are over 58,000 dams constructed that directly or indirectly affect over 60% of the planet's rivers (Grill *et al.*, 2019). Dams change several aspects of a river, including the conversion from a lotic to a lentic environment in the reservoir region (Pelicice, Pompeu & Agostinho, 2015; Loures & Pompeu, 2019), reduced flow and water temperature for stretches downstream of the dam (Cheng *et al.*, 2015; Keppeler *et al.*, 2022), fragmentation and decreased connectivity of organisms between upstream and downstream of the dam (Kitanishi *et al.*, 2012; David *et al.*, 2022), increased sediment and nutrient retention (Palinkas *et al.*, 2019), and homogenization of natural river dynamics between rainy and drought seasons (Poff *et al.*, 2007). In this regard, the recent boom of projects and construction in mega-diverse tropical basins, such as the Amazon, has been a point of intense debate and concern (*e.g.*, Winemiller *et al.*, 2016).

Large tropical river basins are characterized by seasonal flood pulses, that cyclically modify the river flow, along with physicochemical parameters such as pH, temperature, dissolved oxygen, conductivity, and dissolved nutrients, mainly from allochthonous sources when the flood occurs (Ngor *et al.*, 2018; Drake *et al.*, 2021). This seasonal fluctuation is tightly linked with aquatic organisms' biology, which through their evolutionary history have developed strategies to maximize reproductive success (Varpe, 2017; Oliveira *et al.*, 2020). Modifying the natural dynamics of a river with the construction of a dam is expected to directly affect fish populations as well as other aquatic organisms and consequently the ecological processes (Wu *et al.*, 2019; Sousa *et al.*, 2021).

For migratory fish species, the barrier imposed by the dams interrupts upstream and downstream movements, reducing the number of reproducers that can reach spawning areas (Antonio *et al.*, 2007). Another impact is the regulation of the river flow by the dam which can alter the reproductive period by changing the necessary stimuli (*e.g.*, river flow peak) for migration, gonadal maturation, and reproduction (Humphries *et al.*, 2013; Duponchelle *et al.*, 2021). Therefore, this alters the natural synchrony of the reproductive period and consequently decreases reproductive success (Duponchelle *et al*., 2021). On the other hand, many sedentary and opportunistic species do not depend directly on seasonal river variations for reproduction. Evidence suggests that in some cases these species are even favored by the change caused by reservoir construction (Agostinho *et al.*, 2016).

Early stages of the fish life cycle, such as planktonic eggs and larvae (*i.e.*, ichthyoplankton), are particularly sensitive to environmental changes caused by dams (Vasconcelos *et al.*, 2021; Zacardi *et al.*, 2021). For example, the longer residence time associated with reservoirs can cause ichthyoplankton to sink and not complete their development, as they require a period of drift in the water column (Lechner, Keckeis & Humphries, 2016). In addition, larvae can be damaged or even perished when passing through dam turbines, spillways, or fish ladders (Alves *et al.*, 2019). Downstream of the dam, the intensity of natural floods is reduced, leading to changes in the flooded area and reducing the amount of allochthonous contribution (*e.g.*, organic matter in the soil and fruits of the riparian and flooded forests) of the riverbanks and the lateral connectivity with adjacent environments. These environments, such as oxbow lakes and flooded forests, serve as nurseries for fish larvae and juveniles (Valdez *et al.*, 2019; Lopes & Zaniboni-Filho, 2019). They also confer greater protection and adequate food sources for fish larvae growth and subsequent biological recruitment of offspring (Zacardi, Bittencourt & Queiroz, 2020; Hermann *et al.*, 2021). However, the modification of river dynamics can increase the mortality rate of the ichthyoplankton and, ultimately, reduce the recruitment of fish populations.

The reduction in fish recruitment automatically changes the dynamics of fishing. In the Amazon basin, around 93% of all fish landings consist of migrating catfishes and characids, which provide revenues of over US$ 400 million each year and employ hundreds of thousands of people (Duponchelle *et al.*, 2021). Reductions in the fish population are particularly concerning for the riverine population and indigenous people that rely on fish as their main source of income and protein (Loring *et al.*, 2019; Tregidgo *et al.*, 2020).

Belo Monte Hydroelectric Power Plant (BM Complex) is the largest hydroelectric plant in the Amazon and the third largest on the planet, with an installed capacity of up to 11,233.1 MW (Norte Energia, 2021). Its operation began in 2016, but the region has been targeted by the Brazilian government since 1975 to foster the country's economic development (Fearnside, 2017). The design of the BM Complex underwent several changes given the intense debates about the economic feasibility and socio-environmental impacts of the project, which resulted in the release of the installation license only in 2011 (Sabaj Perez, 2015; Fearnside, 2017). The

BM Complex was built as a run-of-the-river (ROR) system, which has been presented as a more sustainable alternative to energy production (Kuriqi *et al.*, 2021). The project's sustainability was always a point of great interest because this region has high rates of fish diversity and endemism, especially for rheophilic fish (~450 species; Camargo, Giarrizzo & Isaac, 2004; Fitzgerald *et al.*, 2018). Because it is a relatively recent development, there is still little published information on the effect of the BM Complex on adult ichthyofauna (Mendes *et al.*, 2021; Keppeler *et al.*, 2022) and none on their reproductive activity. This is concerning given that information about reproductive activity is a crucial element to manage fisheries and accessing fish population health (Zacardi *et al.*, 2020).

Here, we investigated the spatiotemporal variation of ichthyoplankton in the river stretch under the influence of the BM Complex. This area was dammed in 2015 by the Pimental dam, forming the main reservoir (MR). Part of the flow that arrives is diverted to the intermediate reservoir and the Belo Monte dam, where most of the energy is produced (Figure 1). Due to the diversion to the Belo Monte dam, the water flow in the Xingu Big Bend was reduced (Keppeler *et al.*, 2022) and is now referred to as the reduced flow sector (RF). We hypothesized that (i) the RF had a lower occurrence of fish eggs, and lower occurrence and richness of fish larvae than unregulated areas located upstream (UP); (ii) the spawning period in the MR and RF are more parceled than the UP sector; and (iii) the abundance of ichthyoplankton of migratory (*e.g.*, Prochilodontidae) and flood-dependent groups (*e.g.*, Auchenipteridae) is low, especially in sectors near the dam (*i.e.*, MR and RF).

2 METHODS

2.1 Study area

The Xingu River basin drains an area of approximately 504,000 km² and is the second-largest clearwater tributary of the Amazon River (Zuluaga-Gómez *et al.*, 2016). The main river is over 1,600 km long and runs, for most of its course in the S-N direction, from Serra do Roncador, into the Amazon estuary (Latrubesse, Stevaux & Sinha, 2005). The Xingu is a clear water river with low levels of nutrient and suspended sediments, and high light penetration (Ríos-Villamizar *et al.*, 2020). The mean annual precipitation in the region is 1,885 mm, with high seasonality associated with the river discharge. The high water period occurs from December to May (mean discharge reaches ~10,000 m³) whereas the drought season occurs from June to November (down to ~2,000 m³) (Camargo, Giarrizzo & Isaac, 2015).

We studied a river section approximately 70 km long river stretch under the influence of the Belo Monte project. The water is dammed in the main reservoir (MR), a new environment with lentic / semi-lentic conditions. The power station of the Belo Monte dam has 18 Francis turbines with a potential energy production of approximately 11,000 MW. The Pimental dam has only six Bulb turbines with a potential energy production of 233 MW and 18 floodgates. The Pimental dam regulates the water level in the MR and the flow available downstream in the Xingu Big Bend, the reduced flow sector (RF). A fish ladder or the Fish Passage System (FPS), a 1.2 km artificial channel mainly formed by rapids, was built in the Pimental dam to connect the MR to the RF and vice-versa.

