UNIVERSIDADE FEDERAL DO PARÁ

NÚCLEO DE ECOLOGIA AQUÁTICA E PESCA DA AMAZÔNIA - NEAP PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA AQUÁTICA E PESCA - PPGEAP

Ruineris Almada Cajado

Efeito da hidrologia sazonal e dos eventos climáticos anômalos na estrutura da comunidade de larvas de peixes no baixo rio Amazonas

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> Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia Aquática e Pesca, como requisito para obtenção do título de Mestre em Ecologia Aquática e Pesca.
>
> Orientador: Dr. Marcelo Costa Andrade
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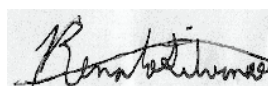
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DEDICATÓRIA

Aos meus pais, **Cristiane** e **Reginaldo**, exemplos de vida, ser humano racional e de bom coração por todos os conselhos e apoio.

EPÍGRAFE

"Dê ao homem um peixe e ele se alimentará por um dia. Ensine um homem a pescar e ele se alimentará por toda a vida."
(Anne Isabella Thackeray Ritchie)

AGRADECIMENTOS

INSTITUIÇÕES DE APOIO E FONTE FINANCIADORA

ESTRUTURA DA DISSERTAÇÃO

Para a estrutura da dissertação, optou-se pela organização na forma de capítulos, os quais foram redigidos nos padrões de artigo científico no formato das revistas em que foram submetidos para publicação. Esse modelo de dissertação encontra-se de acordo com o artigo Art. 66 do regimento do PPGEAP. Ressalta-se, que o primeiro capítulo está submetido e atualmente em revisão (Anexo 1) pela revista *Freshwater Biology* e o segundo capítulo já se encontra publicado na revista *Frontiers in Environmental Science* (DOI: 10.3389/fenvs.2022.1064170 – Anexo 2). O objetivo do primeiro capítulo foi avaliar o efeito da variação sazonal na estrutura taxonômica e funcional de larvas de peixes no trecho baixo do Rio Amazonas. No segundo capítulo foi avaliado o efeito dos eventos climáticos na estrutura taxonômica e funcional das assembleias de larvas de peixes na mesma área de estudo.

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Resumo

A reprodução dos peixes Amazônicos é altamente dependente das variações hidrológicas anuais causadas pelo pulso de inundação. Além disso, a ocorrência de eventos climáticos anômalos tem sido indicado como outro fator preponderante em afetar a dinâmica reprodutiva dos peixes. Embora exista alguma evidência do efeito da hidrologia sazonal e dos eventos climáticos anômalos sobre os parâmetros reprodutivos dos peixes, estudos por uma perspectiva funcional do ictioplâncton (ovos e larvas de peixes) são incipientes na Amazônia. Nesse sentido, o objetivo do estudo foi avaliar o efeito da variação sazonal e dos eventos climáticos anômalos na estrutura taxonômica e funcional de larvas de peixes no trecho baixo do Rio Amazonas. A captura das larvas foi realizada utilizando redes de plâncton cônicas, em torno de uma ilha aluvial localizada próximo a Santarém, Pará. Para avaliar o efeito da hidrologia sazonal, utilizou-se dados de capturas mensais durante dois ciclos hidrológicos entre janeiro e dezembro de 2013 e entre maio de 2017 e abril de 2018. Para as análises referentes aos eventos climáticos anômalos, os dados foram obtidos através de capturas mensais de janeiro a abril em quatro períodos reprodutivos durante os anos de 2013, 2014 (Neutro), 2018 (La Niña) e 2019 (El Niño). Após a identificação, os indivíduos foram classificados de acordo com traços de cada espécie em quatro grupos funcionais (e.g. estratégia de história de vida, hábito alimentar, tipo de migração e uso de micro-'habitat'/posição na coluna d'água). As relações entre a hidrologia sazonal, eventos climáticos anômalos, variáveis ambientais e a estrutura da comunidade das larvas foram avaliadas por análises multivariadas. Os dados evidenciam intensa variabilidade na estrutura da comunidade de larvas entre as diferentes fases hidrológicas e períodos climáticos (Neutro, La Niña e El Niño), com alta influência de variáveis ambientais. As espécies parecem responder a combinações de diferentes variáveis que refletem condições ambientais propícias ao recrutamento biológico de acordo com suas características ecológicas, permitindo a perpetuação ou declínio de sua abundância em cada fase hidrológica e período climático. Alterações na estrutura das assembleias de larvas indicam que a variação do regime hidrológico e a incidência de eventos climáticos anômalos atuam como um filtro na estrutura funcional das assembleias locais e reflete estratégias adaptativas para reduzir a competição interespecífica por espaço e alimento, e maximizar o recrutamento biológico. Portanto, este estudo evidencia a importância da manutenção do regime hidrológico e a necessidade de considerar os eventos climáticos anômalos para a conservação da biodiversidade e dos padrões reprodutivos e de recrutamento dos peixes, que representam importante fonte de alimentação e renda para as populações.

Palavras-chave: Ictioplâncton, reprodução de peixes, Bacia Amazônica, diversidade funcional

Abstract

The reproduction of Amazonian fish is highly dependent on annual hydrological variations caused by the flood pulse. Furthermore, the occurrence of anomalous climatic events has been indicated as another preponderant factor in affecting the reproductive dynamics of fish. Although there is some evidence of the effect of seasonal hydrology and anomalous weather events on the reproductive parameters of fish, studies from a functional perspective of ichthyoplankton (fish eggs and larvae) are incipient in the Amazon. In this sense the objective of the study was to evaluate the effect of seasonal

variation and anomalous climatic events on the taxonomic and functional structure of fish larvae in the lower reaches of the Amazon River. To evaluate the effect of seasonal hydrology, data from monthly captures were used during two hydrological cycles between January and December 2013 and between May 2017 and April 2018. For the analyzes related to anomalous weather events, data were obtained through monthly catches from January to April in four reproductive periods during the years 2013, 2014 (Neutral), 2018 (La Niña), and 2019 (El Niño). After identification, individuals were classified according to traits of each species into four functional groups (e.g., life history strategy, feeding habits, type of migration, and use of micro-habitat/position in the water column). Relationships between seasonal hydrology, anomalous weather events, environmental variables, and larval community structure were evaluated by multivariate analyses. The data show intense variability in the structure of the larval community between the different hydrological phases and climatic periods (Neutral, La Niña, and El Niño), with a high influence of environmental variables. The species seem to respond to combinations of different variables that reflect environmental conditions conducive to biological recruitment according to their ecological characteristics, allowing the perpetuation or decline of their abundance in each hydrological phase and climatic period. Changes in the structure of larval assemblages indicate that the variation in the hydrological regime and the incidence of anomalous climatic events act as a filter in the functional structure of local assemblages and reflect adaptive strategies to reduce interspecific competition for space and food and maximize biological recruitment. Therefore, this study highlights the importance of maintaining the hydrological regime and the need to consider anomalous climatic events for the conservation of biodiversity and reproductive and recruitment patterns of fish, which represent an important source of food and income for populations.

Keywords: Ichthyoplankton, fish reproduction, Amazon Basin, functional diversity

INTRODUÇÃO GERAL

Os ambientes aquáticos amazônicos são dinâmicos e sujeitos a intensas modificações fisiográficas periódicas causadas pelo pulso de inundação (JUNK *et al.*, 2011). O pulso de inundação causa drásticas alterações no fluxo e qualidade da água e, consequentemente, na disponibilidade de nutrientes, recursos alimentares, conectividade lateral e habitats adequados para os peixes (BARBOSA *et al.*, 2015; ESPÍNOLA *et al.*, 2017; HURD *et al.*, 2016).

A hidrologia dinâmica existente na Bacia Amazônica promove alta heterogeneidade ambiental ao longo do ano e afeta significativamente os parâmetros populacionais, padrões de migração, distribuição e abundância da fauna de peixes em seus diferentes estágios do ciclo de vida (larvas, juvenis e adultos) (CASTELLO *et al.*, 2019; RÖPKE *et al.*, 2016). Em particular, as comunidades de larvas de peixes em um determinado período do pulso de inundação refletem amplamente os aspectos populacionais e a dinâmica migratória e reprodutiva dos peixes adultos (CAJADO *et al.*,

2020; REYNALTE-TATAJE *et al.*, 2012; ZACARDI; BITTENCOURT; QUEIROZ, 2020).

Embora a reprodução dos peixes esteja, em geral, intimamente relacionada aos estímulos ambientais impostos pelas variações hidrológicas, as estratégias reprodutivas variam de acordo com suas caraterísticas ecológicas e tolerância fisiológicas (RÖPKE *et al.*, 2017, 2019; SILVA *et al.*, 2020). No período de águas baixas muitas espécies, principalmente de peixes Characiformes de importância comercial se deslocam dos lagos e floresta alagada em direção ao canal principal do rio, onde permanecem até o momento da reprodução durante a enchente (ARAÚJO-LIMA; RUFFINO, 2003; DUPONCHELLE *et al.*, 2021). Posteriormente, seus ovos e larvas são carreados passivamente para as áreas de várzea consideradas locais de berçário e criação dessas espécies (CAJADO *et al.*, 2020; OLIVEIRA *et al.*, 2020; OLIVEIRA; CAJADO; ZACARDI, 2021; ZACARDI; BITTENCOURT; QUEIROZ, 2020). Essa dinâmica é um processo cíclico e ocorre em sinergia com as modulações do pulso de inundação (ZACARDI *et al.*, 2017; ZACARDI; PONTE, 2021). Diferentemente, algumas espécies de bagres migradores se reproduzem durante a vazante como estratégia para evitar que os seus ovos e larvas adentrem na várzea. Isso porque as suas larvas precisam alcançar as áreas de berçário na foz do rio Amazonas que está a milhares de quilômetros dos locais de desova (BARTHEM *et al.*, 2017; GARCÍA-DÁVILA *et al.*, 2015; MIRANDA-CHUMACERO *et al.*, 2020).

Apesar dos efeitos conhecidos, gerados pela hidrologia sazonal, a reprodução dos peixes depende, ainda, de vários fatores, como a incidência de eventos climáticos anômalos (CAJADO *et al*., 2022; CATALDO *et al*., 2022). Os eventos climáticos anômalos, mais conhecidos como Eventos de Oscilação Sul do El Niño (ENSO) estão associados ao aquecimento anormal das águas superficiais que ocorre em intervalos irregulares no Pacífico tropical e podem afetar o clima global (MARENGO *et al*., 2012). Na região norte do Brasil episódios de El Ninõ causam drásticas alterações nos regimes de chuva e consequentemente promovem secas mais extremas do que o normal, enquanto episódios de La Niña possuem efeito contrário (REBOITA *et al*., 2021). A incidência de anomalias climáticas associadas ao ENSO impactam vários aspectos reprodutivos e de recrutamento da ictiofauna. Por exemplo, secas prolongadas e inundações brandas podem causar alta mortalidade de larvas e juvenis, menores proporções de fêmeas com gônadas maduras e diminuição do tamanho na primeira maturidade (CASTELLO *et al*., 2019; RÖPKE *et al*., 2022). Por outro lado, algumas espécies de peixes periódicos e migratórios se beneficiam de maiores áreas de berçário, áreas de alimentação e conectividade entre o canal principal e as várzeas durante eventos de La Niña quando a inundação é intensa

(CAMACHO GUERREIRO *et al.*, 2021; CATALDO *et al.*, 2022).

O uso da abordagem de diversidade funcional, especialmente na Amazônia, atrelada a diversidade taxônomica, é considerada uma ferramenta fundamental para compreender as respostas das comunidades de peixes às flutuações no regime hidrológico. Isso porque predições, por abordagens somente específicas locais podem dificultar o entendimento dos padrões e gerar divergências frente a elevada riqueza de espécies regionais (LAMOUROUX; POFF; ANGERMEIER, 2002). Além disso, *insights* ecológicos baseados em relações funcionais podem ser transferíveis entre regiões biogeográficas (MOI *et al.*, 2022; RÖPKE *et al.*, 2017; SILVA *et al.*, 2020). Contudo, os estudos existentes avaliaram respostas funcionais dos peixes a gradientes ambientais levando em consideração apenas peixes adultos (ARANTES *et al.*, 2018, 2019; FITZGERALD *et al.*, 2017; SILVA *et al.*, 2020). Até o momento, nenhum estudo foi realizado para avaliar a infuência do ciclo hidrológico e dos eventos climáticos anômalos no padrões funcionais das assembleias de larvas de peixes na Bacia Amazônica. Informações como essas podem prover indicativos do efeito de oscilações ambientais na reprodução dos peixes e possibilitar a identificação das condições hidrológicas críticas para a manutenção do recrutamento de espécies com diferentes características ecológicas e assim da elevada diversidade taxônomica e funcional da ictiofauna (GOGOLA *et al.*, 2021; MAPES *et al.*, 2015).

A conservação do ictioplâncton desempenha um papel essencial para a biodiversidade, serviços ecossistêmicos e para a pesca. Isso porque a renovação dos estoques naturais de grande parcela das espécies de peixes importantes para explotação comercial, de subsistência e recreativa no Baixo Amazonas depende do sucesso no recrutamento biológico de sua prole (MARIAC *et al.*, 2021; OLIVEIRA *et al.*, 2022; ZACARDI *et al.*, 2020). Assim, entender a relação entre a estrutura das assembleias de larvas de peixes e flutuações hidrológicas é fundamental para compreender como as espécies e características funcionais estão associadas ao pulso de inundação e aos eventos climáticos anômalos causados pelo El Niño Oscilação Sul (CATALDO *et al.*, 2022; SILVA *et al.*, 2020; WINEMILLER *et al.*, 2014); gerar informações que sirvam como linha de base diante da rápida degradação das várzeas amazônicas e aceleradas mudanças climáticas e hidrológicas (HURD *et al.*, 2016; WINEMILLER *et al.*, 2016); e auxiliar na tomada de decisões em estratéfias de manejo relacionadas a manutenção dos recursos pesqueiros (DUPONCHELLE *et al.*, 2021; GARCÍA-DÁVILA *et al.*, 2015; ZACARDI; BITTENCOURT; QUEIROZ, 2020; ZACARDI; PONTE, 2021). Dessa forma, nesse estudo foi avaliado: 1) O

efeito da variação sazonal na estrutura taxonômica e funcional das assembleias de larvas de peixes no trecho baixo do Rio Amazonas e 2) o efeito dos eventos climáticos na estrutura taxonômica e funcional das assembleias de larvas de peixes na mesma área de estudo.

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CAPÍTULO 1. Formatado, submetido (em 25/07/2022) e em atual processo de revisão pela revista científica **Freshwater Biology -** https://onlinelibrary.wiley.com/page/journal/13652427/homepage/forauthors.html.

Seasonal patterns in the structure of the fish larvae community in the lower Amazon River

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Abstract

1. The aim of this study was to analyze the phenology and functional structure of parental stocks of fish larvae and to evaluate how the species modulate their reproductive activities as a function of the alternation of the hydrological regime in the lower Amazon River.

2. Larvae were captured using conical plankton nets monthly over two hydrological cycles between January and December 2013, and between May 2017 and April 2018. The captures occurred around an alluvial island located near the municipality of Santarém, Pará. After identification, the larvae were classified according to traits of each species of parental into four functional groups (e.g., life history strategy, feeding habits, type of migration, and swimming-performance/microhabitat-use in the water column). The relationships between seasonal hydrology, environmental variables and larvae assembly structure were evaluated by multivariate analyses.

3. A total of 31,347 fish larvae were captured, from nine taxonomic orders, 26 families, 40 genera and 53 species. The larval assemblages showed an intense variability in taxonomic and functional composition between the different phases of the hydrological cycle (rising water, high water, receding water and low water) with high influence of environmental variables. The results show that the reproductive phenology of lower Amazonian fish is complex and different functional groups are distributed among the hydrological phases . The different

ecological characteristics allow the species to withstand specific environmental conditions of each phase.

4. Changes in the structure of larvae assemblages indicates that the variation of the hydrological regime acts as a key ecological factor for understanding the reproductive dynamics of fish and reflects adaptive strategies to reduce interspecific competition for space and food, maximizing biological recruitment. Therefore, the maintenance of natural hydrological fluctuations of Amazonian river systems has a direct implication for the conservation of biodiversity, functions and services of this ecosystem, such as fishing, ecological interactions, and high functional diversity.

Keywords: Amazon basin; Hydrological cycle; Life history; Ichthyoplankton; Functional diversity.

INTRODUCTION

Floodplain ecosystems in the Amazon River Basin are dynamic and subject to intense periodic physiographic changes driven by annual flood pulse (Junk et al., 2011). In floodplains of the Amazon river, seasonal flood pulses affect lateral connectivity between floodplain habitat and river channel with remarkable alterations in water flow and quality as well as availability of nutrients, food resources and habitat for fish across the year (Barbosa *et al.*, 2015; Hurd *et al.*, 2016; Espínola *et al.*, 2017). This dynamic hydrology in the Amazon River promotes high spatial-temporal heterogeneity of habitats, and affects fish population parameters including abundance and distribution over their different stages of the life cycle (larvae, juveniles and adults) (Röpke *et al.*, 2016; Castello *et al.*, 2019). During the high water, for example, many fish enter the floodplain areas in search of abundant food and shelter from predators (Goulding *et al.*, 2019). On the other hand, with the retraction of the waters during the receding water, most of the fish species migrate to the main channel of the river (Duponchelle *et al.*, 2021). Some territorialist groups such as the Cichlidae remain in the lakes (Arantes *et al.*, 2019b). The composition and abundance of larvae fish communities in a given phase of the flood pulse broadly reflect reproductive dynamics and migratory behaviors of the adult fish populations (Reynalte-Tataje *et al.*, 2012; Cajado *et al.*, 2020; Zacardi, Bittencourt & Queiroz, 2020a).

