

UNIVERSIDADE FEDERAL DE MINAS GERAIS  
Instituto de Ciências Biológicas  
Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre

Fernanda de Oliveira Silva

**MIGRAÇÃO DE PEIXES NO RIO JEQUITINHONHA: padrões migratórios e habitats críticos para o recrutamento**

Belo Horizonte

2021

Fernanda de Oliveira Silva

**MIGRAÇÃO DE PEIXES NO RIO JEQUITINHONHA: padrões migratórios e habitats críticos para o recrutamento**

**Versão Final**

Tese apresentada ao Curso de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre da Universidade Federal de Minas Gerais como requisito parcial para obtenção do Grau de Doutora. Área de Concentração: Ecologia e Gestão de Ecossistemas Aquáticos

Orientador: Fernando Mayer Pelicice

Belo Horizonte

2021

043

Silva, Fernanda de Oliveira.

Migração de peixes no rio Jequitinhonha: padrões migratórios e habitats críticos para o recrutamento [manuscrito] / Fernanda de Oliveira Silva. – 2021. 81 f. : il. ; 29,5 cm.

Orientador: Fernando Mayer Pelicice.

Tese (doutorado) – Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas. Programa de Pós-Graduação em Ecologia Conservação e Manejo da Vida Silvestre.

1. Ecologia. 2. Peixes. 3. Migração Animal. 4. Jequitinhonha, Rio. I. Pelicice, Fernando Mayer. II. Universidade Federal de Minas Gerais. Instituto de Ciências Biológicas. III. Título.

CDU: 502.7



UNIVERSIDADE FEDERAL DE MINAS GERAIS  
INSTITUTO DE CIÊNCIAS BIOLÓGICAS  
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, CONSERVAÇÃO E MANEJO DA VIDA SILVESTRE



**Ata da Defesa de Tese**

Nº 199  
Entrada: 2016/2

**FERNANDA DE OLIVEIRA SILVA**

No dia 30 de novembro de 2020, às 14:00 horas, por vídeo conferência, teve lugar a defesa de tese de doutorado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) doutorando(a) FERNANDA DE OLIVEIRA SILVA, orientando do Professor FERNANDO MAYER PELICICE, intitulada: **"Migração de peixes no rio Jequitinhonha: padrões migratórios e habitats críticos para o recrutamento"**. Abrindo a sessão, o(a) Presidente(a) da Comissão, Doutor(a) FERNANDO MAYER PELICICE, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Ângelo Antônio Agostinho (UEM), Paulo Dos Santos Pompeu (UFLA), Alexandre Lima Godinho (UFMG), Fernanda Dotti Do Prado (UNESP) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

- Aprovação da tese, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;
- Reavaliação da tese com avaliação pelos membros da banca do documento revisado, sem nova defesa, no prazo máximo de 30 dias, sob possibilidade de reprovação;
- Reformulação da tese com indicação de nova defesa em data estabelecida a critério do Colegiado em observância às Normas Gerais da Pós-graduação na UFMG e ao Regimento do PPG-ECMVS;
- Reprovação

A banca indica esta tese aos Prêmios CAPES e UFMG de teses? SIM NÃO

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 30 de novembro de 2020.

Assinaturas dos Membros da Banca Examinadora



Documento assinado eletronicamente por **Fernando Mayer Pelicice, Usuário Externo**, em 01/12/2020, às 17:20, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



Documento assinado eletronicamente por **Alexandre Lima Godinho, Professor do Magistério Superior**, em 02/12/2020, às 07:29, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



Documento assinado eletronicamente por **Fernanda Dotti do Prado, Usuário Externo**, em 02/12/2020, às 13:25, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



Documento assinado eletronicamente por **Angelo Antonio Agostinho, Usuário Externo**, em 09/12/2020, às 12:28, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



Documento assinado eletronicamente por **Paulo dos Santos Pompeu, Usuário Externo**, em 09/12/2020, às 13:08, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do [Decreto nº 8.539, de 8 de outubro de 2015](#).



A autenticidade deste documento pode ser conferida no site [https://sei.ufmg.br/sei/controlador\\_externo.php?acao=documento\\_conferir&id\\_orgao\\_acesso\\_externo=0](https://sei.ufmg.br/sei/controlador_externo.php?acao=documento_conferir&id_orgao_acesso_externo=0), informando o código verificador **0448950** e o código CRC **50FDCF4F**.



*Dedicado àquela que tem os lábios mais lindos do mundo: a Curimba!*

## **Agradecimentos**

Meu agradecimento especial vai pro Jequi, que aqui não me refiro apenas ao rio, mas à uma região espetacular. Lá eu fui apresentada a diferentes realidades, desafios, descobertas e pessoas que ampliaram a minha forma de ver o mundo, inclusive sobre minhas capacidades, limitações e privilégios. O Jequi me doutorou na vida! São tantas pessoas que me ajudaram e acolheram que faltaria espaço aqui. Agradeço especialmente ao Neguim (que me ajudou desde o início), Tina, Nicinha, Vila, Salim, Magela, Renato, Seu Mário, Dona Amorosa, Tati, Valdir (que foi importado, mas um grande parceiro) que foram a minha família do Jequi e que carrego pro resto da vida. Ao Alberto e todo o pessoal da usina de Irapé por todo apoio e colaboração. Aos coletores Nêgo, Florêncio, Genísio, Niva, Zé Nilson, Geraldo, Muquim. Aos protagonistas de escamas e de couro, cada vida sacrificada, meu muito obrigada e o famoso “desculpa qualquer coisa”!

Ao Chico, que me conduziu em diversas escolhas felizes. Foi ele quem me levou pro caminho dos peixes, me apresentou o Jequi 11 anos atrás e me sugeriu o Fernando como orientador. Como se não bastasse, a pessoa ainda faz cerveja sem glúten! Muito obrigada por tudo e pela imensa ajuda desde então, Phy!

Ao Fernando, que topou entrar nessa comigo e se tornou um grande amigo (outro presente especial que o Jequi me deu). Muito obrigada por compartilhar tanto conhecimento e tantas outras coisas (menos algumas excentricidades musicais) e pela fantástica companhia nas viagens pelo Jequi. É um privilégio ter sido sua aluna.

À Raquel, que me confiou um projeto tão grande e ainda forneceu todo suporte durante e após a execução. Muito obrigada pela confiança, estímulo, amizade e boas risadas, Quel!

Aos amigos do Peixe Vivo, especialmente Miriam, Alexandre e Ivo que ajudaram ativamente e constantemente, até com as próprias vidas! E ao João, que muito me ajudou e ensinou sobre telemetria.

Aos parceiros do Lapad, especialmente Samara, Evoy, Jade e David (ex Lapad) pela colaboração e ótima acolhida.

Aos membros da banca Angelo e Fernanda, muito obrigada por terem aceitado contribuir com esse trabalho. Ao Sam que me deu a primeira oportunidade de trabalhar com peixes e salvou meu mestrado. Ao Paulo, o onipresente, com quem aprendo cotidianamente. Agradeço também ao Rafa e ao Giba por estarem a postos! Muito obrigada!

À Alexandra Elbakyan, a musa dos pós graduandos, meu muito obrigada!

Aos professores, colegas e agregados da pós ECMVS, especialmente Rafa, Dani, Adriano, Dani, Rosy, Bolo, Massara, Dodora, Lud... Aprendo cotidianamente com vocês. Inclusive a encontrar estímulo pra continuar em tempos tão sombrios.

À mamis e ao Binho. Muito obrigada pelo apoio e presença constantes, inclusive nas diversas atividades relacionadas ao projeto e no Jequi. Obrigada também por entenderem as minhas ausências em vários dos nossos momentos.

Ao Flávio, que foi um companheiro maravilhoso desde o início, sempre me apoiando e acalmando nos momentos de surto. Eu teria divorciado de mim mesma. Obrigada por todo o carinho, suporte e por ter sido luz!

À minha família de quatro patas que tanto alivia os momentos de estresse.

Aos amigos que sempre nos ajudam na nossa caminhada: Cele, que esteve e está sempre presente! Raoni, pelos bate-papos e milhares de ajudas no R. Ao Ivan, companheiro de insônia na madrugada e tensão pré-tese. Dani e Rafa pelos bons papos e várias garrafas de vinho. Maíra, Stephanie, Rapha, Lucas, Ba, Fabi, Dani, Tatau, Nadja, Kelly... muito obrigada pela companhia ao longo da minha trajetória.

À Fapemig, Cemig e Aneel pelo apoio financeiro ao projeto. Muito obrigada!

### **Apoio Institucional**

Esta tese de doutorado foi desenvolvida na Universidade Federal de Minas Gerais, em parceria com as seguintes instituições:

Núcleo de Estudos Ambientais (Neamb), Universidade Federal do Tocantins

Lab. de Biol. e Cultivo de Peixes de Água Doce (LAPAD), Universidade Federal de Santa Catarina

Laboratório de Ictiologia, Universidade Federal de São João del-Rei

### **Apoio financeiro**

Agência Nacional de Energia Elétrica (APQ-03047/2011)

Companhia Energética de Minas Gerais (P&D483 - APQ-03047/2011)

Fundação de Amparo à Pesquisa do Estado de Minas Gerais: (APQ-03047/2011)

Conselho Nacional de Desenvolvimento Científico e Tecnológico (165497/2017-3)



## Resumo

Investigamos o comportamento migratório e fatores que afetam a dinâmica de recrutamento da curimba nativa (*Prochilodus hartii*) do rio Jequitinhonha, uma bacia do semiárido, Brasil, em um contexto de regulação hidrológica e hibridização com espécies não nativas. Para isso, dividimos a tese em dois capítulos. No primeiro, investigamos a dinâmica reprodutiva e de recrutamento da espécie, sua relação com o regime hidrológico e distribuição espacial. Coletamos amostras de ovos, larvas e jovens do ano (YOY) em vários pontos amostrais distribuídos ao longo de 300 km do Rio Jequitinhonha, a montante e a jusante da UHE Irapé. Encontramos maiores densidades de ovos e larvas em locais sem influência do barramento, afetados principalmente pelas variações semanais e diárias no nível da água. A probabilidade de captura de YOY aumentou em 40% quando um riacho lateral estava presente, enquanto a probabilidade de ocorrência de YOY foi afetada pelo tamanho do trecho lótico. A abundância de subadultos não foi correlacionada com nenhuma variável vinculada ao regime de cheias. Esses resultados mostram que curimbas de um rio do semiárido e sem planície de inundação apresentaram relações distintas com o regime de cheias quando comparadas às curimbas de rios de planície. No segundo capítulo, investigamos a dinâmica migratória de *P. hartii* frente aos impactos de alteração de habitat e hibridização com espécies não nativas, por meio do uso de técnicas de telemetria (radio e acústica) e análises genéticas. No estudo de migração, o comportamento de curimbas foi avaliado em 4 grupos de peixes, sendo 2 em trechos a montante e 2 em trechos a jusante da UHE Irapé. A jusante, monitoramos peixes marcados e liberados no canal de fuga da UHE Irapé (RL1) e a 80 km abaixo da barragem, próximo ao seu principal tributário, rio Araçuaí (RL2). A montante, monitoramos peixes oriundos do reservatório (RL3) e transpostos para o reservatório (RL4), simulando um sistema de transposição de peixes. As maiores distâncias deslocadas foram detectadas nos peixes de RL2, e o rio Araçuaí, livre de barramento, mostrou-se como importante rota migratória. Os peixes sob influência direta da

barragem tenderam a mover distâncias mais curtas, tanto no reservatório (RL3) quanto imediatamente abaixo da barragem (RL1). Quase todos os peixes liberados no reservatório não conseguiram migrar para trechos lóticos a montante, especialmente aqueles transpostos (RL4). Detectamos uma alta proporção de hibridização no trecho de jusante, e peixes nativos e híbridos apresentaram comportamento migratório muito semelhante. Considerando os resultados dos dois capítulos, concluímos que existem duas populações independentes na região (uma acima e outra abaixo da barragem), autossustentáveis; no entanto, ambas as populações estão sendo impactadas por ação humana. A modificação e fragmentação do habitat alterou o comportamento migratório e o recrutamento em um longo trecho de rio, particularmente a montante. Além disso, a introgressão genética, principalmente no trecho de jusante, ameaça a permanência de *P. hartii* no Jequitinhonha. Isso indica que medidas de conservação, como a preservação de trechos lóticos, são urgentes para proteger as populações remanescentes a montante e a jusante da barragem.

Palavras-chave: Migração, peixes, rio Jequitinhonha

## **Abstract**

Migration, spawning and recruitment dynamics of Neotropical migratory fishes are widely studied in river-floodplain systems, where the flood pulse and wetlands play a central role. In semi-arid systems, where the flow regime is less predictable and water-bodies intermittent, migratory fishes may employ different migratory behavior and recruitment strategies, although studies on these systems are scarce. Additionally, impacts of habitat fragmentation and species introduction can be intensified in semiarid river systems, making them a study priority. In this thesis, we investigated factors affecting the recruitment dynamics and migratory behavior of curimbas (*Prochilodus hartii*) in a semi-arid river basin (Jequitinhonha River, Brazil) subjected to river regulation and hybridization with non-native species. We sectioned the thesis into two independent studies, presented in two chapters. In the first chapter, we investigated the relationship between flood and recruitment. We sampled eggs, larvae and young of the year (YOY) over 2 years and sub-adult over seven years, at several sites distributed upstream and downstream of a hydroelectric dam, UHE Irapé, about 300 km of the Jequitinhonha River. We found higher densities of eggs and larvae at sites with no influence of river regulation, affected mainly by weekly and daily variations in water level. The probability of YOY detection increased by 40% when a lateral stream was present, and the probability of YOY occupancy was affected by the length of the lotic stretch. Sub-adult abundance was not correlated with any predictor related to the flooding regime. These results show that curimbas from a semi-arid river and without a floodplain had different relationships with the flood regime when compared to curimbas from lowland rivers. In the second chapter, we investigated the migratory behavior of *P. hartii* under impacts of habitat modification and hybridization using telemetry techniques (radio and acoustic) and genetic analysis. We studied four groups based in the release site. We monitored fish in the UHE Irapé tailrace (RL1) and 80 km below the dam, near to the main tributary, Araçuaí River (RL2), downstream to the dam. In the upstream reach, we monitored

fish from the reservoir (RL3) and fish passed to the reservoir (RL4), simulating a fish passage system. The longest distances migrated were detected in RL2 group, and the main free-flowing tributary proved to be an important migratory route. Fish under dam influence tended to move over shorter distances, both in the reservoir and immediately below the dam. Almost all fish released in the reservoir were unable to migrate to upstream lotic stretches, especially those passed from downstream sites. We detected a high proportion of hybridization in the lower reach of the river, and native and hybrids fish showed very similar migratory behavior. Considering all results together, we conclude that there are two segregated populations upstream and downstream the dam. However, both populations are been severely impacted by human interventions. The habitat modification and fragmentation imperiled migratory behavior and recruitment in a long river reach, particularly upstream the dam. Besides that, genetic introgression, especially downstream reaches, threatens the permanence of *P. hartii* in Jequitinhonha River Basin. This indicates that conservation measures, such as the preservation of lotic stretches, are urgent to protect the remaining populations upstream and downstream of the dam.

Key-words: Migration, fish, Jequitinhonha River

## SUMÁRIO

Introdução geral.....	14
Capítulo 1: Recruitment dynamics of a migratory fish in a semiarid river system.....	18
<i>Abstract</i> .....	20
<i>Introduction</i> .....	21
<i>Material and Methods</i> .....	23
<i>Target species</i> .....	23
<i>Study Area</i> .....	24
<i>Abiotic data</i> .....	27
<i>Data analysis</i> .....	28
<i>Eggs and larvae</i> .....	28
<i>Young-of-the-year</i> .....	29
<i>Subadults</i> .....	30
<i>Results</i> .....	30
<i>Eggs and larvae</i> .....	30
<i>Young-of-the-year</i> .....	33
<i>Sub-adults</i> .....	35
<i>Discussion</i> .....	35
<i>References</i> .....	40
Capítulo 2: Migratory behavior of a Neotropical fish under habitat fragmentation and hybridization impacts in a semiarid river system.....	48
<i>Abstract</i> .....	49
<i>Introduction</i> .....	50
<i>Material and methods</i> .....	54
<i>Species</i> .....	54
<i>Study area</i> .....	55
<i>Fish capture, tagging and releasing</i> .....	55
<i>Fish monitoring</i> .....	57
<i>Genetic analysis</i> .....	58
<i>Data processing and analysis</i> .....	60
<i>Results</i> .....	61
<i>Discussion</i> .....	66
<i>References</i> .....	73
Conclusão geral.....	81
<i>Referências bibliográficas</i> .....	83

## **Introdução geral**

A dependência de energia por fonte hidrelétrica se dá principalmente em países em desenvolvimento (Dugan *et al.*, 2010), e o Brasil é o segundo maior produtor de hidroeletricidade no mundo, ficando atrás apenas da China (British Petroleum Company, 2020). Mais de 1.300 barramentos para fim de geração de eletricidade já foram instalados em diversas bacias hidrográficas brasileiras (Aneel, 2019). As espécies de peixes com comportamento reofílico migratório, que necessitam se deslocar entre diferentes tipos de ambientes para completarem seus ciclos de vida, são as mais sensíveis às alterações ambientais, no habitat e na conectividade fluvial, sendo as primeiras a desaparecer após a formação dos barramentos (Lucas and Baras, 2001). Isso acontece porque as barragens, em muitos casos, interferem no ciclo de vida dessas espécies de três formas principais: 1) interrompem os movimentos migratórios (Agostinho, Thomaz and Gomes, 2005), separando sítios de desova dos berçários e dos sítios de alimentação (Pompeu, Agostinho and Pelicice, 2012); 2) alteram o regime hidrológico e os padrões de cheias (Agostinho *et al.*, 2004), os quais mantêm a conectividade lateral dos habitats, fornecem abrigo e alimento aos diversos estágios do ciclo de vida dos peixes (Junk and Wantzen, 2004), e funcionam como gatilho para processos biológicos; 3) modificam as características dos habitats por transformarem ambientes lóticos em lênticos, com condições inapropriadas para a sua residência e aquisição de recursos (Dudley and Platania, 2007; Pelicice, Pompeu and Agostinho, 2015).

Com relação à perturbação imposta a movimentos migratórios, sistemas de transposição para peixes (STPs) vêm sendo construídos com o objetivo básico de reconectar trechos separados pelo barramento (Pompeu *et al.*, 2012). Essa tem sido a segunda medida mitigatória mais utilizada no Brasil (Agostinho, Gomes and Pelicice, 2007), tendo forte apelo popular e determinada por lei em alguns estados (Lei 12.488, de 9/4/1997 em Minas Gerais e Lei 9.798, de 7/10/1997 em São Paulo). No entanto, vários estudos têm questionado a eficácia dos STPs

na manutenção dos estoques de espécies migradoras (Agostinho *et al.*, 2002; A. A. Agostinho *et al.*, 2007; C. S. Agostinho *et al.*, 2007; Lopes *et al.*, 2007; Pelicice and Agostinho, 2012; Silva *et al.*, 2012; Pelicice, Pompeu and Agostinho, 2015), inclusive em nível mundial (Kemp, 2016; Birnie-Gauvin *et al.*, 2018; Wilkes, Mckenzie and Webb, 2018). Mais do que isso, em algumas situações esses sistemas podem atuar como armadilhas ecológicas (Pelicice and Agostinho, 2008; Brito and Carvalho, 2013), causando impactos negativos ao recrutamento, quando peixes são atraídos para regiões com piores condições para reprodução, sem possibilidade de retorno. As principais causas da instalação de STPs que causam impactos sobre a fauna são a ausência de estudos prévios que avaliem claramente os objetivos da transposição, o desconhecimento sobre limitações de funcionamento do STP, o contexto ambiental e a ecologia das espécies locais, além da falta de monitoramento e avaliações periódicas (Pompeu, Agostinho and Pelicice, 2012).

Entender as características dos diferentes tipos de habitats utilizados por espécies migradoras e a disposição espacial dos mesmos em relação a barramentos é fator chave para a decisão acerca de implantação de STPs (Agostinho *et al.*, 2002) ou qualquer outra forma de manejo. Se ambientes propícios à desova e crescimento são inexistentes a montante, por exemplo, um STP não deve ser considerado (Pompeu *et al.*, 2012). Apesar de aparentemente simples, essas análises tornam-se complexas quando aspectos básicos do ciclo de vida das espécies afetadas são desconhecidos. Esse é o caso do rio Jequitinhonha, que tem elevado valor de conservação por estar situado em área de alto endemismo de peixes (Ribeiro, 2006), porém carece de estudos básicos de descrição de espécies (Pugedo *et al.*, 2016). Consequentemente, são raras as informações sobre aspectos biológicos e ecológicos de peixes, mesmo daquelas espécies consideradas abundantes e comercialmente importantes (Andrade, 2018). Essas lacunas de informação tornam as análises sobre o uso de ferramentas de manejo ainda mais complexas,

podendo decretar o insucesso de uma medida (e.g. STPs) caso seja tomada sem informações técnicas suficientes e de qualidade.

O presente estudo, o qual embasa essa tese de doutorado, nasceu de uma demanda da Cemig Geração e Transmissão (Programa Peixe Vivo) em avaliar a necessidade de instalação de um STP na UHE Irapé, uma grande barragem instalada na calha do rio Jequitinhonha, um rio encaixado, sem planícies de inundação significativas, que atravessa parte do semiárido brasileiro. Essa demanda foi uma das condicionantes ambientais da renovação da Licença de Operação da usina. Para atendê-la, foi elaborado um projeto de pesquisa desenvolvido pela Fundação Biodiversitas e que contou com parcerias da Universidade Federal de Santa Catarina, dando apoio aos estudos de ictioplâncton, Universidade Federal de São João del-Rei, apoiando nos estudos de telemetria de peixes, e Universidade Federal do Tocantins, dando apoio no delineamento e condução geral dos estudos. É um dos raros estudos que utilizou abordagem integrativa sobre migração, reprodução e recrutamento para avaliar empiricamente a necessidade de instalação de um STP (Lira *et al.*, 2017), visto que empregou técnicas de telemetria para avaliar a migração, acompanhada de avaliações sobre sítios de desova e crescimento para avaliar o recrutamento. Embora a pergunta sobre a necessidade de transposição de peixes na UHE Irapé tenha sido o pano de fundo do projeto, ele não foi abordado como um dos objetivos na presente tese. Procuramos dar enfoque às características ecológicas da espécie de peixe estudada, suas relações com a hidrologia de um rio em um cenário de clima semiárido, e suas interações com os impactos do barramento e introgressão genética causada por espécies não nativas.

Nesse sentido, o objetivo geral deste trabalho foi avaliar o comportamento migratório e a existência de habitats críticos para o recrutamento (sítios de desova e crescimento) da curimba *Prochilodus hartii* Steindachner, 1875 no trecho de rio influenciado pela Usina Hidrelétrica de Irapé (UHE Irapé), rio Jequitinhonha – MG, a fim de produzir conhecimento acerca da ecologia



dessa espécie e, assim, subsidiar ações de manejo e conservação para os peixes migradores da região. O presente estudo foi estruturado em dois capítulos. No primeiro abordamos a dinâmica de recrutamento da curimba no rio Jequitinhonha (*Recruitment dynamics of a migratory fish in a semiarid river system*). Esse capítulo foi submetido e aceito para publicação no periódico *Inland Waters*. No segundo capítulo avaliamos o comportamento migratório de curimbas (*P. hartii* e híbridos) em trechos do rio Jequitinhonha e seus principais tributários, acima e abaixo da UHE Irapé (*Migratory behavior of a semiarid migratory fish under habitat fragmentation and hybridization impacts*).

