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MIGRAÇÃO DOS GRANDES BAGRES AMAZÔNICOS PELA PERSPECTIVA DOS ISÓTOPOS DE ESTRÔNCIO EM OTÓLITOS

MARÍLIA HAUSER DOS SANTOS

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Orientadora: Prof^{a} Dr^{a} Carolina Rodrigues da Costa Doria
Co-orientador: Dr. Fabrice Duponchelle

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“Cada pessoa deve trabalhar para o seu aperfeiçoamento e, ao mesmo tempo, participar da responsabilidade coletiva por toda a humanidade.”

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RESUMO

A compreensão dos padrões espaciais e temporais dos processos migratórios é fundamental para a elaboração de estratégias de gestão e conservação da ictiofauna. Embora algumas proposições acerca do ciclo de vida dos grandes bagres do gênero *Brachyplatystoma,* grupo de notório papel econômico e ecológico na Amazônia, tenham sido sugeridas, até o momento não há uma validação definitiva sobre o complexo processo migratório dessas espécies. Este estudo objetivou investigar o comportamento migratório de *B. rousseauxii* e *B. platynemum*, ao longo da bacia amazônica a partir da razão de^{87}Sr:^{87}Sr dos otólitos, antes e após o barramento do rio Madeira. A hipótese testada foi de que essas espécies apresentam comportamento de *homing* natal. Para tanto, foram analisados 348 otólitos e 87 amostras de águas ao longo de toda a bacia amazônica, englobando Peru, Bolívia e Brasil. As análises isotópicas de ^{87}Sr:^{86}Sr dos otólitos e águas foram realizadas por meio espectrometria de massa com fonte de plasma e multicoletor, com ablação a laser para os otólitos (MC-LA-ICPMS). Para responder a suposição levantada a respectiva tese foi organizada em quatro capítulos. O primeiro capítulo determinou a idade e crescimento de *B. rousseauxii*, observando-se que essa espécie exibiu duas marcas de crescimento por ano, uma durante a cheia e outra na seca. Todos os indivíduos com mais de 5 anos de idade foram amostrados na Bolívia, confirmando que após a migração para as cabeceiras do Madeira, os adultos permaneceram nessa região todo o ciclo de vida. As informações desse capítulo foram associadas às análises isotópicas dos otólitos permitindo a exata determinação cronológica dos eventos migratórios de *B. rousseauxii*. O segundo capítulo comprovou o *homing* natal de *B. rousseauxii* nas bacias dos rios Madeira e Amazonas por meio da associação do perfil de ^{87}Sr:^{86}Sr dos otólitos e dos seus respectivos mapeamentos de Sr:Ca e Se:Ca (obtidos por microscopia de varredura de fluorescência de raio X - SXFM). O terceiro capítulo investigou e quantificou os diferentes comportamentos migratórios de *B. rousseauxii,* ao longo de toda a bacia amazônica e determinou os impactos das usinas hidrelétricas do rio Madeira sobre esses padrões. *B. rousseauxii* apresentou três comportamentos migratórios distintos: residência, *homing* natal e *straying*. Antes dos barramentos aproximadamente 80% dos indivíduos realizaram *homing* natal no Alto Madeira, e após, todos os indivíduos foram residentes, com a ocorrência de *homers* bloqueados abaixo da usina de Santo Antônio Energia. Estes resultados confirmaram de forma irrefutável os impactos dos barramentos tanto sobre o aporte dos adultos nas porções altas da bacia do rio Madeira, como na migração rio abaixo dos ovos e larvas. Entretanto, a contribuição de 16 % do rio Madeira no recrutamento de *B. rousseauxii* no estuário, após as hidrelétricas, sugerem que pelo menos uma pequena parcela dos juvenis ainda conseguem passar pelas turbinas dessas barragens. O quarto capítulo investigou os processos migratórios de *B. platynemum* e verificou que esta espécie não realiza migrações tão extensas quanto *B. rousseauxii*. A maioria dos indivíduos de *B. platynemum* nascidos no rio Madeira, desenvolveram todo o ciclo de vida nessa bacia, refutando a hipótese de *homing* natal para essa espécie. Diferentemente, verificou-se padrões migratórios mais diversos para a calha principal do rio Amazonas, onde os indivíduos exibiram extensos deslocamentos até as porções baixas dessa bacia. As informações aqui levantadas demonstram a importância da efetividade dos sistemas de transposição de peixes na bacia do rio Madeira e da manutenção da conectividade do sistema fluvial amazônico para o desenvolvimento do ciclo de vida dessas espécies. Salienta-se assim, o quão deletério é o plano hidrelétrico previsto para essa bacia.

Palavras-chave: *Brachyplatystoma* spp, filopatria, microquímica de otólitos, crescimento, usinas hidrelétricas, Amazônia.

ABSTRACT

The understanding of the spatial and temporal patterns of migratory processes is fundamental for the elaboration the strategies of management and conservation of the ichthyofauna. Although some propositions about the life cycle of the goiliath catfish of the genus *Brachyplatystoma*, a group of notorious economic and ecological role in the Amazon, have been suggested until the moment there is no definitive validation about the complex migratory process of this species. This study aimed to investigate the migratory behavior of *B. rousseauxii* and *B. platynemum*, along the Amazon basin from the $^{87}Sr{:}^{86}Sr$ ratio of the otoliths, before and after the construction of hydroeletric dams on the Madeira River. The hypothesis tested was that these species have natal homing behavior. For this purpose were analyzed 344 otoliths and 87 samples of water collected throughout the Amazon basin, including Peru, Bolivia and Brazil. The $^{87}Sr{:}^{86}Sr$ isotopic analyzes of otoliths and waters were performed by mass spectrometry with plasma source and multicoletor, with laser ablation for otoliths (MC-LA-ICPMS). To answer the assumptions raised above, the respective thesis was organized into four chapters. The first chapter determined the age and growth of *B. rousseauxii* and showed that this species exhibited two growth marks per year, one in dry and other in flood season. All individuals older than 5 years old of age were sampled in Bolivia, confirming that once they migrate to the headwaters of Madeira, they remain in this region throughout the life cycle. The information in this chapter was associated with the $^{87}Sr{:}^{86}Sr$ of the otoliths allowing the exact chronological determination of the migratory events of *B. rousseauxii*. The second chapter confirmed the natal homing behavior of *B. rousseauxii* in the Madeira and Amazonas basins by the association of the $^{87}Sr{:}^{86}Sr$ profile of the otoliths and their respective Sr:Ca and Se:Ca mapping (obtained by X - ray fluorescence scanning microscopy - SXFM). The third chapter investigated and quantified the different migratory behaviors of *B. rousseauxii* throughout the Amazon basin and determined the impacts of the Madeira River hydroelectric on these patterns. *B. rousseauxii* exhibited three distinct behaviors: residence, homing natal and straying. Before the dams, approximately 80% of the individuals performed natal homing in the upper Madeira River and after that all the individuals were residents, with the occurrence of homers blocked below the Santo Antônio Energia dam. These results irrefutably confirmed the impacts of the dams both on the transposition upstream Madeira river of the adults, as on the downstream migration of the eggs and larvae. However, the 16% contribution of the Madeira River to the recruitment of *B. rousseauxii* in the estuary, after the dams, suggests that at least a small number of juveniles still get to pass through the turbines. The fourth chapter investigated the migratory processes of *B. platynemum* and verified that this species does not carry out extensive migrations as *B. rousseauxii*. The most of the *B. platynemum* individuals born on the Madeira River developed the whole life cycle in this basin, refuting the natal homing hypothesis for this species. Differently, there were more diverse migratory patterns for the Amazon mainstem River, where the individuals exhibited extensive displacements until the low portions of this basin. The information presented here demonstrates the importance of the effectiveness of fish transposition systems in the Madeira River basin and the maintenance of the connectivity of the Amazonian river system for the development of the life cycle of these species. It should be noted, therefore, how deleterious is the hydroelectric plan for this basin.

Keywords: *Brachyplatystoma* spp, philopatry, microchemistry of otolith, growth, dams, Amazon.

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INTRODUÇÃO GERAL

A migração é uma importante característica do ciclo de vida de muitos peixes dulcícolas e marinhos (HARDEN-JONES, 1968; MILES et al., 2009). A impressionante variedade de padrões migratórios apresentados por espécies ictiícas têm intrigado os cientistas em todo o mundo, os quais descreveram fascinantes estratégias como a anadromia, catadromia, diadromia, potadromia, entre outros (McDOWALL, 1988). Como as espécies migradoras desempenham relevante papel na atividade pesqueira (CAROSFELD et al., 2003; MPA, 2013), a compreensão dos padrões espaciais e temporais dos movimentos dos peixes é fundamental para elaboração de estratégias de gestão e conservação destes recursos (RIEMAN; DUNHAM, 2000; ELSDON; GILLANDERS, 2003).

Na bacia amazônica, a pesca tem um papel fundamental na economia regional movimentando cerca de 389 milhões de reais (ALMEIDA et al., 2010) o que gera mais de 175.000 empregos diretos e indiretos (RUFFINO, 2014). Entre as principais espécies comercializadas nesses mercados estão os Siluriformes que se destacam pelo alto valor do quilo do pescado em relação aos outros grupos de peixes (DORIA et al., 2012). Dentre os gêneros da respectiva ordem, *Brachyplatystoma* spp. figura como o mais valorizado de toda a Amazônia, alcançando valores de desembarques superiores a 40.000t ano-1, segundo estatísticas oriundas apenas da porção brasileira dessa bacia (MPA, 2013; BATISTA et al., 2018).

Além de importância econômica, as espécies desse grupo também exibem relevante função ecológica como predadores de topo da cadeia alimentar (BARTHEM; GOULDING 1997; ANGELINI et al., 2006), e alterações na sua abundância podem ter profundas consequências para os ecossistemas por meio das cascatas tróficas (ESTES et al., 2011; LIMA, 2017).

Mas, sem sobra de dúvidas, uma das características mais intrigantes e ainda enigmática da história de vida desse grupo é o seu complexo processo migratório, o qual é conhecido sobretudo para *B. rousseauxii,* popularmente conhecida como dourada. A partir da distribuição de tamanho dos exemplares capturados nas pescarias dos principais portos pesqueiros, ao longo da calha principal do rio Amazonas, e dos dados de maturação gonadal, Barthem & Goulding (1997) descreveram para essa espécie, um padrão de migração reprodutivo singular e diferente dos já relatados para peixes de água doce. Inclusive, pelo número reduzido de informações, hipotetizaram que *B. platynemum*, uma outra importante espécie econômica desse grupo, sobretudo para o rio Madeira (DORIA; LIMA, 2015; DORIA et al., 2018), também exibiria o mesmo comportamento migratório.

Segundo os autores, os exemplares adultos dessas espécies migram até as cabeceiras dos afluentes do sistema Solimões/Amazonas para se reproduzirem, chegando a percorrer até 4500 km. Após a desova, as larvas e juvenis descem o rio carreados pela corrente, até a região do estuário amazônico, onde se desenvolvem por cerca de dois anos. Estes agora, pré-adultos, iniciam a migração ascendente em direção a Amazônia Central onde utilizam essa nova área por mais um ou dois anos, essencialmente para alimentação e crescimento. Então, por volta de quatro anos quando estão sexualmente maduros, reiniciam o deslocamento rio acima para se reproduzirem nas cabeceiras dos afluentes na Amazônia ocidental. Embora os autores afirmarem que *B. rousseauxii* compõe um único estoque pesqueiro que migra ao longo de todo o sistema amazônico, o comportamento de retornar à região andina para se reproduzir, suscitou entre eles a hipótese de um possível comportamento de *homing* natal para essa espécie na bacia amazônica. Ou seja, após crescerem no estuário, os adultos de *B. rousseauxii* retornariam aos mesmos rios em que nasceram, para se reproduzirem nas cabeceiras andinas, assim como se observa para os salmões (SCHEER, 1939; QUINN, 2005) e enguias (TESCH; WHITE, 2008).

Semelhantemente, a partir de dados merístiscos, morfométricos e de desembarque pesqueiro proveniente dos principais centros de pesca da Amazônia, Alonso (2002) também confirmou que *B. rousseauxii* era composta por um único estoque pesqueiro que migrava ao longo de todo o sistema amazônico.

Por outro lado, a partir de marcadores mitocondriais (D-Loop) Batista & Alves-Gomes (2006) observaram diminuição da variabilidade genética de *B. rousseauxii* do sentido leste (estuário) para oeste (cabeceiras dos afluentes) da bacia amazônica, levantando novamente a hipótese de *homing* natal para a espécie. Entretanto, um dos próprios autores em um estudo posterior e mais abrangente, utilizando marcadores mais sensíveis para identificar diferenças a nível de populações (microssatélites), refutou a respectiva hipótese de *homing* para a dourada na bacia amazônica (BATISTA, 2010). A autora também propôs que *B. rousseauxii* era composta por uma única população panmítica, com considerável fluxo gênico entre o canal principal do Solimões/Amazonas e seus afluentes, consistindo assim em um único estoque pesqueiro.