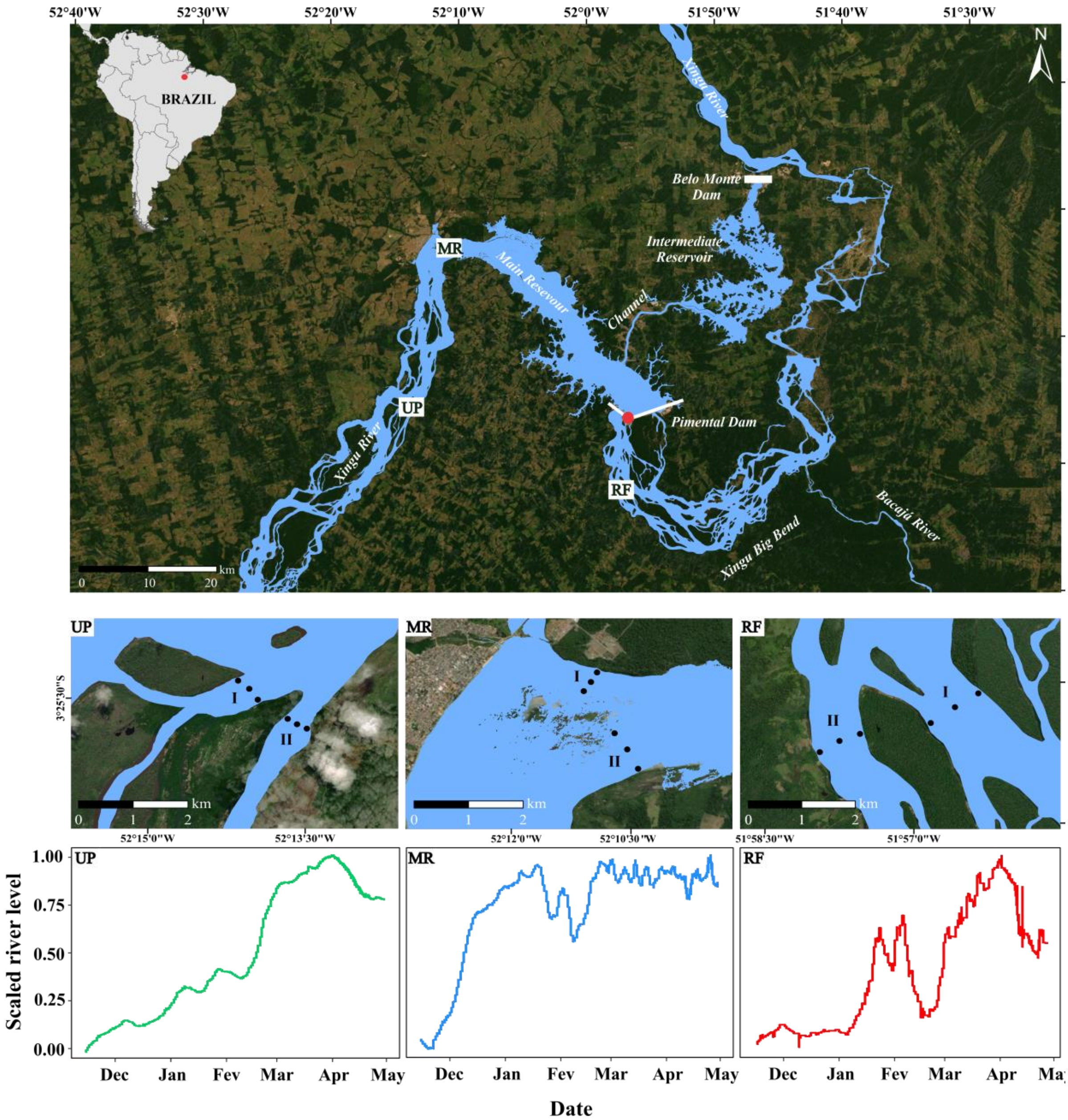

Figure 1 – Study area (upper panel), sampling locations (middle panels), and river level variation (lower panels) in the Middle Xingu River during the sampling period. UP refers to the Upstream sector, MR to the Main Reservoir, and RF to the Reduced Flow sector. Black dots in the middle panels indicate the location of the sampling stations whereas the numbers (I and II) indicate the location of the sampling sites in each river section. The river level is scaled to vary from 0 (minimum) to 1 (maximum). The lower panel's green, blue, and red lines represent water level variation in the UP, MR, and RF sectors, respectively. The red dot demarcated on the Pimental dam represents the location of the fish ladder

2.2 Ichthyoplankton sampling

Three sectors in the Middle Xingu River were sampled: 1) the UP, located upstream of the main reservoir; 2) the MR, formed by the Pimental dam; and 3) the RF, located downstream of the Pimental dam (Figure 1). This division was based on the effects of the Belo Monte operation on river flow, which varied greatly between the sectors during the studying period (Figure 1). Furthermore, the river sectors differ in depth, width, and substrate composition (Table 1), among other environmental variables (Keppeler *et al*. 2022).

Table 1 – Transversal section distance, depth variation, dominant substrate, and marginal vegetation for each of the river sectors sampled in the Middle Xingu River, Brazil.

Sector	Transversal section distance (m)[a]	Variation in depth (m)[b]	Dominant substrates	Marginal vegetation
Upstream (UP)	1127.18	3.01 to 8.74	SD, RC	RF
Main Reservoir (MR)	2155.19	10.27 to 15.07	SD, MD	RF; MS
Reduced flow (RF)	2283.24	2.51 to 6.59	RC, SD	RF

[a] Sum of the width of the river in sites I and II.
[b] Depth variation during the sampling period.
[c] Dominant substrate was visually estimated at each sampling station. The methodology is described in the section *Abiotic co-variables*. SD = sand, RC = rock, MD = mud.
[d] Vegetation found on the riverbanks. RF = Riparian forest; MS = Macrophytes stands.

Simultaneous ichthyoplankton surveys were conducted daily in each sector from November 15th (2020) to 30 April 30th (2021), totalizing 167 sampling days (Figure 2). This period covers the final days of the drought season and the flood season, the main breeding period for most fishes, including migratory species (Duponchelle *et al.*, 2021). We performed horizontal trawling in the subsurface (~5 cm below surface) aboard small motorboats at a constant speed for 10 min, using a 300 μm mesh conical-cylindrical plankton net (1.5 m long and 0.5 m in diameter), with a mechanical flowmeter attached. In each sector, two sites located in different channels of the river were sampled (Figure 2). These sites contain three sample stations: the left bank (LB), the right bank (RB), and the main channel (Figures 1 and 2). In addition to the subsurface samples in the main channel (CS), we conducted midwater samples

(CM) using the plankton net and a depressor weighing 10 kg to stabilize the net. Midwater samples were conducted at 2 m depth at UP and RF, because of the presence of submerged rocks and logs that could damage the plankton net, and 10 m at MR, naturally deeper. To create the treatment replicas were conducted a sample during the day (average interval of 15:00 to 17:00 h) and at night period (21:00 to 23:00 h) (Figure 2). After each sampling event, the material was concentrated in 50 ml sterilized polyethylene pots and fixed in formalin solution at 10%.