Considerando o escasso conhecimento sobre aspectos ecológicos de peixes migradores do rio Jequitinhonha, aliado aos impactos antrópicos já conhecidos na bacia, esperamos que estes estudos sirvam para subsidiar o manejo e a conservação dessa fauna que, além de possuir importância para a integridade ambiental do rio Jequitinhonha, possui relevância como fonte alimentar e de renda para comunidades ribeirinhas.

Capítulo 1: Recruitment dynamics of a migratory fish in a semiarid river system

Manuscrito publicado no periódico *Inland Waters*. DOI:  
10.1080/20442041.2020.1805977



*Jequitinhonha  
Braço do mar  
Leva esse canto prá navegar  
traz do garimpo  
pedra que brilha mais que a luz do luar  
Jequitinhonha, jequitibarro  
mete essa unha, tira da terra  
vida talhada com as mãos*

Paulinho Pedra Azul

## **Recruitment dynamics of a migratory fish in a semiarid river system**

Fernanda de Oliveira Silva<sup>a,f\*</sup>, Francisco Ricardo de Andrade Neto<sup>b</sup>, Samara Hermes Silva<sup>c</sup>, Jade de Oliveira da Silva<sup>c</sup>, Evoy Zaniboni Filho<sup>c</sup>, Ivo Gavião Prado<sup>d</sup>, Alexandre Peressin<sup>b</sup>, Fernando Mayer Pelicice<sup>e</sup>

*<sup>a</sup>Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Universidade Federal de Minas Gerais. Minas Gerais. Brazil. Email: [fernandacachara@gmail.com](mailto:fernandacachara@gmail.com)*

*<sup>b</sup>Programa de Pós-Graduação em Ecologia Aplicada, Universidade Federal de Lavras. Minas Gerais. Brazil.*

*<sup>c</sup>Laboratório de Biologia e Cultivo de Peixes de Água Doce, Universidade Federal de Santa Catarina. Santa Catarina. Brazil*

*<sup>d</sup>Pisces – Consultoria e Serviços Ambientais. Lavras. Minas Gerais. Brazil*

*<sup>e</sup>Núcleo de Estudos Ambientais, Universidade Federal do Tocantins. Tocantins. Brazil*

*<sup>f</sup>Fundação Biodiversitas, Minas Gerais, Brazil*

## **Recruitment dynamics of a migratory fish in a semiarid river system**

### **Abstract**

Recruitment dynamics of Neotropical migratory fishes are widely studied in river-floodplain systems, where the flood pulse and wetlands play a central role. In semiarid systems, where the flow regime is less predictable and water-bodies intermittent, migratory fishes may employ different recruitment strategies. We investigated factors affecting the recruitment dynamics of a migratory fish (*Prochilodus hartii*) in a semiarid river basin (Jequitinhonha River, Brazil) subjected to river regulation. We sampled eggs, larvae, young-of-the-year (YOY), and sub-adults over multiple years and at several sites distributed along 300 km of the Jequitinhonha River. Biotic variables were investigated against 13 predictors through different modeling approaches to examine (i) spawning dynamics and its relationship to the flow regime, (ii) habitat features related to the presence of YOY, and (iii) the relationship between recruitment and floods. Higher densities of eggs and larvae occurred at sites with no influence of river regulation, affected mainly by weekly and daily variations in water level. YOY detection increased by 40% when a lateral stream was present, and occupancy was affected by the length of the lotic stretch. Sub-adult abundance was not correlated with any predictor related to the flooding regime. Our results show that spawning took place at multiple sites, affected mainly by flow variations, while development and recruitment occurred mostly within river channels and in the confluence of small intermittent tributaries, with little dependence on floods. Therefore, fish recruitment in this semiarid system showed different relationships with floods if compared with river-floodplain systems, highlighting the singularity of drylands.

Keywords: Dryland, flow regulation, reproduction, spawning

## Introduction

Migratory fishes employ different strategies to explore variations in the environment and increase the survival of offspring (Winemiller 1989). Upstream migration is a common behavior for many species worldwide (Lucas and Baras 2001; Harvey and Carolsfeld 2003), and in South America, many potamodromous species migrate upstream to spawn in upper reaches and tributaries (Agostinho et al. 2003; Lopes et al. 2018). Eggs released in the current develop into larvae as they drift downstream, and larvae find suitable conditions to grow in floodplain areas, particularly lateral lagoons (Agostinho et al. 2004). This pattern is typical of river-floodplain systems, where predictable hydrological variations (e.g., seasonal variation in water level) drive migration and spawning dynamics (Agostinho et al. 2004; Godinho et al. 2007; Bailly et al. 2008). In these rivers, recruitment of migratory fishes is highly dependent on flood intensity and duration (Agostinho et al. 2004; Bailly et al. 2008) because floods carry larvae toward nursery areas (Suzuki et al. 2010; Reynalte-Tataje et al. 2013; Lozano et al. 2019).

Although this is a common pattern, Neotropical migratory fishes exhibit a diversity of behaviors concerning migration dynamics and habitat types used for spawning and young development (Makrakis et al. 2012; Barthem et al. 2017), since they evolved in systems with distinct flow regimes and habitat distribution. Some rivers (e.g., high gradient and intermittent systems) behave differently from perennial networks or river-floodplain systems (Thorp et al. 1998; Junk and Wantzen 2004). Hydrological regimes vary considerably around the world, with specific flow patterns in space and time (Puckridge et al. 1998; Datry et al. 2016). In general, rivers from drylands (arid and semiarid climates) have variable discharge patterns, with short-term floods during the wet season and limited flow or even dry channels during the dry season (Walker et al. 1995; Puckridge et al. 2010). In addition, they are highly unpredictable, considering that rainfall is irregular, with wide inter-annual variation (Tooth 2000). Under these

conditions, fish must develop life-history traits and strategies to cope with unpredictable flow, limited habitats, and the absence of lateral connectivity (Humphries et al. 1999; Mallen-Cooper and Stuart 2003). One additional complication is that arid and semiarid rivers are highly vulnerable to anthropogenic and environmental alterations (Stromberg et al. 2010; Datry et al. 2011; Zeroual et al. 2013; Mirzabaev et al. 2019), particularly river regulation for water provision and energy production. This activity affects several aspects of the flow regime (e.g., peaks, pulse frequency, duration and amplitude of floods) (Mims and Olden 2013; Ngor et al. 2018; Borba et al. 2019) and connectivity (Helfman 2007; Dudley and Platania 2007; Liermann et al. 2012; Winemiller et al. 2016). Semiarid ecosystems in Brazil, for example, have been subjected to intense environmental degradation (Attayde et al. 2011; Nestler et al. 2012; Sales et al. 2018).

Hydrological specificities and vulnerability to human impacts stress the need to understand how migratory fishes behave and recruit in large semiarid systems, particularly because population dynamics of Neotropical migratory fishes remain poorly known. Such information is crucial to develop management and conservation measures applied to tropical drylands, since most information comes from perennial rivers with predictable flow regime, particularly river-floodplain systems (e.g., Agostinho et al., 2004; Bailly et al., 2008). In this context, this study investigated factors driving the recruitment dynamics of a migratory fish (*Prochilodus hartii*) in a semiarid river (Jequitinhonha River, Brazil) subjected to river regulation. Our objectives were to (i) investigate spawning dynamics and its relationship with the flow regime; (ii) analyze habitat characteristics related to the presence of young-of-the-year (YOY); and (iii) examine the relationship between recruitment and floods. We hypothesize that spawning is controlled by the hydrological regime, while recruitment occurs in the confluence of small tributaries, as floodplain areas and marginal lagoons are lacking in the Jequitinhonha River. In this river system, recruitment dynamics are less dependent on floods and occur in the main channel, being

negatively affected by river regulation. We investigated the following predictions: 1) Spawning occurs at river stretches without dam control, correlating positively with variations in water level, pulse intensity and duration. 2) YOY use the mouth of small tributaries (streams) as nursery grounds when the water level is increased, especially in stretches less affected by the dam. 3) Recruitment (abundance of sub-adults) is not affected by flood duration because lateral environments are absent; instead, flood intensity and number of pulses must explain recruitment, since they create ephemeral and determinant habitats in the littoral zone.

## **Material and Methods**

### ***Target species***

Fishes of the family Prochilodontidae are characterized by having eversive and pronounced lips, equipped with tiny teeth used to scrape the bottom and hard surfaces, where they consume organic matter and periphyton (Castro and Vari 2004). *Prochilodus* is a genus of migratory fishes widely distributed in South America (Resende 2003; Zaniboni-Filho and Schulz 2003; Lopes et al. 2019). They reach medium to large size, employ long-distance migrations to reproduce, and are important for commercial and subsistence fisheries (Castro and Vari 2004). Besides their economic value, the feeding behavior of *Prochilodus* species makes them keystone species in tropical rivers, as they play important roles in the carbon flow and ecosystem functioning (Flecker, 1996; Taylor et al. 2006).

*Prochilodus hartii* Steindachner 1875 is the only species of the genus native to the Jequitinhonha River Basin, but congeneric species were introduced into this basin (Godinho et al. 1999; Pugedo et al. 2016). A genetic study developed by Sales *et al.* (2018) evidenced the hybridization between *P. hartii* and non-native species (*P. argenteus*, *P. costatus*, and *P. lineatus*). Among these *Prochilodus* species, *P. hartii* is the smallest, indicating that non-native *Prochilodus* have higher fecundity and probably greater competitive advantage. The scenario

of introduced kin species and genetic introgression points to a serious conservation issue in the basin.

It is not possible to separate hybrids from the native species using only morphological characters (Sales et al. 2018), especially because morphological diversity is low among *Prochilodus* species (Castro and Vari 2004), and young are difficult to identify at the species level. Due to these limitations, we have decided to consider all individuals (larvae, YOY, and subadults) collected as *Prochilodus hartii*. This decision is biologically justified by the predominance of *P. hartii* in some river reaches (Sales et al 2018) and the similarity between the migration behavior of hybrids and *P. hartii* (unpublished data).

### ***Study Area***

The Jequitinhonha River Basin (JRB) has 70,315 km<sup>2</sup> of drainage area, flowing through sub-humid (upper reach) and semiarid regions (middle and lower reaches) (IBGE 1997). The channel is constrained, without floodplains, receiving several small intermittent tributaries along its course (MMA 2006). JRB drains the Brazilian East Coast, region with many endemic and endangered fish species (Ribeiro 2006; Rosa and Lima 2008; Camelier and Zanata 2014). Although JRB has a low degree of urbanization, it suffers impacts from siltation and sludge contamination (MMA 2006), flow regulation and fish introductions (Pugedo et al. 2016; Andrade et al. 2019). Two hydroelectric dams regulate the main course, Irapé Dam in the upper reach and Itapebi Dam in the lower reach.

The present study was conducted in a long river segment (ca. 300 km) of the Upper-Middle Jequitinhonha River, covering stretches located upstream and downstream from Irapé Dam. This dam created a large accumulation reservoir with 100 km of extension and 280 days of water residence time. This segment includes two main tributaries: the Itacambirucu River, which together with the Jequitinhonha River form the Irapé Reservoir, and the Araçuaí River, an undammed tributary, located 80 km downstream from Irapé Dam (Fig. 1). ***Sampling***



We sampled ichthyoplankton (eggs and larvae) at five sites, being 2 located upstream from Irapé Reservoir: Jequitinhonha River (UPJ) and Itacambiruçu River (UPI). Other sites were located downstream from the dam: one in the tailrace (DAM), and two at the confluence of the Jequitinhonha (DNJ) with the Araçuaí River (DNA) (Fig. 1). All biological material was collected under license from the Brazilian Ministry of Environment (ICMBio/SISBIO No. 42416-4).

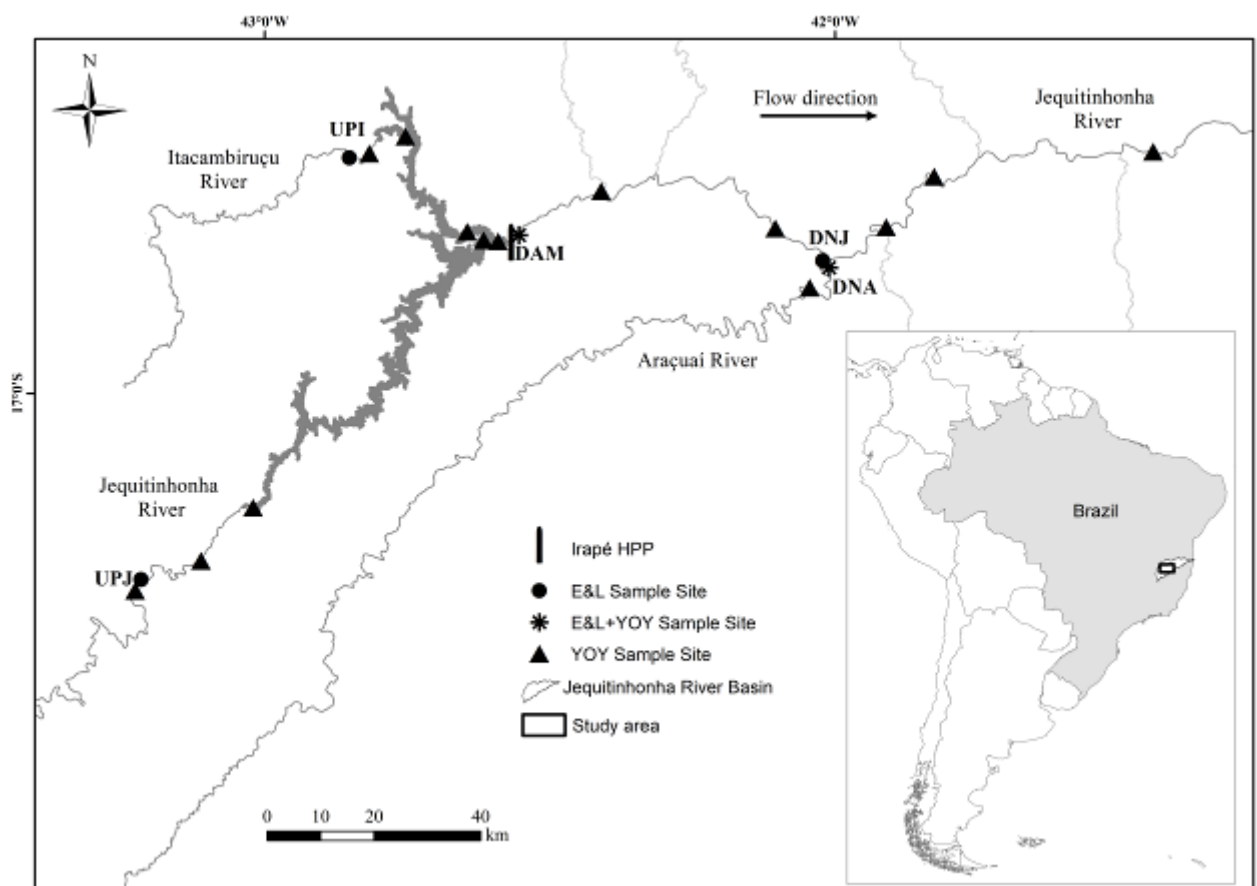


Figure 1. Study area in the Jequitinhonha River Basin. Sampling sites are indicated by symbols: Circles = ichthyoplankton; Asterisks = ichthyoplankton + YOY; Triangles = YOY. UPJ, UPI, DAM, DNA, DNJ: Ichthyoplankton sampling sites (UPJ: 130 km upstream the dam, Jequitinhonha River; UPI: 50 km upstream the dam, Itacambiruçu River; DAM: 500 m downstream the dam, DNA: 80 km downstream the dam, Araçuaí River; DNJ: 80 km downstream the dam, Jequitinhonha River).

We sampled eggs and larvae between October and March (reproductive season) over two consecutive periods: 2014/2015 and 2015/2016. Because spawning is ephemeral and eventual,

we established an intensive sampling protocol. In this sense, sampling occurred every three days during each period, conducted by people from the local community trained by our research team. We used conical-cylindrical plankton nets (0.5 mm mesh) connected to a mechanical flowmeter (General Oceanics) to estimate the volume of filtered water. Sampling occurred at dusk by positioning the net at the subsurface for 10 minutes. Biological samples were preserved in formaldehyde and sorted under a stereomicroscope in the laboratory. Egg identification is challenging and recent genetic studies have evidenced high error rates (Ko et al. 2013; Becker et al. 2015). For this reason, we analyzed eggs generically as "fish eggs". We used this information with caution to discuss the reproduction dynamics of *P. hartii*. Larvae were identified according to Nakatani *et al.* (2001). Egg and larvae densities were standardized as individuals/10 m<sup>3</sup> of filtered water.

We sampled YOY at 16 sites distributed throughout the study area, including the reservoir and lotic stretches upstream and downstream from Irapé Dam (Fig.1). There is no information about length, age, and growth for *P. hartii*, therefore, we used information about *P. lineatus* as reference (Santana 2018). In this sense, we considered as YOY all individuals below 12 cm of standard length. We sampled YOY every 2 or 3 months between February and August, during 2015 (n = 4 months) and 2016 (n = 3 months). We used 5 sets of gill nets (1.2, 1.5, 2 and 2.5 cm mesh sizes; 10 m long each) and seine (5 mm mesh size), which were efficient to catch juveniles in previous trials. We sampled 800 m stretches at each site until all available environments were covered. When a stream with water was present, the sampled area included the stream confluence. Some sites prevented the use of the two methods simultaneously (e.g., reservoir areas, with shores and substrate unsuitable for seining).

We also sampled sub-adults at 3 sites in the reservoir on May, August and November between 2011 and 2018, excepting 2014. Sub-adults are fish with fork lengths among 12 and 22 cm (equivalent to two years old), according to Santana (2018). The subadult data came from

experimental fisheries carried out in the Irapé Reservoir, which employed a set of 20 gill nets (2.4, 3, 4 and 5 cm mesh sizes).

### ***Abiotic data***

Water level data (WL) were obtained from fluviometric stations located near sampling sites and provided by the Agência Nacional das Águas (ANA) and Cemig Geração & Transmissão. From these data we calculated different spatial and hydrological predictors (Table 1).

Table 1. Predictors (name, meaning and method of calculation) used to explain variations in eggs/larvae, YOY and sub-adult density.

<b>Predictor</b>	<b>Meaning</b>	<b>Method of calculation</b>
<b>Ichthyoplankton</b>		
$\Delta$ day	Daily WL variation	Difference between WL in the sampling day and WL in the previous day
$\Delta$ week*	Weekly WL variation	Average $\Delta$ day considering the seven days prior to the sampling day
PulseInt	Pulse intensity	Ratio between $\Delta$ week and average maximum WLs in the past 35 years
PulseDuration	Duration of the pulse	The number of days (within a one-week interval) where the WL remained above the monthly average of the wet season (historical of 35 years).
SS	Sampling site	Sites (UPJ, UPI, DAM, DNJ, DNA)
<b>Young Of the Year - YOY</b>		
WL	Water level variation	Ratio between WL on the sampling day and the WL average during the sampling period.
Stream	Stream presence	Binary variable. Presence (1) or absence (0) of stream with water at the sampling day.
LS	Length of the lotic stretch upstream from the sampling site	Distance from the sampling site until a barrier (dam) or the river source. If the sampling site was in the reservoir, the value was numbered zero. Measured with Geographic Information System – GIS.
Inf	Dam influence	Binary variable. Direct influence of Irapé HPP on river flow (1), or absence of influence (0).
Gear	Sampling method	Seine and/or gillnet. This covariate was used to control the difference in sampling effort
<b>Subadults</b>		
FloodDuration	Duration of the flood	Number of days in the wet season (October to March) the WL remained above the historical average
FloodInt	Intensity of the flood	The ratio between maximum WL and the maximum WLs annual average (historical of 35 years).
Npulses	Number of pulses	The number of complete pulses during the flood period, when the water level reaches values above and below the historical average. Calculated using Pulso software (Neiff & Neiff 2003).

## ***Data analysis***

### *Eggs and larvae*

Eggs and larvae density can be classified as semicontinuous data. This kind of data has two characteristics that make its analysis difficult: (i) Large percentage of zeros (zero inflated); (ii) Strong asymmetry, with many low and few high values (Ingram Jr. et al. 2010), which may deviate even from a log-normal distribution (Duan et al. 1983). Two-part models, or Hurdle models, have been used in different research areas to model semicontinuous data (Collins et al. 2002; Liu et al. 2010; Calama et al. 2011; Smith et al. 2014). These models consider two processes: the first, with binary structure and Bernoulli distribution, examines the occurrence of the event; the second, with log-normal, gamma, inverse Gaussian or other types of distribution, examines its intensity (Liu et al. 2010; Calama et al. 2011; Zuur and Ieno 2016; Nobre et al. 2017). In our study, these processes are represented by the presence and density of eggs/larvae, respectively.

To investigate the first prediction (i.e., flow regime affecting spawning dynamics), we used Two-part models to investigate the relationship between the incidence of eggs/larvae and the predictors SS,  $\Delta$ day,  $\Delta$ week, PulseInt and PulseDuration (Table 1). We used  $\Delta$ week because environmental factors on the sampling day do not affect larvae density, which results from reproductive activity that took place in previous days (Ziober et al. 2012). In addition, we used an one-week window, because the full development of *Prochilodus hartii* larvae may occur within seven days after fertilization (Abdo et al. 2016). Periods were considered as a random variable. Since two-part models allow the use of different variables in each part of the model (Neelon et al. 2016), we removed the predictor SS from the second part, because of the restricted number of observations in the dataset. We used the Zero Adjusted Gamma - ZAGA model of the Generalized Additive Models for Location, Scale and Shape - GAMLSS (Stasinopoulos et al. 2017) in the R software (R Core Team 2018).

### *Young-of-the-year*

Occupancy models are often used to evaluate the probability that a particular sampling locality is occupied by the target species (i.e., incidence of at least one individual) as a function of environmental characteristics (MacKenzie et al. 2002; Moore et al. 2017; Massara et al. 2018). These models are more robust concerning the assumption of imperfect detection, which results in false-zeros or sample zeros (Martin et al. 2005). Detection rates can be obtained by repeated samplings and the use of covariates at sampling occasions, providing better estimates of occupancy (MacKenzie et al. 2017). Because of these characteristics, occupancy models are particularly relevant to analyze juvenile distribution (Rodtka et al. 2015; Weber and Brown 2018), due to sampling limitations related to this life stage (Ryer and Olla 2000; Benson et al. 2005).

To investigate the second prediction (i.e., high WL, stream confluence and long free-flowing river stretches as important nursery grounds), we used occupancy models to analyze the influence of several predictors on the detection and occupancy of *P. hartti* YOY across the 16 sampled sites. First, we evaluated possible changes in site occupancy between the two periods (2015 and 2016) by modeling the extinction and colonization parameters using the Robust Design Occupancy model. Using the Akaike Information Criterion adjusted for small samples (AICc), the model with static occupancy (without colonization and extinction) was the best supported ( $\Delta\text{AICc} = 9.94$  of the model with extinction and colonization estimated), meaning that we did not find difference between the two sampled periods.