Diferentemente, Carvajal-Vallejos e colaboradores (2014) também utilizando marcadores de microssatélites, verificaram um claro padrão de estruturação genética para *B. rousseauxii* na bacia amazônica, com a ocorrência de pelo menos três subpopulações distintas, uma das quais era restrita às porções bolivianas e peruanas do Alto Madeira. Segundo os autores, esse padrão poderia ser explicado por um estilo de vida residente, com os indivíduos desenvolvendo seu ciclo de vida inteiro na bacia do rio Madeira, ou ainda, por um comportamento de *homing* natal, levantando novamente essa hipótese. A partir de então, começou-se a especular a necessidade de aplicação de outras técnicas mais sensíveis para a confirmação dos padrões migratórios de *B. rousseauxii* na bacia amazônica, como por exemplo a microquímica de otólitos, que vem se mostrando eficiente no rastreamento dos diferentes processos de deslocamentos dos peixes (WELLS et al., 2000; GILLANDERS et al., 2001; ELSDON *et al*., 2008).

Os otólitos são pequenas estruturas rígidas localizadas no ouvido interno do peixe, constituídas essencialmente por carbonato de cálcio ($CaCO_3$), tradicionalmente utilizados para a determinação da idade e crescimento desses organismos (PANFILI et al., 2002; POPER et al., 2005). Por ser uma estrutura acelular, metabolicamente inerte, também permite o registro permanente das condições ambientais, assegurando a retenção de substâncias químicas (CAMPANA, 1999). Por exemplo, a medida que o peixe cresce, elementos químicos naturais como estrôncio, bário, chumbo, zinco, entre outros, e seus isótopos, prontamente substituem o cálcio dos otólitos em proporção às suas concentrações dissolvidas no ambiente, ou à ocorrência nos alimentos. Assim, a associação dessas informações à idade que os otólitos fornecem, permite estimar a cronologia exata da exposição do peixe a cada condição ambiental diferente, possibilitando rastrear todo seu o ciclo de vida (GILLANDERS, 2005).

Dentre os elementos comummente utilizados como marcadores para estudar os deslocamentos dos peixes diádromos estão as razões elementares de Ba:Ca e Sr:Ca, as quais variam amplamente entre os ambientes marinhos e dulcícolas (TSUKAMOTO et al., 1998; CAMPANA; THORROLD, 2001; WALTHER; LIMBURG, 2012). No entanto, seu uso em peixes que desenvolvem o ciclo de vida inteiramente dentro da água doce é um pouco mais desafiador, visto à redução dos gradientes químicos em uma bacia hidrográfica, somado ainda aos possíveis efeitos dos processos bióticos (dinâmicas fisiológicas ou alimentares) e abióticos (temperatura) em sua incorporação nos otólitos (TOOLE et al., 1993; TOWNSEND et al., 1995; KAWAKAMI et al., 1998).

Em contraste, a razão isotópica de estrôncio (^{87}Sr:^{86}Sr) não sofre fracionamento biológico significativo durante a captação da dieta ou fontes de água, dependendo quase que exclusivamente da idade e da composição geológica das bacias hidrográficas, e assim, variam muito pouco ao longo dos anos, gerando assinaturas de habitat muito precisas (KENNEDY et al., 1997; 2000; 2002; WALTHER & THORROLD, 2008 WALTHER; LIMBURG, 2012;). Recentes estudos de metodologias de ablação a laser (LA) combinadas com multicoletor

(MC) e espectrometria de massas com plasma indutivamente acoplado (ICPMS), para a medição da razão desses isótopos (^{87}Sr: ^{86}Sr) ao longo de transectos de otólitos, abriram novas perspectivas nas ciências ictiícas, permitindo a reconstrução refinada do uso do habitat durante parte ou toda a vida dos peixes (OUTRIDGE et al., 2002; BARNETT-JOHNSON et al., 2005). Inclusive, a aplicabilidade dessa ferramenta também foi recentemente confirmada na determinação dos padrões migratórios de peixes que vivem em ambientes tão complexos como a bacia amazônica (POUILLY et al., 2014; GARCEZ et al., 2014; SANTOS et al., 2015; HEGG et al., 2015; SOUZA e tal., 2016).

Nessa perspectiva, com base na diferenciação da bacia amazônica em pelo menos 3 grandes subsistemas em função da razão isotópica de ^{87}Sr:^{86}Sr das águas dos rios (Amazonas 0,715-0,712; Madeira e Baixo Negro 0,714-0,727 e tributários do escudo granítico brasileiro 0,724-0,744; PALMER; EDMOND, 1992; SANTOS et al., 2015) Duponchelle e colaboradores (2016) (ver apêndice) confirmaram pela primeira vez o comportamento de *homing* natal para *B. rousseauxii* no Alto rio Madeira a partir da razão desses elementos ao longo dos otólitos. Os autores mostraram a nível de indivíduo que os peixes dessa espécie poderiam migrar mais de 8000 km entre suas zonas de nascimento no alto Madeira e, de berçário no Baixo Amazonas/estuário, somado ao seu retorno como adulto às mesmas zonas onde nasceram dentro do rio Madeira. Interessantemente, esses autores observaram que além do comportamento de *homing* natal, essa espécie também apresentou padrões migratórios distintos, como por exemplo, a presença de *strayers* que são indivíduos que nascem em uma determinada área e falham ao reconhecê-la quando adultos, utilizando rios distintos daqueles de origem para a reprodução.

Embora esse trabalho tenha dado um grande salto de contribuição na compreensão do ciclo de vida de *B. rousseauxii*, o comportamento migratório dessa espécie, e principalmente dos demais bagres do grupo, não foi totalmente elucidado, com vários questionamentos continuando vigentes, além da suscitação de novas perguntas, como por exemplo: em qual idade ocorre os processos migratórios dos indivíduos de *B. rousseauxii*? Esta espécie também exibe comportamento de *homing* natal na calha principal do rio Amazonas? Qual a proporção dos diferentes padrões migratórios de *B. rousseauxii* na bacia amazônica? *B. platynemum* realmente exibe o mesmo padrão migratório de *B. rousseauxii*? Ademais, a recente implementação de um complexo hidrelétrico no rio Madeira, somada a previsão de construção de mais 243 hidrelétricas para toda a Amazônia (LEES et al., 2016), fomentaram novas indagações, agora acerca dos impactos desses empreendimentos sobre as migrações dos grandes bagres.

Nessa perspectiva, ressalta-se a importância do refinamento acerca do ciclo de vida das espécies de *Brachyplatystoma,* grupo de notório papel econômico e ecológico na Amazônia, o qual fornecerá informações essenciais para o manejo desses recursos pesqueiros. Portanto, o presente estudo teve como objetivo geral descrever o padrão migratório dessas espécies a partir da razão de ^{87}Sr:^{86}Sr nos otólitos e testou a hipótese central de que "*B. rousseauxii* e *B. platynemum* apresentam comportamento de *homing* natal na bacia amazônica". Dentre os objetivos específicos buscou-se:

- ✓ Determinar a idade e crescimento de *B. rousseauxii* na bacia do rio Madeira (capítulo 1);
- ✓ Testar o comportamento de *homing* natal de *B. rousseauxii* na calha principal do rio Amazonas (capítulo 2);
- ✓ Quantificar as taxas de homers, residentes e strayers de *B. rousseauxii* na bacia amazônica (capítulo 3)*;*
- ✓ Estimar a contribuição dos rios Madeira e Amazonas no recrutamento de *B. rousseauxii* no estuário (capítulo 3)*;*
- ✓ Verificar se o barramento provocado pelo Complexo Hidrelétrico de Jirau e Santo Antônio estão impedindo a migração rio abaixo dos exemplares juvenis e a migração ascendente dos peixes adultos de *B. rousseauxii* no rio Madeira (capítulo 3)*;*
- ✓ Verificar se a migração de *B. platynemum* é tão extensa quanto a de *B. rousseauxii* (capítulo 4);

Este documento foi organizado de forma a responder os objetivos propostos acima, apresentando as etapas realizadas do projeto de pesquisa e os resultados obtidos, os quais permitiram testar a hipótese levantada.

O primeiro capítulo intitulado "**Idade e crescimento do bagre amazônico migrador *Brachyplatystoma rousseauxii* na bacia do rio Madeira antes da construção das barragens"**, apresentou o estudo inédito de idade e crescimento de *B. rousseauxii* na bacia do rio Madeira e está na forma de artigo científico, já publicado no periódico Neotropical Ichthyology sob o título "**Age and growth of the Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Madeira River basin before the construction of dams**". As informações geradas nesse capítulo foram associadas às análises isotópicas dos otólitos permitindo a exata determinação cronológica dos eventos migratórios desta espécie (capítulos II e III).

O segundo capítulo intitulado **“A associação do mapeamento SXFM de Se:Ca e Sr:Ca de otólitos e seus transectos de ^{87}Sr:^{86}Sr confirmam o *homing* natal transamazônico de um bagre gigante no Alto Amazonas”** apresentou o estudo inédito de *homing* natal de *B. rousseauxii* para a calha principal do rio Amazonas e está na forma de artigo científico visando breve submissão ao periódico Journal Applied Ecology sob o título “Otolith Se/Ca, Sr/Ca SXFM mappings and ^{87}Sr/^{86}Sr transects together confirm trans Amazonian natal homing of goliath catfish in the upper Amazon”.

O terceiro capítulo intitulado “**História de vida de *Brachyplatystoma rousseauxii* sob a perspectiva dos empreendimentos hidrelétricos na Amazônia**” investigou os diferentes comportamentos migratórios de *B. rousseauxii* ao longo de toda a bacia amazônica e os impactos das usinas hidrelétricas do rio Madeira sobre o ciclo de vida dessa espécie.

O quarto capítulo intitulado **“Desvendando os padrões migratórios do grande bagre amazônico *Brachyplatystoma platynemum*, usando análises da ^{87}Sr:^{86}Sr dos otólitos”** apresentou o estudo inédito de migração de *B. platynemum* na bacia amazônica e está na forma de artigo científico aceito para publicação no periódico Aquatic Conservation: Marine and Freshwater Ecosystems sob o título “Shedding light on the migratory patterns of the Amazonian goliath catfish, *Brachyplatystoma platynemum*, using otolith ^{87}Sr:^{86}Sr analyses”.

RERERÊNCIAS

ALMEIDA, O. A.; LORENZEN, K.; MCGRATH, D.; AMARA, L.; RIVERO, S. Importância econômica do setor pesqueiro na calha do rio Amazonas-Solimões. **Papers do Naea**, n. 275, p.1-15, 2010.

ALONSO, J. C. **Padrão espaço-temporal da estrutura populacional e estado atual da exploração pesqueira da dourada *Brachyplatystoma flavicans*, Castelnau, 1855 (Siluriformes: Pimelodidae), no sistema Estuário- Amazonas- Solimões.** Tese de doutorado do Instituto Nacional de Pesquisa da Amazônia/ Fundação Universidade do Amazonas. Manaus, Amazonas, p. 217, 2002.

ANGELINI, R.; FABRE, N. N.; SILVA-JR, U. L. Trophic analysis and shing simulation of the biggest Amazonian cat sh. **African Journal of Agricultural Research**. v.1, p. 151-58, 2006.

BARNETT-JOHNSON, R.; RAMOS, F. C.; GRIMES, C. B.; MAcFARLANE, R. B. Validation of Sr isotopes in otoliths by laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICPMS): opening avenues in fisheries science applications. **Canadian Journal of Fisheries and Aquatic Sciences***,* v. 62, p. 2425-2430, 2005.

BARTHEM, R. B.; GOULDING, M. **Os bagres balizadores: ecologia, migração e Zonservação de peixes amazônicos.** Sociedade Civil Mamirauá/MCT/CNPQ: Brasília, p. 130, 1997.

BATISTA, J. S.; ALVES-GOMES, J. A. Phylogeography of *Brachyplatystoma rousseauxii* (Siluriformes - Pimelodidae) in the Amazon Basin offers preliminary evidence for the first case of “homing” for an Amazonian migratory catfish. **Genetics and Molecular Research**, v. 4, p. 723-740, 2006.

BATISTA, J. **Caracterização genética da dourada - *Brachyplatystoma rousseauxii*, Castelnau, 1855 (Siluriformes: Pimelodidae) na Amazônia por meio de marcadores moleculares mitocondriais e microssatélites: subsídios para conservação e manejo**. Tese de doutorado do Instituto Nacional de Pesquisa da Amazônia/ Fundação Universidade do Amazonas. Manaus, Amazonas, p. 128, 2010.

BATISTA, V.; ALONSO, J. C.; LADLE, R. J.; FABRÉ, N. N. Drivers of the upper River Amazon giant catfish fishery. **Fisheries Management and Ecology**, p. 1–11, 2018.

CAMPANA, S. E. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. **Marine Ecology Progress Series***,* v. 188, p. 263-297, 1999.

CAMPANA, S. E.; THORROLD, S. R. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? **Canadian Journal of Fisheries and Aquatic Sciences***,* v. 58, p. 30-38, 2001.

CAROLSFELD, J.; HARVEY, B.; ROSS, C.; BAER, A. **Migratory shes of South America: Biology, Fisheries and Conservation Status World Fisheries Trust**. Washington: IDRC, World Bank, p. 372, 2003.