The reproduction of fish populations has been shown to be closely related to environmental stimuli imposed by the seasonal hydrology with strategies varying according to their specific ecological characteristics (e.g., migratory behavior) and physiological tolerance (Röpke *et al.*, 2017, 2019; Silva *et al.*, 2020). This variation in reproductive strategies that is associated with distinct ecological characteristics can be illustrated based on examples of fish populations that perform either regional or long-distance migration. In the lower water phase, many species that migrate regionally, including commercially valuable Characiformes fish (e.g., pacu – *Mylossoma albiscopum* (Cope 1872), move from lakes and flooded forests to the main river channel (Araújo-Lima & Ruffino, 2003; Duponchelle *et al.*, 2021). As the water level rises, these species groups migrate longitudinally to reproduce. In the river, their eggs and larvae are passively carried to floodplain areas that act as nursery and breeding sites for these species (Cajado *et al.*, 2020; Oliveira *et al.*, 2020; Oliveira, Cajado & Zacardi, 2021; Zacardi *et al.*, 2020a). This is a cyclic process that occurs in synergy with the modulations of the

flood pulse (Zacardi *et al.*, 2017b; Zacardi & Ponte, 2021). Contrastingly, some species of long distance-migratory catfish (e.g., dourada – *Brachyplatystoma rousseauxii* (Castelnau 1855)) reproduce during the receding water as a strategy to prevent their eggs and larvae from entering the floodplain. This strategy is ought to assure their larvae reach nursery areas thousands of kilometers downstream, at the mouth of the Amazon River (García-Dávila *et al.*, 2015; Barthem *et al.*, 2017; Miranda-Chumacero *et al.*, 2020).

Achieving these sorts of generalization based on ecological strategies of fishes (e.g., short *vs.* long distance migrators) is the central idea of functional diversity approaches (Winemiller *et al.*, 2015; Villéger *et al.*, 2017). Functional diversity approaches can be useful to improve understanding of the responses of fish communities and their reproductive strategies to environmental gradients such as those caused by flood pulse dynamics. Given the extremely high taxonomic diversity of fishes in the Amazon (e.g., 922 species registered in the river Amazonas main channel, alone) (Dagosta & Pinna, 2019), species-specific analyses often provide complex and divergent views of responses of fishes to environmental gradients (Villéger *et al.*, 2010; Sagouis, Jabot & Argillier, 2017). Functional approaches, instead, can facilitate understanding of common patterns of responses across taxa based on similar ecological characteristics driving similar responses (Lamouroux, Poff & Angermeier, 2002). Understanding of functional relationships can yet provide insights that can be comparable among different biogeographic regions (Arantes *et al.*, 2019a; Silva *et al.*, 2020; Moi *et al.*, 2022).

The utility of functional analyses to understand responses of fish communities to environmental gradients has been recognized in the last years (Fitzgerald *et al.*, 2017; Arantes *et al.*, 2018, 2019b; Silva *et al.*, 2020). However, the existent body of knowledge have largely focused on adult fish only. Considerations of other key ontogenetic phases of fish such as the larval phase—ichthyoplankton—are still missing: to date, no studies have assessed patterns of functional structure of fish larvae assemblages in response to the flood pulse in the Amazon river. This information is necessary because can provide indications of the effects of hydrological fluctuations on the reproduction of fish species with different ecological characteristics (i.e., functional groups). This, in turn, would allow to identifying critical hydrological conditions that promote recruitment of various functional groups to ultimately conserve fish production and important fisheries they sustain (Mapes *et al.*, 2015; Gogola *et al.*, 2021).

The successful biological recruitment of offspring of fish populations is essential to maintaining natural stocks of a large portion of species that are important for subsistence, commercial, and recreational fisheries in the Amazon (Zacardi *et al.*, 2020b; Mariac *et al.*, 2021; Oliveira *et al.*, 2022). In this study, to understand the effect of seasonal hydrology on the reproduction of fish assemblages, we evaluated the possible associations between taxonomic and functional composition of the ichthyoplankton with seasonal hydrology in the floodplain of the lower Amazon River. Limnological variables with potential influence on the structure of ichthyoplankton assemblages were also included in our analyses. We collected ichthyoplankton across different phases of the seasonal hydrological cycle to test the hypothesis that the reproductive activity of fishes of different taxonomic and functional groups is associated with specific hydrological conditions that optimize their larval survival. We expect that larvae of fishes belonging to different ecological strategies, or functional groups, will be more abundant in certain seasons as for example, species that migrate regionally will must be associated with the rising water phase. In contrast, the larvae of species that migrate

long distances (intercontinental migrants) must be related to the receding water phase (Barthem *et al.*, 2017). The results of this study can provide a baseline information in face of the rapid degradation of Amazonian floodplains, accelerated climate and hydrological changes, and the possible implantation of hydroelectric plants in several tributaries of the Amazon River (Hurd *et al.*, 2016; Winemiller *et al.*, 2016). Results can also assist with definitions of fisheries management strategies such as seasonal closures to protect spawning fish stocks and habitat conservation to enhance their offspring growth and survival (Zacardi *et al.*, 2017b; Miranda-Chumacero *et al.*, 2020; Duponchelle *et al.*, 2021; Zacardi & Ponte, 2021)

MATERIAL AND METHODS

Study area

This study was conducted in lower Amazon River near the city of Santarém, state of Pará. Specifically, the study was developed in the main channel of the river along marginal areas of a complex of alluvial islands locally known as "Ilha das Marrecas" (2°12'41" S and 2°18'52" S, 54 ° 45'42" W and 54 ° 43'11" W) (Fig. 1).

The water level fluctuation in the region is regulated by a unimodal flood pulse reflecting phases of high and low waters. Due to these oscillations in water level over the year, we observe four well-defined phases of the flood pulse: rising water, high water, receding water and low water. The hydrological phases was adjusted based on the historical analysis of the average water level of the Tapajós River near Santarém (Bentes *et al.*, 2018), which corresponds closest gauge to our study area. To classify the hydrological phases, we used quantitative data of water level obtained from the Brazilian Water Agency (ANA) (http://hidroweb.ana.gov.br) as follows. The 'low water' is the phase with water levels lower than 3.0 m (October, November and December); 'rising water' level vary between 3.0 and 7.0 m (January, February, March and April) with an ascending vector (increasing in water level); 'high water' the level is above 7.0 m (May and June); and 'receding water' levels vary between 7.0 m and 3.0 m (July, August and September) with a descending vector (declining the water level).

Data sampling

We collected ichthyoplankton monthly during two periods: between January and December 2013 and between May 2017 and April 2018. The samplings comprised two complete hydrological cycles. The samplings were carried out in four locations randomly distributed in the river channel on the margins of the archipelago covering microhabitats, characterized by depth close to the margin, current flow, and patterns of sedimentation and/or erosion of the margins as coves = sandy environments with a curvature pattern defined as a function of the number of sediments and hydrodynamics local, ravine = regions turbulent characterized by a constant process of soil erosion on the banks, and restingas = region of low vegetation with a sandy strip of deposition along the river. The collections were performed during daytime (3 to 6 pm) and nighttime (8 to 11 pm; UTC -3) times using vessel at reduced speed and a horizontal trawling with a conical plankton net (300 μm mesh size) performed on the subsurface (0-1 m) of the water column for five minutes. A mechanical flowmeter was attached to the plankton net to provide the volume of filtered water. The net was held against the flow to increase capture efficiency. Fish larvae were euthanized with benzocaine (250 mg. L^{-1}) according to the guidelines of the Conselho Nacional de Controle e

Experimentação Animal do Brasil (Conselho Nacional de Controle e Experimentação Animal, 2015) and then preserved in formalin (10%) and stored in polyethylene bottles labeled to be transported to the laboratory. The collection effort totaled 192 samples (24 months of collection x 4 sampling stations x 2 sampling times – day and night). Concomitantly with the collection of ichthyoplankton, limnological variables such as water temperature (°C), dissolved oxygen (mg. L^{-1}), electrical conductivity ($\mu S. Cm^{-1}$) and potential hydrogen (pH) were recorded. Hydrological data (rainfall index and water levels) for each month of collection were obtained from the website of ANA (Table 1). The license for the collection of biological material was granted by SISBIO / ICMBio / MMA through authorization number 72.330 issued based on Normative Instruction nº 154/2007.

Sample processing

In the laboratory, samples were screened by seizing the fish larvae from the suspended material, debris, and total plankton, under stereoscopic microscope. Subsequently, they were identified at the lowest possible taxonomic level, based on the regressive development sequence technique (Nakatani *et al.*, 2001) and morphological, meristic, and morphometric characteristics, using specialized bibliographies (Araújo-Lima, 1985, 1991; Araújo-Lima, Kirosvsky & Marca, 1993; Lima & Araújo-Lima, 1993; Nascimento & Araújo-Lima, 1993; Nakatani *et al.*, 2001; Leite *et al.*, 2007; Oliveira, Assakawa & Bialetzki, 2008; Oliveira *et al.*, 2021; Garcia *et al.*, 2016; Cajado *et al.*, 2021; Lima *et al.*, 2021; Silva *et al.*, 2021). Thus, the specimens identified at the level of families belonging to Engraulidae, Doradidae and Auchenipteridae were included in the analyses as taxonomic units (e.g., Engraulidae gen. sp.) because larvae of these groups were relatively abundant in the samples, and their exclusion from the analyses could influence ordination results. The taxonomic status of the species followed Fricke, Eschmeyer & van der Laan, (2022) and the classification of families was presented alphabetically according to Betancur *et al.*, (2017).

Functional classification

Each taxonomic unit was classified into four functional groups defined by (1) life history strategy, (2) feeding habits, (3) type of migration and (4) swimming-performance/microhabitat-use strategies according to Arantes *et al.*, (2018), (2019b); Silva *et al.*, (2020). Precisely because this information is effective in elucidating the main ecological mechanisms of species, such as distribution, feeding, and reproduction patterns. Furthermore, the increase or decrease of fish in these functional groups is conditioned by environmental changes that may occur in river systems, such as seasonal hydrological variations (Silva *et al.*, 2020); changes in forest cover (Arantes *et al.*, 2017); Implementation of dams (Arantes *et al.*, 2019a); and changes due to weather events (Ropke *et al.*, 2017; Cajado *et al.*, 2022). Individuals were classified based on species-level information and in cases of unavailable data available information on genera was used. Therefore, for Engraulidae gen. sp., Doradidae gen. sp. and Auchenipteridae gen. sp. functional characteristics were obtained considering traits of typical species for each of these families, based on the fish fauna inventories developed by (Imbiriba *et al.*, 2020; Oliveira *et al.*, 2020) in the study area. For Engraulidae gen. sp. the functional characteristics of the species of the genus *Anchoviella* Fowler 1911 were considered,

which are local migratory fish, periodic strategists with maturation at small size, planktivores and nektonic maneuverable (Silva *et al.*, 2020). While for Doradidae gen. sp., the species *Nemadoras humeralis* (Kner 1855), *Ossancora punctata* (Kner 1855) and *Platydoras costatus* (Linnaeus 1758) were considered, these species have convergent ecological characteristics, because they are sedentary, periodic strategists, omnivores and benthic-slow (Birindelli & Sousa, 2018). For Auchenipteridae gen. sp., the species *Auchenipterichthys longimanus* (Günther 1864) and *Centromochlus heckelii* (De Filippi 1853) were considered, both are sedentary of intermediate strategists, omnivores and benthic-slow (Freitas *et al.*, 2011; Birindelli & Akama, 2018).

The species were classified according to four life history strategies taking into account the maximum body size, size at first maturation, fecundity and parental investment by individual offspring, as previously described by (Winemiller & Rose, 1992; Röpke *et al.*, 2017; Arantes *et al.*, 2018, 2019b): *Intermediate strategists* - have fecundity between 1,000 and 9,000 relatively large oocytes (diameter 1.4-2.0 mm) and intermediate degree of parental care (e.g., internal fertilization, so that oocytes are fertilized before spawn); *Opportunistic* - correspond to fish of small size (26-113 mm standard length (SL), early maturation (<60 mm SL), high and sustained reproductive effort, but low fecundity and no parental care; *Periodic strategists with maturation at small size* (63–148 mm SL) - have fecundity between 6,760 and 74,220 small oocytes (diameter of 0.5–1.3 mm), maximum size between 137–410 mm SL and no parental care; *Periodic strategists with maturation at large sized* (> 164 mm SL) - characterized by having high fecundity between 1,000 and 202,960 small oocytes (diameter 0.7–1.6 mm), without parental care and maximum size > 253 mm SL. Species of life history strategy in equilibrium were not captured due to the ecological characteristics of this group that form couples, usually build nests, take care of the offspring, and do not have planktonic eggs and larvae (Winemiller & Rose, 1992). Hence, the fishing gear employed was not able to capture them, since it was directed to the capture of planktonic organisms.

The species were classified according to six feeding strategies based on dietary information available in the scientific literature (Arantes *et al*., 2019; Ropke *et al*., 2017; Ferreira, Zuanon & Santos, 1998) in: *Herbivores* - which feed predominantly on plant material (seeds, fruits or leaves) and filamentous algae; *Omnivores* - species that have a generalist diet without predominance of plant or animal tissue; *Detritivores* - which predominantly ingest fine particulate organic matter and periphytic algae; *Planktivores* - species that ingest phytoplankton, zooplankton and occasionally small amounts of plant material and debris; *Carnivores* - which feed on fish and numerous aquatic and terrestrial invertebrates (e.g., Ephemeroptera, Chironomidae, Coleoptera, Crustacea etc.); *Piscivores* - which feed on fish at any stage of ontogenetic development, whole or in pieces, including scales and fins.

In addition, migratory strategies were assigned based on dispersion behavior and distances of migrations performed by species. This classification was based on information previously described by Arantes *et al*., (2019) and García-Dávila *et al*., (2018) in: *Sedentary* - resident species that spend their entire life cycle in lowland (from floodplain) habitats, including lakes, eventually performing short-distance movements. These species generally have small body or territorial behavior, and are often associated with substrates or structured habitats (e.g. tree branches and aquatic vegetation); *Short-distance or lateral migrators* (between 100 and 499 km) - fish migrating between river floodplain habitats, including major river channels and lakes, connecting channels and

various vegetated habitats such as flooded forests; *Medium-distance migrators* (between 500 and 1,500 km) - comprise species that perform lateral migrations to floodplain habitats flooded during high water, but also perform longitudinal migrations (often hundreds of kilometers) along river channels during the receding water, to reproduce at the time of rising water; *Long-distance* or *interborder migrators* (>1,500 km) - comprise species that migrate thousands of kilometers along the river channels for trophic, dispersive and reproductive purposes, with the life cycle basically associated with the main channel of the river.

Finally, species were allocated according to five strategies of swimming-performance/microhabitat-use based on morphological characteristics previously described by (Arantes et al., 2019) in: *Nektonic maneuverable* - fishes have laterally compressed body and upper mouth position. The morphological traits associated with efficient swimming performance are based on a hydrodynamic body and feeding within the water column; *Nektonic burst swimmers* - have fusiform body and mouth in terminal position. The morphological traits associated with efficient swimming performance are based on a hydrodynamic body and feeding within the water column; *Epibenthic maneuverable* - relatively deep body and less hydrodynamic than nektonic maneuverable fish, but efficient in making lateral and vertical curves. Eyes positioned more dorsally than laterally; *Benthic-slow* - relatively wide body, dorsally located eyes and inferior mouth, which are characteristic of the inhabitants of the river bottom. Low muscle mass and little area in pectoral and caudal fins. *Benthic-fast* - have relatively wide body, dorsally located eyes and inferior mouth, characteristic of the inhabitants of the river bottom. Higher muscle mass and caudal fin proportion - characteristics associated with a more efficient sustained swim compared to benthic-slow fish; *Surface dwellers* - partially compressed body, usually superior mouth, short or fusiform body. Eyes positioned more dorsally than laterally. A matrix detailed with the functional characteristics of each species is provided in Supplementary material 1.

Data analyses

The abundances of fish larvae were standardized as volume of 10 m^{-3} of filtered water (number of organisms per 10m^{-3}) following Nakatani et al. (2001): $Y = (X/V) \times 10$, where Y represents the density of larvae at 10 m^{-3}, X represents the number of captured larvae and V represents the volume of filtered water. Species that occurred in less than 3% of the samples and samples where no larva was captured were removed from the data set. This criterion was necessary because relatively low-abundance taxa contribute less to the structure of the assembly and may influence the results of the ordination analyses (Gotelli & Ellison, 2013). Due to this criteria, six samples were excluded, and final statistical analysis were based on matrices of 185 samples and 46 species, 18 families, four life history strategy groups, six trophic strategy groups, four migration groups and six groups of swimming-performance/microhabitat-use. The samples were aggregated by hydrological phase, sampling station and daytime (day/night).

The density values of the biological data matrix were log-chord transformed before statistical analyses. This technique combines the logarithmic transformation that makes the distribution of species more symmetrical, reducing the effects of bias caused by abundant species with the chord transformation that removes the double zeros effect from the analysis (Legendre & Borcard, 2018). The environmental data were submitted to z-score transformation to standardize variables scales (Gotelli & Ellison, 2013).

The analytical approach a was based on Arantes et al. (2018) and Silva et al. (2020) which classified the species into functional groups related to trophic strategies, life history, habitat use and migration strategy and used multivariate analyses to investigate relationships between taxonomic structure and these functional groups in response to environmental gradients.

Permutational Multivariate Analyses of Variance (PERMANOVAs) using Bray-Curtis similarity matrix and randomizations (9999 permutations) were used to assess potential differences in temporal distribution patterns (high water, receding, low water and rising water – predictor variables) in the structure fish larvae assemblages (response variables).

Dispersion plots and simple Pearson correlation tests were used to evaluate potential collinearity between explanatory variables. Correlations between variables were <0.4, therefore, all predictor variables were maintained in the analyses. Subsequently, variance inflation factor (VIF) was also evaluated and was generally <3.0, indicating that there was no multicollinearity among the other variables (Bocard, Legendre & Gillet, 2011).

Partial redundancy analyses (pRDAs) were used to evaluate variables that potentially mediate taxonomic and functional structures of fish larvae assemblages. Emphasis was given to seasonal hydrology. The pRDA was performed using the sampling stations and time (day/night) as covariates to reduce the influences of spatial structure and sampling time, respectively. The relationships between larval density (10 m^{-3}) of taxonomic species, families, and functional groups (life history strategy, feeding habits, type of migration and swimming-performance/microhabitat-use) with seasonal hydrology and local environmental variables (rainfall index, electrical conductivity, dissolved oxygen, pH and temperature) were evaluated. Tests with 9999 permutations were used to evaluate the significant effects of environmental variables on biological data. All statistical analyses were performed in the Software R Studio version 4.1.1 using the package Vegan (Oksanen *et al.*, 2018).