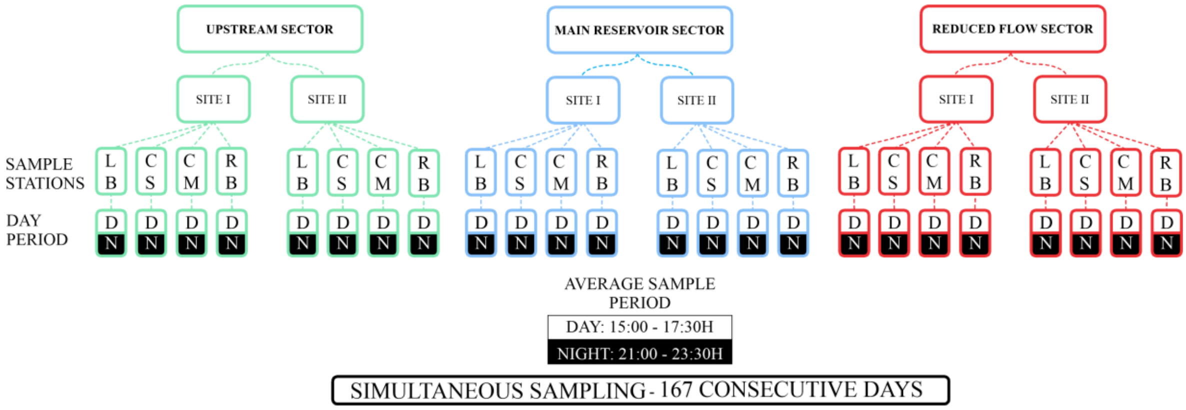

Figure 2 – Summary of the sampling effort conducted to explore ichthyoplankton variation in the Middle Xingu River, Brazil. Samples occurred daily for 167 days. On each day, samples were taken simultaneously in the upstream, main reservoir, and reduced flow sectors during the day (D) and night (N). Each site contained three sample stations: the left bank (LB), the right bank (RB), and the main channel. The main channel was divided into two substations: subsurface (CS) and midwater (CM).

2.3 Sample processing and taxonomic identification

The samples were sorted and divided into fish eggs and larvae. The biological material was quantified, identified, and classified into development stages, according to the terminology described by Nakatani *et al*. (2001): i) embryonic period (egg) - early cleavage stage, early embryo stage, free tail stage, and final embryo; ii) larval period – yolk-sac, preflexion, flexion, and posflexion. The larvae were identified to order, and family levels based on morphological, meristic, and morphometric characteristics, using specialized literature. We worked at this level because most of the individuals could not be identified at the species or genus levels due to the lack of specific literature published for the Amazon species. We use the term "richness" to refer to the number of *taxa* sampled.

2.4 Abiotic co-variables

The influence of environmental variables (herein referred to as co-variables) on the distribution of eggs and larvae was also investigated to control for possible confounding effects. The river level (m) and flow (m^3/s) associated with the sector was obtained daily from fluviometric stations located along the river (Norte Energia, 2021). The water flow for UP and MR sectors varied almost the same (~1,000 to 20,000 m^3/s) and for the RF sector was relatively lower (~800 to ~10,000 m^3/s). As each sector has different depths, only the river level variation was considered to analyze the influence of hydrology on ichthyoplankton (Silva *et al.*, 2020). To assess only the variation, the river level in each sector was scaled to the range 0 and 1, where 0 and 1 indicate, respectively, the minimum and maximum values observed. Due to the few differences between UP and MR sectors, concerning flow, we chose to work only with the river level variation, which was more contrasting (Figure 1). Local precipitation was obtained to analyze the influence of rainy days on spawning activity (Magalhães Lopes *et al.*, 2018). The meteorological stations were located at the Pimental dam and the city of Altamira; the former was used to estimate the precipitation for RF whereas the latter was used to estimate the precipitation for UP and MR sectors.

Samples were classified according to the period of day (*i.e.*, day and night), seeking to observe the variation of the occurrence between the periods (Magalhães Lopes *et al.*, 2018). In addition, we classified samples according to five lunar phases: new moon (1), waxing and waning moons (2), quarters waxing and waning (3), waxing and waning gibbous (4) and full moon (5). This classification can be understood as an ordinal index (herein referred to as lunar index) with higher numbers associated with lighter nights.

Samples were also classified according to the environment of sampling stations: riverbank (left bank and right bank), channel subsurface, and channel midwater. The sediment composition was estimated to analyze whether there is a preference for spawning substrates (Sternecker, Denic & Geist, 2014). Three river bottom samples (separated by 200 m) were collected with a small dradge (5.0 L) and visually estimated (percentage) on the boat, at each sample station and river sector. To increase the detail, a rope with a depressor weighing 10 kg was traversed in the substrate, to feel the presence of unconsolidated (sand or mud) or solid material (gravel or rocks). The sediment samples were classified into three categories: mud, rock, and sand. A principal components analysis was conducted with the mean percentage for each category to reduce the data into two main axes (PCA1 and PCA2). This was necessary given that the three variables associated with the substrate were strongly correlated. PCA1 explained 66% of the data and was positively associated with sandy substrates and negatively related to rocky substrates and PCA2 explained 33% of the data and was positively associated with sandy and rocky substrates and negatively related to mud. The two PCA axes were used as inputs for the statistical analyses described below.

2.5 Data analysis

2.5.1 *Probability of occurrence of fish egg and larvae*

We conducted Bayesian Generalized Linear Mixed Models (GLMM) to explore the occurrence (*i.e.*, presence-absence) of fish eggs and larvae. To explore fish larvae composition, we extended the GLMM to a multivariate context (*i.e.*, a Multivariate Generalized linear Mixed Model – MGLMM). GLMM and MGLMM were carried out in the R package HMSC (Tikhonov *et al*., 2020), which is a powerful tool to explore the association between community and environmental data as well as incorporate the temporal and spatial structure of the data with latent variables (for more details, see Ovaskainen *et al.*, 2017 and Ovaskainen & Abrego, 2020).

For this analysis, we only used eggs and larvae in the first development stages (eggs: early cleavage stage, early embryo stage; larvae: yolk-sac and preflexion) since they encompassed more than 92% of the data. We opted to analyze presence-absence rather than abundance data for three main reasons: 1) data was zero-inflated (Figure S1) with only 14% and 33% of eggs and larvae data, respectively, with non-zero values; 2) presence-absence data was strongly associated with abundance data (Spearman correction = 0.99 and 0.97 for eggs and larvae, respectively) as only 10% and 22% of eggs and larvae data, respectively, was greater than 1; and 3). Exploratory comparisons indicate that models containing abundance and models containing presence-absence data showed similar patterns, but the latter had higher exploratory power and the model chains converged faster. For our MGLMM, we focused only on families with an abundance greater than 1%, since rare *taxa* increase computer processing disproportionately without any relevant gain of information (Brasil *et al.*, 2020; Ovaskainen & Abrego, 2020).

Traditionally, the number of flowmeter rotations is used as ichthyoplankton CPUE (catch per unit effort) indexes to control for the water volume that passes through the net, generating a presumably more robust metric of abundance (*e.g.*, Nakatani *et al*., 2001). However, CPUE indexes assume that the probability of capture increases proportionally with the water volume filtered, which may not be a valid assumption in many cases (Beverton & Holt 1957; Harley, Myers & Dunn, 2001). Besides, it may cause biases in the response variable if there are errors associated with flowmeter rotations readings. Given that exploratory analysis indicated i) a weak association between flowmeter rotations and the probability of ichthyoplankton occurrence and ii) a weak association between CPUE and our predictors of interest, we opted to consider flowmeter rotations as an exploratory variable in the model (see below) and maintain the properties of our response variables (0 – 1) following the approach proposed by Ovaskainen and Abrego (2020).

The fixed and random effect structure of the GLMM and MGLMM were equivalent. Sector (UP, MR, and RF), scaled river level, period of day (day-night), environment (channel subsurface, channel midwater, and riverbanks), precipitation, lunar index, number of flowmeter rotations, and substrate composition (PCA1 and PCA2) were set as fixed effects. We also added an interaction term between scaled river level and river sector in the fixed part of the models once we expected the effect of river level to vary according to the regulation of the Belo Monte operation. The date of sampling and lat-long coordinates were set as random effects in the models to account for the temporal and spatial autocorrelation in the data.

GLMM and MGLMM models were built with Probit distribution and with default non-informative priors following Ovaskainen and Abrego (2020). The posteriori distribution was sampled with five Markov chains, each with 2500,000 interactions, from which 500,000 was burn-in and from the remaining only 250 were rained with the thin value of 10,000. Markov chain convergence of parameters of the models was checked and confirmed with Gelman-Rubin statistics and trace plots.