In the absence of difference between periods, we used the Single Season Occupancy Estimation model considering seven occasions (both periods) to model the occupancy likelihood of YOY as a function of LS and Inf; the probabilities of detection was investigated in function of WL, Stream and Gear (Table 1). We considered Gear as a group; although this predictor is beyond our study question, it was used to control the difference in sampling effort,

since the assumption of constant detectability required in occupancy models was not met (MacKenzie et al. 2017). We started the model selection by varying the detection parameter and, from the best model ranked, we evaluated the most parsimonious for occupancy. We tested the existence of overdispersion (MacKenzie and Bailey 2004) using the Median c-hat test using the Software Mark (White and Burnham 1999), which was also used to run occupancy models.

### *Subadults*

To investigate the third prediction (i.e., relationship between recruitment and flooding regime), we performed Spearman correlation analysis between the number of *P. hartii* captured in each year and the predictors Npulses, Floodduration and FloodInt of the previous two years (Table 1). These predictors were calculated with data retrieved from the fluvimetric station located in the Jequitinhonha River upstream from the reservoir.

## **Results**

### ***Eggs and larvae***

The two spawning seasons (2014/2015 and 2015/2016) were the driest in the past 87 years, with the lowest WL mean and maximum values in the data series (Fig. 2). WL in free-flowing sites showed similar variations in the two spawning seasons, exceeding the maximum historical mean in the Araçuaí River (DNA). On the other hand, sites under dam influence presented small variation, with WL remaining between 47-70% (DAM) and 20-62% (DNJ) of the maximum historical mean (Fig. 3).

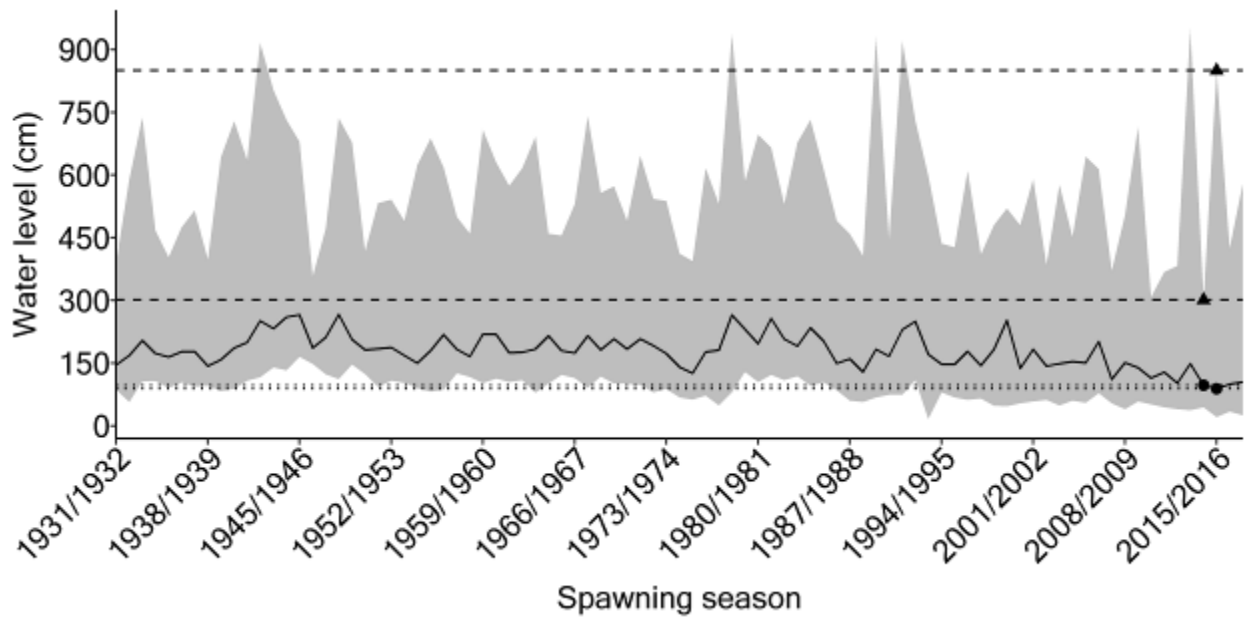


Figure 2. Water level variation (mean: solid line; range: grey area) over 87 consecutive hydrological cycles (spawning seasons: October to March) obtained from the Araçuaí River station, Middle Jequitinhonha River Basin. The maximum (triangle) and minimum (circles) values during the study period (2014/2015 and 2015/2016) are indicated

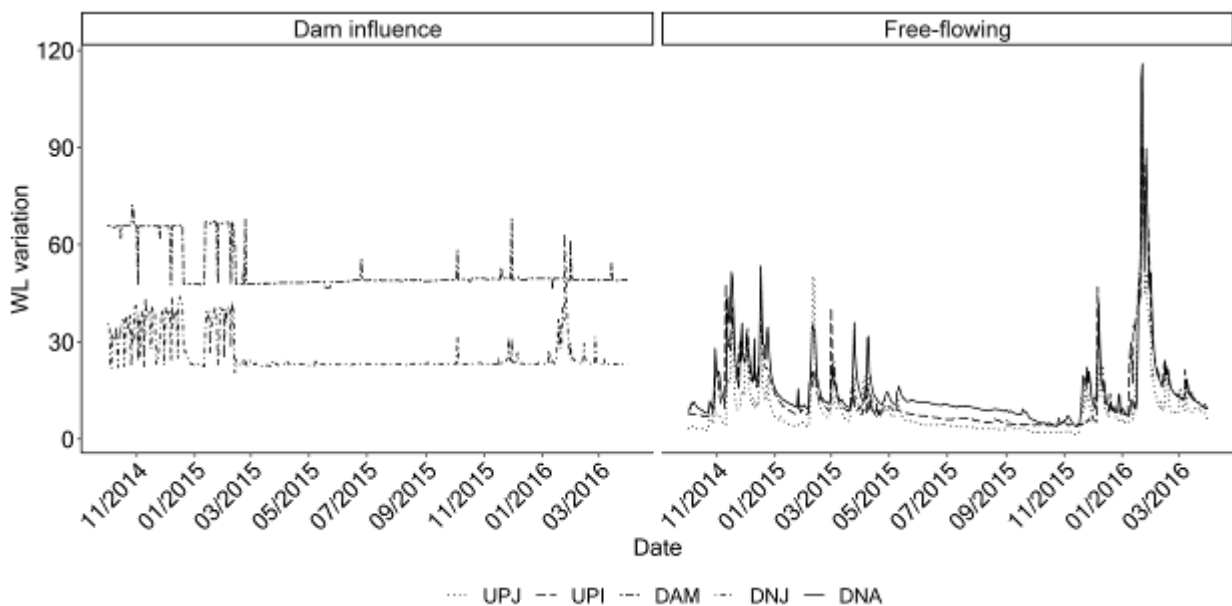


Figure 3. Daily variations in water level (% of the maximum historical mean) from October 2014 to April 2016 at sites that are free-flowing (UPJ, UPI and DNA) and sites under the influence of Irapé Dam (DAM and DNJ).

Of the 557 samples collected, we captured 3,918 fish eggs and 1,266 larvae of *P. hartii* in both reproductive periods. No capture occurred at the DAM site. Higher densities of fish eggs were detected at DNJ, UPI and UPJ (Fig. 4). Larvae occurred in 49 samples (9%) and only one larva was captured at UPI. The DNA and UPJ sites presented the highest larvae densities (Fig. 4).

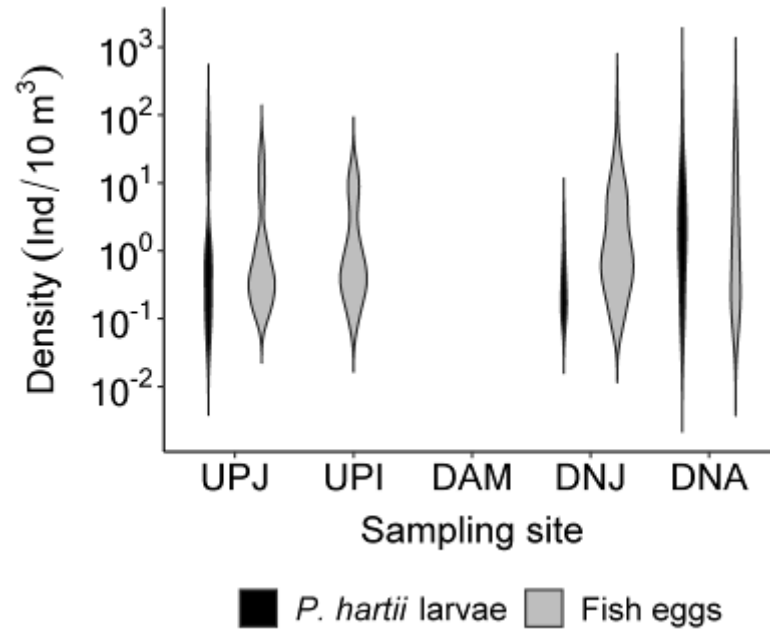


Figure 4. Violin plot of fish egg and *Prochilodus hartii* larvae densities (per 10 m<sup>3</sup> of water) at five sampling sites along the Jequitinhonha River.

Sampling sites (SS) and weekly WL variation ( $\Delta$ week) were the main predictors explaining the presence of eggs and larvae;  $\Delta$ week correlated positively with the two life stages (Table 2). In addition, daily variation ( $\Delta$ day) was also positively related to the presence of larvae. The UPI, UPJ, and DNA sites were less likely to contain fish eggs when compared to DNJ. On the other hand, DNA and UPJ sites were about 7 times more likely to contain *P. hartii* larvae when compared to DNJ (Table 2). The predictor  $\Delta$ week was responsible for most of the variation in egg and larvae density (Table 2). The predictor  $\Delta$ day also correlated positively with egg density, while PulseInt and  $\Delta$ day presented inverse relationships with larvae density (Table 2). Models explained 39 and 34% (Generalized R<sup>2</sup>) of variation in eggs and larvae data, respectively.



Table 2. Results of the Zero Adjusted Gamma models expressed as odds ratio and exponentiated coefficients (semi-continuous component) for fish eggs and *P. hartii* larvae. CI is the confidence interval and bold numbers represent significant relationship ( $p < 0.01$ ).

	Binary part					
	EGGS			LARVAE		
	OR	95% CI	Pr(> z )	OR	95% CI	Pr(> z )
(Intercept)	2.06	1.17   3.64	0.10531	0.013	0.00   0.04	<b>1.9e-08</b>
<i>SS_DAM</i>	4.4e-07	3.2e-100   3.13e+86	0.89334	1.7e-08	6.6e-86   3.4e+98	0.9889
<i>SS_DNA</i>	0.15	0.07   0.29	<b>4.18e-08</b>	6.77	2.42   18.9	<b>0.00029</b>
<i>SS_UPI</i>	0.13	0.07   0.26	<b>2.60e-08</b>	0.11	1.25   96.5	0.0763
<i>SS_UPJ</i>	0.36	0.17   0.76	<b>0.00748</b>	7.3	2.28   24.3	<b>0.00093</b>
<i>PulseInt</i>	0.32	0.13   7.48	0.53919	91.1	3.2e-2   2.5e+5	0.1598
<i>Δweek</i>	1.05	1.02   1.07	<b>0.00061</b>	1.05	1.02   1.09	<b>0.00112</b>
<i>PulseDuration</i>	1.12	0.95   1.31	0.28527	1.09	0.72   1.63	0.6219
<i>Δday</i>	0.99	0.99   1.00	0.61648	1.01	1.00 1.02	<b>0.00139</b>
	Semicontinuous part					
	EGGS			LARVAE		
	Coeff.	95% CI	Pr(> z )	Coeff.	95% CI	Pr(> z )
(Intercept)	1.52	0.86   2.69	0.1474	8.71	2.37   31.9	<b>0.00116</b>
<i>PulseInt</i>	8.9	0.38   209	0.1728	0.001	3.4e-8   0.26	<b>0.02256</b>
<i>Δweek</i>	1.07	1.04   1.10	<b>2.4e-07</b>	1.09	1.05   1.12	<b>2.2e-07</b>
<i>PulseDuration</i>	1.03	0.88   1.22	0.6885	1.47	0.98   2.20	0.06189
<i>Δday</i>	1.01	1.00   1.02	<b>0.0003</b>	0.97	0.96 0.98	<b>5.6e-05</b>

### *Young-of-the-year*

The length of the lotic stretch upstream from the sampling site (LS) ranged between 0 and 295 km, WL ranged from 0.5 to 4.2 m, and flowing streams (Stream) were present from 1 (14%) to 7 (100%) of the sampling occasions. We sampled *P. hartii* YOY on 50% of the sampling sites (8/16), distributed both upstream and downstream from Irapé Dam.

We found no relevant overdispersion (Median chat = 1.12, SE = 0.011), so adjustments were not made to the models. Stream was the only predictor that explained YOY detection, with the highest AICc weight (Table 3). According to the final model, the detection probability increased by 40% when a stream was present ( $0.57 \pm 0.11$  and  $0.17 \pm 0.5$  with and without Stream, respectively). LS was the most important predictor for occupancy (Table 3). The model estimated an occupancy probability of  $0.50 \pm 0.26$  (standard error), similar to naïve occupancy.

The occupancy probability for each site ranged from  $0.00 \pm 0.02$  (sites with no-flowing water located in the reservoir) to  $0.99 \pm 0.005$  (sites with a lotic stretch above 235 km; Fig. 5).

Table 3. Model structure and statistics for the 9 models that evaluated occupancy ( $\Psi$ ) and detection ( $p$ ) probabilities of *P. hartii* YOY. AICc: Akaike's information criterion corrected for small sample size.  $\Delta$ AICc: for the  $i$ th model is computed as  $AICc_i - \min(AIC)$ .  $w$ : AICc weight.  $k$ : number of parameters.  $-2\text{Log(L)}$ : is twice the negative log-likelihood value. WL: water level variation. Stream: stream presence. LS: length of the lotic stretch upstream from the sampling site. Inf: dam influence. Gear: sampling method.

Models for occupancy probability hypothesis				
Model	$\Delta$ AICc	$w$	$k$	$-2\text{Log(L)}$
$\Psi(\text{LS}), p(\text{stream})$	0.000	0.99655	4	100.7166
$\Psi(\cdot), p(\text{stream})$	12.36	0.00205	3	115.8531
$\Psi(\text{inf}), p(\text{stream})$	13.15	0.00140	4	113.8677
Models for detection probability hypothesis				
Model	$\Delta$ AICc	$w$	$k$	$-2\text{Log(L)}$
$\Psi(\text{LS+inf}), p(\text{stream})$	0.0000	0.84653	5	97.8247
$\Psi(\text{LS+inf}), p(\text{WL})$	4.0888	0.10959	5	101.9135
$\Psi(\text{LS+inf}), p(\text{gear})$	7.1393	0.02384	5	104.9640
$\Psi(\text{LS+inf}), p(\cdot)$	7.4874	0.02003	4	108.3510

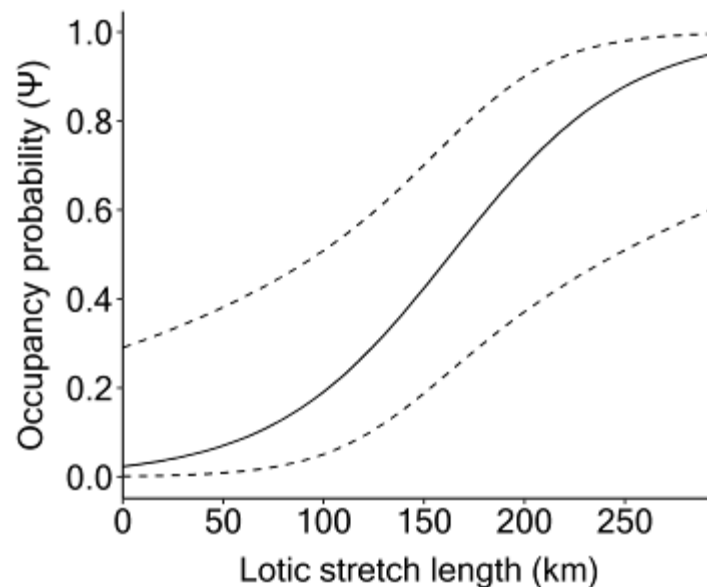


Figure 5. *Prochilodus hartii* YOY occupancy probabilities (mean  $\pm$  95% CI) in relation to the length of the lotic stretch upstream from the sampled site.

### ***Sub-adults***

Subadults sampled in the Irapé Reservoir (n = 172) ranged between 15 and 22 cm fork length, with a median of 20 cm. During the sampling period of 7 years, WL was higher than the historical mean in three years (2009, 2011 and 2013) (Table 4). The years with the highest (91 days) and lowest (14 days) numbers of days when the water level remained above the historical mean were 2011 and 2014, respectively (Table 3). Sub-adult abundance was not correlated (Spearman) with any predictor: FloodDuration (S = 58, p = 0.96), Npulses (S = 43, p = 0.61) or FloodInt (S = 52, p = 0.90).

Table 4. Duration of floods (FloodDuration), Number of pulses (Npulses) and Intensity of floods (FloodInt) during 7 hydrological cycles (spawning seasons) between 2009 and 2016.

<b>Spawning season</b>	<b><i>FloodDuration</i></b>	<b><i>Npulses</i></b>	<b><i>FloodInt</i></b>
2009	36	9	1,23
2010	60	11	0,70
2011	91	8	1,02
2013	38	3	1,31
2014	14	4	0,50
2015	17	2	0,98
2016	23	4	0,46

### **Discussion**

This study brings new information about the reproduction and recruitment of migratory fishes in semiarid rivers without floodplain areas. In general, we observed that spawning, rearing and recruitment dynamics of *P. hartii* in the Jequitinhonha River differ from patterns observed for *Prochilodus* in other Brazilian rivers (Reynalte-Tataje et al. 2008; Bailly et al. 2008; Godinho et al. 2017; Silva and Stewart 2017; Lopes et al. 2019). Results indicated the existence of multiple spawning sites, an activity apparently driven by water level fluctuations. Differing from river-floodplain systems, flood intensity/duration was not related to the abundance of larvae/sub-adult. Moreover, YOY seems to grow in the main channel, near the confluence with small tributaries. We also observed that Irapé Dam affected spawning and

rearing habitats, as no or few larvae and YOY were found in sites under flow regulation, supporting the notion that free-flowing stretches and tributaries work as breeding and nursery sites for migratory fish in catchments altered by dams (Gogola et al. 2010; Reynalte-Tataje et al. 2012; Suzuki et al. 2013). Therefore, recruitment dynamics (i.e., spawning and development) in this Neotropical semiarid river, where floodplains are absent, occur essentially within river channels that present lotic conditions.

In agreement with our first prediction (i.e., spawning in free-flowing stretches, with positive correlation with water level variation, pulse intensity, and duration), sites without dam influence were more suited for reproduction. Eggs and larvae were captured in the main channel and tributaries, but they were absent from sites under flow regulation, particularly at sites close to the reservoir and the dam. The absence of eggs and larvae at the DAM site, in particular, indicates that the reservoir acts as an ecological barrier fragmenting fish populations (Suzuki et al. 2011; Pelicice et al. 2015), especially because eggs were detected in sites located upstream. Also in agreement with our prediction, variations in water level (weekly and daily) correlated positively with both the presence and density of eggs and larvae. This finding may explain why sites with natural water variations (free-flowing), such as UPJ and DNA, had high occurrence and density of eggs and larvae. However, pulse intensity and duration did not correlate with eggs and larvae. Although water level elevation acts as a trigger for spawning (Godinho et al. 2017; Lopes et al. 2018), excessive levels may carry eggs and larvae to unfavorable environments. In the case of the Jequitinhonha River, the stretches studied do not present floodplain areas or lateral habitats such as marginal lagoons. In addition, the duration of peaks was short most of the time, and only once the water level remained 7 consecutive days above the average. Thus, over-bank flows followed by fast retraction may carry eggs and larvae to marginal areas without suitable conditions. We highlight that the investigation of drivers of reproduction is difficult. The low percentage of ZAGA model explanations may be a

consequence of the ephemeral and aggregate nature of ichthyoplankton data. It was demonstrated by Gómez, Calcagno and Fuentes (2011) who found high variability on a same day, among sites and at different depths. This characteristic may explain why some studies do not find relationships between environmental variables, like flow and water level, and ichthyoplankton density (da Silva et al. 2015). Another difficulty concerns with egg identification. Yet, we consider that our approach to using “fish eggs” as a proxy for *P. hartii* eggs was suitable to point out the spatial distribution of spawning sites in the study area. Furthermore, *P. hartii* larvae was the second most abundant taxon in all samples (unpublished data), indicating that our sampling methodology was appropriate for the target species.

In agreement with our second prediction (i.e., small tributaries as nursery grounds, especially in long free-flowing stretches during high water levels), the presence of streams was an important predictor of YOY presence. The mouth of small tributaries, naturally dammed by the Jequitinhonha River, seems to create a backwater environment suitable for larvae development and juvenile growth. There is some evidence of YOY growing in these environments, including migratory fish (Zaniboni-Filho and Schulz 2003; Godinho and Kynard 2009). We noted, however, that such streams in the Jequitinhonha Basin are highly ephemeral and remain dry for most of the time. Yet, in some of them, we collected YOY on all occasions when water flow was present, which indicates their importance as nursery grounds. Contrary to our expectations, the increased water level was not relevant for YOY detection. Humphries, King and Koehn (1999) found out that some semiarid Australian riverine fish are able to recruit within the main river channel during low flow periods. Breeding during more predictable situations (non-flood) can be an important strategy in highly variable systems such as the Jequitinhonha River. The occurrence of reproduction and recruitment in exceptionally dry years is evidence of this possible adaptation. We also observed that YOY occupancy probabilities increased with the length of the lotic stretch upstream, suggesting that free-flowing segments

are crucial for recruitment – as observed in other Neotropical basins (Nunes et al. 2015; Marques et al. 2018; Lopes et al. 2019). Downstream from Irapé Dam, probabilities of sampling YOY in the Jequitinhonha River increased after 100 km, especially after the confluence with the Araçuaí River. The relevance of lotic stretches for young fish was evidenced upstream from Irapé Reservoir, where larvae or YOY was not detected, even though fish eggs were collected in the Itacambiruçu River. The influence of Irapé Reservoir starts 10 km downstream from the UPI site, indicating that the lotic stretch available is too short for the drifting and development of young forms. These results demonstrate the importance of long free-flowing stretches and the presence of confluences to maintain habitat characteristics that are important for the reproduction of migratory fish in embedded river systems.