CARVAJAL-VALLEJOS, F. M.; DUPONCHELLE, F.; DESMARAIS, E.; CERQUEIRA, F.; QUEROUIL, S.; NUÑEZ, J.; GARCIA, C.; RENNO, J. F. Genetic structure in the Amazonian catfish *Brachyplatystoma rousseauxii:* influence of life history strategies. **Genetica**, v. 142, p. 323-336, 2014.

DORIA, C. R. C.; RUFFINO, M. L.; HIJAZI, N. C.; CRUZ, R. L. A pesca comercial na bacia do rio Madeira no estado de Rondônia, Amazônia brasileira. **Acta Amazônia**, v. 42, p. 29-40, 2012.

DORIA, C. R. & LIMA, M. A. L. **Rio madeira: seus peixes e sua pesca.** Porto Velho: EDUFRO. Co-edição: RiMa Editora, p. 153, 2015.

DORIA, C. R. C.; DUPONCHELLE, F.; LIMA, M. A. L.; GARCÌA, A.; CARVAJAL-VALLEJOS, F. M.; MENDEZ, C. C.; CATARINO, M. F.; FREITAS, C. E. C.; VEGA, B.; MIRANDA-CHUMACERO, G.; VAN DAMME, P. A. Review of Fisheries Resource Use and Status in the Madeira River Basin (Brazil, Bolivia, and Peru) Before Hydroelectric Dam Completion. **Reviews In Fisheries Science** , v. 0, P. 1–21, 2018.

DUPONCHELLE, F.; POUILLY, M.; PECHEYRAN, C.; HAUSER, M.; RENNO, J.F.; PANFILI, J.; DARNAUDE, A. M.; GARCIA-VASQUEZ, A.; CARVAJAL-VALLEJOS, F.; GARCIA-DAVILA, C.; DORIA, C.; BERAIL, S.; DONARD, A.; SONDAG, F.; SANTOS, R.V.; NUÑEZ, J.; POINT, D.; LABONNE, M.; BARAS, E. Trans-Amazonian natal homing in giant catfish. **Journal of Applied Ecology**, v. 53, p. 1511-1520, 2016.

ELSDON, T. S.; GILLANDERS, B. M. Reconstructing migratory patterns of fish based on environmental influences on otolith chemistry. **Reviews in Fish Biology and Fisheries**, v. 13, p. 219-235, 2003.

ELSDON, T. S.; WELLS, B. K.; CAMPANA, S. E.; GILLANDERS, B. M.; JONES, C. M.; K. E. LIMBURG, D. H.; SECOR; THORROLD, S. R.; WALTHER, B. D. Otolith chemistry to describe movements and life history parameters of fishes: hypotheses, assumptions, limitations, and inferences. **Oceanography and Marine Biology: An Annual Review**, v. 46, p. 297-330, 2008.

ESTES, J.A.; TERBORGH, J.; BRASHARES, J. S.; POWER, M. E.; BERGER, J.; BOND, W. J.; CARPENTER, S. R. ; ESSINGTON, T. E.; HOLT, R. D.; JACKSON, J. B. C.; MARQUIS, R. J.; OKSANEN, L.; OKSANEN, T.; PAINE, R. T.; PIKITCH, E. K.; RIPPLE, W. J.; SANDIN, S. A.; SCHEFFER, M.; SCHOENER, T. W.; SHURIN, J. B.; SINCLAIR, A. R. E.; SOULE, M. E.; VIRTANEN, R.; WARDLE, D. A. Trophic downgrading of planet Earth. **Science**, v. 333, p. 301-306, 2011.

GARCEZ, R. C. S.; HUMSTON, R.; HARBOR, D.; FREITAS, C. E. C. Otolith geochemistry in young-of-the-year peacock bass *Cichla temensis* for investigating natal dispersal in the Rio Negro (Amazon – Brazil) river system. **Ecology of Freshwater Fish**, v. 24, p. 242–251, 2014.

GILLANDERS, B. M.; FERRELL, D. J.; ANDREW, N. L. Estimates of movement and life-history parameters of yellowtail kingfish (*Seriola lalandi*): How useful are data from a cooperative tagging programme? **Marine & Freshwater Research***,* v. 52: p. 179-192, 2001.

GILLANDERS, B. M. Otolith chemistry to determine movements of diadromous and freshwater fish. **Aquatic Living Resources**, v.18, p. 291-300, 2005.

HARDEN-JONES, F. R. **Fish Migration**. Edward Arnold, London. p. 325, 1968.

HEGG, J. C.; GIARRIZZO, T.; KENNEDY, B. P. Diverse early life-history strategies in migratory Amazonian catfish: implications for conservation and management. **PLoS ONE,** v. 10**,** e0129697, 2015.

KAWAKAMI, Y.; MOCHIOKA, N.; MORISHITA, K.; TAJIMA, T.; NAKAGAWA, H.; TOH, H.; NAKAZONO, A. Factors influencing otolith strontium/ calcium ratios in *Anguilla japonica* elvers. **Environmental Biology of Fishes,** v. 52, p. 299-303, 1998.

KENNEDY, B. P.; FOLT, C. L.; BLUM, J. D.; CHAMBERLAIN, C. P. Natural isotope markers in salmon. **Nature***,* v. 387, p. 766-767, 1997.

KENNEDY, B. P.; BLUM, J. D.; FOLT, C. L.; NISLOW K. H. Using natural strontium isotopic signatures as fish markers: Methodology and application. **Canadian Journal of Fisheries and Aquatic Sciences**, v. 57, p. 2280-2292, 2000.

KENNEDY, B. P.; KLAUE, A.; BLUM, J. D.; FOLT, C. L.; NISLOW, K. H. Reconstructing the lives of fish using Sr isotopes in otoliths. **Canadian Journal of Fisheries and Aquatic Sciences***,* v. 59, p. 925-929, 2002.

LEES, A. C.; PERES, C. A.; FEARNSIDE, P. M.; SCHNEIDER, M.; ZUANON, J. A. S. Hydropower and the future of Amazonian biodiversity. **Biodiversity and Conservation**, v. 25, p. 451-466, 2016.

LIMA, M. A. L. **História do ecossistema e dos recursos pesqueiros frente a implementação de hidrelétricas na bacia do rio Madeira**. Tese de doutorado do Programa de Pós-Graduação Em Desenvolvimento Regional e Meio Ambiente, Universidade Federal de Rondonia, Porto Velo, RO, p. 138, 2017.

McDOWALL R. M. **Diadromy in fishes. Migrations between freshwater and marine environments**. Timber Press, Portland, Oregon, p. 308, 1988.

MILES, N. G; WEST, R. J.; NORMAN, M. D. Does otolith chemistry indicate diadromous lifecycles for five Australian riverine fishes? **Marine and Freshwater Research,** v. 60, p. 904 -911. 2009

MPA. **Boletim estatístico de pesca e aquicultura do Brasil 2011**. Brasília: Ministério da Pesca e Aquicultura, p. 60, 2013.

OUTRIDGE, P. M.; CHENERY, S. R.; BABALUK, J. A.; REIST, J. D. Analysis of geological Sr isotope markers in fish otoliths with subannual resolution using laser ablation-multicollector-ICP-mass spectrometry. **Environmental Geology***,* v. 42**,** p. 891-899, 2002.

PALMER, M. R.; EDMOND, J. M. Controls over the strontium isotope composition of river water. **Geochimica et Cosmochimica Acta,** v. 56, p. 2099–2111, 1992.

PANFILI, J.; PONTUAL, H. D.; TROADEC, H.; WRIGHT, P. J. **Manual of fish sclerochronology.** Ifremer-IRD, Brest, France, p. 463, 2002.

POPER, A. N.; RAMCHARITAR, J.; CAMPANA, S. E. Why otoliths? Insights from inner ear physiology and fisheries biology. **Marine and Freshwater Research**, 56, 497–504, 2005.

POUILLY, M.; POINT, D.; SONDAG, F.; HENRY, M.; SANTOS, R. V. Geographical origin of Amazonian freshwater fishes fingerprinted by ^{87}Sr/^{86}Sr ratios on fish otoliths and scales. **Environmental Science & Technology***,* v. 48, p. 8980-8987, 2014.

QUINN, T. P. **The Behavior and Ecology of Pacific Salmon and Trout**. American Fisheries Society. N/A in Canada, p. 378, 2005.

RIEMAN, B. E.; DUNHAM, J. B. Metapopulations and salmonid fishes: a synthesis of life history patterns and empirical observations. **Ecology of Freshwater Fish**, v. 9, p. 51–64, 2000.

RUFFINO, M. L. Status and trends of the fishery resources of the Amazon Basin in Brazil. Inland fisheries evolution and management. Case studies from four continents. **FAO Technical Paper**, p. 1–19, 2014.

SANTOS, R.V.; SONDAG, F.; COCHONNEAU, G.; LAGANE, C.; BRUNET, P.; HATTINGH, K.; CHAVES, J. G. S. Source area and seasonal 87Sr/86Sr variations in rivers of the Amazon basin. **Hydrological Processes**, v. 29, p. 187–197, 2015.

SCHEER, B.T. Homing instinct in Salmon. **The Quarterly Review of Biology**, v.14, p. 408–430, 1939.

SOUZA, R. G. C; HUMSTON, R.; FREITAS, C. Movement patterns of adult peacock bass *Cichla temensis* between tributaries of the middle Negro River basin (Amazonas – Brazil): an otolith geochemical analysis. **Fisheries Management and Ecology**, v. 23, p. 76–87, 2016.

TESCH, F. W.; WHITE, R. J. **The Eel.** John Wiley & Sons, Oxford, UK, p. 573, 2008.

TOOLE, C. L.; MARKLE, D. F.; HARRIS, P. M. Relationships between otolith microstructure, microchemistry, and early life history events in Dover sole *Microstomus pacificus***. Fishery Bulletin***,* v. 91, p. 732-753, 1993.

TOWNSEND, D. W.; RADTKE, R. L.; MALONE, D. P.; WALLINGA, J. P. Use of otolith strontium: calcium ratios for hindcasting larval cod *Gadus morhua* distributions relative to water masses on Georges Bank. **Marine Ecology Progress Series***,* v. 119, p. 37-44, 1995.

TSUKAMOTO, K.; NAKAI, I.; TESCH, W. V. Do all freshwater eels migrate? **Nature**, v. 396, p. 635-636, 1998.

WALTHER, B. D.; THORROLD, S. R.; OLNEY, J. E. Geochemical signatures in otoliths record natal origins of American shad. **Transactions of the American Fisheries Society**, v. 137, p. 57-69, 2008.

WALTHER, B. D.; LIMBURG, K. E. The use of otolith chemistry to characterize diadromous migrations. **Journal of Fish Biology**, v. 81, p. 796-825, 2012.

WELLS, B. K.; BATH, G. E.; THORROLD, S. R.; JONES, C. M. Incorporation of strontium, cadmium, and barium in juvenile spot (*Leiostomus xanthurus*) scales reflects water chemistry. **Canadian Journal of Fisheries and Aquatic Sciencies,** v. 57, p. 2122-212, 2000.

CAPÍTULO I

Idade e crescimento do bagre amazônico migrador *Brachyplatystoma rousseauxii* na bacia do rio Madeira antes da construção das barragens

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Age and growth of the Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Madeira River basin before the construction of dams

ABSTRACT

The goliath catfish *Brachyplatystoma rousseauxii* has crucial economical and ecological functions in the Amazon basin. Although its life history characteristics have been studied in the Amazon, there is little information in the Madeira River basin, which holds genetically distinct populations and where dams were recently built. Using fish collected in Bolivia, Brazil and Peru, this study provides a validation of growth rings deposition and details the growth patterns of *B. rousseauxii* in the Madeira before the dams' construction. Age structure and growth parameters were determined from 497 otolith readings. The species exhibits two growth rings per year and sampled fish were between 0 and 16 years old. In the Brazilian portion of the basin, mainly young individuals below 5 years old were found, whereas older fish (> 5 years) were caught only in the Bolivian and Peruvian stretches, indicating that after migrating upstream to reproduce, adults remain in the headwaters of the Madeira River. Comparing with previous publications, *B. rousseauxii* had a slower growth and 20 cm lower maximum standard length in the Madeira River than in the Amazon River. This study provides a baseline for future evaluation of changes in population dynamics of the species following dams closure.

Key words: Amazon, Biannual rings, Goliath catfish, Life cycle, Otolith.

RESUMO

Brachyplatystoma rousseauxii é um bagre de importante papel econômico e ecológico na bacia amazônica. Embora existam estudos acerca de sua história de vida na Amazônia, há pouca informação para a bacia do rio Madeira, onde existem populações geneticamente distintas e recentemente foram construídas duas usinas hidrelétricas. Este estudo validou a deposição das marcas de crescimento e detalhou os padrões de desenvolvimento dessa espécie no rio Madeira, antes da construção das barragens. As coletas abrangeram os territórios brasileiro, boliviano e peruano, com a estrutura etária e os parâmetros de crescimento determinados a partir de 497 otólitos. Foram observadas duas marcas de crescimento por ano e indivíduos entre 0 e 16 anos. Na porção brasileira foram encontrados principalmente jovens menores de 5 anos, enquanto que os peixes mais velhos (> 5 anos) foram capturados apenas na Bolívia e Peru, indicando que após a migração reprodutiva, os adultos permanecem nas cabeceiras do rio Madeira. Comparando com estudos prévios realizados na calha principal do rio Amazonas, *B. rousseauxii* apresentou crescimento mais lento e comprimento padrão máximo inferior de 20 cm no rio Madeira. Este estudo fornece uma base para a avaliação futura das mudanças na dinâmica populacional desse espécie após o implementação das barragens.