We assessed the exploratory power (in-sample error) of our GLMM and MGLMM models with the Area Under the Curve (AUC) and Tjur R^2 (Tjur, 2009) using the entire dataset. For predictive power (out-of-sample error), we conducted a 2-fold cross-validation procedure (Ovaskainen & Abrego, 2020) and calculated the average AUC and Tjur R^2 associated.

The predictors' significance was demonstrated when the 95% credible intervals of their respective parameters did not encompass zero. We also calculated the probability that the predictor effect (*i.e.*, slope) is different from zero, following Ovaskainen and Abrego (2020). We considered the predictor significant when the probability was greater than 0.95.

2.5.1 *Parceling of the spawning period*

To compare the level of parceling between the different sectors, we sum all days with the presence of eggs for each sampling station, site, and sector. Then, we model the number of days with eggs present using Bayesian GLMM through the package brms. The river sector was set as a fixed effect and the environment (channel subsurface, channel midwater, and riverbanks) as random intercepts. We used the environment as a random effect in these models because we found consistent differences in the occurrence of eggs between riverbanks and channels (see below).

GLMM models were constructed with Poisson distribution, five chains, non-informative priors, 2,000 interactions, the thinning value of one, and burning of 1,000. We checked and confirmed (< 1.1) the convergence of the models' chains using the potential scale reduction factor on split chains (Rhat).

The exploratory power of the model was assessed with the coefficient of determination (R^2). Predictive power was estimated through approximate leave-one-out cross-validation using the approach proposed by Vehtari, Gelman, and Gabry (2017).

3 RESULTS

A total of 7,849 ichthyoplankton samples were collected during the study period. In the UP sector, 2,567 samples were obtained, in MR, 2,651 samples, and the RF, 2,624. About 60% of the samples did not contain ichthyoplankton.

3.1 Fish eggs

A total of 10,147 fish eggs were collected. Most fish eggs were captured in the RF (47.87%), followed by the UP (27.40%) and the MR (24.74%; Table 2) sectors. The abundance and distribution of fish eggs varied greatly over the sampling period, demonstrating a unique pattern for each sector (Figure 3. a).

Table 2 – Total abundance of the ichthyoplankton sampled in the three studied sectors (Upstream – UP, Main Reservoir – MR, Reduced Flow – RF) of the Middle Xingu River, Brazil. The families indicated by * are the most abundant and are arranged in phylogenetic order according to Nelson *et al.* (2016) and Oliveira *et al*. (2011).

Abundance	**UP**	**MR**	**RF**
Fish eggs	2780	2510	4857
Fish larvae	1519	17222	3856
Fish larvae not identified	304	3859	682
Fish larvae *taxa*	**UP**	**MR**	**RF**
Clupeiformes			
Pristigasteridae	0	1	0
Engraulidae	114	14	5
Characiformes			
Crenuchidae	0	0	1

Erythrinidae	2	15	9
Cynodontidae*	0	208	15
Serrasalmidae*	59	73	180
Hemiodontidae*	337	3800	170
Anostomidae*	56	3597	642
Chilodontidae	1	9	0
Curimatidae*	28	720	50
Prochilodontidae*	1	347	998
Characidae*	259	2693	726
Iguanodectidae	0	3	4
Bryconidae	0	45	6
Triportheidae	52	59	25
Siluriformes			
Ceptopsidae	24	16	2
Trichomycteridae	25	111	7
Loricariidae	0	0	2
Doradidae	0	64	7
Auchenipteridae*	111	634	181
Heptapteridae	0	43	36
Pimelodidae*	11	511	74
Pseudopimelodidae	0	0	5
Gymnotiformes			
Gymnotidae	2	8	1
Hypopomidae	8	11	3
Sternopygidae	5	17	16
Apteronotidae	1	0	0
Cyprinodontiformes			
Rivulidae	1	0	0
Synbranchiformes			
Synbranchidae	0	2	0
Insertae sedis			
Sciaenidae*	118	362	9

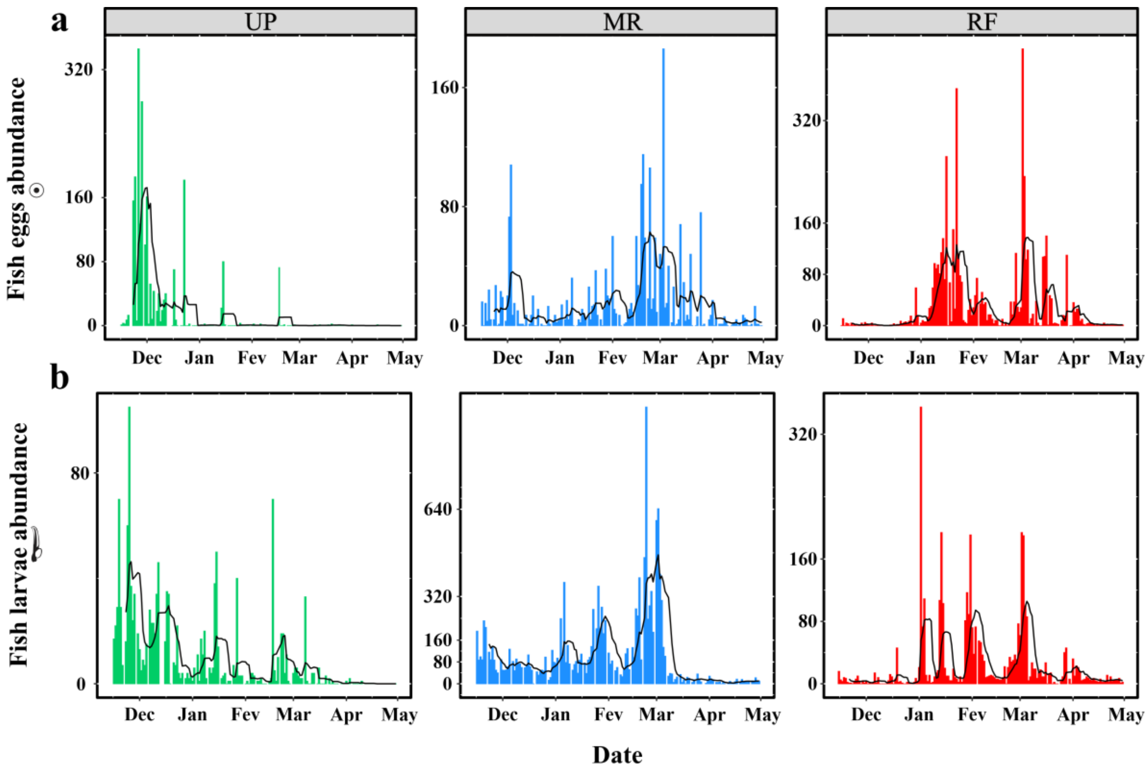

Figure 3 – Daily total abundance of fish eggs (a) and larvae (b) sampled in the three studied sectors (Upstream – UP, Main Reservoir – MR, Reduced Flow – RF) in the Middle Xingu River, Brazil. The black line represents seven days period (1 week) moving average.

3.1.1 *Occurrence of fish eggs*

The GLMM for fish eggs occurrence had an explanatory power of 32% and predictive power of 29%. The relative proportion explained by each variable varied greatly (Figure 4; Table 3). The main effects of river level (Prob = 1.00), sector (Prob = 0.97), and the term interaction between sectors and the river level were significant (Prob [sector*river level] = 1.00) and were the most important components, explaining ~17 of fish eggs occurrence. In the UP sector, the probability of fish egg occurrence was negatively associated with the water level (Figure 5). The opposite trend occurs for the MR and RF sectors, where the occurrence of eggs responded positively to higher river levels (Figure 5).