Our third prediction (i.e., no effect of flood duration on sub-adult abundance, and positive effects of flood intensity and number of pulses) was partially supported. The absence of relationships with all predictors suggests that sub-adults do not benefit from over-bank fluctuations in the water level. Apparently, the energy deriving from external sources is less relevant in these river systems, and offspring may depend especially on autochthonous resources (Thorp and DeLong 1994). Some studies have indicated the importance of autochthonous production as a source of energy in large rivers (Thorp et al. 2006; Doi 2009; Thorp and Bowes 2017), and this may be especially true for the Jequitinhonha River and other systems with similar hydrology (Atlantic basins). In rivers that do not have floodable areas, the mosaic of environments formed by backwaters, rapids, and tributary mouths, may play a critical role for young fish (Ávila-Simas et al. 2014; Lopes and Zaniboni-Filho 2019). King (2004a) points to the relevance of food resources in backwaters and littoral environments (adequate for larvae and YOY development) with little dependence on floodable areas, even in some floodplain rivers. Intense insolation and shallow depths (important for benthic microalgae), for

example, are typically observed along the Jequitinhonha River, which may support instream primary productivity.

*Prochilodus hartii* from the Jequitinhonha River evolved in a semiarid system where perennial habitats are restricted to the main channel, with limited lateral connectivity (e.g., wetlands, lagoons and floodplains), temporary tributaries and unpredictable pulsing flows during the wet season. This particular flow regime and habitat structure seem able to trigger spawning dynamics, disperse eggs and larvae, and create habitats suitable for recruitment, stressing the importance of riverine conditions for the persistence of *P. hartii* populations. Such dynamics differ significantly from *Prochilodus* species living in other basins (e.g., Paraná, São Francisco, and Amazon basins), where they depend strictly on floods and wetlands to complete their life cycle (Gomes and Agostinho 1997; Lopes et al. 2018). Our study observed successful recruitment in the Jequitinhonha River even in exceptionally dry years, indicating that reproductive dynamics are largely unrelated to the occurrence of floods, although recruitment seems to depend on the natural flow regime. Recruitment during more humid years remains as an open question, reinforcing our rudimentary knowledge about biological aspects and flow regime in drylands. In this scenario, recovering and conserving unregulated rivers with their natural flow regime may be the better strategy to maintain migratory fishes in semiarid rivers.

### **Acknowledgments**

Authors thank Companhia Energética de Minas Gerais (Cemig), Agência Nacional de Energia Elétrica (Aneel) and Fundação de Amparo à Pesquisa de Minas Gerais (Fapemig) for financial support. Authors also thank all fishermen who helped with field work, the biologists Miriam Castro and Raquel Loures for technical support, and Raoni Rodrigues and Rodrigo Massara for helping with data analysis. Evoy Zaniboni-Filho and Fernando M. Pelicice received research grants from CNPq. Fernanda O. Silva thanks Capes and CNPq for the scholarship provided.

## References

- Abdo TF, Perrotti PB, Meireles WA, Bazzoli N. 2016. Initial development of *Prochilodus hartii* (Pisces: Prochilodontidae) submitted to induced reproduction. *Zygote*. 24(3):408–417.
- Agostinho AA, Gomes LC, Suzuki HI, Júlio HF. 2003. Migratory fishes of the Upper Paraná river basin, Brazil. In: Carolsfeld J, Harvey B, Ross C, Baer A, editors. *Migr fishes South Am*. Victoria, British Columbia.: World Fisheries Trust; p. 19–98.
- Agostinho AA, Gomes LC, Veríssimo S, Okada EK. 2004. Flood regime, dam regulation and fish in the Upper Paraná River: Effects on assemblage attributes, reproduction and recruitment. *Rev Fish Biol Fish*. 14(1):11–19.
- Andrade FR, Silva LD, Guedes I, Santos AM, Pompeu PS. 2019. Non-native white piranhas graze preferentially on caudal fins from large netted fishes. *Mar Freshw Res*. 70(4):585.
- Antonio RR, Agostinho AA, Pelicice FM, Bailly D, Okada EK, Dias JHP. 2007. Blockage of migration routes by dam construction: Can migratory fish find alternative routes? *Neotrop Ichthyol*. 5(2):177–184.
- Attayde JL, Brasil J, Menescal RA. 2011. Impacts of introducing Nile tilapia on the fisheries of a tropical reservoir in North-eastern Brazil. *Fish Manag Ecol*. 18(6):437–443.
- Ávila-Simas S de, Reynalte-Tataje DA, Zaniboni-Filho E. 2014. Pools and rapids as spawning and nursery areas for fish in a river stretch without floodplains. *Neotrop Ichthyol*. 12(3):611–622.
- Bailly D, Agostinho AA, Suzuki HI. 2008. Influence of the flood regime on the reproduction of fish species with different reproductive strategies in the Cuiabá River, Upper Pantanal, Brazil. *River Res Appl*. 24(9):1218–1229.
- Barthem RB, Goulding M, Leite RG, Cañas C, Forsberg B, Venticinque E, Petry P, Ribeiro MLB, Chuctaya J, Mercado A. 2017. Goliath catfish spawning in the far western Amazon confirmed by the distribution of mature adults, drifting larvae and migrating juveniles. *Sci Rep*. 7(1):41784.
- Becker RA, Sales NG, Santos GM, Santos GB, Carvalho DC. 2015. DNA barcoding and morphological identification of neotropical ichthyoplankton from the Upper Paraná and São Francisco. *J Fish Biol*. 87(1):159–168.
- Benson AC, Sutton TM, Elliott RF, Meronek TG. 2005. Evaluation of Sampling Techniques for Age-0 Lake Sturgeon in a Lake Michigan Tributary. *North Am J Fish Manag* [Internet]. 25(4):1378–1385.
- Borba CS, Latini JD, Baumgartner MT, Gomes LC, Agostinho AA. 2019. Short-term effects in a reduced flow stretch: The case of the Antas River in South Brazil. *River Res Appl*. 35(4):386–395.
- Calama R, Mutke S, Tomé J, Gordo J, Montero G, Tomé M. 2011. Modelling spatial and temporal variability in a zero-inflated variable: The case of stone pine (*Pinus pinea* L.) cone production. *Ecol Modell*. 222(3):606–618.



- Camelier P, Zanata AM. 2015. Biogeography of freshwater fishes from the Northeastern Mata Atlântica freshwater ecoregion: distribution, endemism, and area relationships. *Neotrop Ichthyol.* 12(4):683–698.
- Castro RMC, Vari RP. 2004. Detritivores of the South American fish family Prochilodontidae (Teleostei:Ostariophysi:Characiformes): a phylogenetic and revisionary study. *Smithson Contrib to Zool.*(622):1–189.
- Collins MR, Cooke DW, Smith TIJ, Post WC, Russ DC, Walling DC. 2002. Evaluation of four methods of transmitter attachment on shortnose sturgeon, *Acipenser brevirostrum*. *J Appl Ichthyol.* 18(4–6):491–494.
- Datry T, Arscott DB, Sabater S. 2011. Recent perspectives on temporary river ecology. *Aquat Sci.* 73(4):453–457.
- Datry T, Bonada N, Heino J. 2016. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos.* 125(2):149–159.
- Doi H. 2009. Spatial patterns of autochthonous and allochthonous resources in aquatic food webs. *Popul Ecol.* 51(1):57–64.
- Duan N, Manning WG, Morris CN, Newhouse JP. 1983. A comparison of alternative models for the demand for medical care. *J Bus Econ Stat.* 1(2):115–126.
- Dudley RK, Platania SP. 2007. Flow regulation and fragmentation imperil pelagic-spawning riverine fishes. *Ecol Appl.* 17(7):2074–2086.
- Flecker AS. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology*, 77 (6): 1845–1854.
- Godinho AL, Kynard B. 2009. Migratory fishes of Brazil: Life history and fish passage needs. *River Res Appl.* 25(6):702–712.
- Godinho AL, Kynard B, Godinho HP. 2007. Migration and spawning of female surubim (*Pseudoplatystoma corruscans*, Pimelodidae) in the São Francisco river, Brazil. *Environ Biol Fishes.* 80(4):421–433.
- Godinho AL, Silva CCF, Kynard B. 2017. Spawning calls by zulega, *Prochilodus argenteus*, a Brazilian riverine fish. *Environ Biol Fishes.* 100(5):519–533.
- Godinho HP., Godinho AL., Vono V. 1999. Peixes da bacia do rio Jequitinhonha. In: Lowe-McConnel RH, editor. *Estud ecológicos comunidades peixes Trop.* São Paulo: EDUSP; p. 414–423.
- Gogola TM, Daga VS, da Silva PRL, Sanches P V., Gubiani ÉA, Baumgartner G, Delariva RL. 2010. Spatial and temporal distribution patterns of ichthyoplankton in a region affected by water regulation by dams. *Neotrop Ichthyol.* 8(2):341–349.
- Gomes LC, Agostinho AA. 1997. Influence of the flooding regime on the nutritional state and juvenile recruitment of the curimba, *Prochilodus scrofa*, Steindachner, in upper Paraná River,

Brazil. *Fish Manag Ecol.* 4(4):263–274.

Gómez MI, Calcagno JA, Fuentes CM. 2011. Assessment of an ichthyoplankton net operated at different velocities and durations in the Paraná River. *J Appl Ichthyol.* 27(5):1259–1264.

Harvey B, Carolsfeld J. 2003. *Migratory Fishes of South America*. Victoria (BC): World Fisheries Trust. 372p.

Helfman GS. 2007. *Fish conservation: a guide to understanding and restoring global aquatic biodiversity and fishery resources*. Washington, DC: Island Press.

Humphries P, King A, Koehn J. 1999. Fish, flows and flood plains: links between freshwater fishes and their environment in the Murray-Darling River system, Australia. *Environ Biol Fishes.* 56(1):129–151.

IBGE. 1997. *Diagnóstico ambiental da bacia do rio Jequitinhonha*. Salvador.

Ingram Jr. GW, Richards WJ, Lamkin JT, Muhling B. 2010. Annual indices of Atlantic bluefin tuna (*Thunnus thynnus*) larvae in the Gulf of Mexico developed using delta-lognormal and multivariate models. *Aquat Living Resour.* 23(1):35–47.

Junk WJ, Wantzen KM. 2004. The flood pulse concept: new aspects, approaches and applications - an update. In: Welcomme, R. & Petr T, editor. *Proc Second Int Symp Manag Large Rivers Fish*. Bangkok: Food and Agriculture Organization and Mekong River Commission, FAO Regional Office for Asia and the Pacific; p. 117–149.

King AJ. 2004. Density and distribution of potential prey for larval fish in the main channel of a floodplain river: Pelagic versus epibenthic meiofauna. *River Res Appl.* 20(8):883–897.

Ko HL, Wang YT, Chiu TS, Lee MA, Leu MY, Chang KZ, Chen WY, Shao KT. 2013. Evaluating the accuracy of morphological identification of larval fishes by applying DNA Barcoding. *PLoS One.* 8(1):3–9.

L. Massara R, Paschoal AM de O, L. Bailey L, F. Doherty P, Hirsch A, G. Chiarello A. 2018. Factors influencing ocelot occupancy in Brazilian Atlantic Forest reserves. *Biotropica.* 50(1):125–134.

Liermann CR, Nilsson C, Robertson J, Ng RY. 2012. Implications of Dam Obstruction for Global Freshwater Fish Diversity. *Bioscience.* 62(6):539–548.

Liu L, Strawderman RL, Cowen ME, Shih YCT. 2010. A flexible two-part random effects model for correlated medical costs. *J Health Econ.* 29(1):110–123.

Lopes CA, Zaniboni-Filho E. 2019. Mosaic environments shape the distribution of Neotropical freshwater ichthyoplankton. *Ecol Freshw Fish.* 28(4):544–553.

Lopes J de M, Alves CBM, Peressin A, Pompeu PS. 2018. Influence of rainfall, hydrological fluctuations, and lunar phase on spawning migration timing of the Neotropical fish *Prochilodus costatus*. *Hydrobiologia.* 818(1):145–161.

Lopes J de M, Pompeu PS, Alves CBM, Peressin A, Prado IG, Suzuki FM, Facchin S, Kalapothakis E. 2019. The critical importance of an undammed river segment to the reproductive cycle of a migratory Neotropical fish. *Ecol Freshw Fish*. 28(2):302–316.

Lozano IE, Llamazares Vegh S, Gómez MI, Piazza YG, Salva JL, Fuentes CM. 2019. Episodic recruitment of young *Prochilodus lineatus* (Valenciennes, 1836) (Characiformes: Prochilodontidae) during high discharge in a floodplain lake of the River Paraná, Argentina. *Fish Manag Ecol*. 26(3):260–268.

Lucas MC, Baras E. 2001. *Migration of Freshwater Fishes*. Osney Mead, Oxford: Blackwell Science Ltd.

MacKenzie DI, Bailey LL. 2004. Assessing the fit of site-occupancy models. *J Agric Biol Environ Stat*. 9(3):300–318.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology*. 83(8):2248–2255.

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE. 2017. *Occupancy estimation and modeling. Inferring Patterns and Dynamics of Species Occurrence*. 2<sup>nd</sup> Ed. Burlington, MA, USA. Academic Press.

Makrakis MC, Miranda LE, Makrakis S, Fontes Júnior HM, Morlis WG, Dias JHP, Garcia JO. 2012. Diversity in migratory patterns among Neotropical fishes in a highly regulated river basin. *J Fish Biol*. 81(2):866–881.

Mallen-Cooper M, Stuart IG. 2003. Age, growth and non-flood recruitment of two potamodromous fishes in a large semiarid/temperate river system. *River Res Appl*. 19(7):697–719.

Marques H, Dias JHP, Perbiche-Neves G, Kashiwaqui EAL, Ramos IP. 2018. Importance of dam-free tributaries for conserving fish biodiversity in Neotropical reservoirs. *Biol Conserv*. 224(June):347–354.

Martin TG, Wintle BA, Rhodes JR, Kuhnert PM, Field SA, Low-Choy SJ, Tyre AJ, Possingham HP. 2005. Zero tolerance ecology: Improving ecological inference by modelling the source of zero observations. *Ecol Lett*. 8(11):1235–1246.

Mims MC, Olden JD. 2013. Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshw Biol*. 58(1):50–62.

Mirzabaev A, Wu J, Evans J, García-Oliva F, Hussein IAG, Iqbal MH, Kimutai J, Knowles T, Meza F, Nedjraoui D, et al. 2019. Desertification. In: Shukla PR, Skea J, Buendia EC, Masson-Delmotte V, Pörtner H-O, Roberts DC, Zhai P, Slade R, Connors S, Diemen R van, et al., editors. *Chang L an IPCC Spec Rep Clim Chang Desertif L Degrad Sustain L Manag food Secur Greenh gas fluxes Terr Ecosyst*. p. 249–344.

MMA. 2006. *Caderno da região hidrográfica Atlântico Leste*. Ministério do Meio Ambiente. Brasília.

- Moore MJ, Orth DJ, Frimpong EA. 2017. Occupancy and Detection of Clinch Dace Using Two Gear Types. *J Fish Wildl Manag.* 8(2):530–543.
- Nakatani K, Agostinho AA, Baumgartner G, Bialecki A, Sanches, P. V. Makrakis, M. C. Pavanelli S. 2001. *Ovos e larvas de peixes de água doce: Desenvolvimento e manual de identificação.* Maringá, Brazil: EDUEM.
- Neelon B, O'Malley AJ, Smith VA. 2016. Modeling zero-modified count and semicontinuous data in health services research Part 1: background and overview. *Stat Med.* 35(27):5070–5093.
- Nestler JM, Pompeu PS, Goodwin RA, Smith DL, Silva LGM, Baigún CRM, Oldani NO. 2012. The river machine: a template for fish movement and habitat, fluvial geomorphology, fluid dynamics and biogeochemical cycling. *River Res Appl.* 28(4):490–503.
- Ngor PB, Legendre P, Oberdorff T, Lek S. 2018. Flow alterations by dams shaped fish assemblage dynamics in the complex Mekong-3S river system. *Ecol Indic.* 88:103–114.
- Nobre AA, Melo ECP, Chor D, Griep RH, Carvalho MS, Santos IDS, Fonseca MDJM da. 2017. Multinomial model and zero-inflated gamma model to study time spent on leisure time physical activity: an example of ELSA-Brasil. *Rev Saude Publica.* 51:1–7.
- Nunes DMF, Magalhães ALB, Weber AA, Gomes RZ, Normando FT, Santiago KB, Rizzo E, Bazzoli N. 2015. Influence of a large dam and importance of an undammed tributary on the reproductive ecology of the threatened fish matrinxã *Brycon orthotaenia* Günther, 1864 (Characiformes: Bryconidae) in southeastern Brazil. *Neotrop Ichthyol.* 13(2):317–324.
- Pelicice FM, Pompeu PS, Agostinho AA. 2015. Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. *Fish Fish.* 16(4):697–715.
- Puckridge JT, Costelloe JF, Reid JRW. 2010. Ecological responses to variable water regimes in arid-zone wetlands: Coongie Lakes, Australia. *Mar Freshw Res.* 61(8):832.
- Puckridge JT, Sheldon F, Walker KF, Boulton AJ. 1998. Flow variability and the ecology of large rivers. *Mar Freshw Res.* 49(1):55.
- Pugedo ML, de Andrade Neto FR, Pessali TC, Birindelli JLO, Carvalho DC. 2016. Integrative taxonomy supports new candidate fish species in a poorly studied neotropical region: the Jequitinhonha River Basin. *Genetica.* 144(3):341–349.
- R Core Team. 2018. *R: A language and environment for statistical computing.*
- Resende EK. 2003. Migratory fishes of the Paraguay–Paraná basin excluding the Upper Paraná Basin. In: Carolsfeld J, Harvey B, Ross C, Baer A, editors. *Migr fishes South Am.* Victoria, British Columbia: World Fisheries Trust; p. 99–155.
- Reynalte-Tataje DA, Agostinho AA, Bialecki A. 2013. Temporal and spatial distributions of the fish larval assemblages of the Ivinheima River sub-basin (Brazil). *Environ Biol Fishes.* 96(7):811–822.
- Reynalte-Tataje DA, Agostinho AA, Bialecki A, Hermes-Silva S, Fernandes R, Zaniboni-Filho

E. 2012. Spatial and temporal variation of the ichthyoplankton in a subtropical river in Brazil. *Environ Biol Fishes*. 94(2):403–419.

Reynalte-Tataje DA, Hermes-Silva S, Silva PA, Bialetzki A, Zaniboni-Filho. E. 2008. Locais de crescimento de larvas de peixes na região do alto. In: Zaniboni-Filho E, Nuñez APO, editors. *Reserv Itá Estud Ambient Desenvolvolv Tecnol e Conserv da ictiofauna*. Florianópolis: Editora UFSC; p. 159–193.

Ribeiro AC. 2006. Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: An example of faunal evolution associated with a divergent continental margin. *Neotrop Ichthyol*. 4(2):225–246.

Rodtka MC, Judd CS, Aku PKM, Fitzsimmons KM. 2015. Estimating occupancy and detection probability of juvenile bull trout using backpack electrofishing gear in a west-central Alberta watershed. *Can J Fish Aquat Sci [Internet]*. 72(5):742–750.

Rosa RS, Lima FCT. 2008. Os Peixes Brasileiros Ameaçados de Extinção. In: Machado ABM, Drummond GM, Paglia AP, editors. *Livro Vermelho da Fauna Bras Ameaçada Extinção*. Brasília, DF: MMA. 9–285.

Ryer C., Olla B. 2000. Avoidance of an approaching net by juvenile walleye pollock *Theragra chalcogramma* in the laboratory: the influence of light intensity. *Fish Res [Internet]*. 45(2):195–199.

Sales NG, Pessali TC, Andrade Neto FR, Carvalho DC. 2018. Introgression from non-native species unveils a hidden threat to the migratory Neotropical fish *Prochilodus hartii*. *Biol Invasions*. 20(3):555–566.

Santana HSDE. 2018. Idade e crescimento em peixes: da ciência de base à modelagem populacional. Universidade Estadual de Maringá.

Silva EA, Stewart DJ. 2017. Reproduction, feeding and migration patterns of *Prochilodus nigricans* (Characiformes: Prochilodontidae) in northeastern Ecuador. *Neotrop Ichthyol*. 15(3):1–13.

da Silva PS, Makrakis MC, Miranda LE, Makrakis S, Assumpção L, Paula S, Dias JHP, Marques H. 2015. Importance of Reservoir Tributaries to Spawning of Migratory Fish in the Upper Paraná River. *River Res Appl [Internet]*. 31(3):313–322.

Smith VA, Preisser JS, Neelon B, Maciejewski ML. 2014. A marginalized two-part model for semicontinuous data. *Stat Med*. 33(28):4891–4903.

Stasinopoulos MD, Rigby RA, Heller GZ, Voudouris V, Bastiani F De. 2017. *Flexible Regression and Smoothing: Using GAMLSS in R*. Boca Raton, FL. CRC Press.

Stromberg JC, Lite SJ, Dixon MD. 2010. Effects of stream flow patterns on riparian vegetation of a semiarid river: Implications for a changing climate. *River Res Appl*. 26: 712–729.

Suzuki FM, Pires LV, Pompeu PS. 2011. Passage of fish larvae and eggs through the Funil, Itutinga and Camargos reservoirs on the upper Rio Grande (Minas Gerais, Brazil). *Neotrop*

Ichthyol. 9(3):617–622.

Suzuki FM, Zambaldi LP, Pompeu PS. 2013. Mapping the critical habitats for migratory species of the upper Grande River Region, Minas Gerais State, Brazil. *Appl Ecol Environ Res.* 11(4):645–659.

Suzuki H, Agostinho A, Bailly D, Gimenes M, Júlio-Junior H, Gomes L. 2010. Inter-annual variations in the abundance of young-of-the-year of migratory fishes in the Upper Paraná River floodplain: relations with hydrographic attributes. *Brazilian J Biol.* 69(2 suppl):649–660.

Taylor BW, Flecker AS, Hall Jr RO. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science.* 313: 333–336.

Thorp JH, Bowes RE. 2017. Carbon Sources in Riverine Food Webs: New Evidence from Amino Acid Isotope Techniques. *Ecosystems.* 20(5):1029–1041.

Thorp JH, DeLong MD. 1994. The Riverine Productivity Model: An Heuristic View of Carbon Sources and Organic Processing in Large River Ecosystems. *Oikos.* 70(2):305–308.

Thorp JH, DeLong MD, Greenwood KS, Casper AF. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia.* 117(4):551–563.

Thorp JH, Thoms MC, DeLong MD. 2006. The riverine ecosystem synthesis: Biocomplexity in river networks across space and time. *River Res Appl.* 22(2):123–147.

Tooth S. 2000. Process, form and change in dryland rivers: A review of recent research. *Earth Sci Rev.* 51(1–4):67–107.

Walker KF, Sheldon F, Puckridge JT. 1995. A perspective on dryland river ecosystems. *Regul Rivers Res Manag.* 11(1):85–104.

Weber MJ, Brown ML. 2018. Application of a robust design occupancy model for assessing fish recruitment. *Can J Fish Aquat Sci.* 568:1–8.

White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study.* 46(sup1):120–139.

Winemiller KO. 1989. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia.* 81(2):225–241.

Winemiller KO, McIntyre PB, Castello L, Fluet-Chouinard E, Giarrizzo T, Nam S, Baird IG, Darwall W, Lujan NK, Harrison I, et al. 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science.* 351(6269):128–129.

Zaniboni-Filho E, Schulz UH. 2003. Migratory fishes of the Uruguay river. In: Carosfeld J, Harvey, Ross C, Baer A, editors. *Migr fishes South Am.* Victoria, British Columbia: World Fisheries Trust; p. 157–194.