RESULTS

A total of 31,347 fish larvae was captured, from nine orders, 26 families, 40 genera and 53 species (Table 2). The orders Characiformes and Siluriformes grouped the highest number of families (nine and seven, respectively). These orders comprised 75% of the number of species and approximately 83% of the captured individuals. About 87% of the individuals collected represent commercially valuable fish species that are exploited by commercial and subsistence fisheries in the lower Amazon.

Larval drift occurred throughout every month during our samplings events. The composition varied between the phases of the hydrological cycle (*Pseudo-F* = 15.22; p-value <0.001), demonstrating influences of seasonal hydrology on the structure of fish larvae assemblages.

Seasonal hydrology and local environmental variables explained 19.70% of the variation in species composition and had a significant effect on fish larvae assemblages (Permutation Tests, df = 6, F = 12.90, p-value <0.01). The first two axes of the RDA explained 19.22% of the constrained variation. The taxonomic structure of the larvae

community was strongly related with environmental gradients associated with the hydrological cycle (Fig. 2 a – b; Table 3).

Catfishes *Pimelodus blochii*, *Pseudoplatystoma punctifer* (Pimelodidae), Doradidae gen. sp. (Doradidae) and Auchenipteridae gen. sp. (Auchenipteridae) showed higher reproductive activity during the high-water phase. *Plagioscion auratus*, *P. squamosissimus* (Sciaenidae) and *Hemiodus* sp. (Hemiodontidae) had their reproduction associated with the receding water. The species *Pellona flavipinnis* (Pristigasteridae), Engraulidae gen. sp. (Engraulidae) showed a reproductive peak during low waters, with positive relations to highest temperature values.

On the other hand, *Mylossoma albiscopum* and *M. aureum* (Serrasalmidae) were more strongly associated with transitional phases in water levels the beginning of the rising water and a strong relationship with high water conductivity and dissolved oxygen concentrations. The larvae of *Schizodon fasciatus* (Anostomidae), *Potamorhina altamazonica* and *Psectrogaster amazonica* (Curimatidae) were associated with final phases of the rising water and were positively related to highest pH values (Fig. 2 a, b; Table 2).

The functional structures of the assemblages were also strongly modulated by hydrological variations ($p < 0.001$; Fig. 3a – d; Table 4). Larvae belonging to fish of intermediate life history strategy, sedentary and benthic, as well as omnivores and piscivores feeding habits, tended to be more associated with phase towards high waters. These groups were also related to the higher values of rainfall indices. On the other hand, the interborder migrators (e.g., *Brachyplatystoma* spp.) were related to the beginning of the receding water. The large species of periodic life history in addition to opportunistic, short-distance migrators, carnivores, planktivores and epibenthic maneuverable were associated with receding but also with low water. Furthermore, these groups were positively related to the higher temperatures. Smaller periodic strategists as well as medium-distance migrators, detritivores, herbivores and nektonic maneuverable and burst swimmers were associated with the rising water phase, in addition to higher values of dissolved oxygen, electrical conductivity, and pH.

DISCUSSION

In this study, using information on ichthyoplankton, the effect of seasonal hydrology on fish reproduction in the lower reaches of the Amazon River was evaluated. This is the first study to use a functional approach to investigate ichthyoplankton communities and their relations with hydrology in the Amazon river Basin. The taxonomic and functional composition of the larval community were associated with different phases of the hydrological cycle. Corroborating our hypothesis, differential association of fish larvae assemblage with specific hydrological phases was dependent fishes ecological strategies, and apparently, should favor the survival of offspring in particular phases. These findings contribute to the understanding of the interactions between the hydrological regime and fish reproduction in the Amazon River. In addition, they provide support for the implementation of protective measures during the reproductive season of commercially valuable species in the lower Amazon.

Our results demonstrate that while sedentary, omnivores, piscivores, and benthic species have their reproductive activities associated with the high water, species opportunists, large periodic, migrators of long- and short-distance, carnivores and

planktivores, as well as epibenthic maneuverable are associated with lower water levels. Periodic strategists with maturation at small size, medium-distance migrators, detritivores, herbivores, as well as nektonic burst swimmers and maneuverable reproduce in the rising water.

The reproductive phenology of neotropical ichthyofauna is known to be highly seasonal with remarkable associations of certain species groups and specific seasons (Araújo-Lima & Ruffino, 2003; Ochoa-Orrego, Jiménez-Segura & Palacio, 2015; Zacardi *et al.*, 2017b; Mariac *et al.*, 2021). Consistently, our results showed the occurrence of larvae of different species and functional groups across collection periods, indicating that there is a continuous larval drift along the hydrological cycle.

In the rising water, medium-distance migrators were predominant as indicated by other studies conducted in the Amazon Basin (Ponte, Silva & Zacardi, 2017; Zacardi *et al.*, 2017b a; Mariac *et al.*, 2021). Most species in this group are periodic strategists with maturation at small size, which have their reproduction linked to the seasonal hydrology (Röpke *et al.*, 2019, 2022). Many species of herbivorous (e.g., *M. albiscopum*) and detritivorous (*P. amazonica*) fishes tend to reproduce in the rising water because the overflow of water floods the marginal forest and increases the connection facilitating the access of larvae to floodplains, as observed by Zacardi et al. (2020a). In these areas, larvae exploit different trophic resources such as zooplankton and chironomids associated with aquatic macrophytes and flooded forest (Sánchez-botero et al., 2001; Grzybkowska et al., 2018; Andrade et al., 2019; Oliveira et al., 2021).

Groups of sedentary, omnivores, piscivores and benthic species seemed to maximize fitness and survival of larvae in high water phase. The association of catfish larvae sedentary, omnivorous, strategist intermediate (for example, Auchenipteridae gen. sp.) with the flood season is similar to the findings of Mariac et al. (2021) and Zacardi & Ponte (2021) to other floodplain regions Amazonian. Reproducing during the high waters may be a strategy to avoid intense predation that is common at low waters. Reproducing during the high waters also enhances recruitment because during this phase larvae can explore habitats such as extensive aquatic macrophytes meadows which act as refugee and feeding grounds and favor their development. In addition, during high-water, larvae of piscivores can take advantage of feeding on early stages of small and abundant Characiformes while entering in the floodplain areas (Sánchez-Botero & Araújo-Lima, 2001; Petry, Bayley & Markle, 2003; Bittencourt, 2020; Oliveira *et al.*, 2020). Finally, associations of benthic fish larvae (e.g., *P. blochii*) with high waters corroborates previous studies demonstrating that species of this functional group require minimal hydrological levels to trigger their reproduction (e.g., greater than five meters) (Cañas & Waylen, 2012; García-Dávila *et al.*, 2015; Hermann *et al.*, 2021).

The predominance of larvae of large periodic and long-distance migratory species (e.g., *Brachyplatystoma* spp.) during the receding water highlights the seasonal distribution pattern of larvae of large migratory catfishes (Barthem *et al.*, 2017). During lower water these groups migrate through Solimões-Amazon system to reach spawning areas at upstream reaches and allow the drift and migration of their offspring during the rising waters to nursery sites downstream (García-Dávila *et al.*, 2014, 2015; Cella-Ribeiro *et al.*, 2015). The larval drift of migratory fishes during the receding water can

be considered a strategy to reduce the risks of larvae and juveniles entering floodplains adjacent to the Amazon river and its tributaries (Barthem *et al.*, 2017; Chaves *et al.*, 2017; Goulding *et al.*, 2019). Therefore, the study area at lower reaches of the Amazon river constitutes a key transitional zone between the spawning areas and nursery sites for some of the large migratory catfishes, even more so because most of the larvae of these functional groups were in more advanced stages of development (flexion and post-flexion - ~ 9.0 mm of standard length).During the receding to low-waters, larvae of epibenthic maneuverable fish, short-distance migrators (e.g., *P. squamosissimus*), opportunistic, carnivores and planktivores were predominant probably because they tend to maximize growth, survival and consequently their reproductive success by benefiting from food resources that become abundant in the river channel during these phases. These functional groups may take advantages of large amounts of basal sources of production, including particulate and dissolved organic matter, phytoplankton, zooplankton, and macroinvertebrates that drift from flooded floodplains to the main channel of the river while the water levels are falling (Bonnet et al., 2008; Feitosa et al., 2019).

Fish reproduction were associated with other environmental variables, including conductivity, temperature, dissolved oxygen concentration, pH and rainfall index. This result is consistent with studies showing that the synergy of several mechanisms are responsible for stimulating the reproduction of ichthyofauna in floodplain ecosystems (Reynalte-Tataje *et al.*, 2012; Chaves *et al.*, 2017, 2019; Ponte *et al.*, 2017; Röpke *et al.*, 2022). In addition to seasonal hydrology, variations in environmental factors across seasons probably plays important roles driving fish species spawning and larval survival and development (Baumgartner *et al.*, 2008; Jiménez-Segura, Palacio & Leite, 2010; Zacardi *et al.*, 2017a). For example, the increase in rainfall, pH and electrical conductivity during the flood act as a trigger to stimulate the reproduction of many species of seasonal Amazonian fish (Araújo-Lima & Ruffino, 2003; Ponte *et al.*, 2017). Yet, as discussed by studies conducted in our study area (Arantes *et al.*, 2019b; Silva *et al.*, 2020) due to the region's landscape complexity, and consequently the presence of multiple ecological processes driven by stochastic and mechanistic variables, a large part of the variability in the larvae fish community structure was not explained by our analyses.

Implications for management and conservation

The observed patterns of larval fish assemblage structure and indications of reproduction of the ichthyofauna in association with hydrological phases, highlights the critical need for reassessing fishing policies that are in place. Seasonal fishing ban periods are directed only to species that spawn during rinsing waters (e.g. *S. fasciatus* "aracu", *M. aureum* and *M. albiscopum* "pacu") (Portaria n.º 48, de 5 de Novembro de 2007). However, our results showed that larvae of several species and functional groups are associated with other phases. For example, south American silver croaker (*Plagioscion* spp.), Amazon pellona (*Pellona* spp.) reproduce, principal, during low waters, while tiger sorubim (*Pseudoplatystoma* spp.) and Bloch's catfish (*P. blochi*) reproduced high water. Current legislation thus misses protecting several taxonomic and functional groups when their adults are spawning, and larvae are growing. In addition to our findings, information about the reproductive biology of other commercially valuable and ecologically fundamental fish (e.g., *P. squamosissimus* "pescadas", *P. flavipinnis* "apapa", *P. punctifer* "surubim") (Batista, Isaac & Fabré, 2012; Zacardi, 2020) is available

and can inform management strategies and policy making processes.

The variation of fish reproduction across the hydrological cycle we observed is a result of different ecological characteristics enabling species and functional groups to adapt to particular environmental conditions of each phase. More research is needed fully understand mechanisms driving reproductive partitioning across seasons. However, although we can only speculate, partitioning could be partially an adaptive strategy to reduce competition (e.g. space and food) to ultimately maximize survival rates and biological recruitment. Changes in the natural hydrological regime of the Amazon River can affect reproductive patterns of the ichthyofauna and recruitment of numerous fishery stocks which are fundamental as a source of food and income for populations. Therefore, our study indicates that maintaining natural hydrological fluctuations of Amazonian river systems is vital for the conservation of biodiversity and functions and services they provide (Zacardi et al., 2017a; Goulding et al., 2019; Duponchelle et al., 2021).

ACKNOWLEDGMENTS

Data availability statement

Data are available from the authors upon reasonable request.

Conflict of interest

The authors have no conflicts of interest.

Authors' contributions

Conceptualisation: RAC, DMZ, MCA. Developing methods: DMZ. Conducting the research: RAC, LSO, FKSS. Data analysis: RAC, CCA. Preparation of figures and tables: RAC. Conducting the research, data interpretation, writing: RAC, DMZ, CCA, MCA, LSO, FKSS.

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Table 1. Mean (with standard deviation values) of the water level and limnological variables of the lower Amazon River.

Variable	High water	Receding	Low water	Rising
Water level (cm)	753.54 ± 19.92	558.33 ± 120.69	259.47 ± 60.17	543.11 ± 125.89
Rainfall (mm)	250.13 ± 155.62	142.01 ± 199.61	316.59 ± 120.34	413.87 ± 298.92
Dissolved oxygen (mg/L)	3.96 ± 1.22	4.54 ± 1.68	4.84 ± 0.89	4.17 ± 1.25
Electric conductivity (µS/cm)	45.11 ± 2.59	55.21 ± 9.51	58.38 ± 7.46	43.77 ± 2.50
pH	7.46 ± 0.28	7.45 ± 0.49	7.78 ± 0.75	7.61 ± 0.76
Water Temperature (°C)	29.76 ± 0.68	30.29 ± 0.96	28.47 ± 1.14	29.59 ± 0.67

Table 2. List of species and density (No. of individuals per 10 m-3) of fish larvae sampled during the study on the banks of the Marrecas Island complex, in the lower Amazon River, Pará, Brazil. * N = number of individuals; Abbreviation = referring to the species abbreviations displayed in the ordination of Figure 2a.

Taxons	Abbreviation	N	Density			
			High water	Receding	Low water	Rising
BELONIFORMES		—	—	—	—	—
Belonidae		—	—	—	—	—
Strongylura timucu (Walbaum 1792)	Stt	1	—	0.12	—	—
Hemiramphidae			—	—	—	—
Hyporhamphus brederi (Fernández-Yépez, 1948)	Hyb	1	0.16	—	—	—
CHARACIFORMES		999	5.38	0.66	13.15	211.71
Anostomidae		43	0.14	0.18	—	25.67
Leporinus sp.	Lep	977	3.94	—	4.20	254.98
Rhytiodus microlepis Kner 1858	Rhm	12	—	—	0.33	1.93
Schizodon fasciatus Schultz 1944	Scf	4.619	11.61	0.78	31.06	583.71
Bryconidae		—	—	—	—	—
Brycon amazonicus (Agassiz 1829)	Bca	5	—	—	—	0.56
Characidae		15	0.93	—	0.14	1.76
Curimatidae		34	—	—	0.26	7.54
Potamorhina altamazonica (Cope 1878)	Poa	987	1.23	0.26	1.52	232.47
Potamorhina latior (Spix & Agassiz 1829)	Pol	10	—	—	—	1.59
Psectrogaster amazonica Eigenmann & Eigenmann 1889)	Psa	2.285	4.24	0.17	2.48	436.45
Psectrogaster rutiloides (Kner 1858)	Psr	25	0.22	—	—	36.03
Cynodontidae		—	—	—	—	—
Cynodon gibbus (Spix & Agassiz 1829)	Cyg	3	—	—	—	0.37
Rhaphiodon vulpinus Spix & Agassiz 1829	Rhv	61	—	—	0.63	9.20
Hemiodontidae		105	—	—	0.19	10.93
Anodus elongatus Agassiz 1829	Ane	421	—	3.47	8.32	61.14
Hemiodus sp.	Hem	154	—	4.43	6.57	8.95
Prochilodontidae		—	—	—	—	—
Prochilodus nigricans Spix & Agassiz 1829	Prn	93	—	—	0.74	47.49
Semaprochilodus insignis (Jardine 1841)	Sei	36	—	—	1.87	2.43
Semaprochilodus taeniurus (Valenciennes 1821)	Set	43	0.30	—	0.84	4.60
Serrasalmidae		1	—	—	—	0.12
Mylossoma albiscopum (Cope 1872)	Myl	6.062	4.11	1.73	78.78	1728.28
Mylossoma aureum (Spix & Agassiz 1829)	Myu	5.502	0.52	1.16	238.56	1408.82
Piaractus brachypomus (Cuvier 1818)	Pib	5	0.41	—	—	0.44
Serrassalmus sp.	Ser	3	—	0.29	—	—
Triportheidae		—	—	—	—	—

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Triportheus angulatus (Spix & Agassiz 1829)	Tan	1.758	2.12	32.89	12.72	222.46
Triportheus auritus (Valenciennes 1850)	Tau	109	0.58	0.50	1.88	37.27
CLUPEIFORMES		5	—	0.48	—	0.16
Clupeidae		—	—	—	—	—
Rhinosardinia amazonica (Steindachner 1879)	Rha	22	0.57	1.89	0.45	0.35
Engraulidae		—	—	—	—	—
Engraulidae gen. sp.	Eng	1.096	4.38	57.61	50.49	43.09
Pristigasteridae		—	—	—	—	—
Pellona castelnaeana Valenciennes 1847	Pec	49	0.15	—	0.91	5.03
Pellona flavipinnis (Valenciennes 1837)	Pef	1.557	3.30	13.14	83.46	236.92
GYMNOTIFORMES		—	—	—	—	—
Sternopygidae		—	—	—	—	—
Eigenmannia sp.	Eig	1	—	—	—	0.14
PERCIFORMES		—	—	—	—	—
Sciaenidae		—	—	—	—	—
Pachypops fourcroi (Lacepède 1802)	Paf	8	—	—	—	0.87
Plagioscion auratus (Castelnau 1855)	Pga	152	1.73	20.58	5.61	—
Plagioscion squamosissimus (Heckel 1840)	Pgs	725	1.07	36.48	36.76	32.79
PLEURONECTIFORMES		—	—	—	—	—
Achiridae		—	—	—	—	—
Hypoclinemus mentalis (Günther 1862)	Hym	11	—	1.25	—	0.26
SILURIFORMES		399	3.08	0.09	0.85	46.22
Auchenipteridae		—	—	—	—	—
Auchenipteridae gen. sp.	Auc	1.054	3.88	0.49	—	142.51
Tatia sp.	Tat	3	0.24	—	—	0.14
Trachelyopterus galeatus (Linnaeus 1766)	Trg	10	0.89	0.13	—	0.21
Cetopsidae		16	—	—	—	7.59
Cetopsis coecutiens (Lichtenstein 1819)	Cec	17	—	0.12	0.10	1.95
Doradidae		—	—	—	—	—
Doradidae gen. sp.	Dor	63	2.13	0.71	—	7.58
Heptapteridae		24	—	0.15	—	6.11
Loricariidae		1	—	—	0.11	—
Pimelodidae		65	3.73	0.77	—	5.53
Brachyplatystoma filamentosum (Lichtenstein 1819)	Brf	29	0.24	—	0.34	4.06
Brachyplatystoma juruense (Boulenger 1898)	Brj	80	0.63	6.07	0.52	4.79
Brachyplatystoma sp.	Bra	25	0.43	0.18	0.13	2.22
Brachyplatystoma rousseauxii (Castelnau 1855)	Brr	1	—	—	0.13	—
Calophysus macropterus (Lichtenstein 1819)	Cam	64	0.97	—	0.10	12.77
Hypophthalmus edentatus Spix & Agassiz 1829	Hpe	73	2.46	1.85	1.34	3.28
Hypophthalmus fimbriatus Kner 1858	Hpf	20	0.49	0.66	0.33	0.67
Hypophthalmus oremaculatus Nani & Fuster, 1947	Hpo	14	0.80	0.28	—	—
Phractocephalus hemioliopterus (Bloch & Schneider 1801)	Phh	1	0.15	—	—	—
Pimelodus blochii Valenciennes 1840	Pmb	428	19.53	2.48	2.15	42.20
Pinirampus pirinampu (Spix & Agassiz 1829)	Pnp	2	—	—	—	0.40
Pseudoplatystoma punctifer (Castelnau 1855)	Psp	646	11.25	0.12	0.37	154.07
Pseudoplatystoma tigrinum (Valenciennes 1840)	Pst	50	4.21	—	—	4.32
Sorubim lima (Bloch & Schneider 1801)	Sol	172	1.60	—	—	23.05
Trichomycteridae		2	—	—	0.02	0.16
SYNBRANCHIFORMES		—	—	—	—	—
Synbranchidae		—	—	—	—	—
Synbranchus marmoratus Bloch 1795	Sym	1	0.09	—	—	—
TETRAODONTIFORMES		—	—	—	—	—

Tetraodontidae		—	—	—	—	—
Colomesus asellus (Müller & Troschel 1849)	Coa	62	0.15	—	—	7.37
Unidentified		30	1.98	0.27	3.06	30.98
Total larvae		31,347	106.02	192.29	591.46	6164.82

Table 3. Results of redundancy analyses (RDA) for taxonomic structures of fish larvae assemblages and environmental variables in the lower Amazon. Bold values indicate significance (p<0.05).