Palavras-chave: Amazônia, Bagre gigante, Ciclo de vida, Marcas biannual, Otólito.

INTRODUCTION

Apart from deforestation, habitat degradation, overexploitation and invasive species, hydroelectric impoundments and the resulting disruption of river connectivity are one of the main threats to freshwater biodiversity worldwide (Winemiller *et al.,* 2016). In the Amazon Basin, where more than 175 hydroelectric dams are under construction or in operation, there is growing evidence that planned and current hydroelectric development will likely have massive impacts on the ecosystem and its exceptional biodiversity (Finer, Jenkins 2012; Castello *et al*., 2013; Castello & Macedo, 2016; Lees *et al.,* 2016, Winemiller *et al.,* 2016; Latrubesse *et al.,* 2017).

Most Amazonian commercial fish species perform seasonal migrations, ranging from a few km to several thousands km, for reproductive and/or feeding purposes (Carolsfeld *et al*., 2003) that could be disrupted or imperilled by hydroelectric impoundments (Agostinho *et al*., 2007, 2008; He *et al*., 2017). The large migratory Pimelodid catfishes of the genus *Brachyplatystoma*, also known as goliath catfishes, alone support annual landings above 30,000 tons.year^{-1} (FAO-COPESCAL, 2000). Among these goliath catfishes, *Brachyplatystoma rousseauxii* (Castelnau 1855), popularly known as dourada in Brazil and as dorado or plateado in the other Amazonian countries, is one of the most important species marketed throughout the Amazon basin. It represents nearly 9% of total landings in Bolivia, Brazil, Colombia and Peru, supporting, alone, annual landings of ~ 15,000 tons.year^{-1} (Alonso *et al*., 2009).

This species also performs the most extensive freshwater migration ever described, from the spawning areas in the Andean piedmont of Bolivia, Colombia, Ecuador and Peru, to the nursery areas in the Amazon estuary (Barthem & Goulding, 1997; Duponchelle *et al.*, 2016; Barthem *et al.*, 2017). Barthem, Goulding (1997) first deduced this exceptional life cycle from size frequency and ripe gonad distributions between the estuary and the headwaters of the main Amazon tributaries. Duponchelle *et al.* (2016) confirmed this life cycle at the individual level using otolith $^{87}S_r/^{86}S_r$ ratios, and further demonstrated natal homing behaviour. Using data from spawning adults, drifting larvae and juveniles, Barthem *et al.* (2017) recently showed that the life cycle of *B. rousseauxii* involves a round trip migration of over 11,000 km.

Besides its economic importance, *B. rousseauxii* also plays key ecological functions as top predator of the Amazon main river channels (Barthem, Goulding, 1997; Angelini *et al.*, 2006). Disruption of migration routes for *B. rousseauxii* and its congeners could have profound impacts as loss of apex consumers reduces length of trophic food webs in ecosystems, impacting greatly the abundance and composition of other species through the trophic cascades (Paine, 1966, 1980; Fretwell, 1987; Bauer, Hoye, 2014; Estes *et al.*, 2011).

A more precise understanding of the impact of hydroelectric development in the Amazon basin on the exceptional migratory behaviour of this species would require linking individual movements and age patterns. Knowledge of age and growth plays a key role in understanding fish population dynamics, hence in fisheries management and also provides crucial insights for the conservation of threatened species (Campana, 2001; Hutchinson, TenBrink, 2011). Until now, all studies about age and growth characteristics of *B. rousseauxii* have been carried out along of the Amazon River mainstem using both otoliths (Alonso, 2002) and size frequency distributions (García-Vásquez *et al.*, 2009; Agudelo *et al.*, 2013). However, the existence of a clear genetic differentiation between *B. rousseauxii* from the western Amazon and from the Madeira River (Carvajal-Vallejos *et al.*, 2014) together with a natal homing behaviour in the latter (Duponchelle *et al.*, 2016), called for a specific study of its growth patterns within the Madeira basin.

The present work therefore aimed at validating the periodicity of growth rings formation in otoliths and at testing hypotheses of regional variation in age and growth patterns of *B. rousseauxii* in the Madeira River basin using samples collected in Brazil, Bolivia and Peru before the construction of the Madeira dams.

MATERIALS AND METHODS

FISH SAMPLING AND STUDY AREA

In Bolivia, fish were sampled between February 2005 and March 2009 in Puerto Villaroel (n= 70, Mamoré River), Rurrenabaque (n=5), Cachuela Esperanza (n=37) (both on the Beni River), from local fishermen directly on the fishing ground (which often required several weeks of travel with fishermen) (see Carvajal Vallejos *et al.*, 2014 for details). In Peru, fish were bought to local fishermen in the main landing site of Puerto Maldonado (n=6, Madre de Dios River). Fishing grounds are located within a few dozen kilometres from the city and are usually landed the same day or the following morning. In the middle and lower Madeira basin (i.e. the Brazilian portion of the river), fish were sampled between April 2009 and July 2012, in seven different landing sites (Surpresa n= 11; Iata/Vila Murtinho n=18, Teotônio fall n=7, São Sebastião n =196, São Carlos n=103, Calama n=13 and Humaitá n=11), by Fish Conservation Programs under the covenant of UNIR and RIOMAR and Santo Antônio Energia and Energia Sustentável do Brasil (Fig. 1). During fish landings a local trained collector or a technician from the Ichthyology and Fisheries Laboratory (LIP) of the Federal University of Rondônia (UNIR) recorded the standard length (SL) (mm), date, fishing locality and then extracted the heads of each individual, from which the otoliths were later removed in the LIP/UNIR. To improve growth modeling, juvenile individuals (between 11 cm and 30 cm standard length LS) were collected from the reservoir of the UHE Santo Antônio Energia (place where previously was the Teotonio Fall) with gill nets (mesh size from 30 to 200 mm between opposite knots). Voucher specimens were deposited in the fish collection of Federal University of Rondônia, Porto Velho, Brazil (UFRO-I 14016, UFRO-I 15044, UFRO-I 15175).

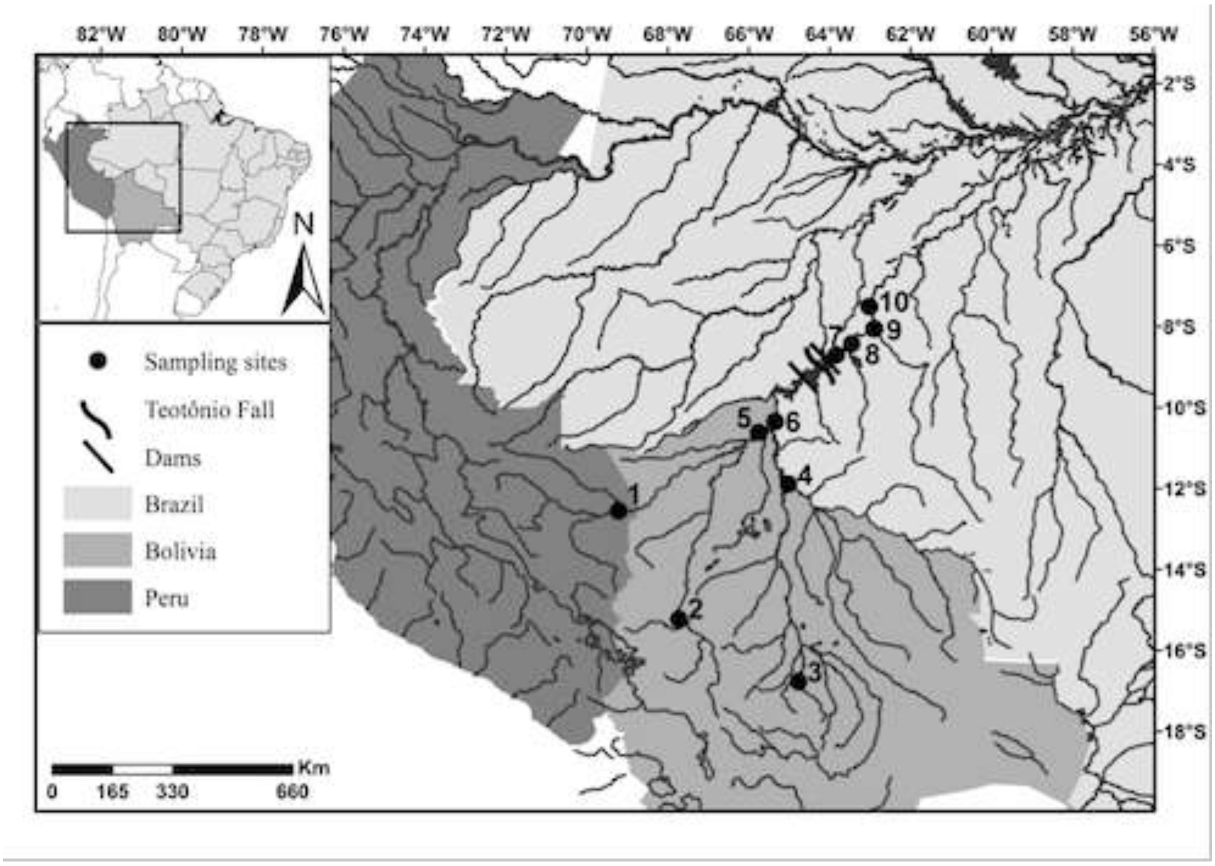

Fig. 1. Map of the sampling sites in the Madeira River basin . 1- Puerto Maldonado, 2- Rurrenabaque, 3-Puerto Villarroel, 4-Surpresa, 5- Cachuela Esperanza, 6-Iata/Vila Murtinho, 7-São Sebastião, 8-São Carlos, 9- Calama and 10- Humaitá.

BIOLOGICAL SAMPLE ANALYSIS

Otolith preparation and interpretation

On each fish, L_S (cm) was measured. The lapillus otoliths were extracted, washed in water, dried and stored in labelled envelopes for later laboratory processing. The otoliths were then embedded in polyester resin and sectioned transversally to a thickness of approximately 0.7 mm using a low-speed metallographic saw (Buehler Isomet and Isomet 1000). The thin sections were then polished (using 1200 and 2400 μm paper, then 1 μm alumin powder) until the core was visible, as detailed in Duponchelle *et al*. (2016). Age and growth characteristics were determined from the examination of 497 individual transverse thin otolith sections. Otolith sections were observed using a stereo microscope and photographed using a Zeiss AxioCam camera under transmitted light. Distances between the core and the growth rings were measured using Axiovision software.

Each growth ring consisted of a pair of one narrow opaque band (dark aspect) and one wide translucent band (light aspect). Opaque bands, or rings, which correspond to seasonal increments, were counted between the core and the edge of the otolith. Photographs were examined twice by two independent readers to determine the number of opaque rings. When there was disagreement between readers about the number of rings, the otolith was re-interpreted and discarded if the readers did not agree. The distance (mm) between the core and the edge of the otolith (otolith radius) and between consecutive rings was measured along the otolith at a pre-determined 110° angle (Fig. 2c).