Zeroual A, Meddi M, Bensaad S. 2013. The impact of climate change on river flow in arid and semiarid rivers in Algeria. In: *IAHS-AISH Proc Reports.* 359: 105–110.

Ziober SR, Bialetzki A, Mateus LA de F. 2012. Effect of abiotic variables on fish eggs and larvae distribution in headwaters of Cuiabá River, Mato Grosso State, Brazil. *Neotrop Ichthyol.*

10(1):123–132.

Zuur AF, Ieno EN. 2016. *Beginner's guide to zero-inflated models with R*. 1st ed. Newburgh, UK. Highland Statistics Ltd.

Capítulo 2: Migratory behavior of a Neotropical fish under habitat fragmentation and hybridization impacts in a semiarid river system



*Sou do Jequitinhonha,  
Sou filho de vaqueiro  
Sou da costa deste rio, onde o sol nasce primeiro  
Também nasci vaqueiro,  
Vaqueiro de cantorias  
Levando por essa estrada, cantigas e poesias  
Canto em versos e trovas,  
Nossas matas tão devastas  
Caviuna, pau brasil, e onde estão nossas cascatas*

Toninho Borges



## Migratory behavior of a Neotropical fish under habitat fragmentation and hybridization impacts in a semiarid river system

### **Abstract**

Habitat fragmentation and species introduction are the main causes of fish population reduction and extinction. These impacts can be intensified in semiarid river systems. The aim of this study was to investigate the migratory behavior of the native fish *Prochilodus hartii* from a semiarid river (Jequitinhonha River, Brazil) in the context of habitat alteration by a large hydroelectric dam (Irapé Dam) and hybridization with non-native species. The study employed radio and acoustic telemetry techniques to investigate fish migration dynamics in the basin, and genetics analyses to differentiate hybrids and native fish. Fish behavior was evaluated for 4 groups: fish released downstream from the dam; near the confluence with the main tributary of the region (Araçuaí River); in the reservoir; and fish passed to the reservoir, simulating a fish passage system. We detected a high proportion of hybridization in the lower reach of the river, and native and hybrids fish showed very similar migratory behavior. The longest distances migrated were detected in the lower reach studied, and the main free-flowing tributary proved to be an important migratory route for reproductive fish. Fish under dam influence tended to move over shorter distances, both in the reservoir and immediately below the dam. Almost all fish released in the reservoir were unable to migrate to upstream lotic stretches, especially those passed from downstream sites. Although we provided evidence about the existence of two independent populations in the region, we detected severe impacts of habitat modification and genetic introgression on this endemic migratory fish, indicating that conservation measures are urgent to protect remnant populations above and below the dam.

## Introduction

Upstream migration is a common behavior for many fish species worldwide (Lucas and Baras, 2001; Harvey and Carolsfeld, 2003). Many South American potamodromous species, for example, migrate upstream to spawn in the main river or in tributaries (Agostinho et al., 2003; Lopes, Alves, et al., 2018). These pelagic-spawning riverine fishes (pelagophils) spawn during high water levels (Dudley and Platania, 2007), they are total spawners, have high fertility and free eggs (Winemiller, 1989), which need turbulent and well oxygenated water for development and drift (Dudley and Platania, 2007). The migratory behavior of Brazilian fishes have been documented in large river systems, especially those with floodplains (Antonio *et al.*, 2007; Godinho, Kynard and Godinho, 2007; Hahn *et al.*, 2011, 2019; Lopes, Pompeu, *et al.*, 2018). These fish show a diversity of behaviors and migrate from dozen to hundreds kilometers (Makrakis *et al.*, 2012), but the main pattern entails upstream migration for spawning, with subsequent dispersal of adults and young to downstream reaches. Although still incipient, some concepts like partial migration (Lopes, Alves, *et al.*, 2018; Hahn *et al.*, 2019), homing (Godinho, Kynard and Godinho, 2007) and metapopulation (Godinho and Kynard, 2006) have been discussed for some fish at some areas.

In semiarid rivers of Brazil, the presence of migratory behavior in fish species have been assumed based on indirect evidence or extrapolations from other basins (Godinho, Godinho and Vono, 1999). The presence of some genera (e.g., *Prochilodus*, *Megaleporinus*) in these systems indicate that the migratory behavior is present. Semiarid rivers are hydrologically peculiar systems, where the flow regime is highly variable, with intense floods during few days of the cycle, and the occurrence of severe droughts (Walker, Sheldon and Puckridge, 1995; Leite and Fujaco, 2010). Rivers in the Brazilian semiarid region have constrained channels, without the presence of floodplains (Maltchik and Medeiros, 2006). Since semiarid rivers have different hydrology, migratory fish species may have developed specific behaviors and adaptations to cope with unpredictable flow patterns and the lack of critical habitats that are commonly found

in river-floodplain systems (Mallen-Cooper and Stuart, 2003). However, scientific information is significantly silent about the behavior of migratory fishes in semiarid rivers in Brazil. Understanding how migratory fishes behave in these systems is a fundamental step to make a broader picture of fish migrations in South America. Moreover, this information is crucial to set management and conservation actions, particularly because semiarid rivers have been significantly impacted by changes in water flow, fragmentation, regulation and habitat degradation (Maltchik and Medeiros, 2006).

Dams change hydrological patterns, river connectivity and habitat availability, being the main cause of migratory species reduction and collapse (Dudley and Platania, 2007; Helfman, 2007; Liermann et al., 2012). When implemented in cascade, the sum of their impacts has the potential to cause local extinctions (Ferguson et al., 2011; dos Santos et al., 2017; Loures and Pompeu, 2018; Oliveira et al., 2018). The consequences for migratory species in modified stretches are many, and include: the blockage of migratory routes (Haraldstad *et al.*, 2019; van Puijenbroek *et al.*, 2019); changes in the flow regime and environmental cues (Dudley and Platania, 2007); divergences between upstream (lacustrine) and downstream (riverine) habitats (Pelicice et al., 2015); segregation of populations (Lopes et al., 2019); extensive fish aggregations downstream (Gehrke, Gilligan and Barwick, 2002; Suzuki *et al.*, 2017), changes in genetic diversity and behavior (Junker et al., 2012; Van Leeuwen et al., 2018). Migratory pelagophils fishes, in particular, are highly threatened by dams. The lentic environment created by large reservoirs works as a filter to drifting eggs and larvae, and creates a behavioral barrier for adults in upstream and downstream migration (Antonio et al., 2007; Pelicice, Pompeu and Agostinho, 2015; Lopes et al., 2019). Different scenarios can modulate the behavior of migratory fish in rivers affected by impoundments, including reservoir size (Lopes, 2017; De Fries et al., 2019), presence of tributaries (Brito and Carvalho, 2013; Ribeiro, 2013), and the morphological complexity of the water body (Pavlov, Mikheev and Kostin, 2019). This

information is unavailable for semi-arid rivers, although these systems, with variable flow and long dry periods, are usually under pressure for flow regulation. As consequence, migratory fish populations in these rivers must be severely impacted by river fragmentation and flow regulation.

Besides habitat alteration and fragmentation, introduction of alien species is another threat to migratory fish in Neotropical systems. The number of introduced fish species have increased over the past 200 years, and current rates surpass historical trends, without signs of decrease (Seebens et al., 2017). Fish introductions have occurred mainly via escapes from fish farms (Azevedo-Santos et al., 2015; FAO, 2020), and some basins are highly invaded (Garcia *et al.*, 2018). In Brazilian semi-arid region, for example, official programs support aquaculture of alien species introduced several fish species in ponds and reservoirs built for water supply (Agostinho et al., 2007; (Attayde, Brasil and Menescal, 2011). including semi-arid systems (Attayde, Brasil and Menescal, 2011). The success of each introduction is dependent on a number of factors, including the receiving environment and ecological characteristics of the invader (Alves et al., 2007; Carvalho et al., 2014; Teixeira et al., 2019), and the ecological consequences are many. One of the consequences is the hybridization with native species (Vitule, Freire and Simberloff, 2009), which can result in genetic introgression and extinction (Todesco et al., 2016). Introgression has the potential to cause life-history and demographic changes in native populations when they reproduce with individuals from other species (Prado et al., 2012; Kovach et al., 2015) or with domesticated individuals from the native species (Horká et al., 2015; Bolstad et al., 2017; Glover et al., 2020). Migratory species from river-floodplain systems, which are highly value by fisheries, have been successfully introduced in different watersheds in Brazil, including semiarid rivers (Godinho, Godinho and Vono, 1999; Alves et al., 2007; Silva et al., 2012; Sales et al., 2018). There is evidence that these species can hybridized with native species and induce introgressive mechanisms (Sales *et al.*, 2018), but

little is known about their interaction with native populations. The occurrence of hybridization indicate the migratory behavior is synchronized between native and non-native populations, although no study investigated this question.

The combination of negative conditions (e.g., environmental degradation, vulnerability to impacts, knowledge gaps) makes Brazilian semiarid rivers a priority for research, particularly to understand how dams and species invasions impact native migratory fish (Silva et al., 2020). In this scenario, this study investigated the migratory behavior of the native *Prochilodus hartii* Steindachner 1875 in the Jequitinhonha River, semiarid region, in the context of habitat alteration by a large hydroelectric dam (Irapé Hydropower Plant - IHP) and hybridization with non-native *Prochilodus* species. The study employed radio and acoustic telemetry techniques to investigate fish migration dynamics in the basin, covering a long river segment (ca. 300 km) above and below the dam, including the main channel and tributaries. In particular, we tagged fish in sites downstream (lotic) and upstream (impoundment) from the dam, and simulated a fish passage in the upstream direction by releasing tagged fish in the reservoir. Also, native and hybrid fish were differentiated by genotyping process. Based on information provided previously, we hypothesized that the stretch immediately downstream from the dam, with altered environmental conditions, is inhospitable for migratory fish. Fish move to regions located far downstream, where environmental characteristics preserve lotic conditions. The presence of a large free-flowing tributary (Araçuaí River), in this case, attract fish and work as an alternative migratory route, where *P. hartii* complete its life cycle. Fish passed to the reservoir upstream, with lentic characteristics without directional flow, have erratic behavior and are not able to reach upstream reaches of the basin. In contrast, populations from the upstream section remain in the impounded area during non-reproductive periods, but use lotic stretches upstream to spawn. Finally, due to the high degree of genetic introgression between *P. hartii* and non-native *Prochilodus*, these fish use the same breeding sites and display the

same migratory behavior. Our predictions are: i) Fish in lotic stretches of the Jequitinhonha River, downstream of the IHP, will use the tributary Araçuaí River as the preferential route and will migrate over longer distances than upstream fish. ii) Fish from lotic stretches passed to the reservoir will present a higher diversity of movements than fish tagged in the reservoir, but they will not reach stretches upstream. iii) Hybrids and native fish will have the same migratory behavior (routes, distances and timing).

## **Material and methods**

### ***Species***

*Prochilodus* is a genus of migratory fishes widely distributed in South America (Resende, 2003; Zaniboni-Filho and Schulz, 2003; Lopes, Pompeu, et al., 2018). They reach medium to large size, employ long-distance migrations to reproduce, and are important for commercial and subsistence fisheries (Espinach Ros et al., 1998; Castro and Vari, 2004). Besides their economic value, the feeding behavior of *Prochilodus* makes them keystone species in tropical rivers, as they play important roles in the carbon flow and ecosystem functioning (Flecker, 1996; Taylor et al. 2006).

*Prochilodus hartii* Steindachner 1875 is endemic to the Pardo and Jequitinhonha basins, the only native *Prochilodus* species in these catchments. *Prochilodus* is among the most studied migratory fish in Brazil, but the migratory behavior for *P. hartii* remains unknown. Its eggs are non-adhesive with large perivitelline space (Abdo *et al.*, 2016), similar to other migratory species (Rizzo *et al.*, 2002), indicating that *P. hartii* also employs similar behavior concerning migration (upstream movements) and spawning (pelagophils).

Some *Prochilodus* species were introduced to the Jequitinhonha River Basin (Godinho, Godinho and Vono, 1999; Pugedo *et al.*, 2016). A genetic study developed by Sales *et al.* (2018) evidenced the hybridization between *P. hartii* and non-native species (*P. argenteus*, *P. costatus*, and *P. lineatus*). Among these *Prochilodus* species, *P. hartii* is the smallest, indicating that non-

native *Prochilodus* have higher fecundity and probably some competitive advantage. The scenario of introduced kin species and genetic introgression points to a serious conservation issue in the basin. Due to the impossibility of separating hybrids from the native species using only morphological characters (Prado *et al.*, 2012; Sales *et al.*, 2018), we used the generic term “curimba” (local name for *Prochilodus*) to refer to hybrids and native fish indistinctly. We referred to *P. hartii* and hybrids separately only when genetic data identified each group (see below).

### ***Study area***

The Jequitinhonha River Basin (JRB) drains the East Atlantic Basin complex, a region with many endemic and endangered fish species (Ribeiro, 2006; Camelier and Zanata, 2014; Reis *et al.*, 2016). The watershed is home to different vegetation and biomes, such as savanna, xeric and rainforests (Ferreira, 2011), with climate changing from sub-humid (Upper reach) to semi-arid (Middle and Lower reaches) (IBGE, 1997). The Jequitinhonha River is 920 km long, and its drainage is strongly affected by geological features, with steep valleys and embedded channels (IBGE, 1997).

This study was conducted in the Upper and Middle reaches of the JRB, in the area directly and indirectly affected by Irapé Hydropower Plant (IHP). It included lotic stretches of the Jequitinhonha River upstream and downstream from the dam, the impoundment and main tributaries (Itacambiruçu, upstream; Araçuaí, downstream). Irapé Reservoir flooded a segment of approximately 100 km of the Jequitinhonha River and 45 km of the Itacambiruçu River (Fig. 1). It is a large storage reservoir, and depths reach more than 200 m near the dam. The lotic stretch downstream IHP is drained by small tributaries and the Araçuaí River, the main tributary in the region, distant 80 km from Irapé dam (Fig. 1).

### ***Fish capture, tagging and releasing***

During the tagging period, curimbas were captured with cast net, gillnet and drift nets in the beginning of two breeding seasons: Oct/15 to Feb/16 and Oct/16 to Feb/17. Fish were

captured in three sites: TG1 - up to 2 rkm (river kilometers) downstream from Irapé dam; TG2 – Jequitinhonha River 12 rkm downstream from the Araçuaí River confluence; TG3 – Irapé Reservoir, up to 5 rkm upstream from Irapé dam (Fig. 1).

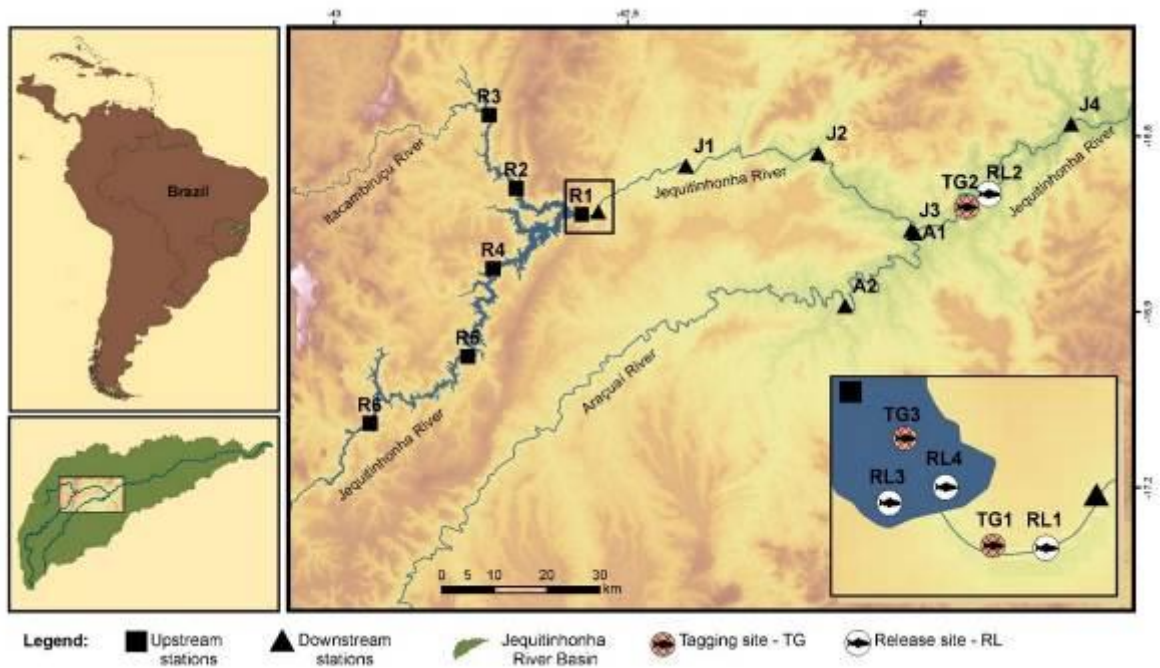


Fig1: Map of the study area in the Jequitinhonha River Basin. Squares indicate acoustic stations upstream from Irapé Dam, and triangles indicate radio stations downstream from Irapé Dam. R: stations at the reservoir, J: stations at the Jequitinhonha River, A: stations at the Araçuaí River. In detail (bottom, right) are the locations of tagging (TG) and releasing (RL) sites close to the dam, upstream and downstream from IHP.

Fish were initially anesthetized with eugenol solution (0.05 mg/l). After weighing and measuring, fish received in the gills a solution of 0.035 mg/l eugenol during the surgery for the implantation of the transmitter in the body cavity, following procedures outlined by Lopes et al. (2016). Fish were tagged with radio (Lotek Wireless Inc., MST-930, weight in air = 4 g; pulse rate= 12, 12.5 and 13 s; minimum lifetime= 476 days) or acoustic transmitters (Lotek Wireless Inc., JSATS L-AMT-8.2, weight in air = 2 g; pulse rate= 7 sec; minimum lifetime= 681 days), depending on the release site. A small incision was made in the lateral side of the body, posterior to the pelvic fins, and the transmitter was inserted in the body cavity. Sex was assigned for mature individuals during surgery, based on macroscopic characteristics of the



gonads. It was not possible to determine the sex of non-reproductive fish, and they were classified as unidentified sex – NI. The incision was sutured with monofilament nylon sutures. Fish were also marked with external tags (Hallprint©, model PDS small tipped dart tags) with returning information in case the fish was caught by fishermen. A small fragment of the caudal fin was taken for genetic analysis. After tagging, fish were transferred to a tank with river water, to recover prior to release.

We used radio transmitters in the segment downstream from the dam, and acoustic transmitters in the segment upstream. Fish were released at 4 distinct sites (Fig. 1):

RL1: Fish captured and released in TG1, to investigate migratory dynamics downstream from the dam;

RL2: Fish captured and released in TG2, to investigate migratory dynamics near the confluence with the Araçuaí River;

RL3: Fish captured and released in TG3, to investigate migratory dynamics in the impoundment and upstream sites;

RL4: Fish captured in TG1 and released in the Irapé reservoir, to investigate the behavior of fish passed upstream, simulating a fish passage system.

Fish capture, handling and tagging procedures were licensed by the Brazilian Ministry of Environment (ICMBio/SISBIO: 42416-4).

### ***Fish monitoring***

Curimbas movements along the study area were determined using acoustic telemetry in the Irapé reservoir and upstream sites, and radio telemetry in the long segment downstream from IHP dam. Different techniques were chosen according to the best detection efficiency found after tests at each environment (impoundment versus river channel). We installed acoustic and radio fixed stations along 220 rkm of the study area, at 13 sites (Fig. 1). We installed 17 acoustic receivers (Lotek WHS 4000L) at 6 sites along the Irapé reservoir (R1 to

R6, Fig. 1), using arrays of 2 to 4 receivers depending on reservoir width. Additionally, one acoustic receiver was installed 1 rkm downstream from the Irapé HP, in order to record fish released at RL3 and RL4 that eventually passed downstream through the turbines. Each acoustic receiver stayed submerged approximately 15 meters below the surface, attached to a system of 12 mm polypropylene rope, mooring and buoys. The system was designed to follow variations in the water level of the reservoir.

Seven fixed radio stations were installed on the riverbank at 6 locations downstream from the Irapé Dam (Fig. 1). Each station consisted of one radio receiver (Lotek SRX800-D) connected to 2 four-elements Yagi antenna (one directed upstream and another downstream). Fixed stations at Araçuaí (A1) and Jequitinhonha (J3) were installed close to the Araçuaí River confluence, but with independent receivers and antennas (Fig. 1).

Radio and acoustic fixed stations were operational from September 2015 to March 2018. We downloaded data from the fixed stations (radio and acoustic) every month on the reproductive season (October to March) and bimonthly on the non-reproductive season (April to September). Additionally, we tracked radio tagged fish by boat and airplane in the reach downstream from the dam to complement passive monitoring by fixed stations. We covered 370 rkm of the Jequitinhonha River and 120 rkm of the Araçuaí River by airplane, and 280 rkm of the Jequitinhonha River by boat, totalizing 6 tracks for each method. We did not track fish in the reservoir due to the large size of the area and the small detection range of the acoustic receiver. However, bi-monthly tracks were made between the R1 station and the dam.

### ***Genetic analysis***

Methodology was performed as described by Pimentel *et al.*, (2018). Fragments of fish fin (12.5-mm<sup>2</sup>) from samples previously collected and stored in 70% ethanol (v/v) were washed with ultrapure water, incubated with 50 µl of NaOH (50 mM), vortexed for 10 s, incubated at 95 °C for 10 min, and vortexed again for 10 s. Then, 7.5 mL of Tris-HCl (0.5 M, pH 8.0) were

added to each sample and vortexed for 15 s. We purified DNA from the supernatants using Agencourt AMPure XP magnetic beads (Beckman Coulter, Brea, CA, United States), according to the manufacturer's protocol. DNA was quantified using Qubit 2.0 (Invitrogen, Carlsbad, CA, United States) and its purity was evaluated using NanoDrop 2000 (ThermoScientific, Waltham, MA, United States). For genotyping, Illumina's overhang adapter complementary to the 'index' was added to the primers (Forward: 5'-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGC locus-specific forward primer-3', and Reverse: 5'-GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGC locus-specific reverse primer sequence-3'). The primers with the overhang adapters were incorporated into the target DNA through 30 PCR cycles (10 ng of DNA, pre-mix 4B (Phoneutria Biotecnologia e Serviços LTDA, Brazil), 5 pmol of each primer, 5% of DMSO, final volume of 20 µl. Cycling: 95 °C for 2 min, 30 cycles at 95 °C for 30 s, 58 °C for 20 s and 72 °C for 30 s. Final step was 72 °C for 5 min.). A specific primer (index) containing the MiSeq adapter (which individualizes samples in the NGS procedures) was attached to amplicons through 10 PCR amplification cycles. We used PrcF6 5'-ACTCCCACCACTAACTCCC and PrcR2 5'-TCATATTGTGCGACCCCCAC to amplify the mitochondrial DNA of *Prochilodus sp.*, and 08F 5'-GGGATGCAAAGGGACATGAC and 08R 5'-AAAGCCATGCGTCCATTGAG, 10F 5'-TGACGCCTCGCTATATCAGG and 10R 5'-GACCCATCATCTGTGCAAGG, 21F 5'-AGGTTGGGTGTGCTAGAGAG and 21R 5'-CTCAGCCACAGATGCATGAC, 31F 5'-CACAGTAAGGACATCGCTGC and 31R 5'-AGGACTGGAGTTGTGCACC, primers that preferentially amplify *P. argenteus* and *P. constatus*, in special loci 16, 10 and 21. The non-amplification of two or more loci, characterized the genomic sample as being *P. hartii*. The amplification and sequencing process was repeated to confirm the results. After 3 repetitions of amplification and sequencing, samples with inconclusive results were not considered in this study. Locus 38, with primers 38F 5'-AAGAGATGGGTGACTGCGTG and 38R 5'-

TCAGCACTTCACTCCCTTGG was used as a positive control for amplifying the genomic DNA of *Prochilodus argenteus*, *costatus* and *hartii*. Genotyping libraries were diluted using the Illumina buffer to attain the final concentration of 10 pMol DNA in a final volume of 1 ml. Sequencing was performed with 600 µl of the final solution using a nano kit (v. 2, 1M) and the MiSeq platform (Illumina). Bioinformatics analysis was performed essentially as described by Pimentel *et al.* (2018) and made by Phoneutria Biotecnologia e Serviços LTDA.