Variable	Species			Families		
	Variance	F	Pr (>F)	Variance	F	Pr (>F)
Water level (cm)	0.15	14.34	**0.00**	0.21	22.27	**0.00**
Rainfall (mm)	0.20	1.78	0.05	0.25	1.10	0.34
Dissolved oxygen (mg.L^{-1})	0.19	2.08	**0.02**	0.25	1.99	0.05
Electric conductivity (µS.cm^{-1})	0.09	19.57	**0.00**	0.11	24.53	**0.00**
pH	0.18	6.65	**0.00**	0.23	6.34	**0.00**
Water Temperature (°C)	0.19	2.93	**0.00**	0.24	4.09	**0.00**

Table 4. Results of redundancy analyses (RDA) for functional structure of fish larvae assemblages and environmental variables in the lower Amazon. Bold values indicate significance (p<0.05).

Variable	Life history			Feeding			Microhabitat use			Migratory		
	Variance	F	Pr (>F)	Variance	F	Pr (>F)	Variance	F	Pr (>F)	Variance	F	Pr (>F)
Water level (cm)	0.10	4.02	**0.01**	0.21	14.89	**0.00**	0.12	27.10	**0.00**	0.21	7.72	**0.00**
Rainfall (mm)	0.10	0.95	0.40	0.25	3.60	**0.00**	0.16	2.51	**0.04**	0.30	2.25	0.09
Dissolved oxygen (mg.L^{-1})	0.10	1.58	0.20	0.27	2.35	**0.04**	0.17	1.00	0.38	0.29	1.66	0.17
Electric conductivity (µS.cm^{-1})	0.06	11.95	**0.00**	0.15	32.26	**0.00**	0.15	7.20	**0.00**	0.27	13.73	**0.00**
pH	0.09	6.92	**0.00**	0.24	9.67	**0.00**	0.17	2.31	0.06	0.29	7.73	**0.00**
Water Temperature (°C)	-	-	-	0.26	3.33	**0.01**	0.17	1.00	0.39	0.19	42.92	**0.00**

Figure legends

Figure 1. Study area highlighting the sampling locations, inlets areas (a), restinga swamps areas (b) and steep ruts (c), the banks of the Complex of Ilha das Marrecas in the lower Amazon River in Pará, Brazil.

Figure 2. Redundancy analysis (RDA) showing associations between environmental variables and taxonomic structure of fish larvae assemblages at (a) species level and (b) families. A detailed list of the species and their respective abbreviation is available in Table 1. The least representative species and families were removed from the graphic to facilitate visualization of information.

Figure 3. Redundancy analysis (RDA) showing associations between environmental variables and the functional structure of fish larvae assemblages. (a) life history strategy, (b) feeding habits, (c) swimming-performance/microhabitat-use, and (d) migration.
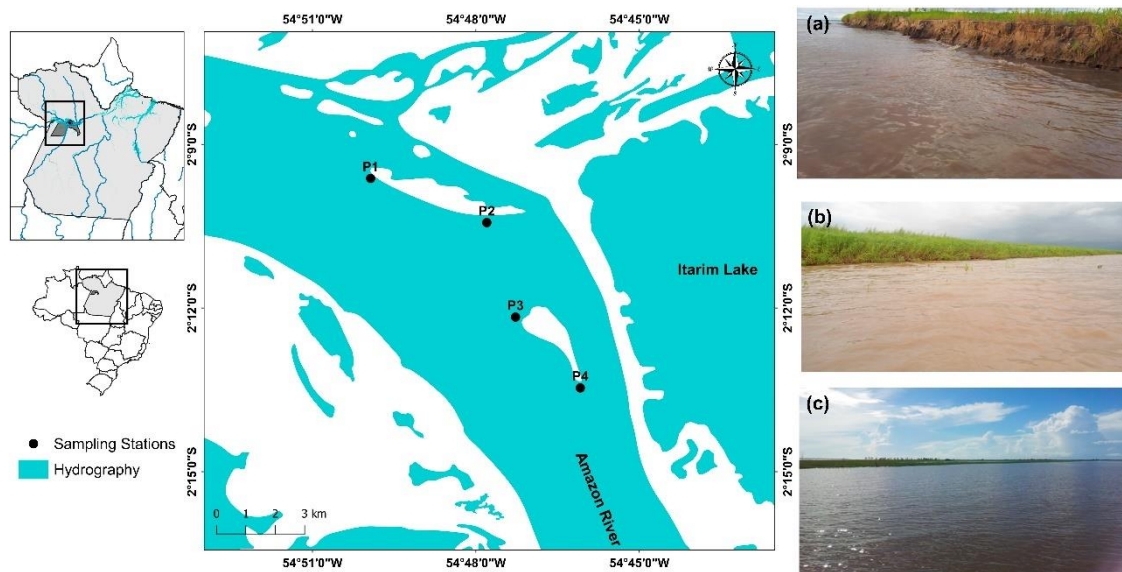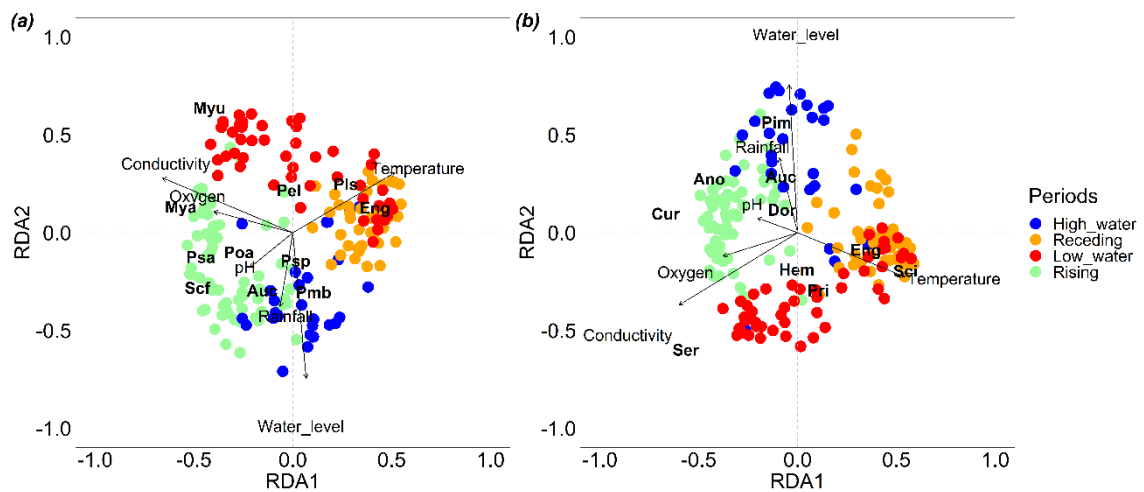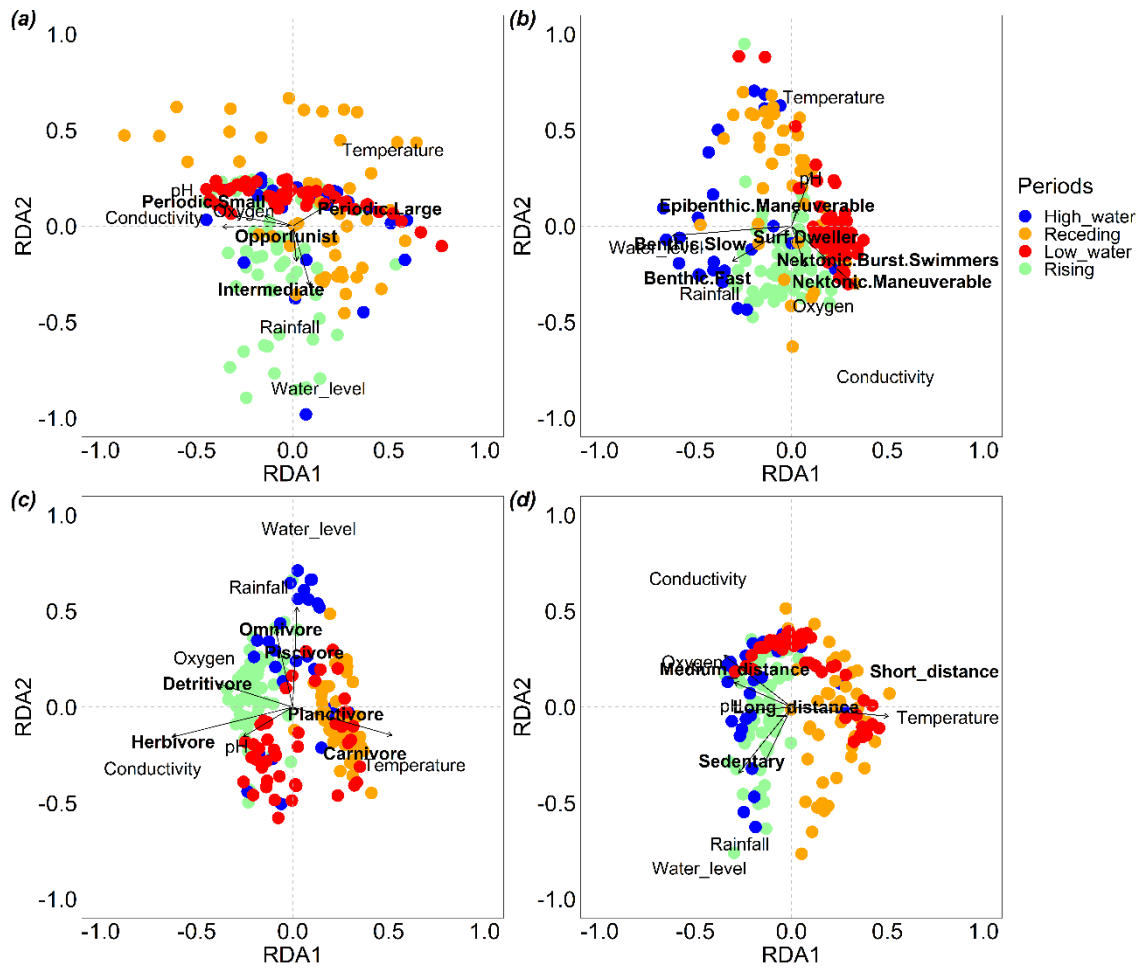
Figures

Figure 1

Figure 2

Figure 3

Effects of anomalous climatic events on the structure of fish larvae assemblages in the eastern Amazon

Ichthyoplankton and climatic events

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Abstract

The reproduction of neotropical fish is linked to environmental stimuli that act as triggers in this process. Thus, it is possible to affirm that specific environmental changes can delimit most fish's period and reproductive success. El Niño Southern Oscillation phenomena (ENSO) influence rainfall and, consequently, hydrological dynamics, affecting several fish population aspects, especially reproductive aspects. However, in the Amazon, empirical evidence of the effect of anomalous climatic events on fish reproduction is incipient. In this sense, we investigated the taxonomic and functional structure of parental fish larvae stocks and how species modulate their reproductive activities before (2013 and 2014) and during La Niña (2018) and El Niño (2019) events. The data evidence that the larval assemblages suffered alterations in the taxonomic and functional composition between the three analyzed periods and a pattern of temporal distribution with a high influence of environmental variables. Flow, pH, and electrical conductivity were the most important variables to modulate fish reproductive intensity between periods. The species seem to respond to combinations of these variables that reflect environmental conditions conducive to biological recruitment according to their ecological characteristics, allowing the perpetuation or decline of their abundance in each period. All species of commercial interest associated with the neutral period showed a sharp decline in the subsequent moments. These results suggest that the incidence of anomalous climatic events added to regional fisheries exploitation can negatively affect the phenology and demographic patterns of larvae assemblages on a short temporal scale.

During the neutral period, the community was dominated by larvae of periodic large, herbivores, piscivores, epibenthic maneuverable, and nektonic burst swimmers. The decrease in the abundance of certain functional groups at the neutral and La Niña period favored an accelerated ecological succession during the El Niño period, due to the increase of species from basal trophic levels (planktivores), generalists (omnivores), highly resilient (intermediate strategists), sedentary, short-distance migrants and little commercially exploited. Thus, the results contribute to the understanding of the interactions between anomalous climatic events and the reproduction of fish with different ecological characteristics in the Amazon River.

1   Introduction

El Niño Southern Oscillation (ENSO) events are associated with abnormal surface water warming that occurs at irregular intervals in the tropical Pacific and can affect global climate (Marengo et al., 2012). Severe ENSO seasons affect not only the Pacific Ocean but the inland waters of the entire planet (Ward et al., 2014). In the northern region of Brazil, El Niño episodes cause drastic changes in rainfall patterns and consequently promote more extreme droughts than normal, while La Niña episodes have the opposite effect (Reboita et al., 2021). In Amazonian river systems, ENSO effects are reflected by changes in flow conditions, limnological variables, lateral connectivity, and seasonal biogeochemical cycles (Towner et al., 2021). During El Niño, the absence of rain causes, among others, severe droughts, decreased lateral connectivity, intense forest fires, and reduced floodplain areas. Meanwhile, the La Niña seasons are marked by high hydrological and flow levels, large amounts of rainfall, increased biological productivity, and a diversity of habitats suitable for the development of associated organisms (Towner et al., 2021). Additionally, La Niña seasons are related to abundant fishing harvests in the Amazon (Isaac et al., 2016).

Although the Amazon ichthyofauna is very adapted to the intense hydrological dynamics that naturally occur in this system, due to the periodicity of the flood pulse, studies indicate that extreme climatic events can cause significant and lasting changes in the taxonomic composition and functional diversity of the fish community in floodplain environments (Freitas et al., 2013; Röpke et al., 2017). The way the ichthyofauna responds to the existing environmental conditions during anomalous hydrological events is related to the ecological characteristics of each species and that often allow them to support or not such conditions (Chessman, 2013; Chea et al., 2020). The climatic anomalies associated with ENSO impact several population aspects of fish, especially reproductive ones. For example, prolonged droughts and mild floods can cause high mortality of larvae and juveniles, lower proportions of females with mature gonads, and decreased size at first maturity (Castello et al., 2019; Röpke et al., 2022). On the other hand, some species of periodic and migratory fish benefit from larger nursery areas, feeding areas, and the connectivity between the main channel and the floodplains during La Niña events when the flood is intense (Oliveira et al., 2014; Camacho Guerreiro et al., 2021; Cataldo et al., 2022).

Although studies indicate the existence of the effect of La Niña and El Niño on the reproductive success of ichthyofauna, few investigations have been carried out on this topic, especially in the Amazon. Empirical information from the perspective of the ichthyoplankton community stands out as a fundamental tool to assess the effect of changes in environmental gradients on fish reproduction (Cajado et al., 2020; Tyler et al., 2021). Ichthyoplankton dynamics reflect the status of commercially and ecologically

important fish populations and provide predictive answers about potential future recruitment (Zacardi et al., 2017a; Humphries et al., 2020).

Understanding the response of the fish community to climatic anomalies through a functional face applied to ichthyoplankton becomes fundamental because it makes it possible to identify a more predictable response of biological communities to environmental changes (Arantes et al., 2019a; Gogola et al., 2021). Information of this nature would contribute to the understanding of the effect of climate change on the reproductive aspects of Neotropical fish. This fact is aggravated because, in recent decades, events such as ENSO have become increasingly intense and frequent in the tropics due to increasing changes in the global climate (Espinoza et al., 2019); and thus, studies of their effects on ichthyoplankton communities can help in decision-making for effective management measures for the conservation of fisheries resources.