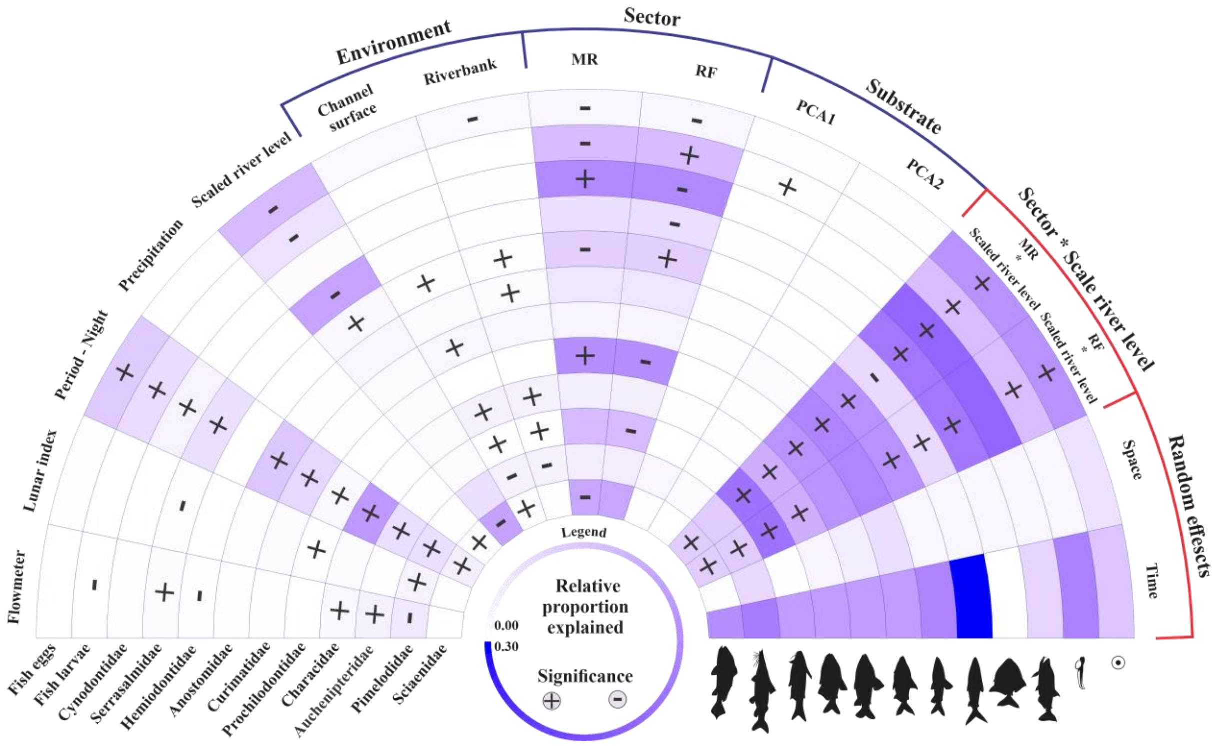

Figure 4 – Associations between the occurrence of fish eggs, larvae, the 10 most abundant fish larvae families, and environmental variables. For the variable sector, were used the Upstream (UP), Main Reservoir (MR), and Reduced Flow (RF) sectors. Positive and negative significant relationships (95% credibility interval not encompassing zero) are displayed with positive (+) and negative (-) signals, respectively. The relative proportion explained varied from zero (white) to 0.30 (blue). For categorical variables, one of the levels is considered a baseline (Night period: day; Environment: midwater samples; Sector: UP; Sector*Scaled river level: UP*Scaled river level) to which the other levels of the categorical variable are compared (*e.g.*, Period-Night refers to the comparison between day and night). Temporal and spatial random effects were utilized to improve model performance.

Table 3 - List of models created for explaining the occurrence of fish larvae and eggs. Explanatory (in-sample error) and Predictive power (out-of-sample error), which were measured using the Area Under the Curve (AUC) and Tjur's coefficient of determination (Tjur R^2), are provided for each model. For the fish larvae model, we used a multivariate analysis (MGLMM), so we provided AUC and Tjur R^2 values for each family. In addition, the average across families is shown, followed by minimum and maximum values in parentheses.

	Explanatory power		**Predict power**	
	AUC	**TJurR²**	**AUC**	**TJurR²**
Fish eggs	0.903	0.322	0.879	0.287
Fish larvae	0.847	0.328	0.884	0.314
Fish larvae families	0.862 (0.735 - 0.961)	0.242 (0.101 - 0.366)	0.825 (0.701 - 0.938)	0.198 (0.081 - 0.325)
Cynodontidae	0.961	0.317	0.938	0.256
Serrasalmidae	0.808	0.101	0.773	0.081
Hemiodontidae	0.869	0.366	0.839	0.325
Anostomidae	0.859	0.320	0.834	0.298
Curimatidae	0.860	0.229	0.818	0.189
Prochilodontidae	0.954	0.321	0.927	0.243
Characidae	0.735	0.152	0.701	0.131
Auchenipteridae	0.867	0.247	0.815	0.171
Pimelodidae	0.875	0.220	0.817	0.169
Sciaenidae	0.834	0.148	0.793	0.121

The abundance of fish eggs (~93%) was higher during the night period, with a significant difference between periods (Prob = 1.00), explaining ~5% of the data (Figure 4). Environment was considered a significant predictor (Prob [CM-CS] = 0.07; Prob [CM-riverbank] = 0.99) but explained less than 1% of the data. Channels tended to have a frequency of fish eggs twice as high as the riverbanks. Flowmeter, lunar index, precipitation, and substrate composition were not significantly associated with the occurrence of fish eggs. Temporal (*i.e.*, sample date) and spatial (*i.e.*, sampling stations location) components had a contribution of ~5% and ~3%, respectively (Figure 4).

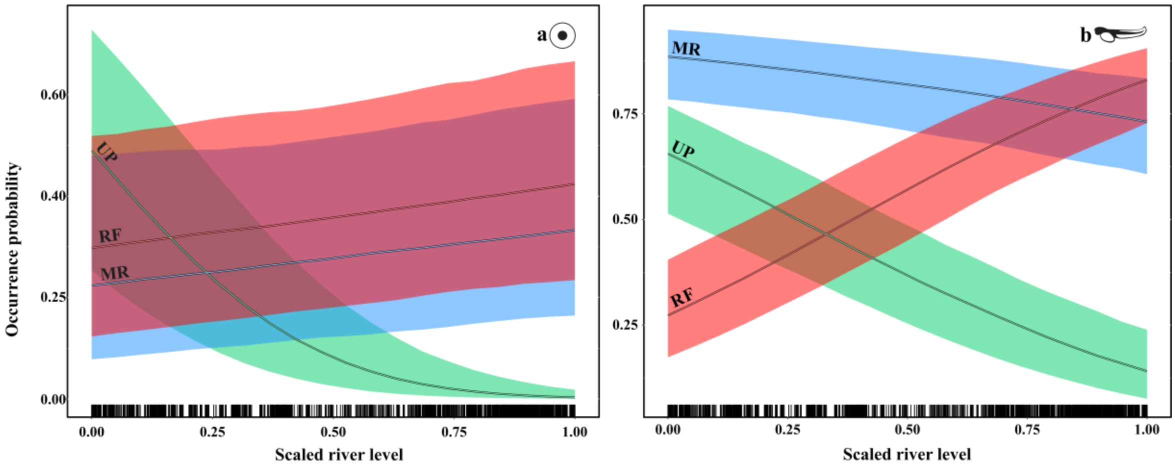

Figure 5 – Marginal effect of river level and sector (Upstream - UP, Main Reservoir - MR, and Reduced Flow - RF) on the occurrence of fish eggs (a) and larvae (b) in the Middle Xingu River, Brazil. Colored areas represent the 95% credibility intervals for each sector. The marginal effect was calculated by setting the period of the day to night, environment to the riverbank, precipitation, lunar index, number of flowmeter rotations, and substrate composition to average values.