### ***Data processing and analysis***

Data from radio receivers were validated considering at least 2 consecutive records within the pulse rate range and within an interval of 300 seconds. Data from acoustic receivers were processed using the JSATS Autonomous Receiver Data Filtering Software, developed by Pacific Northwest National Laboratory, Richland, Washington (PNNL), due to the high frequency of false detections in these datasets. First, we analyzed the dataset from receivers that remained in the study area for 2 months prior to the release of tagged fish. We used this dataset to set the most parsimonious configuration of the filtering process, i.e., the number of records within a pulse rate range necessary to eliminate all of the false positive detections (Deng *et al.*, 2017). After that, we filtered the dataset from all the receivers during the study period.

We applied GLM (Gamma distribution) to test the effects of type of fish (hybrids and native) and release site on distance migrated. This test was applied to investigate the first (fish downstream from the dam migrate over longer distances) and third (hybrids and native fish migrate the same distances) predictions.

Chi-square test was applied to evaluate the third prediction (hybrids and native fish will take the same routes). We tested if fish frequencies differed between type of fish (hybrids and native) and routes taken for fish at each release site. We assigned as a route the fish track between the release site and fixed stations, as well as fish movements between fixed stations, considering the most upstream and downstream fixed stations visited.

We also used Chord diagrams to investigate the first and second (fish passed to the reservoir present a higher diversity of movements, but they do not reach stretches upstream) predictions. Chord diagram displays the relationships between the proportion of fish at each release sites and their respective destinations (in this case, each fixed station). Chord diagrams were built using migest package (Abel, 2019).

We investigated possible differences in timing of migration between native and hybrids (third prediction) by calculating the number of fish detected by each fixed station, per day, during the study period. As fish have not moved over long distances in most sites, we used only fish from RL2 to investigate this question. All analyses were run in R software (R Core Team, 2018).

## **Results**

From 406 tagged fish, we had combined information about migration and genetics for 256 (63%), being 48 from RL1, 100 from RL2, 47 from RL3 e 61 from RL4. A lower proportion of hybrids was found close to the dam: 20% at TG1 and 18% at TG3. Differently, 62% of the fish captured at TG2 were assigned as hybrids. The main species introduced and detected among hybrid fish was *Prochilodus argenteus*.

It was not possible to identify the sex of most of individuals tagged at TG1 and TG3. Also, the majority of fish at these points were smaller than 300 mm SL (Fig. 2). On the contrary, most of fish tagged at TG2 were larger than 300 mm, being 73% males and 10% females (Fig. 2). Only 35% of tagged fish provided information for more than 100 days. RL3 was the environment where we followed fish for a shorter period of time (Fig 3).

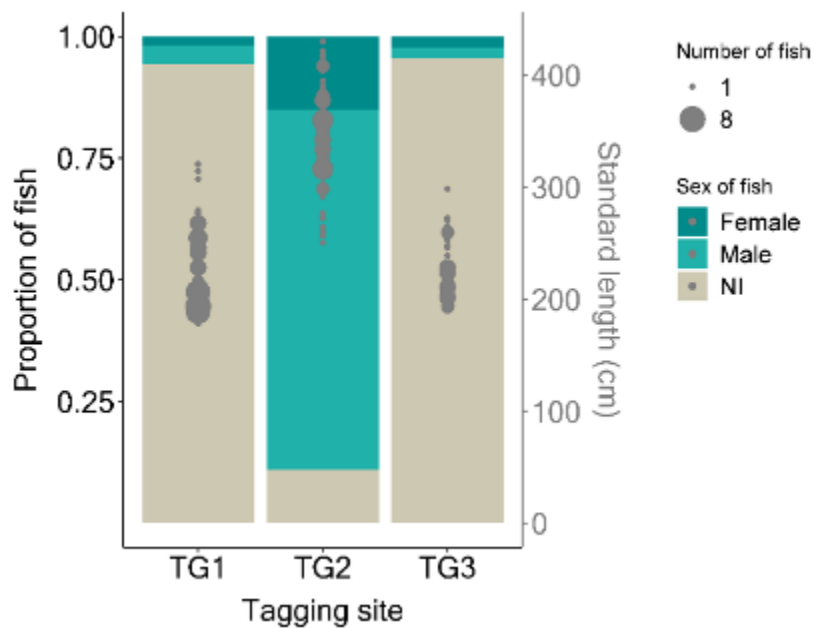


Fig. 2: Standard length (cm) and proportion of sex (male, female or NI: non-identified) at each tagging site. TG1: tailrace of Irapé HP; TG2: downstream from Araçuaí River confluence; TG3: reservoir.

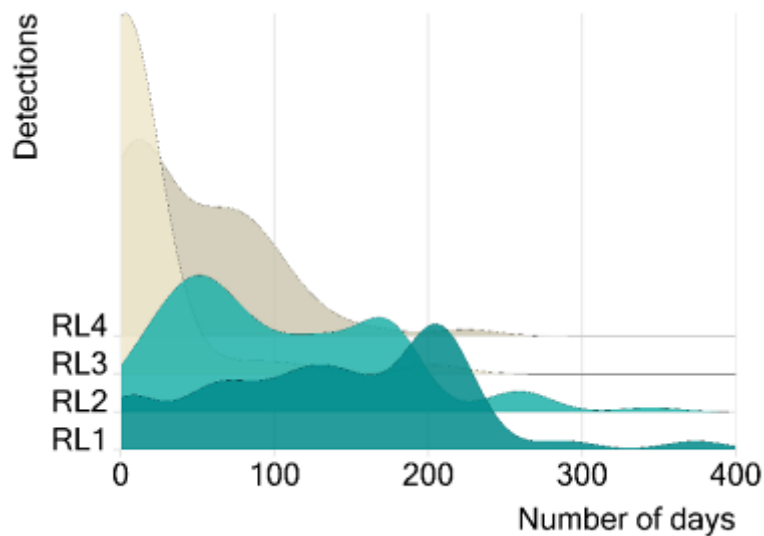


Fig. 3: Number of detections of tags over time, considering tags from each release site. Number of days is the time elapsed between tagging and the last detection.

The distance migrated was not different among hybrids and *P. hartii*, but differed at RL2 (Table 1). In general, fish did not show long displacements (RL1:  $\bar{x}$ =9.3 km,  $\tilde{x}$ =0.7 km; RL3:  $\bar{x}$ =3.7 km;  $\tilde{x}$ =0.5 km; RL4:  $\bar{x}$ =10.4 km,  $\tilde{x}$ =0.5 km), except fish tagged and released at RL2, which showed longer displacements (RL2:  $\bar{x}$  =71 km;  $\tilde{x}$  =53 km) (Fig. 4).

Table 1: Results of GLM Gamma analysis that tested the effects of type of fish (native versus hybrid) and release site on distance migrated.

Predictor	Coefficient	Std. Error	t-value	p-value
Intercept	2.28602	0.38862	5.882	1.29e-08*
Hybrid	-0.05599	0.37724	-0.148	0.8821
Site_T2	2.01431	0.47676	4.225	3.35e-05*
Site_T3	-0.94918	0.53395	-1.778	0.0767
Site_T4	0.07789	0.50215	0.155	0.8769

Hybrids and *P. hartii* showed similar migratory behavior, since they have taken similar routes after released in each site (RL1:  $X= 0.92$ ,  $df= 3$ ,  $p= 0.82$ ; RL2:  $X= 9.03$ ,  $df= 14$ ,  $p= 0.83$ ; RL3:  $X= 2.17$ ,  $df= 2$ ,  $p= 0.33$ ; RL4:  $X= 9.87$ ,  $df= 11$ ,  $p= 0.54$ ). Overall, fish at RL1 remained close to the dam ( $d < 5$  km), 7 individuals migrate 6 to 15 km and only 2 fish migrated over long distances in the downstream direction (Fig. 4 and 5). One curimba passed by A1 and returned upstream to the release site. The other passed through A2 (Fig. 5), reaching 105 km upstream from the Araçuaí confluence, where it was detected for the last time 100 days after tagging. Fish at RL2 site showed a diversity of migratory behaviors, but as expected, most fish visited the Araçuaí River (Fig. 5). Some fish visited the Jequitinhonha River, remaining close to the confluence with the Araçuaí River, and a low percentage reached J2. No fish from RL2 migrated to the Irapé Dam (Fig. 5).

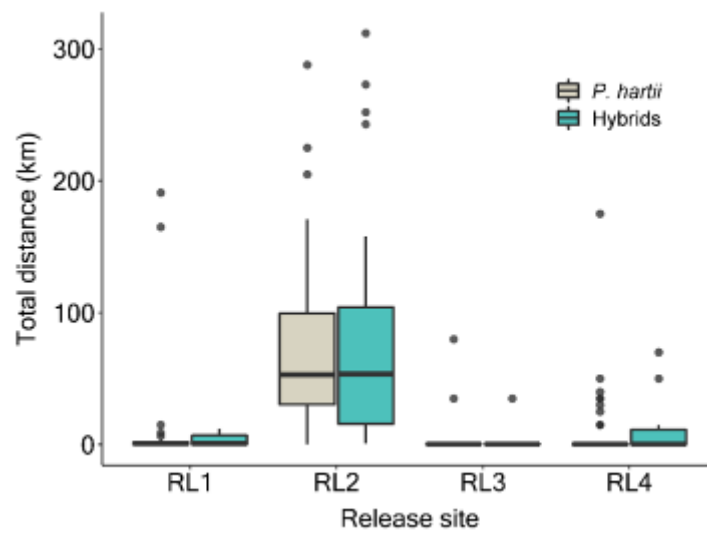


Fig.4: Total distance traveled by hybrids and *P. hartii*, considering each release site.

Fish from RL3 moved over shorter distances along the reservoir. All individuals passed the first station (R1) and the majority dispersed in the first third of the reservoir. Few fish reached the transition region of the Itacambiruçu (R3; n=2) and Jequitinhonha (R6; n=1) rivers (Fig. 6). Almost half of RL4 fish passed through R1 station and stayed in the first third of the reservoir. Third percent remained near to the dam and never approached the R1 station. Two percent (n=1) and 7% (n=4) reached the final stretch of the reservoir in the Jequitinhonha and Itacambiruçu rivers, respectively (Fig. 6).



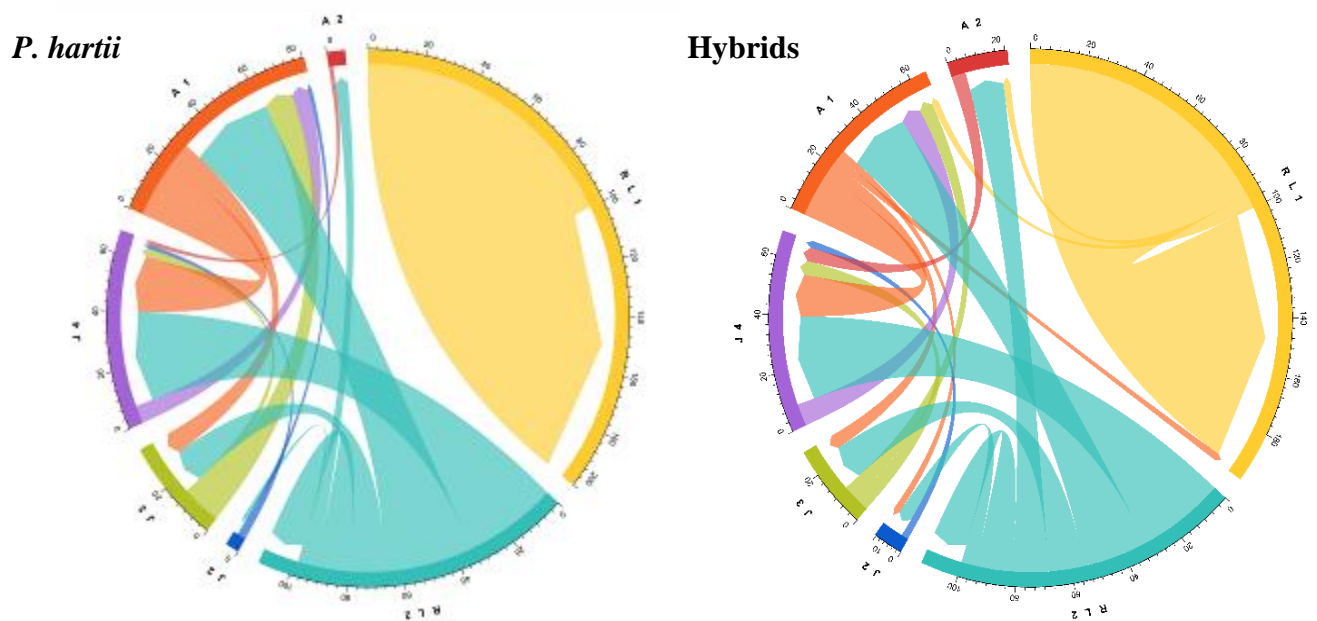


Fig. 5: Migratory routes of *P. hartii* and hybrids fish tagged at TG1 and TG2 and released at sites RL1 and RL2, respectively, downstream from Irapé Dam. Stations J2, J3 and J4 are located at the Jequitinhonha River, and A1 and A2 are stations located at the Araçuaí River.

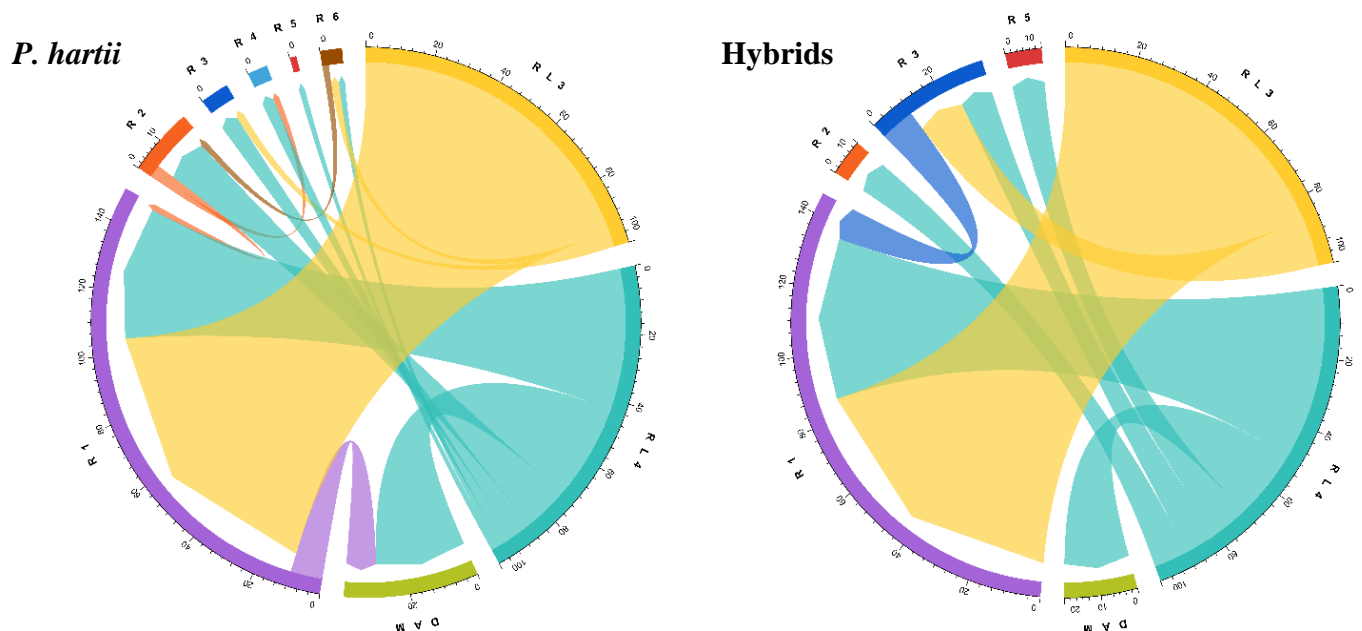


Fig. 6: Migratory routes of *P. hartii* and hybrids fish tagged at TG3 and TG1 and released at RL3 and RL4, respectively, upstream from Irapé Dam. R1 is the station located 500 m upstream from Irapé dam; DAM is the area between the dam and R1 station; R2 and R3 are stations in the Itacambiruçu reservoir; R4, R5 and R6 are stations in the Jequitinhonha reservoir.

Timing of migration was evaluated using only J4 and A1 stations, since they were the most visited. Higher proportion of *P. hartii* and hybrid fish migrated on the same days (Fig. 7) to the Araçuaí River (A1) and to the downstream segment of the Jequitinhonha River (J4).

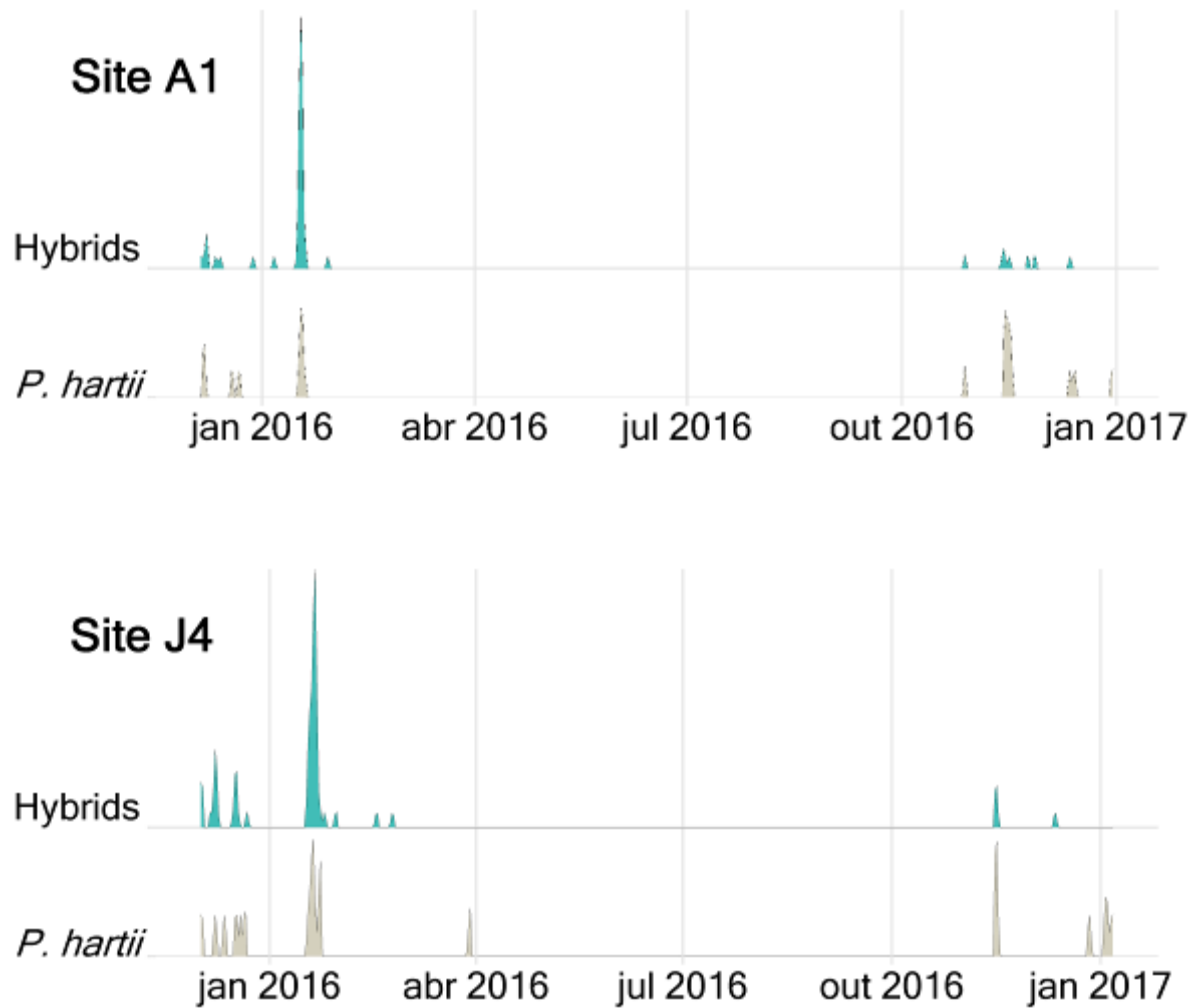


Fig. 7: Proportion of fish tagged at TG2 detected at A1 and J4 stations between December 2015 and January 2017. The figure shows daily records.

## Discussion

Our study is the first to investigate the migratory behavior of *P. hartii* (curimba) in the Jequitinhonha River, a species under impacts of biotic invasion, flow regulation and

fragmentation. We detected a high proportion of hybridization between native and introduced curimbas, especially in the lower stretch of the Jequitinhonha River. One important finding was that hybrid and native fish showed a very similar migratory behavior in all studied sites. A more diverse migratory behavior, which involved longest distances, were detected in the lower reach of the study area. The Araçuaí tributary, the main free-flowing river in the region, proved to be an important migratory route for reproductive fish. On the other hand, curimbas in stretches under dam influence tended to stay close to the release site, both in the reservoir and below the dam.

Our first prediction, that fish at lotic stretches downstream from the dam (RL1 and RL2) should migrate over longer distances and use the Araçuaí River as a main route, was partially confirmed. Most fish at RL1 stayed close to the dam, with only two fish migrating long distances downstream and visiting the Araçuaí River. In other basins, the behavior of *Prochilodus* spp. downstream from dams have shown varied patterns, ranging from a high proportion of sedentary fish in the tailrace (Godinho and Kynard, 2006; Ribeiro, 2013) to a large percentage of fish migrating downstream and/or using tributaries (Antonio *et al.*, 2007; Ribeiro, 2013). These results show how habitat fragmentation, depending on dam position and operation, can disrupt the life cycle of migratory fishes (Agostinho *et al.*, 2002; Van Leeuwen *et al.*, 2018). In general, fish tagged at RL1 were smaller than fish at RL2, and sexually immature. These findings agree with those of Abdo, Marcon and Bazzoli (2018), which observed inactive *P. hartii*, or with gonads at initial maturation stages, close to the Irapé Dam. One possible explanation for this scenario is that individuals that come to the tailrace are dispersing with no reproductive motivation, probably young recruited downstream in the region of the Araçuaí River. Although there was no evidence of recruitment in the Jequitinhonha River upstream from the Araçuaí River, larvae were detected at the J3 site (Silva *et al.*, 2020),

indicating that some curimbas spawn in this reach. These larvae can be from fish coming downstream from Araçuaí River, migrating upstream to spawn (J3 and J2 sites).