In this study, we evaluated the possible influences of ENSO on the taxonomic and functional structure of the fish larvae community in the surroundings of a Lower Amazon River floodplain. Environmental variables with potential influence on the structure of ichthyoplankton assemblages were also included in our analyses. We collected ichthyoplankton in three hydrological periods: neutral, La Niña, and El Niño during the rising of river water, the reproductive phase of most fish species in the Lower Amazon (Zacardi et al., 2017b), to test the hypothesis that anomalous climatic events significantly affect fish reproduction, with changes in demographic aspects and in the taxonomic and functional structure of fish larvae assemblages. We expect that the response of species to climate change will be influenced by their functional traits. For example, pelagic fish larvae must be associated with different periods than benthic species, because the former may be more sensitive to changes in water masses than the latter, which have more geographically fixed, near-bottom habitat requirements (Duarte et al., 2020, 2022; Silva et al., 2020). In addition, periodic species, as well as medium-distance migrators, should be more abundant during La Niña, due to favorable conditions for the reproduction of these fish, such as greater amounts of rainfall and river flow (Zacardi et al., 2017b; Humphries et al., 2020). Finally, we believe that commercially exploited species will have their reproduction more affected, given that previous studies have observed the effect of climatic events on the reproductive parameters of these fish (Röpke et al., 2022)

2   Material and methods

2.1.1 Study area

Amazon River, responsible for almost 95% of all discharge in the Amazon basin, with an average flow of 209,000 (m^{-3}. s), is classified as a whitewater river, having high dissolved oxygen concentrations and conductivity electrical, almost neutral pH, and large concentrations of nutrient-rich sediments, making it a highly dynamic and productive river (Barthem and Fabré, 2004; Junk et al., 2011). Due to the local characteristics of the river's hydrodynamics, erosion processes, transport, and sediment deposition on the archipelago, this environment has annual changes in its structure. These changes generate a mosaic of habitats in the floodplain (i.e., channels, marginal lakes, extensive aquatic macrophytes stands) that favor success in the life cycle of many regional species (Zacardi et al., 2017b; Oliveira et al., 2020). It should be noted that the floodplain in the Amazon River is locally called "várzea" which represents regions of the fluvial plain flooded by white water rivers rich in sediments, coming from the Andes, which fertilize the soil favoring the growth and establishment of extensive areas of aquatic vegetation (Piedade

et al., 2020), colonized by an association of invertebrates (entomofauna) and periphyton in the root system serving as food sources for many aquatic biota organisms (Sánchez-Botero et al., 2007; Magalhães et al., 2015).

The local climate is classified as the Am type in the Köppen system, that is, rainy tropical, with a restricted annual temperature range and mean monthly precipitation of over 60 mm. Mean air temperature is approximately 27.7°C and related humidity, is 86%, varying little during the year, while annual rainfall is approximately 2,000 mm (Costa et al., 2013).

The archipelago of the Ilha das Marrecas is an important fluvial and lake fishing area in the Lower Amazon, with the city of Santarém being the main fish market for landing and marketing fish (Pereira et al., 2019). Fisheries in the study area sustain per capita fish consumption rates of 40–94 kg.yr^{-1}, well above the global average of 16 kg.yr^{-1} (Isaac et al., 2016). The fishing activity occurs intensively for eight months throughout the year and the composition of the species caught varies between the hydrological phases, but basically focuses on medium and large migratory species, representatives of the families Serrasalmidae (e.g., *Mylossoma* spp) Anostomidae (e.g., *Schizodon* spp.), Pimelodidae (e.g., *Brachyplatystoma* spp., *Pseudoplatystoma* spp.), Pristigasteridae (e.g., *Pellona* spp.), Sciaenidae (e.g., *Plagioscion* spp.) and Curimatidae (e.g., *Psectrogaster* spp.) (Isaac et al., 2016). Fisheries productivity is associated with several factors, but in general, the highest catches per unit of effort are associated with lower values of flow, river level, rainfall, and higher temperatures (Pinaya et al., 2016).

2.1.2 Data sampling

Ichthyoplankton were collected monthly during four reproductive periods between January and April 2013, 2014, 2018, and 2019. Sampling was carried out over four stations randomly distributed in the river channel at the edge of the archipelago. The collections were carried out during the daytime (3 pm to 6 pm) and nighttime (8 pm to 11 pm, UTC -3) aboard a local vessel at reduced speed, through horizontal trawls carried out in the subsurface (0-1 m) of the water column for five minutes using a conical plankton net with 300 μm mesh size and coupled mechanical flowmeter to obtain the volume of filtered water. The net was always held against the flow to increase capture efficiency. Fish larvae were euthanized with benzocaine (250 mg. L-1) and then preserved in formalin (10%) and stored in polyethylene bottles labeled to be transported to the laboratory. The collection effort totaled 128 samples at the end of the study (16 months of collection x 4 sampling stations x 2 sampling times - day and night), and all samples contained fish larvae.

Concomitantly with the collection of ichthyoplankton, limnological variables such as water temperature (°C), dissolved oxygen (mg. L^{-1}), electrical conductivity (μS. cm^{-1}) and potential hydrogen (pH) were recorded using a multiparameter. Hydrological data (rainfall index, flow, and water levels) for each month of collection were obtained from the website of Brazilian Water Agency - ANA (http://hidroweb.ana.gov.br). The ENSO phenomena data were obtained by the National Oceanic and Atmospheric Administration - NOAA (www.psl.noaa.gov/data/climateindices/list/). The ENSO values were quantitatively expressed by the Oceanic Niño Index (ONI), where values greater than or equal to 0.5 represent El Niño events and values less than or equal to -0.5 La Niña events (values between -0.5 and 0.5 represent neutral periods when none of the events occur). Based on this index, the reproductive periods (months from January to April) of 2013 and

2014 were considered neutral, while 2018 was considered La Niña and 2019 El Niño. The license for the collection of biological material was granted by SISBIO / ICMBio / MMA through authorization number 72.330 issued based on Normative Instruction nº 154/2007

2.1.3 Sample processing

In the laboratory, samples were screened by seizing the fish larvae from the suspended material, debris, and total plankton, under stereoscopic microscope. Subsequently, they were identified at the lowest possible taxonomic level, based on the regressive development sequence technique (Nakatani et al., 2001) and morphological, meristic, and morphometric characteristics, using specialized bibliographies. The larvae classified as "unidentified" or at the order level corresponded to individuals with damaged structures and/or at a very early stage of development and made up less than 10% of the collected material. Thus, the specimens identified at the level of families belonging to Engraulidae, Doradidae and Auchenipteridae were included in the analyses as taxonomic units (e.g., Engraulidae gen. sp.) because larvae of these groups were relatively abundant in the samples, and their exclusion from the analyses could influence ordination results. The taxonomic status of the species followed (Fricke et al., 2022)

2.1.4 Functional classification

We assumed that captures of fish larvae in plankton reveal the adults individuals of the species are in reproductive activity in the region at a certain phase of the hydrological cycle. This assumption is reasonable because the structure of ichthyoplankton communities results from patterns in the reproductive behavior and gene flow of adults (Zacardi et al., 2020; Mariac et al., 2021). Thus, functional traits we used here were selected according to the biological aspects of adult fish and their relationship with ecosystem and community functions (Rosado et al., 2013; Winemiller et al., 2015; Gogola et al., 2021).

Each taxonomic unit was classified into four functional groups defined by (1) life history strategy, (2) feeding habits, (3) type of migration and (4) swimming-performance/microhabitat-use strategies according to (Arantes et al., 2018, 2019b; Silva et al., 2020) (Table 1). Individuals were classified based on species-level information and in cases of unavailable data available information on genera was used. Therefore, for Engraulidae gen. sp., Doradidae gen. sp. and Auchenipteridae gen. sp. functional characteristics were obtained considering traits of typical species for each of these families, based on the fish fauna inventories developed by (Imbiriba et al., 2020; Oliveira et al., 2020) in the study area. For Engraulidae gen. sp. the functional characteristics of the species of the genus *Anchoviella* Fowler 1911 were considered, which are local migratory fish, periodic strategists with maturation at small size, planktivores and nektonic maneuverable (Silva et al., 2020). While for Doradidae gen. sp., the species *Nemadoras humeralis* (Kner 1855), *Ossancora punctata* (Kner 1855) and *Platydoras costatus* (Linnaeus 1758) were considered, these species have convergent ecological characteristics, because they are sedentary, periodic strategists, omnivores and benthic-slow (Birindelli and Sousa, 2018). For Auchenipteridae gen. sp., the species *Auchenipterichthys longimanus* (Günther 1864) and *Centromochlus heckelii* (De Filippi 1853) were considered, both are sedentary of intermediate strategists, omnivores and benthic-slow (Freitas et al., 2011; Birindelli and Akama, 2018).

The species were classified according to four life history strategies considering the maximum body size, size at first maturation, fecundity and parental investment by individual offspring, as previously described by (Winemiller and Rose, 1992; Röpke et

al., 2017; Arantes et al., 2018, 2019b): Intermediate strategists - have fecundity between 1,000 and 9,000 relatively large oocytes (diameter 1.4-2.0 mm) and intermediate degree of parental care (e.g., internal fertilization, so that oocytes are fertilized before spawn); Opportunistic - correspond to fish of small size (26-113 mm standard length (SL), early maturation (<60 mm SL), high and sustained reproductive effort, but low fecundity and no parental care; Periodic strategists with maturation at small size (63–148 mm SL) - have fecundity between 6,760 and 74,220 small oocytes (diameter of 0.5-1.3 mm), maximum size between 137-410 mm SL and no parental care; Periodic strategists with maturation at large sized (> 164 mm SL) - characterized by having high fecundity between 1,000 and 202,960 small oocytes (diameter 0.7-1.6 mm), without parental care and maximum size > 253 mm SL (Supplementary material 1). Species of life history strategy in equilibrium were not captured due to the ecological characteristics of this group that form couples, usually build nests, take care of the offspring, and do not have planktonic eggs and larvae. Hence, the fishing gear employed was not able to capture them, since it was directed to the capture of planktonic organisms.

The species were classified according to six feeding strategies based on dietary information available in the scientific literature in: Herbivores - which feed predominantly on plant material (seeds, fruits or leaves) and filamentous algae; Omnivores - species that have a generalist diet without predominance of plant or animal tissue; Detritivores - which predominantly ingest fine particulate organic matter and periphytic algae; Planktivores - species that ingest phytoplankton, zooplankton and occasionally small amounts of plant material and debris; Carnivores - which feed on fish and numerous aquatic and terrestrial invertebrates (e.g., Ephemeroptera, Chironomidae, Coleoptera, Crustacea etc.); Piscivores - which feed on fish at any stage of ontogenetic development, whole or in pieces, including scales and fins.

In addition, migratory strategies were assigned based on dispersion behavior and distances of migrations performed by species. This classification was based on information previously described by García-Dávila et al. (2018) and Arantes et al. (2019b) in: Sedentary - resident species that spend their entire life cycle in lowland (from floodplain) habitats, including lakes, eventually performing short-distance movements. These species generally have small body or territorial behavior, and are often associated with substrates or structured habitats (e.g. tree branches and aquatic vegetation); Short-distance or lateral migrators (between 100 and 499 km) - fish migrating between river floodplain habitats, including major river channels and lakes, connecting channels and various vegetated habitats such as flooded forests; Medium-distance migrators (between 500 and 1,500 km) - comprise species that perform lateral migrations to floodplain habitats flooded during high water, but also perform longitudinal migrations (often hundreds of kilometers) along river channels during the receding water, to reproduce at the time of rising water; Long-distance or interborder migrators (>1,500 km) - comprise species that migrate thousands of kilometers along the river channels for trophic, dispersive and reproductive purposes, with the life cycle basically associated with the main channel of the river.

Finally, species were allocated according to five strategies of swimming-performance/microhabitat-use based on morphological characteristics previously described by (Arantes et al., 2019b) in: Nektonic maneuverable - fishes have laterally compressed body and upper mouth position. The morphological traits associated with efficient swimming performance are based on a hydrodynamic body and feeding within

the water column; Nektonic burst swimmers - have fusiform body and mouth in terminal position. The morphological traits associated with efficient swimming performance are based on a hydrodynamic body and feeding within the water column; Epibenthic maneuverable - relatively deep body and less hydrodynamic than nektonic maneuverable fish, but efficient in making lateral and vertical curves. Eyes positioned more dorsally than laterally; Benthic-slow - relatively wide body, dorsally located eyes and inferior mouth, which are characteristic of the inhabitants of the river bottom. Low muscle mass and little area in pectoral and caudal fins. Benthic-fast - have relatively wide body, dorsally located eyes and inferior mouth, characteristic of the inhabitants of the river bottom. Higher muscle mass and caudal fin proportion - characteristics associated with a more efficient sustained swim compared to benthic-slow fish; Surface dwellers - partially compressed body, usually superior mouth, short or fusiform body. Eyes positioned more dorsally than laterally.

2.1.5 Data analyses

The abundances of fish larvae were standardized as volume of 10 m^{-3} of filtered water (number of organisms per $10m^{-3}$) following Nakatani et al. (2001): $Y = (X/V) \times 10$, where Y represents the density of larvae at 10 m^{-3}, X represents the number of captured larvae and V represents the volume of filtered water. The final statistical analysis consisted of matrices of 128 samples and 55 species, four life history strategy groups, six trophic strategy groups, four migration groups and six swimming/microhabitat use groups. Samples were aggregated by climatic period (Neutral, La Niña and El Niño), sampling season and time of day (day/night). For the ordination analyses (RDA and PCA) the environmental data were submitted to z-score transformation to standardize variables scales (Gotelli and Ellison, 2013). Dispersion plots and simple Pearson correlation tests were used to evaluate potential collinearity between explanatory variables before analysis. Subsequently, variance inflation factor (VIF) also evaluated the presence of multicollinearity between the variables, considering values up to 3.0 as the limit of multicollinearity (Bocard et al., 2011). Was metrics water level with the flow were highly collinear ($r^2 = 0.92$), and therefore, the water level was excluded from the analysis as it contained the highest VIF (9.94). After removing water level, all variables showed low correlations (<5) and VIF lower than three.

The Principal Component Analysis (PCA) was used to reduce the dimensions of variables environmental and examine the existence of environmental differences between periods. Axes with eigenvalues greater than 1.0 were used for interpretation, according to the Kaiser-Guttman criterion. Only variables with score coefficients >0.4 were considered biologically important (Gotelli and Ellison, 2013).

Differences in temporal distribution patterns (Neutral, La Niña, and El Niño - predictor variables) in the taxonomic and functional structure of fish larvae assemblages (response variables) were evaluated using abundance data (larvae density.10m^{-3}) and analyzed using a model-based multivariate approach (Warton et al., 2015) with the R package *mvabund* (version 4.1.3). The *mvabund* package uses simultaneous generalized linear models (GLMs), which specify the mean-variance relationship in the data (*manyglm*), which for the larval density data was a negative binomial distribution with a log-link function (confirmed by examining residual plots during model validation) (Warton et al., 2015). In addition, a distance-based approach, multivariate and univariate GLMs, using the same linkage function as in the previous model, was fitted to test the effect of ONI and environmental variables (electrical conductivity, pH, dissolved oxygen,

rainfall, and flow) on the assemblage of fish larvae. The contributions of taxa to the sum of logarithmic odds ratios (or sum of multivariate deviations) for period effects (Neutral, La Niña and El Niño), ONI, and environmental variables significant were investigated (with a correction applied to p- values to account for multiple tests). The nature of the significant contributions of taxa to the inter-period differences in the multivariate model was also investigated by fitting univariate models for each significant taxon in the *mvabund*.

A non-metric multidimensional scaling ordination (nMDS) was used to visualize the variations in the taxonomic composition of the larval assemblage between periods. To visualize the effects of variables from the best-fit GLM model variables on fish larvae assemblages the variables were plotted using Partial Redundancy Analysis (pRDAs) with emphasis on ONI, whose significance is evaluated by a test with 999 permutations. For the ordering for pRDA, the density values of the biological data matrix were log-chord transformed. This technique combines the logarithmic transformation that makes the distribution of species more symmetrical, reducing the effects of bias caused by abundant species with the chord transformation that removes the double zeros effect from the analysis (Legendre and Borcard, 2018). The pRDA was performed using the sampling stations, years, months, and time (day/night) as covariates to reduce the influences of spatial structure, interannual, monthly and sampling time, respectively. The relationships between larval density (10 m⁻³) of taxonomic species, and functional groups (life history strategy, feeding habits, type of migration and swimming-performance/microhabitat-use) with the Oceanic Niño Index and local environmental variables (flow, rainfall index, electrical conductivity, dissolved oxygen, pH and temperature) was evaluated. For the composition graph in RDA, only the species that showed significant differences between the three periods using the GLM model were used, precisely to facilitate the interpretation of the results graphically. These statistical analyses were performed in the Software R version 4.1.1 using the package Vegan (Oksanen et al., 2018).

3   Results

Environmental variables differed between the periods studied. The first two axes of PCA explained approximately 55% of the data variability. The La Niña period presented higher values of electrical conductivity, pH, and rainfall that were positively associated with PC1, while El Niño presented higher values of temperature, ONI, dissolved oxygen, and flow, variables associated more with PC2, except for flow that was negatively more associated with PC1 (Figure 2; Table 1). The neutral period recorded a gradient associated with the intermediate conditions environmental between the two periods of ENSO.

A total of 50,484 fish larvae classified in nine orders, 27 families, 40 genera and 55 species were captured (Supplementary Material 1). The composition and abundance of larval assemblages differed significantly between the neutral (2013 and 2014), La Niña (2018) and El Niño (2019) periods (LR = 763.5, p-value = 0.001) (Fig 3). The assemblage differences between each period were driven by the significant contributions of 20 species (Fig. 4). The mean density of larvae captured in the neutral period (123.05 larvae 10m⁻³) was 13 times greater than the La Niña period (17.88 larvae.10m⁻³) and about six times greater than the El Niño period (39.88 larvae.10m⁻³).