3.1.2 *Parceling of the spawning period*

The GLMM built to explain the spawning days had a high conditional (Fixed + Random effects) explanatory and predictive power of ~72% and ~56%, respectively. Marginal (only fixed effects) explanatory and predictive power had values of ~32% and ~15%, respectively. The sector had a significant effect on the spawning period, with higher values found for MR (~65 days) and RF (~73 days), and lower for the UP (~26 days) sector. Random intercept values indicated that the spawning period was considerably higher at channel environments (CM=3.67 [3.52, 3.82], CS= 3.51 [3.35, 3.66]) than riverbank (2.81 [2.66, 2.97]).

3.2 Fish larvae

A total of 27,442 fish larvae were collected, mainly in the MR (76.82%), followed by the RF (16.53%) and UP (6.64%; Table 2). Similar to the fish eggs, the number and distribution of fish larvae varied in space and time (Figure 3. b). About 80% of the fish larvae were identified (22,597), which generated a taxonomic list with six orders and one *Incertae sedis*, subdivided into 30 families (Table 2). Characiformes and Siluriformes had the highest number of cataloged families (13 and 8, respectively). Characiformes had the highest abundance (84.75%), with seven of the 10 most abundant families (>1% of total abundance), followed by Siluriformes (11.32%) and *Incertae sedis* (2.21%).

3.2.1 *Occurrence of fish larvae*

The GLMM for fish larvae had an explanatory power of 33% and a predicted power of 31% (Table 3). The main effect of the sector (Prob = 1.00), river level (Prob = 1.00), and the term interaction (Prob [sector*river level] = 1.00) were significant and the most important components in the model, explaining a total of from ~15% of larvae occurrence variation (Figure 4). The UP sector had a sharp decline in larvae occurrence with the increase in river level (Figure 5). Conversely, the occurrence of fish larvae in the RF sector tended to increase with river level whereas was almost constant in the MR sector (Figure 5). MR sector tended to have a higher occurrence of fish larvae than the UP and RF sectors.

The abundance of fish larvae (~86%) was higher during the night period (Prob = 1.00), explaining ~3% of the data (Figure 4). The rest of the environment variables explained less than 1% of the fish larvae occurrence. Flowmeter values were significant (Prob = 0.98) and had a negative relationship with the occurrence of larvae and higher occurrences were related to sand substrates (PCA1; Prob = 0.99). Environment, lunar index, and precipitation were not significantly associated with the occurrence of fish larvae. Temporal and spatial components had a contribution of 12% and less than 1% in the explanation, respectively.

3.2.2 *Composition and richness of fish larvae*

The MGLMM model used to model the occurrence of fish larvae families had an average explanatory power of ~24% and a predicted power of ~20% (Table 3). The family with the highest amount of variation explained was Hemiodontidae (explanatory power = ~37%, predictive power = ~33%), followed by Prochilodontidae (32% and 24%) and Anostomidae (~32% and ~30%), and the lowest was Serrasalmidae (~10% and ~8%).

Predictions of our MGLMM model suggested that fish larvae richness increased with river level at MR and RF, but it went down with the increase of the river level in the UP sector (Figure 6). The MR and RF sectors showed the highest taxonomic richness, with 25 families each, but the composition differs, and the UP sector had a total of 20 families (Table 2).

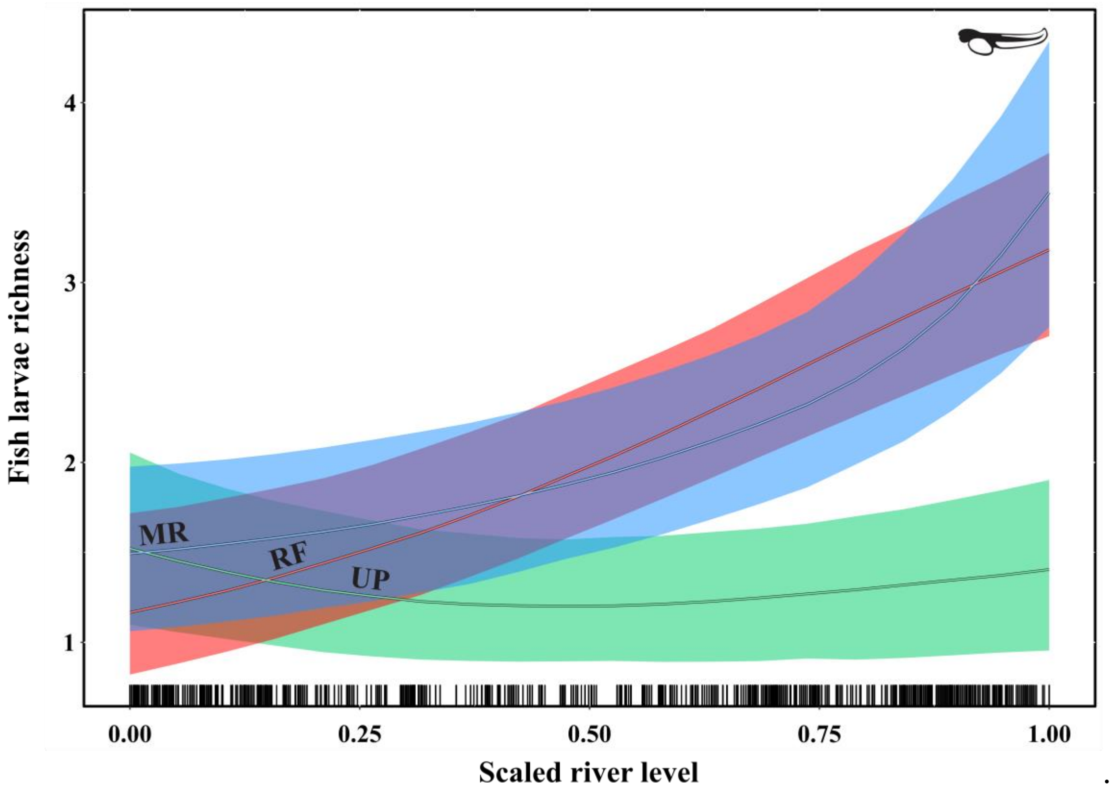

Figure 6 – Marginal effect of river level and sector (Upstream -UP, Main Reservoir - MR, and Reduced Flow RF) on fish larvae richness in the Middle Xingu River, Brazil. Colored areas represent the 95% credibility interval for each sector. The marginal effect was calculated by setting the period of the day to night, environment to the riverbank, precipitation, lunar index, number of flowmeter rotations, and substrate composition to average values.

The main effect of the sector, river level, and the interaction term between them explained an average relative proportion of 6.37% ± 3.12% of the fish larvae family's data. Fish larvae occurrence in the UP sector was constantly low for all families, except for Hemidontidae, which increased the occurrence at higher river levels. Families that significantly increase in occurrence with river level in MR sector were Anostomidae, Auchenipteridae, Characidae, Curimatidae, Cynodontidae, Hemiodontidae, Prochilodontidae, Sciaenidae, and Serrasalmidae (Figure 5). We also found increases in larvae occurrences with river level at the RF sector for the families Anostomidae, Auchenipteridae, Characidae, Hemiodontidae, Pimelodidae, Sciaenidae, and Serrasalmidae (Figure 4). Prochilodontidae showed a lower probability of occurrence at high river levels in the RF sector compared to the UP sector (Figure 4), despite the higher abundance (Table 2). Hemiodontidae was the only family that was significantly negative relative to the increase in river level in the RF sector.