Fish from RL2 migrated over longer distances and used the Araçuaí tributary as a main destination, supporting our first prediction. The use of tributaries as a migration route downstream from dams has been shown for other curimba species in different watersheds (Godinho and Kynard, 2006; Antonio *et al.*, 2007; Ribeiro, 2013). Additionally, fish at RL2 showed a variety of behaviors, and a large proportion moved toward downstream reaches. Probably these fish used the Jequitinhonha River near the confluence with the Araçuaí River as spawning site. It is important to note that none RL2 fish reached Irapé PP tailrace, with the longest displacement reaching 30 km downstream from the dam. It reinforces that reaches downstream from dams have poor environmental quality and are not suitable for fish in reproductive activity. Some studies have reported curimbas presenting low fecundity and high levels of follicular atresia at the tailrace of dams (Agostinho *et al.*, 1993; Arantes *et al.*, 2010; Perini *et al.*, 2013). The low water temperature and dissolved oxygen resulting from the deep water intake of some hydropower plants like IHP are likely responsible for negative effects on the reproduction of fish downstream from dams (Arantes *et al.*, 2010; Abdo, Marcon and Bazzoli, 2018). A small proportion of RL2 fish (13%) stayed close to the release site and there are many possible reasons for this behavior, including negative effects of the surgery, post-release mortality, or sedentary behavior. The presence of sedentary and migratory behavior in the same population, also known as partial migration (Chapman *et al.*, 2012), have been discussed for some Brazilian potamodromous fish (Lopes, Alves, *et al.*, 2018; Hahn *et al.*, 2019). In our study, one individual stayed in the release site for 2 years, then captured by a fisher, suggesting some resident behavior. We recorded long displacements in the Jequitinhonha River, showing that this fish can explore long lotic reaches when they are available. The migratory distances travelled by curimbas differ among studies, being shorter in

dammed rivers (Espinach Ros *et al.*, 1998; Godinho and Kynard, 2006; Antonio *et al.*, 2007; Brito and Carvalho, 2013; Ribeiro, 2013; Lopes, 2018). The life-history strategy of some migratory species may adjust in face of environmental change and habitat losses, with individuals changing migratory routes, distance travelled and spawning sites (Junge *et al.*, 2014). However, migratory pelagophils need lotic stretches to spawn, requiring a minimum length of lotic habitats in the region (Agostinho *et al.*, 2016, Silva *et al.*, 2020; Lopes, Pompeu, *et al.*, 2018). If these essential conditions are absent, recruitment is prevented and populations decline or collapse (Pelicice and Agostinho, 2008; Pompeu, Agostinho and Pelicice, 2012). At the scenario of habitat modification caused by Irapé dam, the Araçuaí River seems to be an important migratory route, providing spawning and nursery habitats for curimbas in the Jequitinhonha River Basin – together with other small watercourses that flow into the main channel (Silva *et al.*, 2020). This show the relevance of free-flowing rivers for the conservation of migratory fish (Casarim *et al.*, 2018).

In agreement with our second prediction, fish passed to the impoundment (RL4) presented a greater diversity of displacements than fish locally tagged in the reservoir (RL3), indicating that fish from lotic environments, when released in lentic environments, can become disoriented (Antonio *et al.*, 2007; Lopes, 2017). Few fish from RL4 (8%) reached the reservoir transition zone, differing from translocated fish at smaller reservoir, where a high proportion of fish can cross the entire water body (Brito and Carvalho, 2013; Ribeiro, 2013; De Fries *et al.*, 2019), even immature fish (Ribeiro, 2013). Reservoir fish (RL3) stayed at the first third of the reservoir, with few reaching the transition zone. Fish that moved away from the reservoir, either RL3 or RL4, moved toward the Itacambiruçu River, which is closer to the dam. However, the length of the lotic stretch in the Itacambiruçu upstream from Irapé reservoir seems to be insufficient for ichthyoplankton drifting and development (Silva *et al.*, 2020). Thus, those fish that reach lotic stretches with optimal conditions for reproduction find poor conditions for

recruitment. Also, only two RL4 and none RL3 fish returned to the dam region. These results show that crossing the water body in the upstream direction is only one of the problems faced by migratory fish in large reservoirs, because lentic waters create hydrological and limnological obstacles to downstream movements for different life stages (Pelicice, Pompeu and Agostinho, 2015). It is important to note that Irapé reservoir does not have expressive tributaries, where the Itacambiruçu is the larger, although flooded by the reservoir. Therefore, the Jequitinhonha River main channel, upstream from the reservoir, remains as the most appropriate site for migratory fishes (Silva *et al.*, 2020). In this scenario, Irapé reservoir have the potential to work as a sink system (Pulliam, 1988) for RL3 and RL4 fish, since few fish migrated upstream, and they have not moved toward the Jequitinhonha River. Gilroy and Edwards (2017) stated that source-sink dynamics are more neglected in the tropics, which can underestimate the impacts caused by human-driven habitat changes. In this context, it is very important to confirm this hypothesis in the Irapé Reservoir to set effective conservation efforts.

In agreement with our third prediction, we did not detect differences between native and hybrid curimbas regarding the distance travelled, timing of migration and routes taken. Although introduced *Prochilodus* species are originated from river-floodplain systems, which differ from the Jequitinhonha River (Silva *et al.*, 2020), their hybrids behaved in the same way as *P. hartii*. It indicates that introduced *Prochilodus* reproduce together with *P. hartii*, probably forming mixed shoals. In some situations, hybridization can produce individuals with reproductive and behavioral differences, even lower fitness, which can be negatively selected (Levin, 2002; Corsi, Eby and Barfoot, 2013; Pärssinen *et al.*, 2020). However, in many cases hybridization and introgression can impair native/parental species (Taylor *et al.*, 2006; Muhlfeld *et al.*, 2009; Prado *et al.*, 2012; Kovach *et al.*, 2015). This seems to be the situation in the Jequitinhonha River, where hybridization, mainly with *P. argenteus*, has the potential to cause genetic erosion and the extinction of pure lineages of *P. hartii*, at least in some portions

of the basin. The same reproductive behavior among hybrids and native fish indicate that they will continue to hybridize, especially because they use the same spawning sites. The higher fecundity of *P. argenteus* (Arantes *et al.*, 2013) is another factor that may impact *P. hartii* populations. The genetic introgression in *P. hartii* populations is spreading fast in the lower stretches of the basin. The native proportion of curimbas has been decreasing since the work of Sales *et al.* (2018). It is important to note that the proportion of hybrids in the Jequitinhonha River must be much higher than observed in this work, because we tagged only phenotypes similar to *P. hartii*. The morphological differentiation between native and hybrids is very difficult (Prado *et al.*, 2012; Sales *et al.*, 2018), and we released many captured fish because they seemed to differ from *P. hartii*, particularly pure introduced species.

This is the first study that investigated migratory patterns of *P. hartii* in the Jequitinhonha River, showing how migration interacts with impoundments and invasive species. The migratory patterns of curimbas in the studied area, when combined with the results of Silva *et al.* (2020), revealed the following scenario. There are two independent populations fragmented by Irapé Dam, one upstream and another downstream. These populations are self-sustainable, since there are reproduction and recruitment in both stretches, and the dam has no fish passage system. In the upstream reach, the Itacambiruçu River and the reservoir seemed inappropriate for recruitment. In this way, due to the absence of relevant tributaries, the reservoir stock seems to depend on recruitment that takes place in the Jequitinhonha River upstream. In the downstream reach, the Araçuaí River is the main reproductive stock, and this tributary proved to be a migration route, spawning and recruitment area. However, this reach also had the highest proportion of hybridization with non-native species, providing high introgression rates and threatening pure *P. hartii* lineages. Although some RL2 fish used the Jequitinhonha River for reproduction, none moved to the Irapé dam, indicating that it is unfavorable for spawning and recruitment (Abdo, Marcon and Bazzoli, 2018). Curimbas found

in this stretch are apparently young dispersing through the basin, and not adult fish engaged on reproductive dynamics. In addition, the Irapé HP tailrace can provide some risk of death and injury. Dam operations can affect fish in the tailrace through mechanical impacts or decompression (Andrade *et al.*, 2012; Loures and Godinho, 2017). Dead curimbas were eventually observed floating downstream from Irapé Dam, probably because of interactions with the turbines (Silva, FO; personal information). However, it is still unclear whether injuries were caused to fish located upstream or downstream from the dam.

*Prochilodus hartii* populations are disturbed by habitat changes, especially in the impoundment and the upstream reach of Irapé Dam, and by hybridization pressure in the lower reaches of the basin. These impacts are of great magnitude, severe and difficult to solve. Due to the phenotypic and behavioral similarity between hybrids and native fish, the control of hybridization is virtually impossible. Regarding the impacts of habitat modification, fish passes have been recommended to restore the migratory flow in areas fragmented by dams, despite its ineffectiveness for the conservation of Neotropical fishes in the context of dams with large reservoirs (Pelicice and Agostinho, 2008; Pompeu, Agostinho and Pelicice, 2012; Pelicice, Pompeu and Agostinho, 2015). In the Jequitinhonha scenario, populations are self-sustainable in both upstream and downstream reaches, indicating that a fish passage system is not required for demographic purposes. Moreover, RL1 curimbas are not reproductive individuals looking for spawning sites, meaning that there is no fragmentation between spawning and feeding sites, as each population found these habitats in both upstream and downstream reaches. A fish pass could be justified to provide genetic flow and avoid isolation of populations and the loss of genetic diversity (Pompeu, Agostinho and Pelicice, 2012). However, fish passed upstream became disoriented and an exceedingly small proportion reached lotic stretches upstream. In addition, downstream stocks are more impacted by genetic introgression, and a fish passage system would allow the dispersion of hybrids to the upstream reach of the basin, threatening



the genetic structure of native curimbas. In this sense, alternative management actions must be pursued. We agree with Sales *et al.* (2018) that *P. hartii* is a threatened species and actions to protect native stocks are mandatory and urgent. For that, we recommend the following priority actions: 1) Studies about the origin of RL1 fish, in the way to understand if this stock is progressively hybridizing; 2) Protection and environmental recovery of reaches in the Jequitinhonha River upstream from Irapé Dam, where hybridization rate is lower and populations are recruiting; 3) Prioritize the restoration and conservation of the Araçuaí River due to its relevance for the maintenance of curimbas in the downstream reach. The Araçuaí River basin is intensely modified by eucalyptus plantations, soil erosion and intense water deficit (evapotranspiration greater than precipitation in the last 50 years), which is progressively reducing the Araçuaí River flow (Leite and Fujaco, 2010). As management actions like fish passes and hybridization control would be innocuous in the current scenario, we consider that protection of curimbas stocks, especially where they have lower introgression rate, should be priority. For this, conservation planning for free-flowing reaches must be associated with water and land use planning in a way to preserve a very particular semi-arid system and its endemic ichthyofauna.

## References

- Abdo, T. F. *et al.* (2016) 'Initial development of *Prochilodus hartii* (Pisces: Prochilodontidae) submitted to induced reproduction', *Zygote*, 24(3), pp. 408–417. doi: 10.1017/S0967199415000337.
- Abdo, T. F., Marcon, L. and Bazzoli, N. (2018) 'Downstream effects of a large reservoir on the reproductive activity of *Prochilodus hartii* (Pisces: Prochilodontidae)', *Animal Reproduction Science*, 190(February), pp. 102–107. doi: 10.1016/j.anireprosci.2018.01.013.
- Abel, G. J. (2019) 'migest: Methods for the Indirect Estimation of Bilateral Migration.' Available at: <https://cran.r-project.org/package=migest>.
- Agostinho, A. *et al.* (1993) 'Avaliação da atividade reprodutiva da comunidade de peixes dos primeiros quilômetros a jusante do reservatório de Itaipu', *Rev Unimar*, 15(Suppl), pp. 175–189. Available at: <ftp://ftp.nupelia.uem.br/users/agostinhoaa/publications/020-UNIMAR->

Agostinho-et al.pdf.

Agostinho, A. A. *et al.* (2002) 'Efficiency of fish ladders for neotropical ichthyofauna', *River Research and Applications*, 18(3), pp. 299–306. doi: 10.1002/rra.674.

Agostinho, A. A. *et al.* (2003) 'Migratory fishes of the Upper Paraná river basin , Brazil', in Carolsfeld, J. *et al.* (eds) *Migratory fishes of South America*. Victoria, British Columbia.: World Fisheries Trust, pp. 19–98.

Alves, C. B. M. *et al.* (2007) 'Impacts of Non-Native Fish Species in Minas Gerais, Brazil: Present Situation and Prospects', in *Ecological and Genetic Implications of Aquaculture Activities*. Dordrecht: Springer Netherlands, pp. 291–314. doi: 10.1007/978-1-4020-6148-6\_16.

Andrade, F. De *et al.* (2012) 'Evaluation of techniques used to protect tailrace fishes during turbine maneuvers at Três Marias Dam , Brazil', *Neotropical Ichthyology*, 10(4), pp. 723–730.

Antonio, R. R. *et al.* (2007) 'Blockage of migration routes by dam construction: Can migratory fish find alternative routes?', *Neotropical Ichthyology*, 5(2), pp. 177–184. doi: 10.1590/S1679-62252007000200012.

Arantes, F. P. *et al.* (2010) 'Profiles of sex steroids, fecundity, and spawning of the curimatã-pacu *Prochilodus argenteus* in the São Francisco River, downstream from the Três Marias Dam, Southeastern Brazil', *Animal Reproduction Science*, 118(2–4), pp. 330–336. doi: 10.1016/j.anireprosci.2009.07.004.

Arantes, F. P. *et al.* (2013) 'Spawning induction and fecundity of commercial native fish species from the São Francisco River basin, Brazil, under hatchery conditions', *Agricultural Sciences*, 04(08), pp. 382–388. doi: 10.4236/as.2013.48055.

Attayde, J. L., Brasil, J. and Menescal, R. A. (2011) 'Impacts of introducing Nile tilapia on the fisheries of a tropical reservoir in North-eastern Brazil', pp. 437–443. doi: 10.1111/j.1365-2400.2011.00796.x.

Azevedo-Santos, V. M. *et al.* (2015) 'How to avoid fish introductions in Brazil: Education and information as alternatives', *Natureza e Conservacao*. Associação Brasileira de Ciência Ecológica e Conservação, 13(2), pp. 123–132. doi: 10.1016/j.ncon.2015.06.002.

Bolstad, G. H. *et al.* (2017) 'Gene flow from domesticated escapes alters the life history of wild Atlantic salmon', *Nature Ecology and Evolution*, 1(5), pp. 1–5. doi: 10.1038/s41559-017-0124.

Brito, S. G. and Carvalho, E. D. (2013) 'Reproductive migration of fish and movement in a series of reservoirs in the Upper Parana River basin, Brazil', *Fisheries Management and Ecology*, 20(5), pp. 426–433. doi: 10.1111/fme.12030.

Camelier, P. and Zanata, A. M. (2014) 'Biogeography of freshwater fishes from the Northeastern Mata Atlântica freshwater ecoregion: distribution, endemism, and area relationships', *Neotropical Ichthyology*, 12(4), pp. 683–698. doi: 10.1590/1982-0224-20130228.

Carvalho, D. C. *et al.* (2014) 'Analysis of propagule pressure and genetic diversity in the invasibility of a freshwater apex predator: The peacock bass (genus *Cichla*)', *Neotropical*

*Ichthyology*, 12(1), pp. 105–116. doi: 10.1590/S1679-62252014000100011.

Casarim, R. *et al.* (2018) ‘Fish movement patterns in a Neotropical free-flowing tributary located downstream from a large dam’, *Marine and Freshwater Research*, 69(10), p. 1626. doi: 10.1071/mf17216.

Castro, R. M. C. and Vari, R. P. (2004) ‘Detritivores of the South American fish family Prochilodontidae (Teleostei:Ostariophysi:Characiformes): a phylogenetic and revisionary study’, *Smithsonian Contributions to Zoology*, (622), pp. 1–189. doi: 10.5479/si.00810282.622.

Chapman, B. B. *et al.* (2012) ‘Partial migration in fishes: Causes and consequences’, *Journal of Fish Biology*, 81(2), pp. 456–478. doi: 10.1111/j.1095-8649.2012.03342.x.

Corsi, M. P., Eby, L. A. and Barfoot, C. A. (2013) ‘Hybridization with rainbow trout alters life history traits of native westslope cutthroat trout’, *Canadian Journal of Fisheries and Aquatic Sciences*, 70(6), pp. 895–904. doi: 10.1139/cjfas-2012-0312.

Dala-Corte, R. B. *et al.* (2020) ‘Thresholds of freshwater biodiversity in response to riparian vegetation loss in the Neotropical region’, *Journal of Applied Ecology*, pp. 0–2. doi: 10.1111/1365-2664.13657.

Deng, Z. D. *et al.* (2017) ‘Comparing the survival rate of juvenile Chinook salmon migrating through hydropower systems using injectable and surgical acoustic transmitters’, *Scientific Reports*. doi: 10.1038/srep42999.

Dudley, R. K. and Platania, S. P. (2007) ‘FLOW REGULATION AND FRAGMENTATION IMPERIL PELAGIC-SPAWNING RIVERINE FISHES’, *Ecological Applications*, 17(7), pp. 2074–2086. doi: 10.1890/06-1252.1.

Espinach Ros, A. *et al.* (1998) ‘Migration pattern of the sábalo *Prochilodus lineatus* (Pisces, Prochilodontidae) tagged in the lower Uruguay River’, *SIL Proceedings, 1922-2010*, 26(5), pp. 2234–2236. doi: 10.1080/03680770.1995.11901143.

FAO (2020) *Database on introductions of aquatic species (DIAS)*, FAO Fisheries and Aquaculture Department. Rome. Available at: <http://www.fao.org/fishery/topic/14786/en>.

Ferguson, J. W. *et al.* (2011) ‘Potential effects of dams on migratory fish in the Mekong River: Lessons from salmon in the Fraser and Columbia Rivers’, *Environmental Management*, 47(1), pp. 141–159. doi: 10.1007/s00267-010-9563-6.

Ferreira, V. de O. (2011) ‘Unidades de paisagem da bacia do rio Jequitinhonha, em Minas Gerais: subsídios para a Gestão de Recursos Hídricos’, *Caminhos de Geografia*, 12(37), pp. 239–257. Available at: [file:///C:/Daniel/PA Gr?o Mogol/Refer?ncias/FerreiraSilva2012.pdf](file:///C:/Daniel/PA%20Gr%20o%20Mogol/Refer%20ncias/FerreiraSilva2012.pdf).

De Fries, L. *et al.* (2019) ‘Movement and longitudinal distribution of a migratory fish (*Salminus brasiliensis*) in a small reservoir in southern Brazil’, *Neotropical Ichthyology*, 17(3), pp. 1–12. doi: 10.1590/1982-0224-20180119.

Garcia, D. A. Z. *et al.* (2018) ‘Introductions of non-native fishes into a heavily modified river: rates, patterns and management issues in the Paranapanema River (Upper Paraná ecoregion, Brazil)’, *Biological Invasions*, 20(5), pp. 1229–1241. doi: 10.1007/s10530-017-1623-x.

- Gehrke, P. C., Gilligan, D. M. and Barwick, M. (2002) 'Changes in fish communities of the Shoalhaven River 20 years after construction of Tallowa Dam, Australia', *River Research and Applications*, 18(3), pp. 265–286. doi: 10.1002/rra.669.
- Gilroy, J. J. and Edwards, D. P. (2017) 'Source-Sink Dynamics: a Neglected Problem for Landscape-Scale Biodiversity Conservation in the Tropics', *Current Landscape Ecology Reports*. *Current Landscape Ecology Reports*, 2(1), pp. 51–60. doi: 10.1007/s40823-017-0023-3.
- Glover, K. A. *et al.* (2020) 'The future looks like the past: Introgression of domesticated Atlantic salmon escapees in a risk assessment framework', *Fish and Fisheries*, (May), pp. 1–15. doi: 10.1111/faf.12478.
- Godinho, A. L. and Kynard, B. (2006) 'Migration and Spawning of Radio-Tagged Zulega *Prochilodus argenteus* in a Dammed Brazilian River', *Transactions of the American Fisheries Society*, 135(3), pp. 811–824. doi: 10.1577/T04-176.1.
- Godinho, A. L., Kynard, B. and Godinho, H. P. (2007) 'Migration and spawning of female surubim (*Pseudoplatystoma corruscans*, Pimelodidae) in the São Francisco river, Brazil', *Environmental Biology of Fishes*, 80(4), pp. 421–433. doi: 10.1007/s10641-006-9141-1.
- Godinho, H. P. ., Godinho, A. L. . and Vono, V. (1999) 'Peixes da bacia do rio Jequitinhonha', in Lowe-McConnell, R. H. (ed.) *Estudos ecológicos de comunidades de peixes tropicais*. São Paulo: EDUSP, pp. 414–423.
- Hahn, L. *et al.* (2011) 'Use of radiotelemetry to track threatened dorados *Salminus brasiliensis* in the upper Uruguay River, Brazil', *Endangered Species Research*, 15(2), pp. 103–114. doi: 10.3354/esr00363.
- Hahn, L. *et al.* (2019) 'Biotelemetry reveals migratory behaviour of large catfish in the Xingu River, Eastern Amazon', *Scientific Reports*, 9(1), pp. 1–15. doi: 10.1038/s41598-019-44869-x.
- Haraldstad, T. *et al.* (2019) 'Migratory passage structures at hydropower plants as potential physiological and behavioural selective agents', *Royal Society Open Science*, 6(11). doi: 10.1098/rsos.190989.
- Harvey, B. and Carolsfeld, J. (2003) *Migratory Fishes of South America*.
- Helfman, G. S. (2007) *Fish conservation: a guide to understanding and restoring global aquatic biodiversity and fishery resources*. Washington, DC: Island Press is.
- Horká, P. *et al.* (2015) 'Radio-telemetry shows differences in the behaviour of wild and hatchery-reared European grayling *Thymallus thymallus* in response to environmental variables', *Journal of Fish Biology*, 86(2), pp. 544–557. doi: 10.1111/jfb.12575.
- IBGE (1997) *Diagnóstico Ambiental Da Bacia Do Rio Jequitinhonha*.
- Junge, C. *et al.* (2014) 'Assessing the consequences of habitat fragmentation for two migratory salmonid fishes', *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24(3), pp. 297–311. doi: 10.1002/aqc.2391.
- Junker, J. *et al.* (2012) 'River fragmentation increases localized population genetic structure

and enhances asymmetry of dispersal in bullhead (*Cottus gobio*)', *Conservation Genetics*, 13(2), pp. 545–556. doi: 10.1007/s10592-011-0306-x.

Kovach, R. P. *et al.* (2015) 'Dispersal and selection mediate hybridization between a native and invasive species', *Proceedings of the Royal Society B: Biological Sciences*, 282(1799). doi: 10.1098/rspb.2014.2454.