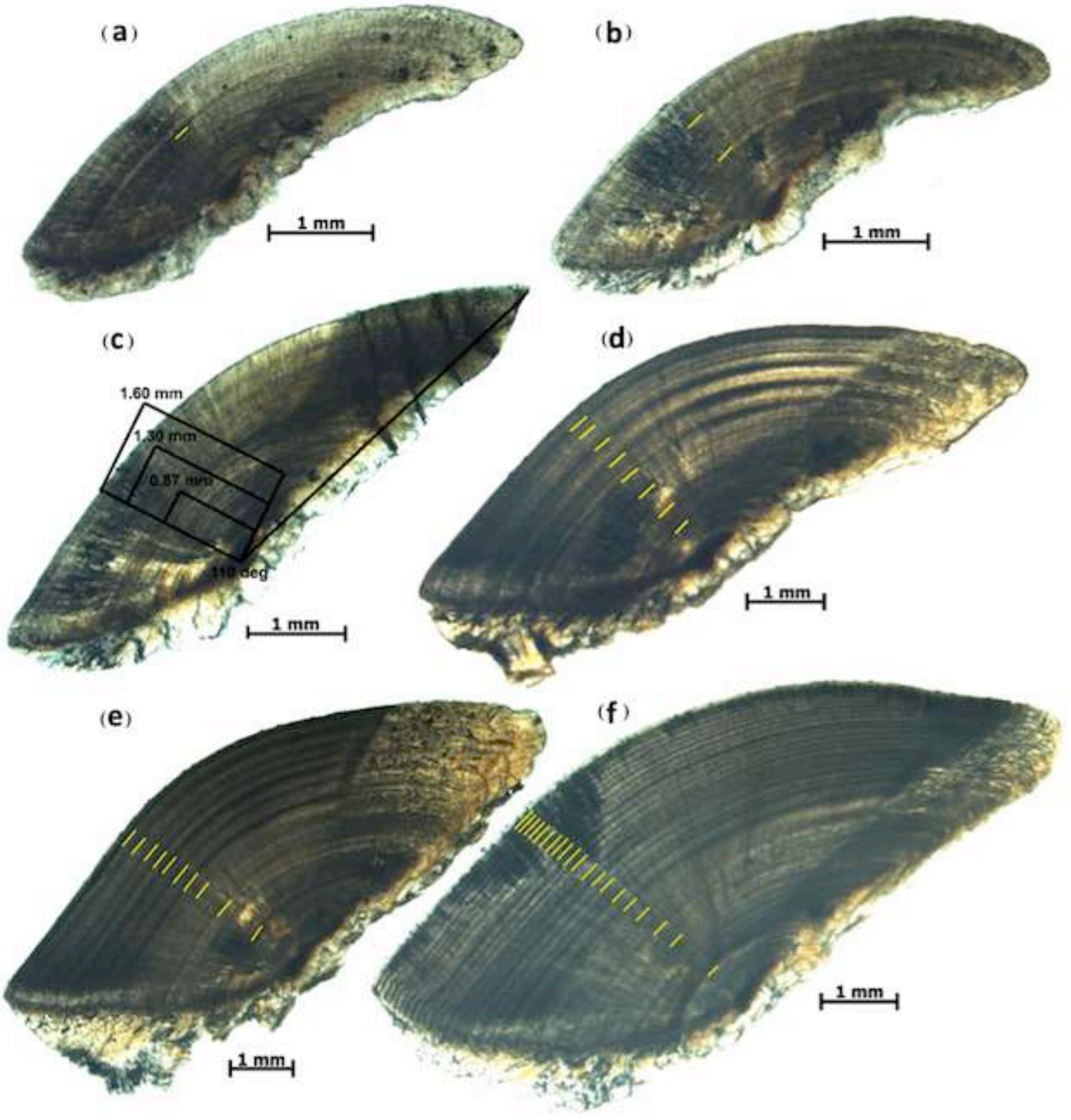

Fig. 2. Transverse thin sections of *B. rousseauxii'*s otoliths showing: **a**. one ring; **b.** and **c**. two rings; **d.** eight rings; **e.** ten rings; and **f**. twenty rings. The yellow line marks the rings.

The individual age in months was then calculated taking into account the date of capture, the number of growth rings and the mean hatching date for the populations: January (Van Damme *et al*., 2011). For the estimation of the mean observed length-at-age, age groups were determined as follows: age-group 0 corresponded to fish whose calculated age was between 0.1 and 0.9 years, age-group 1 corresponded to fish whose calculated age was between 1.0 and 1.9 years, and so on.

HYDROLOGICAL DATA

Data on the hydrological cycles of the Madeira river basin were provided by the Geological Survey of Brazil/CPRM (Companhia de Pesquisa de Recursos Minerais). The data came from the Porto Velho station (Fig. 4).

STATISTICAL ANALYSIS

Validation of ring formation

The periodicity of translucent ring deposition was determined through the monthly relative marginal increment ratio (RMI): $\text{RMI}=(R_T-R_N)/(R_N-R_{N1})$, where R_T is the total radius of the otolith, R_N is the distance from the core of the otolith to the last ring and R_{N1} is the distance from the core to the penultimate ring (Haimovici, Reis, 1984; Fabré, Saint-Paul, 1998). RMI mean monthly values were compared using one-way-ANOVA with Tukey's post hoc test. A significant decrease followed by an increase in RMI values was interpreted as the formation of a seasonal translucent ring.

Considering the differences in sampling period and hydrological cycle between the upper and the middle/lower Madeira basin, only individuals sampled in the Brazilian Amazon (see Fig. 1) were used in this analysis. The validation analysis was first carried out for two consecutive years between 2010 and 2012, but as the same tendency was observed in both years, the data were pooled into a single annual cycle to increase the number of specimens analysed at each month.

The von Bertalanffy growth function (VBGF) was calculated using a non-linear estimation (quasi-Newton method), which was calculated as equation (2): $L_t= L_\infty\,[1 - e^{-K(t-t0)}]$, where L and t are L_S (cm) and age t (years) of the fish respectively, L_∞ is the asymptotic L_S; K is the growth coefficient representing how fast L_∞ is reached and t_0 is the theoretical age at which L_S =0.

The age at first sexual maturity (A_{50}) was calculated from the VBGF as follows (Duponchelle *et al.*, 2007; García-Vásquez *et al.*, 2009): $A_{50} = \{-\ln[1 - (L_{S50}\, L_{S\infty}^{-1})]K^{-1}\} + t_0$, where L_{S50} is the size at first sexual maturity and L_{oo} and K are parameters from the VBGF. Size at first sexual maturity for the females of this species in the Madeira River was previously estimated at 73 cm L_S from the same data set (Duponchelle *et al.*, 2016).

For comparison purposes, VBGF parameters of *B. rousseauxii* in the Amazon River mainstem (Alonso, 2002), expressed in fork length (L_F), were converted to L_S using the equation provided in García-Vásquez *et al.* (2009): $L_S = 0.965\ L_F - 1.504$, $r^2 = 0.997$, $P < 0.001$. The growth parameters of the VBGF curves were compared between sexes using the likelihood ratio test (Tomassone *et al.*, 1993) and applying the weighted sum of squares of Kimura (1980). For *k* populations, the likelihood ratio test S_{ML} was compared with χ^2 using 3 degrees of freedom (3 parameters): $S_{ML} = \sum_{i=1}^{k} n_i * [ln(S_c^2) - ln(S_k^2)]$, where n_i is the number of individuals of the k^{th} population, S_c^2 is the residual variance of the pooled model (for all populations), and S_k^2 is the residual variance of the models of the *k* populations, with k = 2 here.

RESULTS

Over the study period, 562 otoliths of *B. rousseauxii* (11–120 cm L_S) were analysed, of which 65 (11.6 %) were discarded because they could not be interpreted. Of the 497 fish used, 142 were females (L_S range 67–120 cm, mean ± SD; 93 ± 9.6 cm), 95 were males (L_S range 49–112 cm, mean ± SD, 81± 12.2 cm), and 260 could not be sexed (L_S range 11–119 cm, mean ± SD, 79 ± 19.2 cm).

INTERPRETATION OF GROWTH RINGS AND VALIDATION

The alternation of a narrow opaque (dark) band with a wide translucent (light) band constituted a growth ring, for age estimation (Fig. 2). Otoliths with more than four growth rings exhibited two development patterns: the first with wide translucent bands up to the fourth or fifth growth rings and then the second, with a progressively decreasing width of the translucent bands until they became approximately of the same size as the opaque bands (Fig. 2).

The first growth ring formed on mean±SD of 0.85 ± 0.106 mm from the core, the second at 1.3 ± 0.097 mm, the third at 1.7 ± 0.088 mm, and despite overlap in the ring radius distributions, a clear modal progression could be observed, with the mean inter-rings radius distances progressively decreasing (Fig. 3)

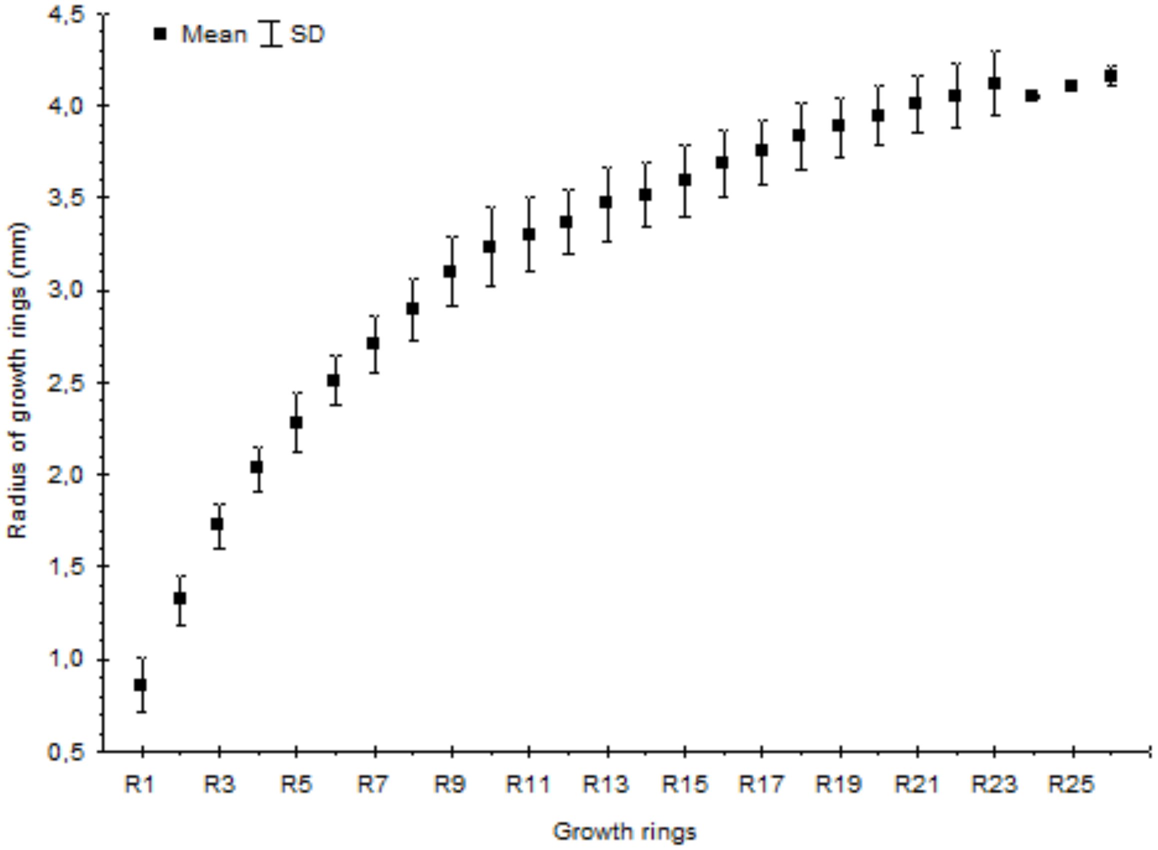

Fig. 3. Mean and standard deviation (SD) of each growth ring radius in otoliths of *B. rousseauxii* from the Madeira River basin.

Three different types of rings could be observed: single (*S*), double (*D*) and triple (*T*) (Fig. 4a). *D* rings were observed in large proportions in the first four growth rings and their occurrence decreased afterwards until the 8th ring. From the 9th ring onwards, all rings were *S* rings. *T* rings were observed only in the first two growth rings and were most frequent in the first one (Fig. 4b).

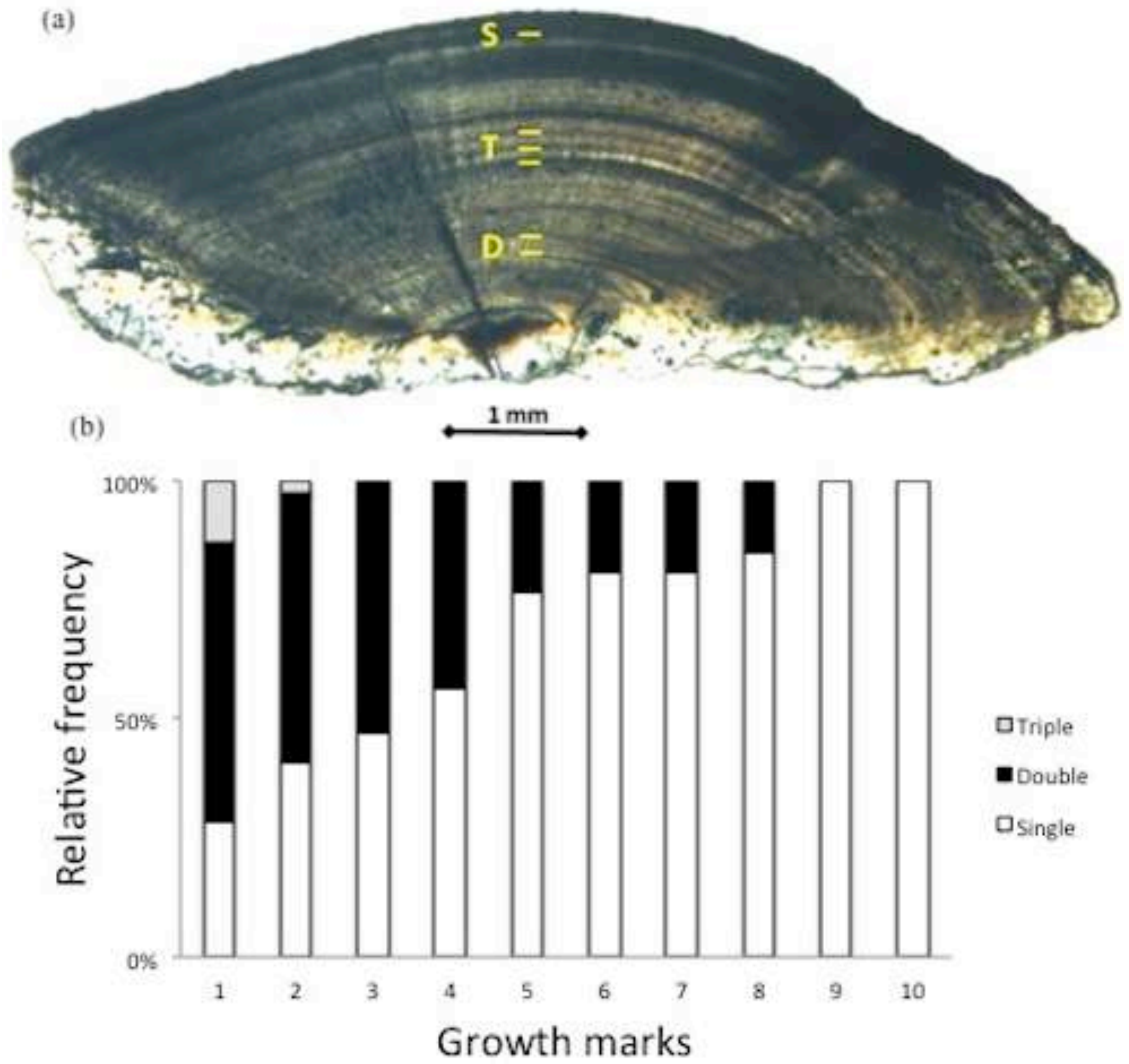

Fig. 4a. Different types of growth rings; and **b.** their relative proportions, in transverse thin sections of *B. rousseauxii* from the Madeira River basin. *S*-single, *D*-double, *T*-triple rings.