ONI and local environmental variables explained 9.66% of the change in species composition and had, except temperature and dissolved oxygen, significant effect on fish

larval assemblages (RDA: permutation tests, df = 7, F = 3.55, p-value < 0.001). The first two axes of the RDA explained 13.44% of the restricted variation. The taxonomic structure of the larval assemblage was strongly associated with the environmental conditions arranged along the temporal gradient (Table 2; Figure 5). The larvae of the Characiformes *Mylossoma aureum*, *M. albiscopum*, *Schizodon fasciatus*, *Leporinus* sp., *Anodus elongatus*, Siluriformes *Pseudoplatystoma punctifer*, *Sorubim lima*, and Clupeiformes *Pellona flavipinnis*, *P. castelnaeana* and Engraulidae gen. sp. were more representative in the neutral period and showed a sharp decline in their abundances in subsequent periods (LR: p-value <0.05) (Figure 4). Interestingly, all these species, except Engraulidae gen. sp., are highly commercially exploited in the Lower Amazon region. The curimatid *Psectrogaster amazonica* we associated with the La Niña period and were positively associated with high gradients of electrical conductivity (LR = 42.78, p-value = 0.001) and pH (LR = 12.43, p-value = 0.04). While Auchenipteridae gen. sp., *Pimelodus blochii*, and *Hemiodus microlepis* increased in abundance during the El Niño period, a fact evidenced by the association of these species with high ONI (Figure 5). Furthermore, the abundance of these species decreased with higher pH values (LR: p-value <005).

The functional structures of the assemblages also changed between periods (LR = 739.4, p-value = 0.001) and were strongly modulated by ONI and local environmental variables (RDA: permutation tests, df = 7, F = 4.53, p-value < 0.001) that explain 11.61% of the change in the functional structure of the larval assemblage. Larvae of fish large periodicals, herbivores, piscivores, epibenthic maneuverable, and nektonic burst swimmers were more abundant during the neutral epoch and were negatively associated with electrical conductivity and pH and positively to the flow (p-value <0.05) (Table 3). Larvae of fish migratory medium-distance, with a life history strategy periodic of small-sized, and maneuverable nektonic predominated during the La Niña season (2018), in addition, they were positively related to the high gradients of pH, electrical conductivity, and negatively to the flow. While larvae of species with intermediate life history strategy, sedentary, short-distance migratory, planktivores, omnivores as well as benthic slow and benthic fast species, were associated with El Niño (2019), a fact observed by the positive correlations of these groups with high ONI, in addition to being positively related to higher values of flow and temperature and negatively to rainfall, electrical conductivity, and pH (p-value <0.05) (Figure 6 a-b). Larvae of fish opportunistic life-history, as well as long-distance migrators, carnivores, and Surface dwellers, were not affected by the periods. However, they were negatively influenced by pH and electrical conductivity. Only long-distance migrants and Surface dwellers were not influenced by the variables included in our models.

4   Discussion

The patterns of association of larval community to hydrological periods are dependent on the ecological strategies of each species and show that climatic events modulate the structure of larval fish assemblages, corroborating our hypothesis. These findings contribute to an understanding of interactions between anomalous climatic events and fish reproduction in the Amazon River. Larvae of large periodic fish, piscivores, herbivores, maneuverable epibenthic, and nektonic burst swimmers predominated in the neutral period. On other hand, larvae of small periodicals and medium-distance migrators were more abundant in the La Niña period. In addition, larvae of fish with basal feeding habits (planktivores), generalists (omnivores), intermediate strategists, short-distance, and sedentary migrators, as well as benthic and commercially unexploited species, dominated assemblages during El Niño.

The environmental conditions were characteristic of each period, but the flow and precipitation values diverged from the proposed models for Amazon region throughout the seasonal cycle (Towner et al., 2021). Higher flows were observed during El Niño despite lower amounts of rainfall. Recent studies have documented abnormal precipitation in Andean regions caused by Pacific Decadal Oscillation (PDO), and ENSO in positive phases (Rodríguez-Morata et al., 2019; Mohammadi et al., 2020). This may favor higher temperatures in this period and, consequently, rapid melting of glaciers that contribute as one of the sources of water for the Amazon River, as observed by Rocha et al., 2019. It is known that the Andean thaw acts as a regulator of the hydrological regime and strongly affects geomorphology, biochemistry, and ecology of headwater tributaries of the Amazon basin (Filizola and Guyot, 2011; Vauchel et al., 2017), exporting a source of sediments, organic matter, and nutrients to the lower sectors of this basin.

The higher values of pH and electrical conductivity during La Niña possibly associated with high rainfall recorded during this period. The rainfall regime is a main regulatory agent of water courses, being responsible for the distribution of nutrients and ions in the water column, affecting concentrations of physicochemical variables in rivers (Esteves, 1998; Zuliani et al., 2016). According to Carvalho et al. (2000), during increased precipitation, pH tends to rise and approach neutrality, as there is a greater dilution of dissolved compounds and faster flow. This is caused by the increase in the volume of water which causes the acidity of the water to decrease. However, rainfall is responsible for leaching the soil from adjacent regions, influencing the periodic supply of suspended solids, particulate inorganic matter, and natural calcium carbonate in the region, and increasing turbidity (Silva et al., 2008). Thus, the electrical conductivity that depends on the ionic composition of water bodies is also influenced by the volume of local rainfall.

Our results showed that in the neutral period the mean density of larvae was much higher than in the La Niña and El Niño periods. This high variability in abundance between different periods has also been recorded in other river systems (Bednarski et al., 2008; Marschall et al., 2021). Changes in the flow and amount of rainfall have been suggested as plausible explanations for the variation in fish reproductive success in rivers with floodplain areas (King et al., 2009; Andrews et al., 2020; Stoffers et al., 2022). In fact, most species associated with the neutral period showed a positive relationship to flow, pH, and electrical conductivity, but precipitation was less important. In Amazonian rivers, increased flow, which is correlated at river level, is the main mechanism for transporting eggs and larvae to floodplain areas (Oliveira et al., 2020; Zacardi et al., 2020). It is noteworthy that the early stages of fish are critical due to their high susceptibility to predation and the need for readily available food resources for growth (Grenouillet and Pont, 2001; Montenegro et al., 2020). Therefore, the floodplain is considered an excellent nursery and natural breeding ground during the initial cycle of fish development (Bittencourt et al., 2020; Zacardi et al., 2020).

The studies by Baumgartner et al. (2008) and Tondato et al. (2010) also recorded the association of pH and electrical conductivity with the abundance of fish larvae, however, the effect of these variables on fish reproduction is not known for sure, but somehow, they induce migration and spawning for some species. Additionally, the decrease in larvae of fish of commercial interest after the neutral period may indicate some connection with fishing carried out in the region. Zacardi et al. (2018) verified the relationship between the production of landed fish and the abundance of larvae in the lower stretch of the Amazon River and observed that the fishing effort undertaken on adults compromises the spawning stock and, consequently, the annual recruitment of

resources. The reproductive parameters of commercially exploited species are more susceptible to the effects of climatic events (Röpke et al., 2022), suggesting that environmental factors and fishing intensity can act simultaneously for the failure or success of fish recruitment in each period. Therefore, relatively minor changes in the reproductive success of large periodic can lead to poor recruitment for at least two years (Bayley et al., 2018; Castello et al., 2019; Cataldo et al., 2022).

The inferred effects of climatic events on the biodiversity of fish larvae indicate that the environmental conditions associated with ENSOs act as a filter in the functional structure of local assemblages, as observed in studies involving adult fish in the Amazon (Freitas et al., 2013; Röpke et al., 2017). Several functional groups had reproduction strongly associated with periods of high flux values, as they exploit favorable conditions for the transport of larvae to locations conducive to development. The large-size periodics decreased in abundance during ENSOs. These fish are more exploited by fisheries, in addition, they have a slow life cycle, being more sensitive to environmental changes (e.g., decreased flow) and anthropogenic pressures (Castello et al., 2019; Camacho Guerreiro et al., 2021). Larvae of many fish epibenthic maneuverable, herbivorous, and piscivorous benefit from increased flows as they are carried by rising water levels into recent floodplains to explore structurally complex habitats. For example, herbivore larvae (e.g., *Mylossoma* spp.) tend to colonize aquatic vegetation in search of refuge and food (Bittencourt et al., 2020; Oliveira et al., 2020), and piscivorous larvae maximize their survival by capturing abundant prey in the various habitats and micro-habitat of the floodplain (Tondato et al., 2010; Nunn et al., 2012; Grzybkowska et al., 2018).

On the other hand, although the lower flows during La Niña may indicate some disadvantages in dispersal mechanisms, the offspring of small periodic fish can take advantage of the low abundances of predatory fish larvae, such as piscivores and large periodic, to maximize recruitment. This strategy guarantees good ecological conditions and advantages for the survival of small periodic since predation is one of the main mortality factors during the initial ontogeny of fish (Nunn et al., 2012; Cajado et al., 2018; Humphries et al., 2020).

The El Niño period, in turn, was less favorable to the reproduction of some previously abundant functional groups (e.g., periodicals, medium-distance migrators, herbivores, and maneuverable epibenthic), suggesting that the combination of environmental conditions favorable to the reproduction of most of these groups did not occur effectively. This result corroborates the view that, regardless of anomalous hydrological periods, there is scaling at the time of spawning season between species (Shuai et al., 2016; Barthem et al., 2017; Tyler et al., 2021) and functional similarity reflects the preference between reproductive periods. For example, the associations of slow benthic and fast benthic fish larvae, as well as sedentary ones with the high fluxes in El Niño corroborate previous studies that demonstrate that species of these functional groups require minimum hydrological levels to trigger their reproduction (for example, greater than five meters) (Cañas and Waylen, 2012; Hermann et al., 2021). This allows the larvae to enter the floodplain areas and explore the spatial patterns and nature of resources essential for successful recruitment, as reported by Duarte et al. (2020, 2022) and Zacardi and Ponte (2021). Thus, the period and extent of the flooding over the river plain significantly contribute to the generation and maintenance of the biodiversity of the Amazon ichthyofauna (Röpke et al., 2017; Frederico et al., 2021).

These examples further indicate that changes in environmental conditions

associated with ENSOs favor some functional groups but are detrimental to others. However, a deeper understanding of how climatic events influence the structure of fish descendants can be obtained from the expansion of the sampling effort in spatial and temporal scales, inclusion of interactions between factors such as seasonal periods, water level elevation intervals, river, prey availability, lateral connectivity, and forest cover.

5   Conclusion

The variation in the taxonomic and functional structure of the fish larvae community between periods highlights the potential for extreme weather events as a factor affecting fish reproduction in the Amazon River. Despite this evidence, further studies are needed to better understand the processes that shape the reproductive dynamics of fish under anomalous hydrological conditions in the Amazon basin. Although we can only assume, the interaction between hydrological variations and factors such as changes in local environmental variables, ecological relationships, and fisheries seem to enable the success of certain functional groups in each period. The findings of this study can serve as a baseline to assist the implementation of protective measures on reproductive fish stocks, for example, in times of ENSO under atypical flow conditions and changes in environmental characteristics, where the intensity of reproduction and the biological recruitment is predictable, and thus adjust the duration of fish reproduction protection periods. An alternative widely used in the region as an effective action for the conservation of species and the sustainable use of fisheries resources.

Data availability statement

Data are available from the authors upon reasonable request.

Author Contributions

Conceptualisation: RAC, DMZ, MCA. Developing methods: RAC, DMZ, LSO, FKSS. Conducting the research: RAC, LSO, FKSS. Data analysis: RAC. Preparation of figures and tables: RAC. Conducting the research, data interpretation, writing: RAC, DMZ, MCA, LSO, FKSS.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Legend of figures

Figure 1. Study area, "Ilha das Marrecas" complex, lower stretch of the Amazon River, Pará, Brazil.

Figure 2. PCA analysis among variables environmental in the three sampled periods (neutral, La Niña, and El Niño) during the rising water in the Lower Amazon.

Figure 3. Non-metric multidimensional scaling ordinations (nMDS) visualizing period effects on fish assemblage composition. MAL – *Mylossoma albiscopum*, MAU – *M. aureum*, SCF – *Schizodon fasciatus*, PSA – *Psectrogaster amazonica*, POA – *Potamorhina altamazonica*, POL- *P. latior*, AUC – Auchenipteridae gen. sp., TAN – *Triportheus angulatus*, TAU – *T. auritus*, ENG – Engraulidae gen. sp., LES – *Leporinus* sp., PLF – *Pellona flavipinnis*, PEC – *P. castelnaeana*, PMB – *Pimelodus blochii*, PSP – *Pseudoplatystoma punctifer*, ANE – *Anodus elongatus*, CAM – *Calophysus* cf. *macropterus*, HEM – *Hemiodus microlepis*, PRN – *Prochilodus nigricans*, CYG – *Cynodon gibbus*, HEI – *Hemiodus immaculatus*, HES – *Hemiodus* sp., RHA –

Rhinosardinia amazonica, BRJ – *Brachyplatystoma juruense*, PLS – *Plagioscion squamosissimus* and DOR – Doradidae gen. sp.

Figure 4. Summary of results from individual multivariate GLM for period effects on larval assemblage composition, the percent contribution of univariate model deviance of significant taxa to the parameter deviance in the multivariate model, and the associated *p*-value. Figures of the fish were adapted from Galvis et al. (2006) and Santos et al. (2006).

Figure 5. Redundancy analysis (RDA) showing the association between environmental variables and the taxonomic structure of fish larvae assemblages. Only the most representative species were displayed in the graph. A detailed list of species is available in Supplementary Material 1 and their abbreviations are in the legend of figure 2.