The period of the day was a relevant variable to explain the larvae occurrence for most families (average relative proportion of 2.24% ± 1.90%) (Figure 5). Of the identified larvae, 87% were collected during the night period. Only the occurrence of Hemiodontidae larvae was not affected by day and night periods. The rest of the fixed variables explained less than 1% of the variation in fish larvae occurrence. Temporal and spatial components explained 7.10% ± 4.03% and 1.17% ± 1.24% of the fish larvae occurrence data, respectively. The temporal component was especially important for Hemiodontidae, explaining ~25% of occurrences.

4 DISCUSSION

Our intensive daily sampling of ichthyoplankton during the rainy season demonstrated that there were profound temporal and spatial variations in fish reproductive activity in the area influenced by the Belo Monte dams. The sampling effort allowed us to correlate hourly variations in ichthyoplankton abundance with hydrological metrics and other environmental variables. In general, fish eggs and larvae were found in all sectors, demonstrating that reproductive activity still occurred after the impoundment. Contrary to what we hypothesized, the sectors closer to the Pimental dam (*i.e.*, MR and RF), which are more strongly regulated by the dam operation, tended to have a higher abundance and richness of ichthyoplankton than the UP sector. Conversely, we found support for the hypothesis of a spawning parceling in the MR and RF sectors following the less predictable variation in water level caused by the Pimental dam. In addition, we found that fish reproductive activities were strongly connected with river level, but each sector showed its own dynamic. The probability of ichthyoplankton occurrence increased with the water level in the sectors closer to the Pimental dam (MR and RF sectors) but reduced in the UP sector. Together, these results corroborate with previous studies regarding the strong influence of dams on the dynamic of ichthyoplankton (Azevedo-Santos *et al.*, 2021; Vasconcelos *et al.*, 2022) and provide pivotal information to create better guidelines for the establishment of more sustainable dams and protocols to improve the monitoring of the ichthyofauna.

The probability of fish egg occurrence and larvae richness in the RF was ~2 times higher than in the UP sector. This indicates that the RF is an important area of fish reproduction, independently of the water level reduction that occurred after the construction of the Pimental dam. Although the fish eggs and larvae may be drifted from more upstream regions, this is unlikely because most of them are from early development stages. The high reproductive effort in the RF may be associated with the higher diversity of habitats and fish in this sector, which is considered a hotspot of biodiversity and endemism (Fitzgerald *et al.*, 2018). On the other hand, the Pimental dam may be acting as a barrier, reducing fish migrations upstream and forcing fish to reproduce downstream. Although the fish ladder exists and is an important connector in other rivers (Agostinho *et al.*, 2011; Bao *et al.*, 2019), there is still no study testing its efficiency in the Xingu River. In this sense, it is possible that adult fishes, unable to pass the dam, accumulate in the RF sector and spawn with the correct environmental stimuli (Liu *et al.*, 2021).

The probability of occurrence of fish eggs and larvae was also higher in the MR when compared to the UP sector. A high abundance of eggs and larvae in reservoirs is not uncommon (Cataldo *et al.*, 2022; Vasconcelos *et al.*, 2022). Reservoirs typically retain ichthyoplankton due to the reduction in water velocity (Pelicice *et al.*, 2015; Silva *et al.*, 2020). From December to February, the river level in the MR sector increased abruptly to accumulate water for Belo Monte's energy production activity and probably caused the ichthyoplankton to accumulate, especially on the riverbanks. According to Araújo *et al*. (2019), the residence time in the MR is approximately three days, which is relatively low when compared to other reservoirs (Marques *et al.*, 2018; Silva *et al.*, 2020). It is because the BM Complex was designed as a Run-of-the-River (ROR) system. In this sense, the retention of ichthyoplankton may be minimized, but there is still little evidence supporting the lower impact of this type of dam on fish communities and reproduction (Barros & Rosman, 2018). In the Paraná River basin, southern Brazil, a study showed that the local ROR dam had greater fish community instability over the years, despite less variation in hydrological conditions, compared to a conventional dam (*i.e.*, storage system; Baumgartner *et al.*, 2020). There is an urgent need for studies that compare the impacts of conventional and run-of-river dams over long periods, particularly, in highly diverse tropical rivers (Keppeler *et al*., 2022).

The high ichthyoplankton occurrence at the reservoir may also be associated with the presence of macrophyte banks and flooded grasses on the riverbanks of the sampling stations, which could serve as a place for larvae accumulation, mainly for protection and food (Kimura *et al.*, 2021). Another possibility is the high aquatic production of the reservoir in the early stages of the BM Complex. The fish abundance and biomass are usually high in the first years after impoundment because nutrients leach from dead, submerged vegetation, and soil organic materials (Agostinho *et al.*, 2016). However, this peak in fish production is temporary and tends to decline as nutrients are depleted (Agostinho *et al.*, 2016). Few sedentary and opportunistic fish species (*i.e.*, that depend little on hydrological variations) are expected to thrive in reservoirs after the maturation of the system (Turgeon, Turpin & Gregory-Eaves, 2019).

A high abundance of ichthyoplankton does not necessarily indicate higher reproductive success. Previous studies suggest that the mortality rates of fish eggs and larvae are disproportionally high in reservoirs. Reservoirs may act as a trap because fish eggs and larvae sink in the water column and tend to perish due to unfavorable environmental conditions (*e.g.*, low oxygen, temperature), predation, and starvation (Pelicice, Pompeu & Agostinho, 2015). The drift eggs and larvae that make up the end of the reservoirs may still be damaged by the turbines of the dam (Alves *et al.*, 2019). But there are already results that Bulb-type turbines do less damage to the ichthyoplankton that drift by them (Vasconcelos *et al.*, 2022). Another possibility is that part of the ichthyoplankton drifted to the Intermediate Reservoir, which may be considered a more inhospitable environment due to its longer residence time (~20 days; Araújo *et al.*, 2019). Overall, was found few larvae in advanced stages in the RF sector, which corroborate with the hypothesis that most of the ichthyoplankton are not able to pass the Pimental dam and reach ideal areas for their development, such as flooded forest and floodplain lakes.

We found reproductive asynchrony along the river, with fish spawning before the flood pulse in the UP sector and during the flood pulse in the MR and RF sector. In addition, the reproductive effort was parceled in the MR and RF, where the number of days with the reproductive event was higher than in the UP sector. The reproductive synchrony of a species increases the chances of success of the offspring, especially by decreasing predation rates (Ims, 1990). Therefore, the fish community, especially migratory, responds synchronously to the natural seasonal variations of the river through reproductive migrations, gonadal maturation, spawning, and initial development of eggs, larvae, and juveniles (Duponchelle *et al.*, 2021). In this sense, the asynchrony between the river sectors studied and within the MR and RF sector, which is associated with the dams' operation, may lead to the decreased reproductive success of fish in the Middle Xingu River. Ultimately, this may lead to a reduction in fish populations and, consequently, the fish stock, affecting riverine populations that depend directly and/or indirectly on fishing for their food and income (Sousa *et al*., 2021).

The composition of fish larvae changed between the river sectors. The new lentic or semi-lentic conditions in the MR sector favor the spawning of several fish groups, including many opportunistic and sedentary fishes that are known to thrive in these novel systems, such as scianids (*e.g.*, freshwater drums), hemiodontids (*e.g.*, halftooths) and characids (e.g., tetras) (Sá-Oliveira *et al.*, 2015; Zacardi & Ponte, 2016; Cajado *et al.*, 2021). Curimatids (*e.g.*, toothless characins), which are detritivorous fish, also had a higher occurrence of fish larvae in the MR sector, probably reflecting high population sizes fueled by increasing levels of decomposing material (Farago *et al.*, 2020). Interestingly, was also observed a higher occurrence of larvae from fish families that contain migratory species, such as Pimelodidae

(Hahn *et al.*, 2019), and high dependence on marginal habitats, such as Auchenipteridae and Anostomidae (Freitas *et al.*, 2015; Zacardi *et al.*, 2017b). The factors underlying the increase in these fish families are not completely clear but may involve some of the processes discussed above.