The RMI (carried out on 357 individuals) significantly varied among months (one-way ANOVA, $F_{11,345}$= 2.07, $P < 0.01$), with lowest mean values in April (mean = 71.76 ± SD) and September (mean =72.10 ± SD) (Fig. 5). This indicates the formation of two opaque rings per year, hence two periods of reduced growth: one during the high-waters in April and the second during the low water period in September.

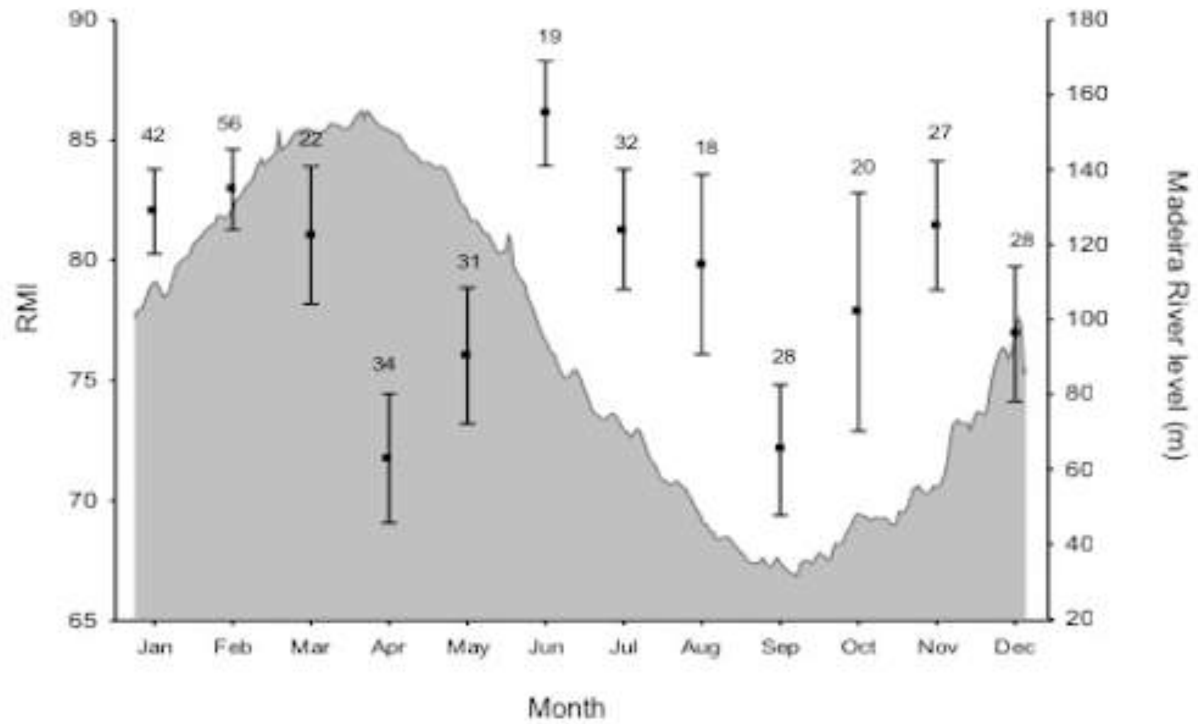

Fig. 5. Mean monthly relative marginal increment (RMI ± S.D.) of 357 *B. rousseauxii*'s otoliths in relation to the hydrological cycle in the Madeira River basin. The values above bars indicate the number of otoliths analysed each month.

GROWTH AND AGE AT MATURITY

Although more than half the fish used in this study could not be sexed, a gender specific analysis was still possible (Fig. 6a-b), with the following VBGF parameters for females (L_∞ = 108.3 cm, K = 0.55, t_0 = 0.029) and males (L_∞ = 96.2 cm, K = 0.57, t_0 = -0.065), using the same unsexed individuals under 60 cm L_S to improve modelling for each sex. Females grew significantly faster than males (S_{ML} = 111.5, $P < 0.001$). The difference between sexes ranged, on average, from ~ 5 cm at two years old, to ~12 cm at 10 years old and greater (Tab. 1).

Tab. 1. Standard length-at-age of *B. rousseauxii* in the Madeira River basin and along the Amazon River mainstem (from the Estuary to Iquitos; Alonso 2002), calculated from the VBGF. Total refers to females + males + unsexed individuals.

Age (years)	Length-at-age (cm)					
	Madeira			Amazon †		
	Total	Females	Males	Total	Females	Males
1	45.3	44.8	43.8	52.2	54.7	49.4
2	70.3	71.7	66.6	73.2	76.4	69.0
3	84.4	87,2	79.4	88.8	92.2	83.6
4	92.4	96.1	86.7	100.3	103.6	94.5
5	96.9	101.3	90.8	109.0	112.0	102.7
6	99.5	104.2	93.2	115.4	118.0	108.8
7	100.9	106.0	94.5	120.2	122.4	113.4
8	101.8	106.9	95.2	123.7	125.6	116.8
9	102.2	107.5	95.7	126.3	127.9	119.4
10	102.5	107.9	95.9	128.3	129.5	121.3
11	102.6	108.0	96.0	129.8	130.8	122.7
12	102.7	108.2	96.1	130.8	131.7	123.8
13	102.8	108.2	96.1	131.7	132.0	124.6
14	102.8	108.3	96.2	132.3	132.8	125.2
15	102.8	108.3	96.2	132.7	133.1	125.7

*Although Alonso (2002) did not observe fish older than 8 years, we know from other studies using length-frequency analyses (García-Vásquez *et al.*, 2009, Agudelo *et al.*, 2013) that this species grow at least as old as 13 years in the Amazonas, hence we calculated length-at-age up to 15 years old as well, using VBG parameters taken from Alonso.

Considering females, males and unsexed individuals together, the VBGF for *B. rousseauxii* in the Madeira River basin yielded the following parameter estimates: L_∞ = 102.84 cm L_S, K = 0.57 and t_0 = 0.021 (Fig. 6c). The species grew quickly during the first three years and the asymptotic phase of the growth curve was reached after five years.

Remarkably, there was only a small overlap in age distribution (3-5 years) between the middle and lower Madeira (Brazil) and the upper Madeira (Bolivia and Peru). In Brazil, fish were mainly young, between 0 and 5 years old, whereas older fish (> 6 years old) were only captured in Bolivia and Peru. Interestingly, as growth reached a plateau after 5 years, fish were not really larger in the upper basin, but were much older at a given length than in the middle and lower portion of the basin in Brazil. In fact, fish above ~ 80 cm could have any age between 3 and 15 years (Fig. 6c).

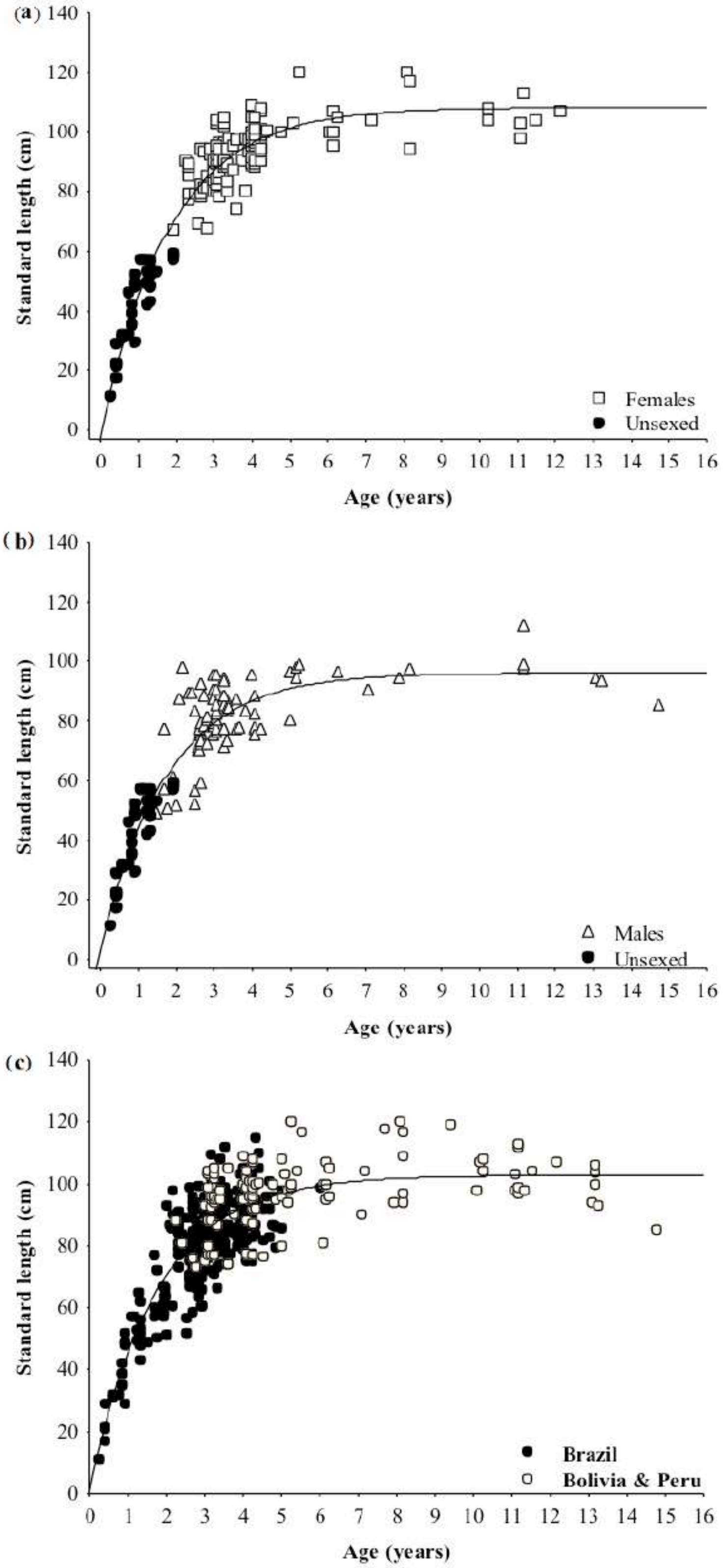

Fig. 6. Length-at age distribution and von Bertalanffy growth function (solid lines) of *B. rousseauxii*: **a.** females (N = 142); **b.** males (N = 95); and **c**. females, males and unsexed individuals pooled (N = 497) in the lower / middle (Brazil) and in the upper (Bolivia and Peru) Madeira River basin. In order to improve modelling for females (**a**) and males (**b**), unsexed individuals < 60 cm (black dots) were also used.

This also reflected in the relationship between fish standard length and otolith radius, with a strongly increased variance in otolith radius above 80 cm (Fig. 7a). Although otolith radius grew proportionately with age, its variability also tended to increase with age (Fig. 7b). The oldest fish sampled was a 15 years old male, rather small for its age, 85.4 cm L_S, whereas the largest fish sampled (a female of 120 cm) was only 8 years old. Female *B. rousseauxii* reached the mean size at first sexual maturity (L_{50} = 73 cm L_S) at 2.2 years old in the Madeira basin.