Figure 6. Redundancy analysis (RDA) showing the association between environmental variables and the functional structure of larval assemblages. (a) life history strategy, (b) feeding habits, (c) swimming/microhabitat use, and (d) migration.
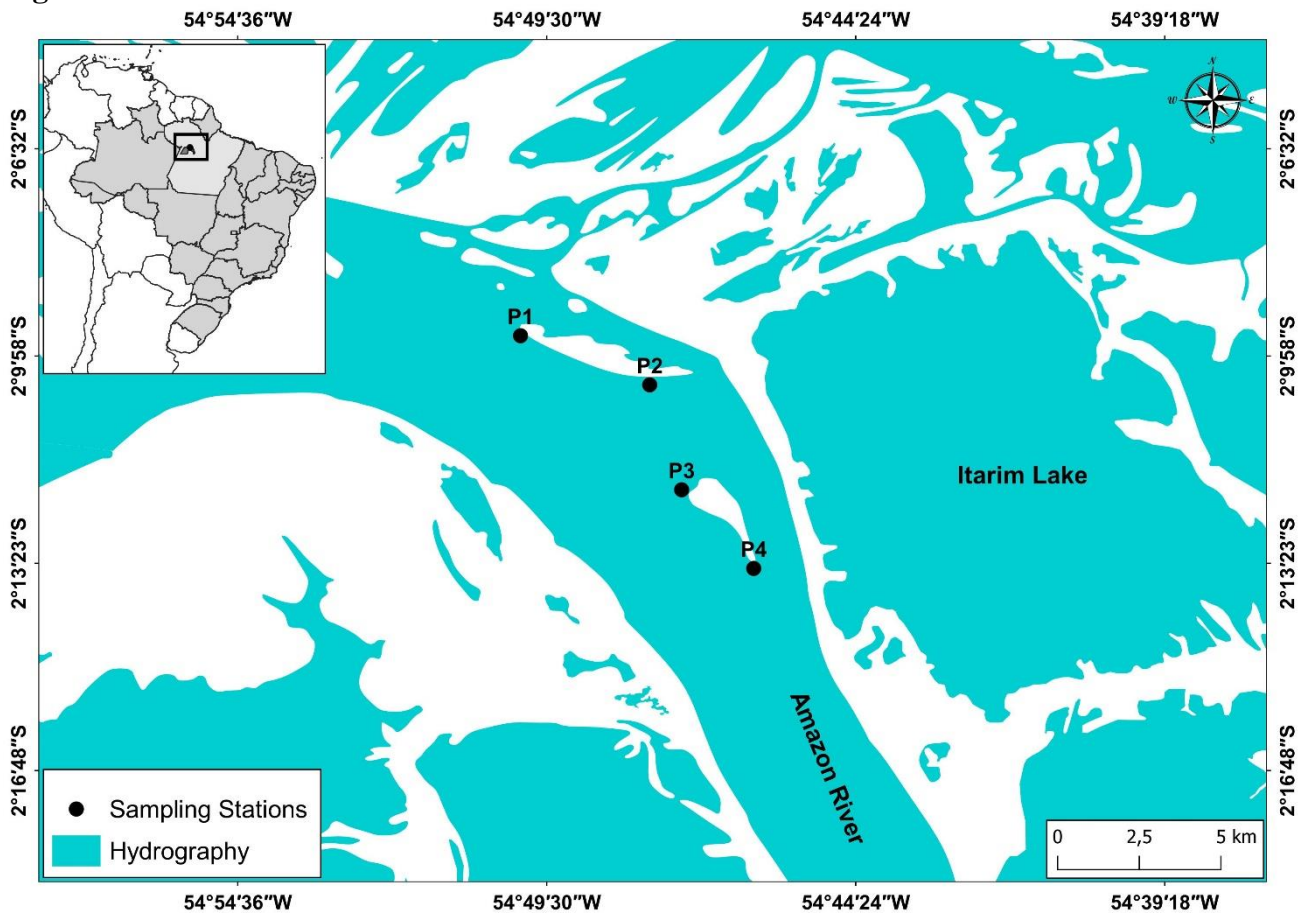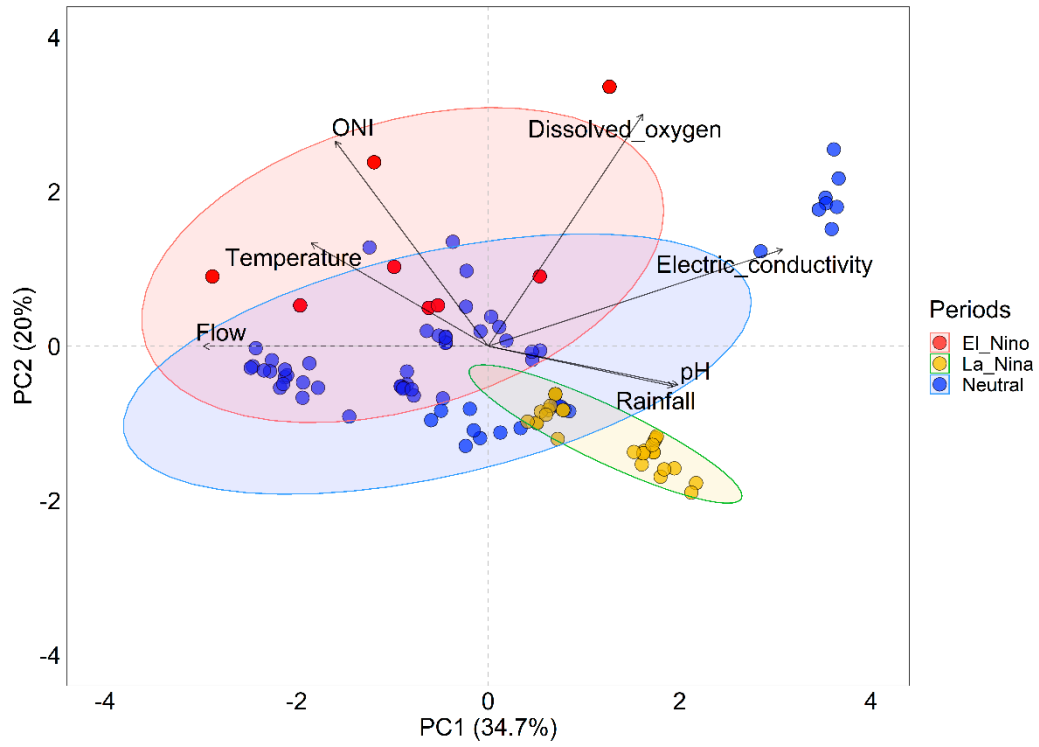
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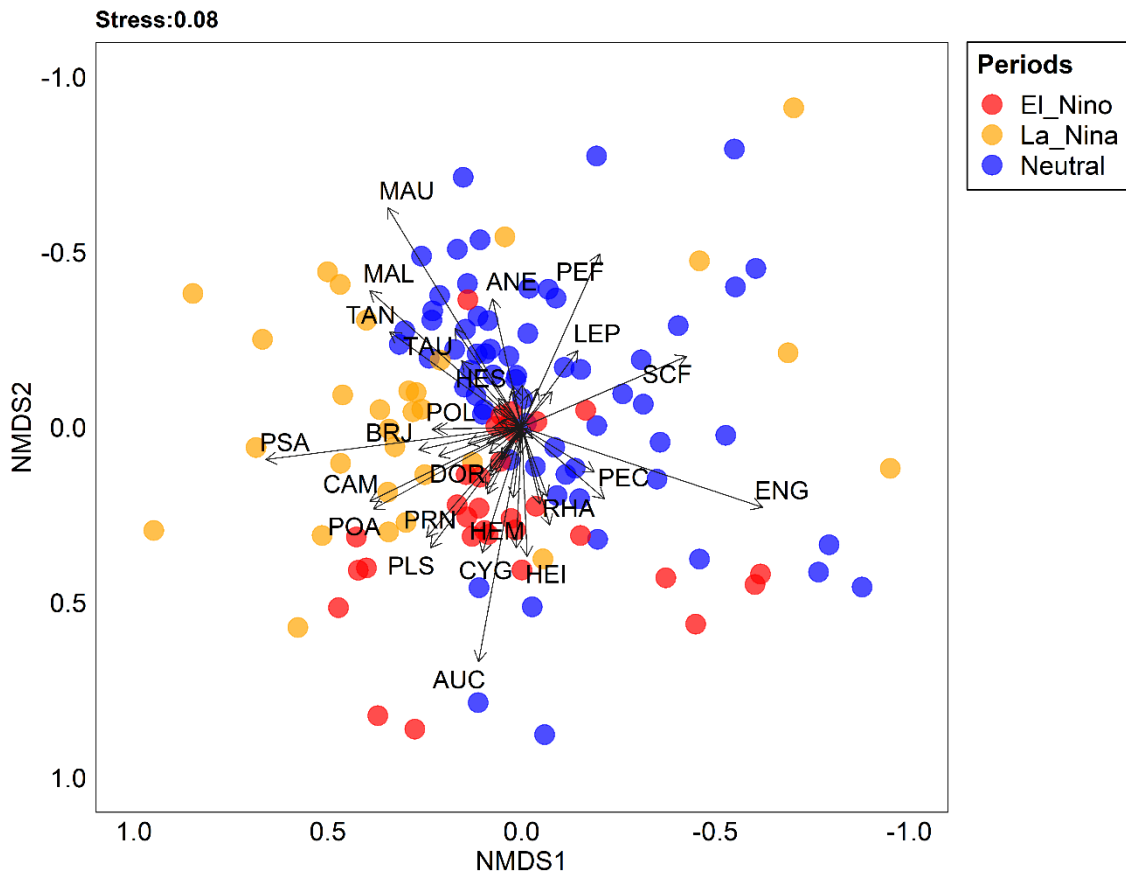
Figure 1
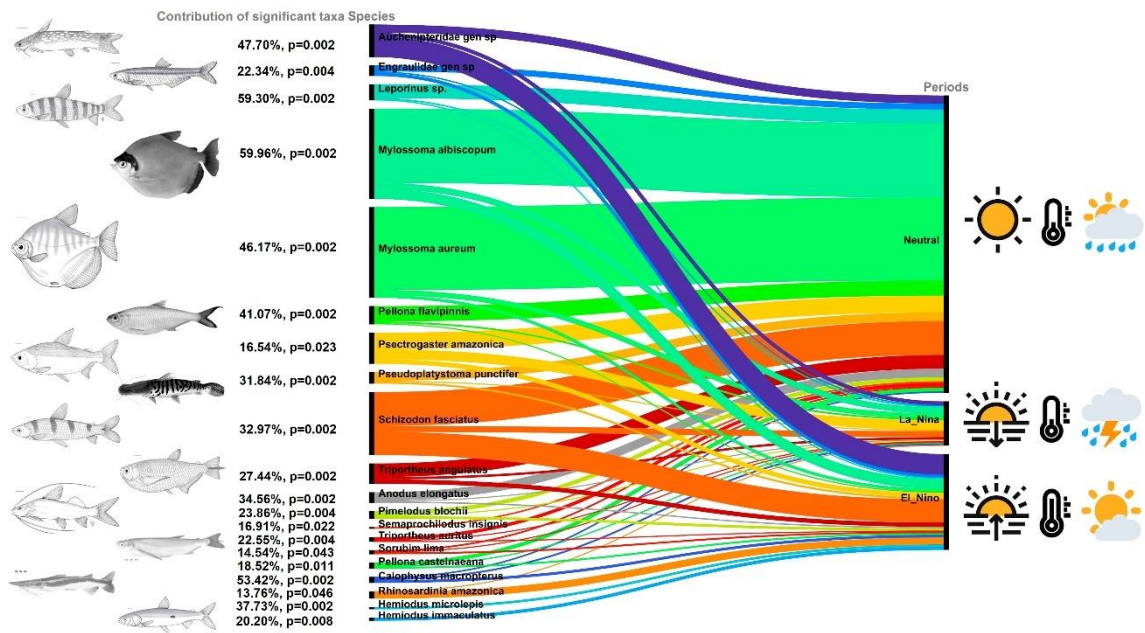
Figure 2

Figure 3

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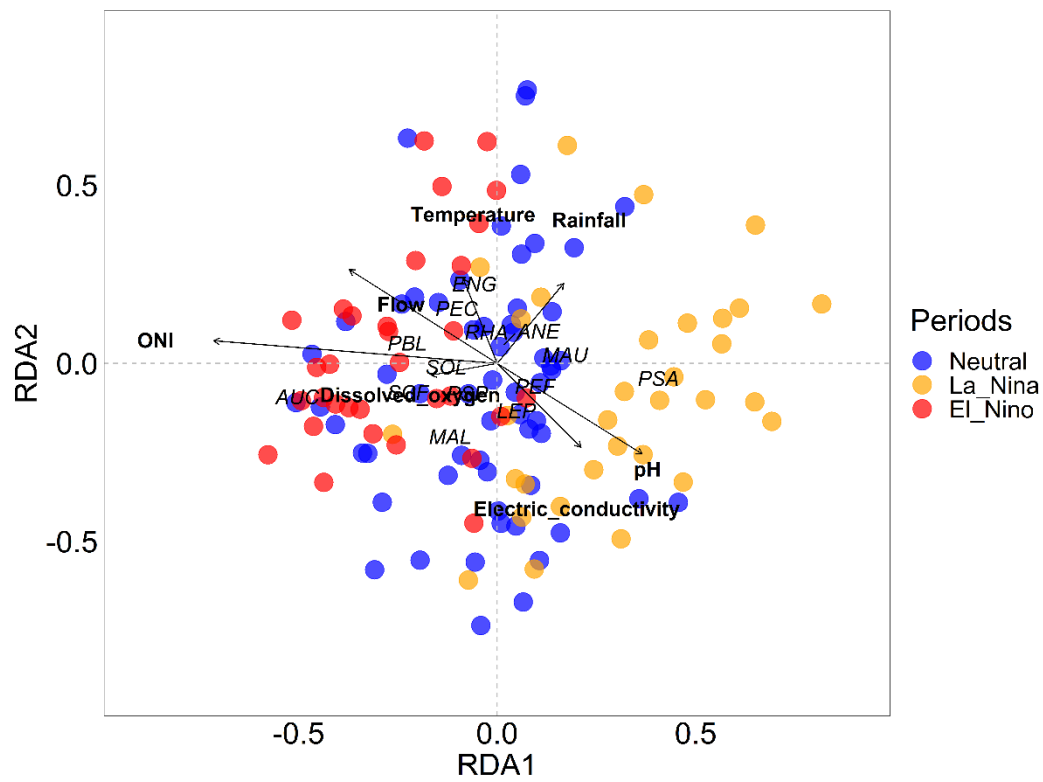
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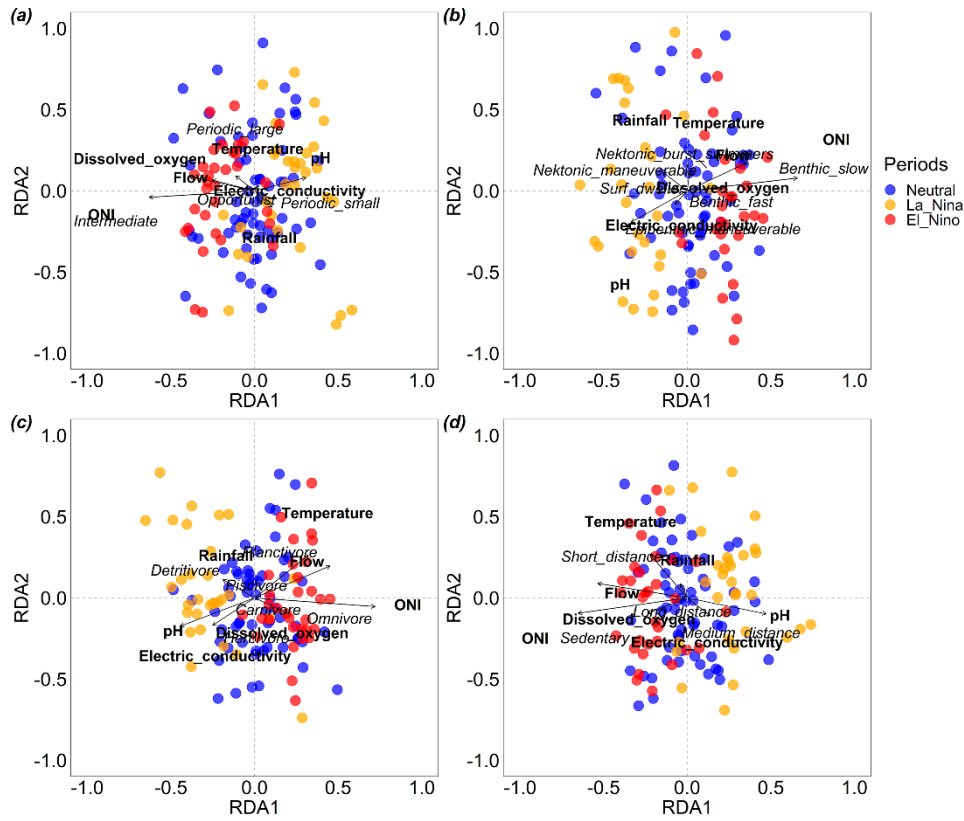
Figure 6

Table 1. Mean and standard deviation values of the flow and limnological variables of the lower Amazon River between three periods (neutral, La Niña, and El Niño).

Variable	Neutral	La Niña	El Niño
Flow ($m^{-3}.s^{-1}$)	185369.93± 37284.40	175717.48 ± 28208.92	205228.98 ± 28800.45
Rainfall (mm)	333.18 ± 147.18	326.11 ± 61.85	263.94 ± 78.96
Dissolved oxygen ($mg.L^{-1}$)	6.76 ± 5.39	4.97 ± 0.63	9.97 ± 8.12
Electric conductivity ($\mu S.cm^{-1}$)	55.46 ± 9.19	57.91 ± 1.41	53.66 ± 4.98
pH	6.70 ± 0.54	8.52 ± 0.09	7.54 ± 0.64
Water Temperature (°C)	29.12 ± 1.27	27.99 ± 0.69	28.81 ± 0.73

Table 2. Summary of GLM for the effects of environmental variables and periods on the taxonomic structure of fish larvae assemblages in the Lower Amazon. DO = Dissolved Oxygen, EC = Electrical Conductivity, FL = Flow, pH = Hydrogenonic Potential, ONI = Oceanic Nino Index, RF = Rainfall, TE = Temperature, A = association with the neutral period (color blue), El Niño (color black) and La Niña (color yellow). R = type of positive (color green) or negative (color red) relationship with the environmental variable. Values in bold indicate significance. The abbreviation of the species names can be found in the legend of Figure 3.

Species	DO Dev	DO P	R	EC Dev	EC P	R	FL Dev	FL P	R	pH Dev	pH P	R	ONI Dev	ONI P	R	RF Dev	RF P	R	TE Dev	TE P	R	A
ANE	4.53	0.83		1.58	0.97		18.59	**0.00**		13.55	**0.03**		7.66	0.31		0.54	1.00		4.33	0.84		blue
AUC	0.92	1.00		1.49	0.97		6.68	0.36		22.98	**0.00**		39.27	**0.00**		3.67	0.94		5.36	0.68		black
CAM	0.62	1.00		6.51	0.32		3.38	0.91		9.83	1.12		21.05	**0.04**		0.44	1.00		8.77	0.24		blue
ENG	6.77	0.48		9.19	0.16		6.57	0.37		15.51	**0.02**		0.14	0.99		2.56	0.98		1.17	1.00		blue
HEI	0.04	1.00		5.62	0.45		16.14	**0.01**		0.00	1.00		17.40	0.07		0.00	1.00		0.80	1.00		blue
HEM	0.28	1.00		7.23	0.23		1.29	1.00		0.44	0.97		46.15	**0.00**		0.23	1.00		4.15	0.85		black
LEP	0.03	1.00		16.84	**0.01**		4.13	0.78		47.62	**0.00**		10.94	0.19		1.62	1.00		0.46	1.00		blue
MAL	1.47	1.00		55.89	**0.00**		22.05	**0.00**		58.61	**0.00**		8.14	0.31		0.70	1.00		0.54	1.00		blue
MAU	1.37	1.00		45.06	**0.00**		54.51	**0.00**		10.52	0.09		13.98	0.12		1.03	1.00		0.30	1.00		blue
PBL	3.32	0.94		1.76	0.97		0.43	1.00		34.48	**0.00**		1.22	0.98		3.99	0.92		1.26	1.00		blue
PEC	2.96	9.58		1.28	0.97		0.91	1.00		6.11	0.41		0.12	0.99		12.01	0.09		0.55	1.00		blue
PEF	0.17	1.00		38.92	**0.00**		0.23	1.00		17.87	**0.01**		8.78	0.28		6.20	0.60		4.46	0.82		blue
PSA	10.54	0.13		42.78	**0.00**		0.21	1.00		12.43	**0.04**		7.68	0.31		0.00	1.00		0.05	1.00		yellow
PSP	0.06	1.00		26.17	**0.00**		1.57	1.00		21.95	**0.00**		3.49	0.75		1.69	1.00		0.57	1.00		blue
RHA	0.01	1.00		16.48	**0.01**		0.98	1.00		7.72	0.24		11.15	0.19		0.00	1.00		4.99	0.75		blue
SCF	9.87	0.15		7.21	0.23		3.46	0.90		22.33	**0.00**		0.26	0.99		0.31	1.00		0.77	1.00		blue
SEI	6.16	0.58		0.44	1.00		0.18	1.00		13.65	**0.03**		2.05	0.93		15.27	**0.03**		0.39	1.00		blue
SOL	2.24	0.99		3.78	0.74		0.58	1.00		11.83	**0.05**		4.05	0.69		0.07	1.00		2.24	0.99		blue
TAN	11.12	0.10		16.93	**0.01**		16.09	**0.01**		18.08	**0.01**		0.52	0.99		3.00	0.97		0.07	1.00		blue
TAU	4.13	0.87		31.16	**0.00**		11.08	**0.05**		7.87	0.24		2.87	0.24		8.39	0.33		3.40	0.95		blue

Table 3. Summary of GLM for the effects of environmental variables and periods on the functional structure of fish larvae assemblages in the Lower Amazon. DO = Dissolved Oxygen, EC = Electrical Conductivity, FL = Flow, pH = Hydrogenonic Potential, ONI = Oceanic Nino Index, RF = Rainfall, TE = Temperature, A = association with the neutral period (color blue), El Niño (color black) and La Niña (color yellow), and absence of association significative with periods (color gray). R = type of positive (color green) or negative (color red) relationship with the environmental variable. Values in bold indicate significance.