Van Leeuwen, C. H. A. *et al.* (2018) 'Habitat fragmentation has interactive effects on the population genetic diversity and individual behaviour of a freshwater salmonid fish', *River Research and Applications*, 34(1), pp. 60–68. doi: 10.1002/rra.3226.

Leite, M. G. P. and Fujaco, M. A. G. (2010) 'A long-term annual water balance analysis of the Araçuaí River Basin, Brazil', *Journal of Geographical Sciences*, 20(6), pp. 938–946. doi: 10.1007/s11442-010-0822-5.

Levin, D. A. (2002) 'Hybridization and extinction: in protecting rare species, conservationists should consider the dangers of interbreeding, which compound the more well-known threats to wildlife.', *Am. Sci.*, 90(3), pp. 254–261. Available at: [http://find.galegroup.com/itx/infomark.do?&contentSet=IAC-Documents&type=retrieve&tabID=T002&prodId=EAIM&docId=A85185144&source=gale&srcreprod=EAIM&userGroupName=nd\\_ref&version=1.0](http://find.galegroup.com/itx/infomark.do?&contentSet=IAC-Documents&type=retrieve&tabID=T002&prodId=EAIM&docId=A85185144&source=gale&srcreprod=EAIM&userGroupName=nd_ref&version=1.0).

Liermann, C. R. *et al.* (2012) 'Implications of Dam Obstruction for Global Freshwater Fish Diversity', *BioScience*, 62(6), pp. 539–548. doi: 10.1525/bio.2012.62.6.5.

Lopes, J. D. M. *et al.* (2019) 'Upstream and downstream migration speed of *Prochilodus costatus* (Characiformes: Prochilodontidae) in upper São Francisco basin, Brazil', *Neotropical Ichthyology*, 17(2), pp. 1–10. doi: 10.1590/1982-0224-20180072.

Lopes, J. de M. (2017) *Dinâmica migratória e reprodutiva de uma espécie reofílica de peixe (Prochilodus Costatus) no Alto São Francisco, MG: Diferenças entre populações locais e transpostas e implicações para a instalação de um sistema de transposição de peixes na UHE Três Mari*. Universidade Federal de Lavras.

Lopes, J. de M., Alves, C. B. M., *et al.* (2018) 'Influence of rainfall, hydrological fluctuations, and lunar phase on spawning migration timing of the Neotropical fish *Prochilodus costatus*', *Hydrobiologia*, 818(1), pp. 145–161. doi: 10.1007/s10750-018-3601-4.

Lopes, J. de M., Pompeu, P. S., *et al.* (2018) 'The critical importance of an undammed river segment to the reproductive cycle of a migratory Neotropical fish', *Ecology of Freshwater Fish*, (September), pp. 1–15. doi: 10.1111/eff.12454.

Lopes, J. M. *et al.* (2016) 'Effect of anesthetic, tag size, and surgeon experience on postsurgical rEffect of anesthetic, tag size, and surgeon experience on postsurgical recovering after implantation of electroniccovering after implantation of electronic tags in a Neotropical fish', *Neotropical Ichthyology*, 14(3). doi: 10.1590/1982-0224-20150189.

Loures, R. C. and Godinho, A. L. (2017) 'Risk of fish death at Brazilian hydropower plants', in *Risk assessment of fish death at hydropower plants in southeastern Brazil*. Belo Horizonte: Companhia Energética de Minas Gerais, pp. 19–36. doi: 10.5935/978-85-87929-62-4.2016.1.

Loures, R. C. and Pompeu, P. S. (2018) 'Long-term study of reservoir cascade in south-eastern

Brazil reveals spatio-temporal gradient in fish assemblages', *Marine and Freshwater Research*. doi: 10.1071/MF18109.

Lucas, M. C. and Baras, E. (2001) *Migration of Freshwater Fishes*. Osney Mead, Oxford: Blackwell Science Ltd. doi: 10.1643/0045-8511(2002)002[0878:]2.0.CO;2.

Makrakis, M. C. *et al.* (2012) 'Diversity in migratory patterns among Neotropical fishes in a highly regulated river basin', *Journal of Fish Biology*, 81(2), pp. 866–881. doi: 10.1111/j.1095-8649.2012.03346.x.

Mallen-Cooper, M. and Stuart, I. G. (2003) 'Age, growth and non-flood recruitment of two potamodromous fishes in a large semi-arid/temperate river system', *River Research and Applications*, 19(7), pp. 697–719. doi: 10.1002/rra.714.

Maltchik, L. and Medeiros, E. S. F. (2006) 'Conservation importance of semi-arid streams in north-eastern Brazil: implications of hydrological disturbance and species diversity', *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16(7), pp. 665–677. doi: 10.1002/aqc.805.

Muhlfeld, C. C. *et al.* (2009) 'Hybridization rapidly reduces fitness of a native trout in the wild', *Biology Letters*, 5(3), pp. 328–331. doi: 10.1098/rsbl.2009.0033.

Nilsson, C. *et al.* (2005) 'Fragmentation and flow regulation of the world's large river systems', *Science*, 308(5720), pp. 405–408. doi: 10.1126/science.1107887.

Oliveira, A. G. *et al.* (2018) 'Long-term effects of flow regulation by dams simplify fish functional diversity', *Freshwater Biology*, 63(3), pp. 293–305. doi: 10.1111/fwb.13064.

Pärssinen, V. *et al.* (2020) 'Maladaptive migration behaviour in hybrids links to predator-mediated ecological selection', *Journal of Animal Ecology*, (January), pp. 1–9. doi: 10.1111/1365-2656.13308.

Pavlov, D. S., Mikheev, V. N. and Kostin, V. V. (2019) 'Migrations of Fish Juveniles in Dammed Rivers: the Role of Ecological Barriers', *Journal of Ichthyology*, 59(2), pp. 234–245. doi: 10.1134/S0032945219020140.

Pelicice, F. M. and Agostinho, A. A. (2008) 'Fish-passage facilities as ecological traps in large neotropical rivers', *Conservation Biology*, 22(1), pp. 180–188. doi: 10.1111/j.1523-1739.2007.00849.x.

Pelicice, F. M., Pompeu, P. S. and Agostinho, A. A. (2015) 'Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish', *Fish and Fisheries*, 16(4), pp. 697–715. doi: 10.1111/faf.12089.

Perini, V. da R. *et al.* (2013) 'Profiles of sex steroids, fecundity and spawning of a migratory characiform fish from the Paraguay-Paraná basin: A comparative study in a three-river system', *Fish Physiology and Biochemistry*, 39(6), pp. 1473–1484. doi: 10.1007/s10695-013-9800-z.

Pimentel, J. S. M. *et al.* (2018) 'High-Throughput Sequencing Strategy for Microsatellite Genotyping Using Neotropical Fish as a Model', *Frontiers in Genetics*, 9. doi: 10.3389/fgene.2018.00073.

Pompeu, P. S., Agostinho, A. A. and Pelicice, F. M. (2012) 'Existing and future challenges:

The concept of successful fish passage in South America', *River Research and Applications*, 28(4), pp. 504–512. doi: 10.1002/rra.1557.

Prado, F. D. do *et al.* (2012) 'Detection of hybrids and genetic introgression in wild stocks of two catfish species (Siluriformes: Pimelodidae): The impact of hatcheries in Brazil', *Fisheries Research*, 125–126(September 2019), pp. 300–305. doi: 10.1016/j.fishres.2012.02.030.

Pugedo, M. L. *et al.* (2016) 'Integrative taxonomy supports new candidate fish species in a poorly studied neotropical region: the Jequitinhonha River Basin', *Genetica*, 144(3), pp. 341–349. doi: 10.1007/s10709-016-9903-4.

van Puijenbroek, P. J. T. M. *et al.* (2019) 'Species and river specific effects of river fragmentation on European anadromous fish species', *River Research and Applications*, 35(1), pp. 68–77. doi: 10.1002/rra.3386.

Pulliam, R. (1988) 'Sources, sinks, and population regulation', *The American Naturalist*, 132(5), pp. 652–661.

R Core Team (2018) 'R: A language and environment for statistical computing'. Vienna, Austria: R Foundation for Statistical Computing.

Reis, R. E. *et al.* (2016) 'Fish biodiversity and conservation in South America', *Journal of fish biology*, 89(1), pp. 12–47. doi: 10.1111/jfb.13016.

Resende, E. K. (2003) 'Migratory fishes of the Paraguay–Paraná basin excluding the Upper Paraná Basin', in Carolsfeld, J. *et al.* (eds) *Migratory fishes of South America*. Victoria, British Columbia: World Fisheries Trust, pp. 99–155.

Ribeiro, A. C. (2006) 'Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: An example of faunal evolution associated with a divergent continental margin', *Neotropical Ichthyology*, 4(2), pp. 225–246. doi: 10.1590/S1679-62252006000200009.

Ribeiro, T. (2013) *Migração de peixes neotropicais em rio com barramentos sucessivos*. Universidade Federal de Minas Gerais.

Rizzo, E. *et al.* (2002) 'Adhesiveness and surface patterns of eggs in neotropical freshwater teleosts', *Journal of Fish Biology*, 61(3), pp. 615–632. doi: 10.1006/jfbi.2002.2085.

Sales, N. G. *et al.* (2018) 'Introgression from non-native species unveils a hidden threat to the migratory Neotropical fish *Prochilodus hartii*', *Biological Invasions*, 20(3), pp. 555–566. doi: 10.1007/s10530-017-1556-4.

dos Santos, N. C. L. *et al.* (2017) 'Environmental filters predict the trait composition of fish communities in reservoir cascades', *Hydrobiologia*, 802(1), pp. 245–253. doi: 10.1007/s10750-017-3274-4.

Seebens, H. *et al.* (2017) 'No saturation in the accumulation of alien species worldwide', *Nature Communications*, 8, pp. 1–9. doi: 10.1038/ncomms14435.

Silva, F. de O. *et al.* (no date) 'Recruitment dynamics of a migratory fish in a semi-arid river system'.

- Silva, L. G. M. *et al.* (2012) 'Fish passage post-construction issues: analysis of distribution, attraction and passage efficiency metrics at the Baguari Dam fish ladder to approach the problem', *Neotropical Ichthyology*, 10(4), pp. 751–762. Available at: <http://www.scielo.br/pdf/ni/v10n4/08.pdf>.
- Suzuki, F. M. *et al.* (2017) 'Factors Influencing Movements of Two Migratory Fishes within the Tailrace of a Large Neotropical Dam and their Implications for Hydropower Impacts', *River Research and Applications*, 33(4), pp. 514–523. doi: 10.1002/rra.3105.
- Taylor, E. B. *et al.* (2006) 'Speciation in reverse: Morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair', *Molecular Ecology*, 15(2), pp. 343–355. doi: 10.1111/j.1365-294X.2005.02794.x.
- Teixeira, D. F. *et al.* (2019) 'Invasion dynamics of the white piranha (*Serrasalmus brandtii*) in a Neotropical river basin', *Biological Invasions*, 0123456789. doi: 10.1007/s10530-019-02138-y.
- Todesco, M. *et al.* (2016) 'Hybridization and extinction', *Evolutionary Applications*, 9(7), pp. 892–908. doi: 10.1111/eva.12367.
- Vitule, J. R. S., Freire, C. A. and Simberloff, D. (2009) 'Introduction of non-native freshwater fish can certainly be bad', *Fish and Fisheries*, 10(1), pp. 98–108. doi: 10.1111/j.1467-2979.2008.00312.x.
- Walker, K. F., Sheldon, F. and Puckridge, J. T. (1995) 'A perspective on dryland river ecosystems', *Regulated Rivers: Research & Management*, 11(1), pp. 85–104. doi: 10.1002/rrr.3450110108.
- Winemiller, K. O. (1989) 'Patterns of variation in life history among South American fishes in seasonal environments', *Oecologia*, 81(2), pp. 225–241. doi: 10.1007/BF00379810.
- Zaniboni-Filho, E. and Schulz, U. H. (2003) 'Migratory fishes of the Uruguay river', in Carosfeld, J. *et al.* (eds) *Migratory fishes of South America*. Victoria, British Columbia: World Fisheries Trust, pp. 157–194.



## Conclusão geral

Esse projeto de tese foi desenvolvido com o objetivo de compreender o ciclo de vida da curimba *Prochilodus hartii* no rio Jequitinhonha, um sistema fluvial com características diferentes dos rios de planície de inundação, para onde a maior parte dos estudos de migração e recrutamento de peixes são desenvolvidos. Embora seja o primeiro trabalho a descrever aspectos básicos relacionados a migração, reprodução e recrutamento de *P. hartii*, é importante salientar que ele foi desenvolvido em um ambiente já impactado pela fragmentação, alteração de hábitat e introdução de espécies, que colocam *P. hartii* em grau significativo de ameaça. Com isso, a informação gerada nesse documento se refere a um fragmento de uma história que não pôde ser contada por completo. Esta tem sido, infelizmente, a realidade dos estudos descritivos e ecológicos para muitas espécies de peixes, que só ocorrem após impactos instalados. Apesar dessa questão, nossos resultados representam avanço significativo no entendimento do comportamento migratório e recrutamento da curimba na área afetada pela UHE Irapé, e esperamos que nossos achados forneçam subsídio para conservação desse peixe migrador nativo do Jequitinhonha.

O atual cenário mostra que, apesar dos impactos, dois trechos significativos para a manutenção de curimbas ainda existem acima e abaixo da barragem da UHE Irapé. Eles são o (i) rio Jequitinhonha entre a sua nascente e o reservatório da UHE Irapé, e (ii) o seu principal tributário a jusante dessa usina, o rio Araçuai. Esses segmentos apresentam características hidrológicas naturais, que funcionam como gatilhos para a migração e desova, e com trechos fluviais suficientes para a deriva e desenvolvimento dos ovos e larvas, além de locais para abrigo e crescimento de juvenis. Apesar de altamente relevantes, processos de assoreamento e redução do fluxo tem se intensificado, bem como a interferência da UHE Irapé na hidrologia do rio Jequitinhonha abaixo da barragem. Ações de recuperação ambiental e proteção dos trechos lóticos são indispensáveis para a manutenção de curimbas no Alto e Médio Jequitinhonha. O presente estudo não contemplou o trecho abaixo da UHE Itapebi, na região baixa da bacia, permanecendo importante lacuna sobre o recrutamento e persistência de populações de curimbas no segmento inferior do rio Jequitinhonha.

Nosso estudo também revelou que curimbas do Jequitinhonha, e provavelmente as curimbas das bacias do Atlântico Leste, não são dependentes da intensidade e duração das cheias como as curimbas de rios de planície de inundação (e.g., *P. lineatus* na bacia Paraná, ou *P. costatus* na bacia São Francisco). Esse resultado era esperado, visto que planícies não são ambientes comuns ou extensivos no Alto e Médio Jequitinhonha. No entanto, a dinâmica

reprodutiva da curimba estudada esteve associada ao regime hidrológico, uma vez que o aumento no nível da água se mostrou importante para desencadear o processo reprodutivo. Compreender como a ictiofauna se relaciona com a variação ambiental natural é primordial para a indicação de qualquer medida mitigadora ou de manejo. Entretanto, o manejo da ictiofauna no país tem se baseado em protocolos padronizados (e.g., STPs ou estocagem; Agostinho et al., 2007), os quais não levam em consideração a fauna e hidrologia do local alvo. No caso do rio Jequitinhonha, por exemplo, detectamos um trabalho de modelagem para a indução de cheias artificiais no trecho a jusante de UHE Irapé (Fernandes and Marques, 2011). Os autores propuseram um modelo de cheias artificiais sem utilizar qualquer informação biológica das espécies locais, apenas transferindo para o Jequitinhonha informações atreladas ao conceito de planície de inundação e sua importância para o recrutamento. A adoção de medidas de manejo sem critérios técnicos e sem monitoramento trazem riscos relevantes: 1) além de não serem efetivas, podem acarretar prejuízos às populações alvo do manejo. Exemplos são STPs construídos em trechos que não propiciam que as espécies completem o ciclo de vida, causando movimentação em via única ou depleção de estoques; o mesmo pode acontecer em atividades de peixamento, ocasionando perda da variabilidade genética de estoques nativos; 2) geram a falsa sensação de que qualquer impacto pode ser mitigado, e que as medidas tomadas, sem respaldo técnico, estão resolvendo o problema. Ao contrário disso, pesquisas vêm mostrando que as ações implementadas para mitigação de impactos por barramentos têm sido infrutíferas, por vezes danosas. Nesse cenário onde o manejo é aplicado de maneira indevida, os problemas ambientais persistem ou são agravados, como se registrou em muitos trechos das bacias do rio Paraná, São Francisco e Tocantins (C. S. Agostinho *et al.*, 2007; Pelicice, Pompeu and Agostinho, 2015).

Como conclusão, ações de manejo e conservação devem considerar o atual cenário das populações de *P. hartii* recrutando nos fragmentos fluviais do rio Jequitinhonha, bem como os impactos causados pela barragem e peixes invasores. Não recomendamos a instalação de um STP na UHE Irapé, visto que existe recrutamento nos dois lados da barragem, e um STP poderia permitir a dispersão de curimbas não-nativas para o Alto Jequitinhonha. Uma melhor estratégia para a região é a conservação, proteção e recuperação ambiental de trechos com características fluviais naturais para assegurar a permanência de peixes migradores. Ainda, recomendamos a adoção de atividades fiscalizadoras e educativas de forma a inibir novas introduções e a implementação de medidas de remoção seletiva dos peixes não-nativos, de forma a diminuir pressões de propágulo no processo de invasão biológica. Ressaltamos que nenhuma medida será capaz de recuperar as populações de *P. hartii* ao nível anterior aos impactos, uma vez que

as populações estão terminantemente fragmentadas e reduzidas pelos efeitos da barragem da UHE Irapé. Além disso, essas populações estão sob risco de extinção genética devido ao rápido avanço do processo de hibridização na bacia. Dessa forma, as ações de conservação devem fomentar a manutenção de populações relictuais de *P. hartii*. Essas ações são mandatórias e urgentes, especialmente considerando o agravante que os poucos remanescentes lóticos estão cada vez mais impactados pela alteração por uso e ocupação do solo, além da invasão por múltiplas espécies não-nativas.

### Referências bibliográficas

Agostinho, A. A. *et al.* (2002) 'Efficiency of fish ladders for neotropical ichthyofauna', *River Research and Applications*, 18(3), pp. 299–306.

Agostinho, A. A. *et al.* (2004) 'Flood regime, dam regulation and fish in the Upper Paraná River: Effects on assemblage attributes, reproduction and recruitment', *Reviews in Fish Biology and Fisheries*, 14(1), pp. 11–19.

Agostinho, A. A. *et al.* (2007) 'Fish ladder of Lajeado Dam : migrations on one-way routes ?', *Neotropical Ichthyology*, 5(2), pp. 121–130.

Agostinho, A. A., Gomes, L. C. and Pelicice, F. M. (2007) 'Ecologia e Manejo de Recursos Pesqueiros em Reservatórios do Brasil', *UEM*, p. 501.

Agostinho, A. A., Thomaz, S. M. and Gomes, L. C. (2005) 'Conservation of the Biodiversity of Brazil's Inland Waters', *Conservation Biology*, 19(3), pp. 646–652.

Agostinho, C. S. *et al.* (2007) 'Selectivity of fish ladders: a bottleneck in Neotropical fish movement', *Neotropical Ichthyology*, 5(2), pp. 205–213.

Andrade, F. R. (2018) *Estudos ecológicos dos peixes da bacia do rio Jequitinhonha*. Universidade Federal de Lavras. Lavras.

Birnie-Gauvin, K. *et al.* (2018) 'Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene', *Aquatic Conservation: Marine and Freshwater Ecosystems*,

British Petroleum Company (2020) *BP statistical review of world energy*. London. Available at: <https://www.bp.com/content/dam/bp/business-sites/en/global/corporate/pdfs/energy-economics/statistical-review/bp-stats-review-2020-full-report.pdf>.

Brito, S. G. and Carvalho, E. D. (2013) 'Reproductive migration of fish and movement in a series of reservoirs in the Upper Parana River basin, Brazil', *Fisheries Management and Ecology*, 20(5), pp. 426–433.

Dudley, R. K. and Platania, S. P. (2007) 'Flow regulation and fragmentation imperil pelagic-spawning riverine fishes', *Ecological Applications*, 17(7), pp. 2074–2086.

Dugan, P. J. *et al.* (2010) 'Fish Migration, Dams, and Loss of Ecosystem Services in the Mekong Basin', *Ambio*, 39, pp. 344–348.

Fernandes, N. R. C. and Marques, G. F. (2011) 'Integration OS Gis and Hydraulic Modeling To Evaluate the Cost of Ecological stream flow recovery in Irapé dam, Brazil', in, pp. 4162–4171.

Junk, W. J. and Wantzen, K. M. (2004) 'The flood pulse concept: new aspects, approaches and applications - an update', *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries*, (January 2004), pp. 117–149.

Kemp, P. S. (2016) 'Meta-analyses, Metrics and Motivation: Mixed Messages in the Fish Passage Debate', *River Research and Applications*, 32(10), pp. 2116–2124.

Lira, N. A. *et al.* (2017) 'Fish passages in South America: an overview of studied facilities and research effort', *Neotropical Ichthyology*, 15(2), pp. 1–14.

Lopes, C. M. *et al.* (2007) 'Fish passage ladders from Canoas Complex – Paranapanema River : evaluation of genetic structure maintenance of *Salminus brasiliensis* (Teleostei : Characiformes )', 5(2), pp. 131–138.

Lucas, M. C. and Baras, E. (2001) *Migration of Freshwater Fishes*. Osney Mead, Oxford: Blackwell Science Ltd.

Pelicice, F. M. and Agostinho, A. A. (2008) 'Fish-passage facilities as ecological traps in large neotropical rivers', *Conservation Biology*, 22(1), pp. 180–188.

Pelicice, F. M. and Agostinho, C. S. (2012) 'Deficient downstream passage through fish ladders: the case of Peixe Angical Dam, Tocantins River, Brazil', *Neotropical Ichthyology*, 10(4), pp. 705–713.

Pelicice, F. M., Pompeu, P. S. and Agostinho, A. A. (2015) 'Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish', *Fish and Fisheries*, 16(4), pp. 697–715.

Pompeu, P. S., Agostinho, A. A. and Pelicice, F. M. (2012) 'Existing and future challenges: The concept of successful fish passage in South America', *River Research and Applications*, 28(4), pp. 504–512.

Pugedo, M. L. *et al.* (2016) 'Integrative taxonomy supports new candidate fish species in a poorly studied neotropical region: the Jequitinhonha River Basin', *Genetica*, 144(3), pp. 341–349.

Ribeiro, A. C. (2006) 'Tectonic history and the biogeography of the freshwater fishes from the coastal drainages of eastern Brazil: An example of faunal evolution associated with a divergent continental margin', *Neotropical Ichthyology*, 4(2), pp. 225–246.

Silva, L. G. M. *et al.* (2012) 'Fish passage post-construction issues: analysis of distribution, attraction and passage efficiency metrics at the Baguari Dam fish ladder to approach the problem', *Neotropical Ichthyology*, 10(4), pp. 751–762.

Wilkes, M. A., Mckenzie, M. and Webb, J. A. (2018) 'Fish passage design for sustainable hydropower in the temperate Southern Hemisphere: an evidence review', *Reviews in Fish Biology and Fisheries*. Springer International Publishing, 28(1), pp. 117–135.