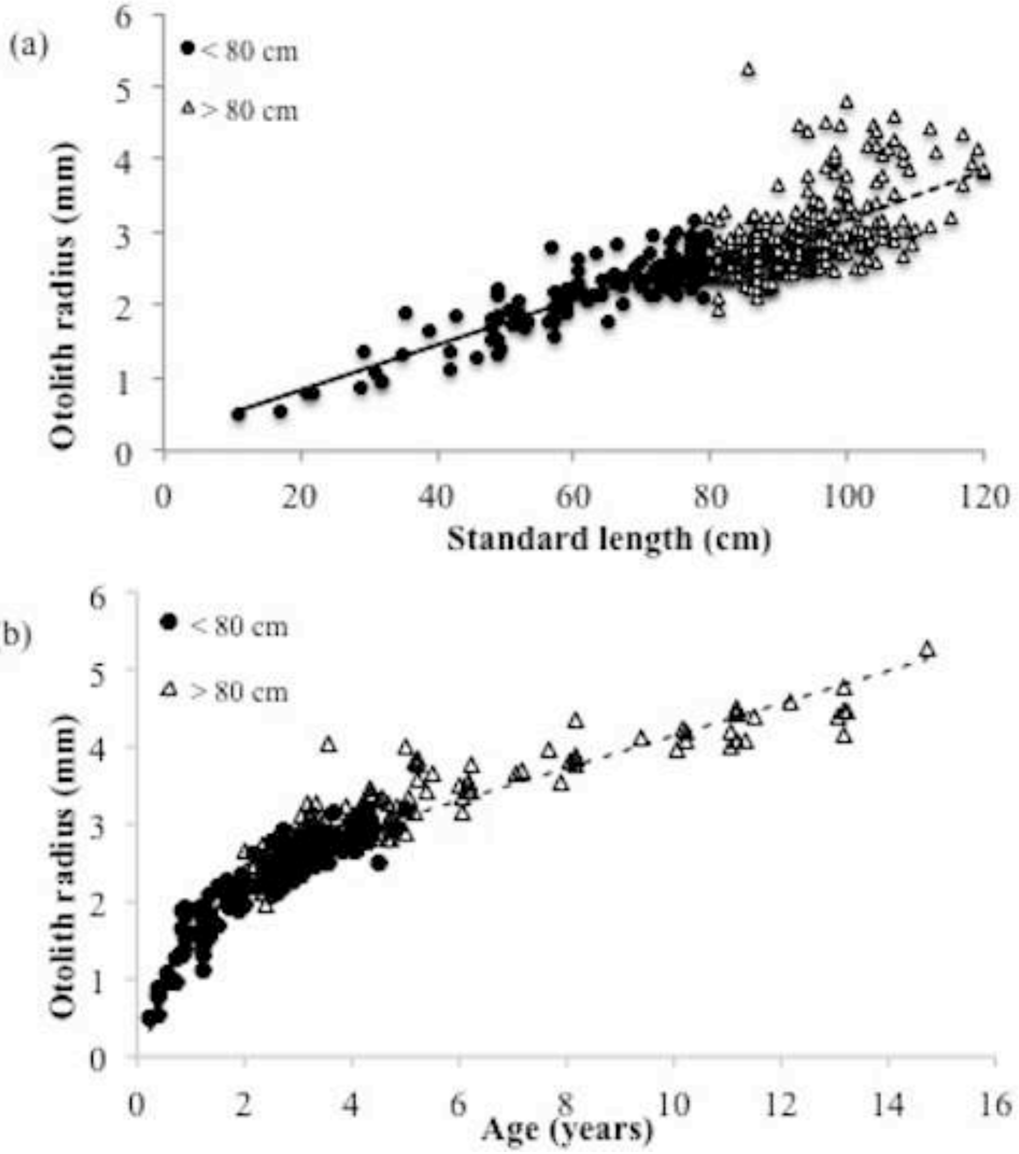

Fig. 7. a. Relationship between fish standard length and otolith radius for *B. rousseauxii* below 80 cm (black circles, black line: $y = 0.031x + 0.209$, $r^2 = 0.805$, $P < 0.001$) and above 80 cm (white triangles, broken line: $y = 0.034x - 0.223$, $r^2 = 0.328$, $P < 0.001$); and **b.** relationship between fish age and otolith radius for *B. rousseauxii* below 80 cm (black circles, black line: $y = 0.887\ln(x) + 1.567$, $r^2 = 0.879$, $P < 0.001$) and above 80 cm (white triangles, broken line: $y = 0.209\ln(x) + 2.055$, $r^2 = 0.822$, $P < 0.001$), both in Madeira River basin.

DISCUSSION

INTERPRETATION OF GROWTH RINGS AND VALIDATION

The identification of the first growth ring is relatively difficult in *B. rousseauxii*, owing to many intermediate opaque bands (Fig. 2), along with *D* or *T* rings (Fig. 4). Intermediate bands could be due to fluctuating environmental conditions (mainly salinity) in the Amazon estuary (the species' nursery area, Alonso, 2002) and to the potential variations in competition for food with marine species (Barthem, Goulding, 1997). Furthermore, the formation of the very first growth ring would be associated with the stress caused by increased salinity in the estuary during incursions of oceanic waters in August-September when freshwater flows decline (Alonso, 2002). Indeed, although *B. rousseauxii* is a potamodromous species, it can be observed down to the 20 m isobath in the estuary, where the salinity reaches almost 35 (psu) (Sanyo, 1998). Under stress conditions, animals often divert growth energy to maintain the homostatic equilibrium (Fuzzen *et al.,* 2011), which for teleost fish represents between 20 and 50% of the total energy budget (Boeuf & Payan, 2001).

Most otoliths exhibited two clearly defined development patterns: the alternation of a large translucent band and a small opaque band until the fourth or fifth opaque band, followed afterwards by opaque and translucent bands of approximately equal width. This reduction in growth rate after the fourth or fifth ring was also observed in *B. rousseauxii* from the Amazon River mainstem, and interpreted as an energetic consequence of leaving the rich estuary area followed by the cost of the first upstream migration (Alonso, 2002), and ultimately, life in a fluvial system. This behaviour was recently confirmed by microchemical otolith analyses (Duponchelle *et al.*, 2016; Hermann *et al.*, 2016), and probably also applies to fish from the Madeira basin.

The present study demonstrates a clear biannual formation of growth rings for *B. rousseauxii* in the Madeira River basin, as already reported in the Amazon River mainstem (Alonso, 2002). One ring formed during the high waters and the other during the low water period, emphasizing the close relationship between the seasonal hydrologic cycle, controlled by the flood pulse (Junk *et al.*, 1989), and the life cycle of tropical freshwater fishes (Lowe-Mc Connell, 1999). Although some biases can be associated with the use of RMI analyses in age validation (Campana, 2001), other methods such as mark recapture are impossible to implement in a species whose life cycle encompasses almost the whole Amazon basin. The fact that the results are consistent with previous, independent, studies in the Amazon mainstem using both otoliths (Alonso, 2002) and length-frequency analyses (García-Vásquez *et al.*, 2009; Agudelo *et al.*, 2013), tend to support the credibility of the validation carried out in the present study.

The number of growth rings formed during a complete annual cycle in the otoliths and other body hard parts (mainly scales and vertebrae) of Amazonian fishes is particularly interesting. All fish studied in western Amazonia, close to the Andes, display a single growth ring per year during the low water period, whether they belong to the Characiformes, *Prochilodus nigricans* in Bolivia (Loubens, Panfili, 1992) and Ecuador (Silva, Stewart, 2006), *Colossoma macropomum*, *Piaractus brachypomus*, and *Pygocentrus nattereri* in Bolivia (Loubens, Panfili 1997, 2001; Duponchelle *et al.*, 2007, respectively), the Siluriformes, *Pseudoplatystoma fasciatum* and *Pseudoplatystoma tigrinum* in Bolivia (Loubens, Panfili, 2000), the Perciformes, *Plagioscion squamosissimus* in Bolivia (Loubens, 2003) or the Osteoglossiformes, *Osteoglossum biccirhossum* in Peru (Duponchelle *et al.*, 2012).

On the other hand, fish of these same orders, and sometimes the same species, tend to present two growth rings per annual cycle in central Amazonia, Brazil: in Characiformes, *P. nigricans* (Oliveira, 1996), *C. macropomum* (Villacorta-Correa, 1997), *Semaprochilodus insignis* (Viera, 1999); in Siluriformes: *Calophysus macropterus* (Pérez, Fabré, 2009), *Hypophthalmus marginatus* (Cutrim, Batista, 2005); and in Osteoglossiformes: *Arapaima* sp. (Arantes *et al.*, 2010). One of these biannuali usually forms during the low water season as well, similar to the only annual ring formed in western Amazonian fishes, and the other ring forms during the flood. The interpretation of these two periods of reduced growth varies according to studies or species: it could be associated with food limitations during the low water period and with reproductive activities during the flood, according to Pérez, Fabré (2009) and Arantes *et al.* (2010), or to reproductive migrations during the low waters and food limitations during the flood according to Cutrim, Batista (2005). Notable exceptions in central Amazonia are *Schizodon fasciatus*, which forms a single ring per year during the flood (Fabré, Saint Paul, 1998) and *Cichla temensis*, which forms a single ring during the receding water period (Campos *et al.*, 2015).

The nature of *B. rousseauxii*'s life cycle, however, prevents its categorization as either from central or western Amazonia, as it encompasses both and also includes the estuary. Besides the particular environmental conditions of the estuary and their influence on the formation of the first few growth rings (Alonso, 2002), subsequent periods of growth rings formation appear to reflect two annual periods of reduced growth in *B. rousseauxii*'s life cycle. One of these periods is likely associated to the low availability of its main prey fishes, which move into the floodplains during the high-waters (Goulding, 1979; Barthem, Goulding, 1997; Junk *et al.*, 1997).

The reason why a second annual ring forms during the low water season in *B. rousseauxii* could also relate to food limitation, although not for the same causes. During the low water season, the concentration in the main river channels of fish upon which *B. rousseauxii* preys is supposed to be maximum and should therefore provide optimum growth conditions. This is also the period of the hydrological cycle, however, when all the other large predatory species, including all large catfishes (*Brachyplatystoma* spp., *Pseudoplatystoma* spp. and *Zungaro zungaro*) (Doria, Lima, 2015) and river dolphins (Silva *et al.*, 2008; Crema *et al.*, 2014) are concentrated in the river channels and compete over the same resources. Although *B. rousseauxii* is an apex predator, this competitive situation could result in an unfavourable ratio of energy expenditure over food availability and hence, in a reduced growth rate. Similar patterns of reduced growth rate in fishes under increased densities and related competition has been widely reported in the literature, for Chinook Salmon (Mazur *et al.*, 1993), Brown Trout (Vøllestad *et al.*, 2002) and other salmonids (Taniguchi, Nakano, 2000; Puffer *et al.*, 2015).

GROWTH

Despite the fact that more than half the fish could not be sexed, the growth dimorphism in favour of females, already reported in the Amazon River mainstem (Alonso, 2002; García-Vásquez *et al.*, 2009; Agudelo *et al.*, 2013) was also observed in the Madeira basin. Females did grow faster than males. Fish from the Madeira, however, had an overall slower growth that fish from the Amazon River mainstem (Tab. 1). The difference ranged, on average, from about 10 cm at one year old to 25 cm at 15 years old for females, from over 5 cm at one year old to ~ 30 cm at 15 years old for males, and from 7 cm at one year old to nearly 30 cm at 15 years old for females, males and unsexed individuals together. This important difference also translates in the maximum observed lengths between the two systems: *B. rousseauxii* of 150 cm L_S are, or at least were, regularly observed in the upper Amazon (García-Vásquez *et al.*, 2009; Agudelo *et al.*, 2013), whereas they barely reach 130 cm L_S in the upper Madeira (Van Damme *et al.*, 2011; Carvajal-Vallejos *et al.*, 2014). Out of the ~ 500 individuals analysed for the present study none was larger than 120 cm L_S. This growth difference is further emphasized by the differences in level of exploitation between the two systems. Indeed, fisheries usually harvest the largest specimens and often induce a decrease in the maximum size of exploited populations (Rochet, Trenckel, 2003). Fishery exploitation is close to over-exploitation in both the Peruvian (García-Vásquez *et al.*, 2009) and Colombian (Agudelo *et al.*, 2013) waters, whereas it started later and remains relatively weak in the Bolivian Amazon (Goulding, 1979; Van Damme *et al.*, 2011). Yet, in spite of a lower exploitation pressure, the maximum sizes are smaller in the upper Madeira.

Growth differences could also result from genetic determinism or phenotypic plasticity in response to environmental differences. Although three genetically distinct populations of *B. rousseauxii* are present in admixture in the Madeira, the numerically dominant genotype is the same in the Madeira as that in the Peruvian Amazon (Carvajal-Vallejos *et al.*, 2014). Yet all three genotypes attain smaller maximum lengths in the Madeira than in the upper Amazon, suggesting that the observed growth differences are rather a consequence of less favourable environmental conditions in the Madeira.

It is the river with the highest sediment load in the Amazon basin (Latrubesse *et al.*, 2005), which might impact primary production and ultimately ecosystem productivity, resulting in less favourable trophic conditions. A high sediment load could also affect gills efficiency by reducing oxygen intake and metabolism (Val *et al.*, 2005). Bolivia has one of the largest floodplains of the Amazon basin (Hamilton *et al.*, 2004), but unlike the flooded forest of the floodplain in Central Amazonia (Goulding, 1990), it consists of a flooded savannah, which might not be as productive as the flooded rainforests of Central Amazonia.