Functional groups	DO Dev	DO P	R	EC Dev	EC P	R	FL Dev	FL P	R	pH Dev	pH P	R	ONI Dev	ONI P	R	RF Dev	RF P	R	TE Dev	TE P	R	A
Intermediate	0.92	0.68		1.45	0.35		6.83	0.08		23.25	**0.00**		39.50	**0.01**		3.60	0.22		5.39	0.14		black
Opportunist	0.04	0.85		0.03	0.35		0.11	0.23		0.06	0.05		0.24	0.50		0.08	0.22		0.20	0.89		gray
Periodic large	0.07	0.85		60.79	**0.00**		2.74	0.23		45.93	**0.00**		2.53	0.50		3.62	0.22		0.04	0.98		blue
Periodic small	1.12	0.68		50.77	**0.00**		8.11	0.06		43.72	**0.00**		5.12	0.40		2.70	0.22		0.01	0.98		yellow
Carnivore	2.25	0.53		9.73	**0.01**		2.84	0.48		0.41	0.59		14.27	**0.01**		0.35	0.84		0.22	0.94		gray
Detritivore	7.21	1.00		41.46	**0.00**		0.11	0.96		12.77	**0.01**		5.59	0.36		0.69	0.80		0.00	0.94		gray
Herbivore	2.44	0.53		55.81	**0.00**		19.93	**0.00**		43.75	**0.00**		5.90	0.36		2.10	0.47		0.07	0.94		black
Omnivore	1.70	0.53		25.20	**0.00**		0.21	0.96		55.61	**0.00**		5.27	0.36		0.01	0.90		1.20	0.66		blue
Piscivore	0.00	0.98		51.65	**0.00**		0.44	0.94		35.33	**0.00**		3.78	0.42		10.43	**0.02**		2.03	0.56		blue
Planctivore	2.42	0.53		1.49	0.28		0.01	0.96		32.46	**0.00**		0.18	0.69		2.60	0.47		7.15	0.72		blue
Benthic fast	0.36	0.85		26.43	**0.01**		1.95	0.46		30.19	**0.00**		0.37	0.94		3.09	0.36		1.18	0.69		black
Benthic slow	1.03	0.76		0.52	0.53		10.58	**0.03**		26.89	**0.00**		41.81	**0.00**		3.41	0.36		8.45	0.07		black
Epib. maneuverable	5.35	0.18		20.62	**0.01**		1.05	0.46		36.69	**0.00**		0.01	0.99		0.58	0.72		0.77	0.69		blue
Nektonic b. swimmers	2.16	0.58		2.06	0.39		20.54	**0.00**		7.96	0.58		0.00	1.00		0.01	0.93		9.15	0.06		blue
Nektonic maneuverable	0.11	0.85		62.94	**0.00**		8.45	0.05		43.95	**0.00**		10.06	0.22		3.02	0.36		0.48	0.69		yellow
Surf dweller	0.47	0.84		0.72	0.44		0.02	0.46		0.13	0.85		0.05	0.97		0.05	0.85		0.00	0.69		gray
Long distance	0.24	0.68		2.59	0.23		1.93	0.46		0.36	0.57		3.48	0.33		0.00	0.94		2.82	0.22		gray
Medium distance	1.88	0.61		59.10	**0.00**		9.24	**0.04**		45.99	**0.00**		5.58	0.33		1.11	0.06		0.15	0.74		yellow
Sedentary	0.96	0.68		0.52	0.49		10.82	**0.03**		25.70	**0.00**		41.01	**0.00**		3.68	0.25		8.21	**0.04**		black
Short distance	1.40	0.68		12.53	**0.03**		0.04	0.91		37.35	**0.00**		0.25	0.78		9.42	**0.04**		7.83	**0.04**		black

CONSIDERAÇÕES FINAIS

A flutuação sazonal do nível da água representa um fator ecológico chave na estruturação das assembleias de larvas de peixes. Os padrões sazonais de reprodução das espécies ocorrem de acordo com suas características ecológicas que possibilita com que elas suportem as condições ambientais em cada estação sazonal.

A presença de larvas durante todos os meses de estudo sugere que os peixes se reproduzem em todas as fases hidrológicas, no baixo Rio Amazonas. A variação da estrutura taxonômica e funcional da comunidade de larvas associadas a cada fase hidrológica evidencia a necessidade crítica de reavaliar as políticas pesqueiras em vigor, como o período defeso, prática amplamente utilizada, no Baixo Amazonas, para proteger os peixes durante a época de reprodução.

As mudanças na composição taxonômica e funcional das larvas de peixes entre os períodos climáticos, demonstram o potencial dos ENOS em afetar a estrutura dos estoques parentais das espécies. A pouca abundância, principalmente, de larvas de peixes de interesse comercial associada aos eventos climáticos indica que a pesca e os ENOS atuam simultaneamente nos processos reprodutivos da ictiofauna. Corroborando estudos prévios no médios amazonas, esses resultados sugerem que períodos de ENOS devem servir como preditores para definir a duração do período de proteção a reprodução dos peixes.

Este estudo evidencia a importância da manutenção do regime hidrológico e a necessidade de considerar os eventos climáticos anômalos para a conservação da biodiversidade e dos padrões reprodutivos e de recrutamento dos peixes, que representam importante fonte de alimentação e renda para as populações.

Capítulo 1: Material suplementar

Table S1- Fish species, family and trophic, migratory, life history and microhabitat use strategies.

Family Species	Life history strategy	Trophic strategies	Migratory behaviors	Swimming behavior/microhabitat use
Achiridae				
Hypoclinemus mentalis	Opportunistic	Carnivore	Sedentary	Benthic slow
Anostomidae				
Leporinus sp.	Periodic-large	Omnivore	Medium distance	Epibenthic maneuverable
Rhytiodus microlepis	Periodic-small	Herbivore	Medium distance	Nektonic burst swimmers
Schizodon fasciatus	Periodic-small	Herbivore	Medium distance	Epibenthic maneuverable
Auchenipteridae				
Auchenipteridae gen. sp.	Intermediate	Omnivore	Sedentary	Benthic slow
Tatia sp.	Intermediate	Omnivore	Sedentary	Benthic slow
Trachelyopterus galeatus	Intermediate	Omnivore	Sedentary	Benthic slow
Belonidae				
Belonion apodion	Periodic-small	Piscivore	Sedentary	Nektonic burst swimmers
Strongylura timucu	Periodic-small	Piscivore	Sedentary	Nektonic burst swimmers
Bryconidae				
Brycon amazonicus	Periodic-large	Detritivore	Medium distance	Epibenthic maneuverable
Cetopsidae				
Cetopsis coecutiens	Periodic-small	Carnivore	Short distance	Benthic slow
Clupeidae				
Rhinosardinia amazonica	Periodic-small	Planktivore	Short distance	Nektonic maneuverable
Curimatidae				
Potamorhina altamazonica	Periodic-small	Detritivore	Medium distance	Nektonic maneuverable
Potamorhina latior	Periodic-small	Detritivore	Medium distance	Nektonic maneuverable
Psectrogaster amazonica	Periodic-small	Detritivore	Medium distance	Nektonic maneuverable

Psectrogaster rutiloides	Periodic-small	Detritivore	Medium distance	Nektonic maneuverable
Cynodontidae				
Cynodon gibbus	Periodic-large	Piscivore	Medium distance	Nektonic maneuverable
Rhaphiodon vulpinus	Periodic-large	Piscivore	Medium distance	Nektonic maneuverable
Doradidae				
Doradidae gen. sp.	Periodic-small	Omnivore	Sedentary	Benthic slow
Engraulidae				
Engraulidae gen. sp.	Periodic-small	Planktivore	Short distance	Nektonic maneuverable
Hemiodontidae				
Anodus elongatus	Periodic-small	Planktivore	Short distance	Nektonic burst swimmers
Hemiodus sp.	Periodic-small	Omnivore	Short distance	Nektonic burst swimmers
Pimelodidae				
Brachyplatystoma filamentosum	Periodic-large	Piscivore	Long distance	Benthic fast
Brachyplatystoma juruense	Periodic-large	Piscivore	Long distance	Benthic fast
Brachyplatystoma rousseauxii	Periodic-large	Piscivore	Long distance	Benthic fast
Brachyplatystoma sp.	Periodic-large	Piscivore	Long distance	Benthic fast
Calophysus macropterus	Periodic-large	Omnivore	Medium distance	Benthic fast
Hypophthalmus edentatus	Periodic-large	Planktivore	Medium distance	Epibenthic maneuverable
Hypophthalmus fimbriatus	Periodic-large	Planktivore	Medium distance	Epibenthic maneuverable
Hypophthalmus oremaculatus	Periodic-large	Planktivore	Medium distance	Epibenthic maneuverable
Pimelodus blochii	Periodic-small	Omnivore	Medium distance	Benthic fast
Pinirampus pirinampu	Periodic-large	Piscivore	Medium distance	Benthic fast
Pseudoplatystoma punctifer	Periodic-large	Piscivore	Medium distance	Benthic fast
Pseudoplatystoma tigrinum	Periodic-large	Piscivore	Medium distance	Benthic fast
Phractocephalus hemioliopterus	Periodic-large	Piscivore	Medium distance	Benthic fast
Sorubim lima	Periodic-large	Piscivore	Medium distance	Benthic fast
Pristigasteridae				
Pellona castelnaeana	Periodic-large	Piscivore	Short distance	Nektonic maneuverable
Pellona flavipinnis	Periodic-large	Piscivore	Short distance	Nektonic maneuverable
Prochilodontidae				

Prochilodus nigricans	Periodic-large	Detritivore	Medium distance	Epibenthic maneuverable
Semaprochilodus insignis	Periodic-large	Detritivore	Medium distance	Epibenthic maneuverable
Semaprochilodus taeniurus	Periodic-large	Detritivore	Medium distance	Epibenthic maneuverable
Sciaenidae				
Pachypops fourcroe	Periodic-large	Carnivore	Short distance	Epibenthic maneuverable
Plagioscion auratus	Periodic-large	Carnivore	Short distance	Epibenthic maneuverable
Plagioscion squamosissimus	Periodic-large	Carnivore	Short distance	Epibenthic maneuverable
Serrasalmidae				
Mylossoma albiscopum	Periodic-small	Herbivore	Medium distance	Nektonic maneuverable
Mylossoma aureum	Periodic-small	Herbivore	Medium distance	Nektonic maneuverable
Piaractus brachypomus	Periodic-large	Herbivore	Medium distance	Surf dweller
Serrassalmus sp.	Intermediate	Piscivore	Short distance	Nektonic maneuverable
Sternopygidae				
Eigenmannia sp.	Intermediate	Omnivore	Sedentary	Benthic slow
Synbranchidae				
Synbranchus marmoratus	Intermediate	Piscivore	Sedentary	Benthic slow
Tetraodontidae				
Colomesus asellus	Periodic-small	Omnivore	Sedentary	Benthic slow
Triportheidae				
Triportheus angulatus	Periodic-small	Omnivore	Medium distance	Nektonic maneuverable
Triportheus auritus	Periodic-small	Omnivore	Medium distance	Nektonic burst swimmers

Capítulo 2: Material suplementar

Effects of anomalous climatic events on the structure of fish larvae assemblages in the eastern Amazon

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Table S1- Fish species and trophic, migratory, life history and microhabitat use strategies.

Species	Life history strategy	Trophic strategies	Swimming behavior/microhabitat use	Migratory behaviors
Acestrorhynchus sp.	Periodic small	Piscivores	Nektonic burst swimmers	Short distance
Anodus elongatus	Periodic small	Planktivores	Nektonic burst swimmers	Short distance
Auchenipteridae gen. sp.	Intermediate	Omnivores	Benthic slow	Sedentary
Brachyplatystoma filamentosum	Periodic large	Piscivores	Benthic fast	Long distance
Brachyplatystoma juruense	Periodic large	Piscivores	Benthic fast	Long distance
Brachyplatystoma sp.	Periodic large	Piscivores	Benthic fast	Long distance
Brycon amazonicus	Periodic large	Omnivores	Epibenthic maneuverable	Medium distance
Calophysus macropterus	Periodic large	Omnivores	Benthic fast	Medium distance
Centromochlus sp.	Intermediate	Omnivores	Benthic slow	Sedentary
Cetopsis coecutiens	Periodic small	Carnivores	Benthic slow	Short distance
Colomesus asellus	Periodic small	Omnivores	Benthic slow	Sedentary
Cynodon gibbus	Periodic large	Piscivores	Nektonic maneuverable	Medium distance
Doradidae gen. sp.	Periodic small	Omnivores	Benthic slow	Sedentary
Eigenmannia sp.	Intermediate	Omnivores	Benthic slow	Sedentary

Engraulidae gen. sp.	Periodic small	Planktivores	Nektonic maneuverable	Short distance
Hemiodus immaculatus	Periodic small	Omnivores	Nektonic burst swimmers	Short distance
Hemiodus microlepis	Periodic small	Omnivores	Nektonic burst swimmers	Short distance
Hemiodus sp.	Periodic small	Omnivores	Nektonic burst swimmers	Short distance
Hemiodus unimmaculatus	Periodic small	Omnivores	Nektonic burst swimmers	Short distance
Hypoclinemus mentalis	Opportunistic	Carnivores	Benthic slow	Sedentary
Hypophthalmus edentatus	Periodic large	Planktivores	Epibenthic maneuverable	Medium distance
Hypophthalmus fimbriatus	Periodic large	Planktivores	Epibenthic maneuverable	Medium distance
Hypophthalmus oremaculatus	Periodic large	Planktivores	Epibenthic maneuverable	Medium distance
Hyporhamphus brederi	Intermediate	Piscivores	Nektonic burst swimmers	Sedentary
Leporinus sp.	Periodic large	Omnivores	Epibenthic maneuverable	Medium distance
Microphilypinus tapajosenses	Opportunistic	Carnivores	Benthic slow	Sedentary
Myloplus asterias	Intermediate	Herbivores	Nektonic maneuverable	Medium distance
Mylossoma albiscopum	Periodic small	Herbivores	Nektonic maneuverable	Medium distance
Mylossoma aureum	Periodic small	Herbivores	Nektonic maneuverable	Medium distance
Pachypops fourcroi	Periodic large	Carnivores	Epibenthic maneuverable	Short distance
Pellona castelnaeana	Periodic large	Piscivores	Nektonic maneuverable	Short distance
Pellona flavipinnis	Periodic large	Piscivores	Nektonic maneuverable	Short distance
Piaractus brachypomus	Periodic large	Herbivores	Surf dweller	Medium distance
Pimelodus blochii	Periodic small	Omnivores	Benthic fast	Medium distance
Pinirampus pirinampu	Periodic large	Piscivores	Benthic fast	Medium distance
Plagioscion auratus	Periodic large	Carnivores	Epibenthic maneuverable	Short distance
Plagioscion squamosissimus	Periodic large	Carnivores	Epibenthic maneuverable	Short distance
Potamorhina altamazonica	Periodic small	Detritivores	Nektonic maneuverable	Medium distance
Potamorhina latior	Periodic small	Detritivores	Nektonic maneuverable	Medium distance
Prochilodus nigricans	Periodic large	Detritivores	Epibenthic maneuverable	Medium distance
Psectrogaster amazonica	Periodic small	Detritivores	Nektonic maneuverable	Medium distance
Psectrogaster rutiloides	Periodic small	Detritivores	Nektonic maneuverable	Medium distance
Pseudoplatystoma punctifer	Periodic large	Piscivores	Benthic fast	Medium distance
Pseudoplatystoma tigrinum	Periodic large	Piscivores	Benthic fast	Medium distance

Rhaphiodon vulpinus	Periodic large	Piscivores	Nektonic maneuverable	Medium distance
Rhinosardinia amazonica	Periodic small	Planktivores	Nektonic maneuverable	Short distance
Rhytiodus microlepis	Periodic small	Herbivores	Nektonic burst swimmers	Medium distance
Schizodon fasciatus	Periodic small	Herbivores	Epibenthic maneuverable	Medium distance
Semaprochilodus insignis	Periodic large	Detritivores	Epibenthic maneuverable	Medium distance
Semaprochilodus taeniurus	Periodic large	Detritivores	Epibenthic maneuverable	Medium distance
Sorubim lima	Periodic large	Piscivores	Benthic fast	Medium distance
Tatia sp.	Intermediate	Omnivores	Benthic slow	Sedentary
Trachelyopterus galeatus	Intermediate	Omnivores	Benthic slow	Sedentary
Triportheus angulatus	Periodic small	Omnivores	Nektonic maneuverable	Medium distance
Triportheus auritus	Periodic small	Omnivores	Nektonic maneuverable	Medium distance

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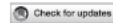| Submission Status	Under Review
Manuscript ID	FWB-P-Jul-22-0327
Submitted On	25 July 2022 by Ruineris Cajado
Submission Started	25 July 2022 by Ruineris Cajado

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ANEXO 2

Effects of anomalous climatic events on the structure of fish larvae assemblages in the eastern Amazon

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The reproduction of neotropical fish is linked to environmental stimuli that act as triggers in this process. Thus, it is possible to affirm that specific environmental changes can delimit most fish's period and reproductive success. El Niño Southern Oscillation phenomena (ENSO) influence rainfall and, consequently, hydrological dynamics, affecting several fish population aspects, especially reproductive aspects. However, in the Amazon, empirical evidence of the effect of anomalous climatic events on fish reproduction is incipient. In this sense, we investigated the taxonomic and functional structure of parental fish larvae stocks and how species modulate their reproductive activities before (2013 and 2014) and during La Niña (2018) and El Niño (2019) events. The data evidence that the larval assemblages suffered alterations in the taxonomic and functional composition between the three analyzed periods and a pattern of temporal distribution with a high influence of environmental variables. Flow, pH, and electrical conductivity were the most important variables to modulate fish reproductive intensity between periods. The species seem to respond to combinations of these variables that reflect environmental conditions conducive to biological recruitment according to their ecological characteristics, allowing the perpetuation or decline of their abundance in each period. All species of commercial interest associated with the neutral period showed a sharp decline in the subsequent moments. These results suggest that the incidence of anomalous climatic events added to regional fisheries exploitation can negatively affect the phenology and demographic patterns of larvae assemblages on a short temporal scale. During the neutral period, the community was dominated by larvae of periodic large, herbivores, piscivores, epibenthic maneuverable, and nektonic burst swimmers. The decrease in the abundance of certain functional groups at the neutral and La Niña period favored an accelerated ecological succession during the El Niño period, due to the increase of species from basal trophic levels (planktivores), generalists (omnivores), highly resilient (intermediate strategists), sedentary, short-distance migrants and little commercially

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