Was found a higher occurrence of Prochilodontidae and Serrasalmidae larvae in the RF when compared to the other sectors. Prochilodontidae species found in the Xingu River are all migratory, such as *Prochilodus nigricans* Spix & Agassiz 1829 and *Semaprochilodus brama* (Valenciennes 1850) (Norte Energia, 2021). This fish group has a strong reproductive seasonality (Zacardi *et al.*, 2017a; Magalhães Lopes *et al.*, 2018), demonstrating the need for stretches of uninterrupted river for optimal reproduction. Although it is possible that Prochilodontidae larvae originated from upstream sectors (the development from egg to early larvae stages is around three days; Silva *et al.*, 2022) we suspect that the migration of adult fishes is being mostly blocked by the dam. Therefore, they reproduced downstream to the Pimental dam (Yang, Yang & Chang, 2008). On the other hand, Serrasalmidae species encompass predators (piranhas) and herbivorous fishes (pacus) that do not perform long migrations (Godinho & Kynard, 2009). Their high occurrence could be associated with the presence of rapids and flood forests in this sector, which are habitat and feeding grounds for pacus (Andrade *et al*., 2019). However, it is noteworthy that a recent study indicates a reduction in the occurrence of pacus after the Belo Monte operation due to an overall reduction in flooded forest habitats (Keppeler *et al*., 2022).

The only fish family that was associated with the UP sector was Hemiodontidae. This was surprising because we expected a higher diversity of ichthyoplankton in this sector, which is less impacted by the dams (*e.g.*, Keppeler *et al*., 2022). A study conducted by Zacardi and Ponte (2016), before dam construction, showed that hemidontids were the most abundant family, so this trend may have remained in the UP and MR sectors. But several factors may be associated with the low occurrence and richness of ichthyoplankton in the UP sector. For example, it is possible that we missed some initial reproduction events at the beginning of the hydrological cycle. Another possibility is that the Pimental dam is blocking the migration of periodic, migratory species which have a large contribution to the ichthyoplankton composition (Barthem *et al.*, 2017; Van Damme *et al.*, 2019; Zacardi *et al.*, 2021). Nevertheless, other relevant anthropic impacts may reduce ichthyoplankton and fish abundance in the region, such as fisheries, and land use (Isaac *et al.*, 2015; Rizzo *et al.*, 2020; Duponchelle *et al.*, 2021). Future studies should explore ichthyoplankton data from before and after the dam operation to better understand the dynamic of ichthyoplankton in this river sector.

The co-variables included in the models were overall less important than the variation of river level and sector in explaining the variations in occurrence, and composition of the ichthyoplankton. Among the co-variables, the period of the day was the most important. The results indicated that fish spawning and larvae presence are more likely to occur at night, corroborating previous studies (Zacardi & Ponte, 2016). Spawning at night may reduce the levels of predation on fish eggs whereas the higher frequency of larvae at night is associated with vertical migration. Fish larvae migrate to the surface at night to reduce their risk of predation while they forage on phytoplankton and zooplankton (Picapedra, Sanches & Lansac-Tôha, 2018; Silva & Bialetzki, 2019). The water transparency of the Xingu River may have influenced the diurnal abundance since the larvae could more easily avoid the plankton net during the day, but not at the night (Araujo-Lima *et al.*, 2001). The type of environment was also an important covariate. The results indicated that the main channel is used for spawning and the riverbanks are sites of larval concentration (Mounic-Silva & Leite, 2013; Zacardi *et al.*, 2017a; Minghui *et al.*, 2020). The midwater environments were important for Pimelodidae larvae which prefer deeper regions for drifting and support low oxygen levels (Chaves *et al.*, 2017; Hermann *et al.*, 2021). The other covariates, such as flowmeter values, lunar index, and substrate explained a lower proportion of the data.

5 CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our results showed that the composition, richness, and occurrence of ichthyoplankton were higher in the MR and RF, two river sectors under a greater influence of the Belo Monte operation than the UP. This indicated that despite the anthropogenic impacts, the MR and RF sectors are still relevant for fish reproduction in the region. In addition, we found a reproductive period desynchrony between the sectors and more parceling reproduction in the MR and RF sectors, which can have deleterious consequences in the long term. In this sense, we suggest that the Belo Monte operation mimic the natural flow regime in the MR and RF (Xingu Big Bend) sectors, with its seasonal variability, size, frequency, and duration, to reduce asynchrony between sectors and allow fish access to nursery and feeding grounds. Furthermore, in the next years Norte Energia S.A., the concessionaire of the BM Complex, plans to keep to the consensus hydrograph as specified in the environmental impact assessment study (Rima, 2009). According to the plan, two hydrographs, Hydrograph A with a minimum peak flow of 8000 m^3s and Hydrograph B with a minimum peak flow of 4000 m^3s, should be replaced annually (IBAMA, 2014). If applied, Hydrographs A and B would reduce the minimum peak flow reported following the BM Complex operation by 35% to 67%, respectively (Keppeler *et al.*, 2022). Since there is a possibility of modifying the current hydrograph and dam impacts on fish communities may take years to unfold (Oliveira *et al.*, 2018), ongoing monitoring is advised to better assess the magnitude of the ecological changes and guide future hydrological projects in tropical basins.

ACKNOWLEDGMENTS

We are grateful for the financial support of this study by Norte Energia S.A through the Fundação de Amparo e Desenvolvimento da Pesquisa (FADESP). We would also like to thank the sampling team for the 6 months of daily dedication: Sérgio Messias, Ruineris Cajado, Fernando Guido, Paulo Bezerra, and Jerry Max Corrêa. And the constructive comments on early versions of the manuscript by Drs. Maristela Makrakis, Raphael Macieira, Suzana Bittencourt and Tatiana Pereira. Sampling was authorized by the Programa de Conservação da Ictiofauna da Área de Influência da UHE Belo Monte (Code 4276).

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SUPPLEMENTARY INFORMATION

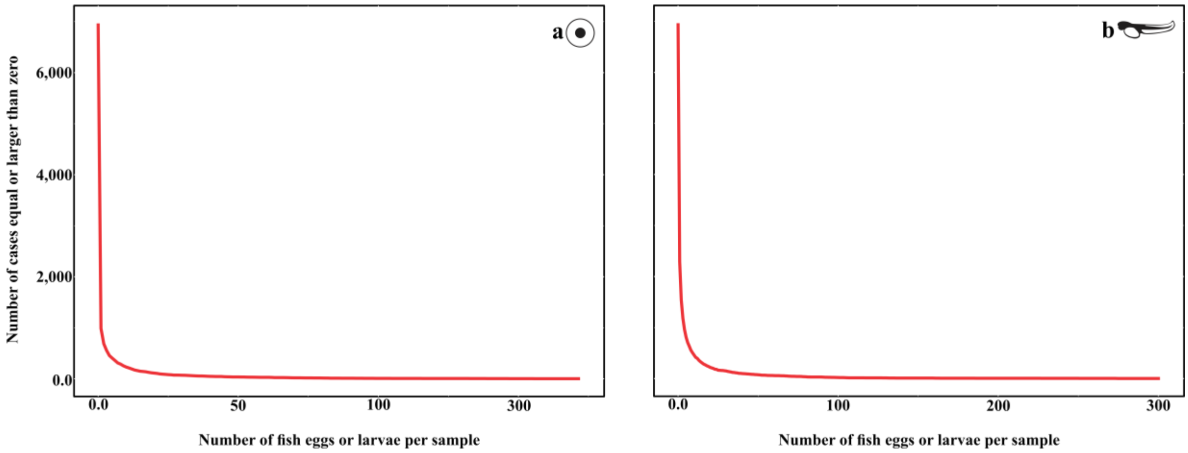

Figure S1 – Number of cases where the number of fish eggs (a) or larvae (b) were equal or larger than zero per sample.