Another explanation could lie in a poorer nutritious value of the prey fishes consumed in the Madeira vs the Amazon systems. Whereas *B. rousseauxii* predominantly feeds upon detritivorous-herbivorous (*Brycon* spp., *Mylossoma* spp.) and omnivorous (*Triportheus* spp.) migratory Characiformes in the Amazon River mainstem (Barthem, Goulding, 1997; García-Vásquez *et al.*, 2009), its main prey fishes in the Madeira River are the carnivorous *Pimelodina flavipinnis* and *Hypophthalmus marginatus* (Cella-Ribeiro *et al.*, 2016). These last two species are invertivorous (Santos *et al.*, 2006) and planktivorous (Carvalho, 1980; Cutrim, Batista, 2005; Cella-Ribeiro *et al.*, 2016), respectively. At each transfer from one level of the food web to the upper level, a large part of the energy is lost in heat (Odum, 1988), which should reduce the energy content of species higher in the food web. Vismara, *et al.* (2004) indeed observed a decreased caloric content from herbivorous to carnivorous fish species in the upper Paraná River floodplain. Hence, foraging on carnivorous species in the Madeira River instead of on detritivorous-herbivorous species in the Amazon River mainstem might partly account for the slower growth of *B. rousseauxii* in the Madeira.

A complementary potential explanation is that the Bolivian Amazon is the southernmost region of the Amazon basin. As such, it is subjected to frequent episodes of cold fronts from the south occurring during approximately 40% of winter days and 10% of summer days (Ronchail, 1989). These cold fronts result in important temperature decreases of up to 20°C from one day to another and lasting a few days (Ronchail, 1989; Lupo *et al.*, 2001), that are likely to affect fish growth. The potential explanations listed in this last paragraph are not mutually exclusive and could add up to explain the slower growth of *B. rousseauxii* in the Madeira.

A slower growth was also detected in the first year of life, which is supposed to be passed in the Amazon estuary for all fish. The geographic separation between the adults in the headwaters and the juveniles in the estuary for *B. rousseauxii* is believed to reduce competition over food and space with other young large catfish stages and to provide particularly favourable trophic conditions for the young stages (Barthem, Goulding, 1997). Recent studies using $^{87}S_{r}/^{86}S_{r}$ ratios in *B. rousseauxii* otoliths (Hegg *et al.*, 2015; Duponchelle *et al.*, 2016), however, suggested that not all fish enter the estuary and that some could use upstream areas within the Amazon as nursery. Although there is no evidence to support this hypothesis, nursery areas for *Brachyplatystoma* young stages hatched in the upper Madeira might, in general, be located upstream of the estuary, resulting in slower growth and higher competition with other catfish young stages compared to those that reside in the estuary.

In addition to growth differences found in the two systems, one of the most interesting results of this study was the clear age segregation between the lower and upper Madeira. Apart from one specimen, all fish caught in the Brazilian portion of the Madeira were less than 5 years old, including the larger ones, whereas most large individuals caught in Bolivia and Peru were between 5 and 15 years old. This clearly confirms that after their upstream reproductive runs in the upper Mamoré, Béni and Madre de Dios Rivers, *B. rousseauxii* specimens do not go back down to central Amazonia, which had already been suggested by recent otolith microchemistry analyses (Duponchelle *et al.*, 2016). Furthermore, this result also indicates that once they enter the Madeira, or home back to the Madeira, they do not just stay in the Madeira basin, they remain within the upper portion of the basin, within Bolivia and Peru.

This crucial information for fisheries management should actually be put in a past tense as the construction of two hydroelectric dams in the Brazilian portion of the Madeira, Santo Antônio and Jirau dams, have profoundly modified the situation. The fishways in Santo Antonio and Jirau have been found ineffective for accommodating the upstream passage of large catfishes, including *B. rousseauxii*, and many fishing communities above the dams report that these species have disappeared from the catches (Fearnside, 2014, 2015). The adverse environmental conditions in the upstream reservoirs of the dams are also expected to compromise severely the downstream migration and survival of *B. rousseauxii* larvae and juveniles (Baras, Lucas, 2001; Carolsfeld *et al.*, 2003; Pelicice *et al.*, 2015), especially in view of the small size of migrants (Barthem *et al.*, 2014; Cella-Ribeiro *et al.*, 2015; Duponchelle *et al.*, 2016).

This study is the first to describe the growth patterns of *B. rousseauxii's* in the Madeira River. It provides important new information about the life-history characteristics of this species and contributes to a better understanding of its complex life cycle. It will serve as a base line for monitoring the development of *B. rousseauxii*'s life-history dynamics in the upper Madeira basin after the dams. These results have profound consequences for the fisheries management, especially considering the current and planned hydropower development scenario in the Amazon basin. As already warned by Duponchelle *et al.* (2016) and re-emphasized here, the Madeira dams threaten the life cycle of this flagship top predator species, which may cause deleterious cascading effects through the Amazonian aquatic food webs.

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REFERENCES

Agostinho AA, Gomes LC, Pelicice FM. Ecologia e Manejo de Recursos Pesqueiros em Reservatórios do Brasil. Maringá: Eduem; 2007.

Agostinho AA, Pelicice FM, Gomes LC. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Braz. J. Biol. 2008; 68(Suppl.4): 1119–1132.

Agudelo E, Joven-León AV, Bonilla-Castillo CA, Petrere, M Jr, Peláez M, Duponchelle F (2013) Breeding, growth and exploitation of *Brachyplatystoma rousseauxii* in the Caqueta River, Colombia. Neotrop Ichthyol. 2013; 11(3): 637–647.

Alonso, JC. Padrão espaço-temporal da estrutura populacional e estado atual da exploração pesqueira da dourada *Brachyplatystoma flavicans*, Castelnau, 1855 (Siluriformes: Pimelodidae), no sistema estuário-Amazonas-Solimões. [PhD Thesis]. Manaus, AM: Instituto Nacional de Pesquisas da Amazônia; 2002.

Alonso JC, Camacho KA, Núñez-Avellaneda M, Agudelo E, Galarza E, Oliveros LA, Natagani K. Recursos Hídricos y Ecosistemas Acuáticos. In: Programa de las Naciones Unidas para el Medio Ambiente, Organización del Tratado de Cooperación Amazónica, Centro de Investigación de la Universidad del Pacífico, editors. Perspectivas del Medio Ambiente en la Amazonía. Lima: PNUMA/(OTCA/CIUP; 2009. p.146-161.

Angelini R, Fabré NN, Silva-JR UL. Trophic analysis and fishing simulation of the biggest Amazonian catfish. African Journal Of Agricultural Research. 2006; 1(5):151-158

Arantes CC, Castello L, Stewart DJ, Cetra M, Queiroz HL. Population density, growth and reproduction of *Arapaima* in an Amazonian river-floodplain. Ecology of Freshwater Fish. 2010; 19(3): 455-465.

Baras E, Lucas MC. Impacts of man's modifications of river hydrology on the migration of freshwater fishes: a mechanistic perspective. Ecohydrology Hydrobiology. 2001; 1(3): 291-304.

Barthem R, Goulding M. The Catfish Connection: Ecology, Migration, and Conservation of Amazon Predators. New York, NY: Columbia University Press; 1997.

Barthem R, da Costa MC, Cassemiro F, Leite RG, Silva Jr N. Diversity and Abundance of Fish Larvae Drifting in the Madeira River, Amazon Basin: Sampling Methods Comparison. In: Grillo, O, editor. Biodiversity - The Dynamic Balance of the Planet. Intech; 2014. p.137-158.

Barthem R, Goulding M, Leite RG, Cañas C, Forsberg EV, Petry P, Ribeiro MLB, Chuctaya J, Mercado A. Goliath catfish spawning in the far western Amazon confirmed by the distribution of mature adults, drifting larvae and migrating juveniles. Scientific Reports. 2017; 7, doi: 101038/srep41784.

Bauer S, Hoye BJ. Migratory animals cou-ple biodiversity and ecosystem functioning worldwide. Science. 2014; April 344(6179): 1242552.

Boeuf G, Payan P. How should salinity influence fish growth? Comp Biochem Physiol Part C. 2001; 130(4): 411–423.

Campana SE. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods J Fish Biol., 2001; 59(2): 197–242.

Campos CP, Freitas CEC, Amadio S. Growth of the *Cichla temensis* Humboldt, 1821 (Perciformes: Cichlidae) from the middle rio Negro, Amazonas, Brazil. Neotrop Ichthyol. 2015; 13(2): 413-420.

Carolsfeld J, Harvey B, Ross C, Baer A. Migratory fishes of South America: Biology, Fisheries and Conservation Status World Fisheries Trust.Washington: IDRC, World Bank; 2003.

Carvajal-Vallejos FM, Duponchelle F, Desmarais E, Cerqueira F, Querouil S, Nuñez J, García C, Renno JF. Genetic structure in the Amazonian catfish *Brachyplatystoma rousseauxii*: influence of life history strategies. Genetica. 2014; 142(4): 323-336.

Carvalho FM. Alimentação de Mapará (*Hypophthalmus edentatus* Spix 1829) do Lago Castanho, Amazonas (Siluriformes Hypophthalmidae). Acta Amazonica. 1980; 10 (3): 545-555.

Castello L, Macedo MN. Large-scale degradation of Amazonian freshwater ecosystems. Global Change Biology. 2016; 22(3): 990-1007.

Castello L, McGrath DG, Hess LL, Coe MT, Lefebvrel PA, Petry P, Macedo MM, Renó, VF Arantes, CC. The vulnerability of Amazon freshwater ecosystems Conservation Letters. 2013; 6(4): 217–229.

Cella-Ribeiro A, Assakawa LF, Torrente-Vilara G, Zuanon J, Leite RG, Doria C, Duponchelle F. Temporal and spatial distribution of young *Brachyplatystoma* spp (Siluriformes: Pimelodidae) along the rapids stretch of the Madeira River (Brazil) before the construction of two hydroelectric dams. J Fish Biol. 2015; 86 (4): 1429-1437.

Cella-Ribeiro A, Torrente-Vilara G, Lima-Filho JA, Doria CRC. Ecologia e Biologia de Peixes do Rio Madeira. Porto Velho: EDUFRO; 2016.

Crema LC, Quaresma AC, Silva VMF. Nem tudo que nada é peixe: os mamíferos aquáticos amazônicos. Recursos Hídricos y Ecosistemas Acuáticos. In: Lopes A, Piedade MTF, editors. Conhecendo as áreas úmidas amazônicas: uma viagem pelas várzeas e igapós. Manus: INPA Editora; 2014. p. 85-94.

Cutrim L, Batista VS. Determinação de idade e crescimento do mapará (*Hypophthalmus marginatus*) na Amazônia Central. Acta Amazônica. 2005; 35(1): 85–92.

Doria CRC, Lima MAL. Rio Madeira: seus peixes e sua pesca Porto Velho: EDUFRO/RIMa Editora; 2015.

Duponchelle F, Lino F, Hubert N, Panfili J, Renno JF, Baras E, Torrico JP, Dugué R, Nuñez J. Environment-related life history trait variations of the red-bellied piranha, *Pygocentrus nattereri*, in two river basins of the Bolivian Amazon. J Fish Biol. 2007; 71(4): 1113–1134.

Duponchelle F, Ruiz-Arce A, Waty A, Panfili J, Renno J F, Farfan F, García-Vásquez A, Chu Koo F, Garcia Davila C, Vargas G, Ortiz A, Pinedo R, Nuñez J. Contrasted hydrological systems of the Peruvian Amazon induce differences in growth patterns of the silver arowana, *Osteoglossum bicirrhosum*. Aquatic Living Resources. 2012; 25(1): 55-66.

Duponchelle F, Pouilly M, Pécheyran C, Hauser M, Renno JF, Panfili J *et al.* Trans-Amazonian natal homing in giant catfish. J Appl Ecol. 2016; 53:1511-1520.

Estes, JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ *et al.* Trophic downgrading of planet earth. Science. 2011; 333 (6040): 301-306.

Food and Agriculture Organization of the United Nations (FAO-COPESCAL). Inform del taller regional sobre el manejo de lãs pesquerías de bagres migratórios del Amazonas (Iquitos-Perú) Informe de campo F-5: Comisíon de pesca continental para a América Latina FAO; 2000.

Fabré NN, Saint-Paul U. Annulus formation on scales and seasonal growth of the Central Amazonian anostomid *Schizodon fasciatus*. J Fish Biol. 1998; 53 (1): 1-11.

Fearnside PM. Brazil's Madeira River dams: A setback for environmental policy in Amazonian development. Water Alternatives. 2014; 7(1): 154-167.

Fearnside PM. Hidrelétricas na Amazônia: impactos ambientais e sociais na tomada de decisões sobre grandes obras-Vol 1. Manaus: Editora do INPA; 2015.

Finer M, Jenkins CN. Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. PLoS ONE. 2012; 7(4): e35126.

Fretwell S. Food chain dynamics: the central theory of ecology? Acta Oecol Scand. 1987; 50 (3): 291-301.

Fuzzen MLM, Bernier NJ, Kraak GVD. Stress and reproduction. In: Norris DO, Lopez KH, editors. Hormones and reproduction of vertebrates, vol 1. Academic Press; 2011. p. 103-118.

García Vásquez A, Alonso JC, Carvajal F, Moreau J, Nuñez J, Renno JF, Tello S, Montreuil V, Duponchelle F. Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. J Fish Biol. 2009; 75(10); 2527–2551.

Goulding M. Ecologia da pesca do rio Madeira. Manaus: CNPq/INPA; 1979.

Goulding M. Amazon: The Flooded Forest New York: Sterling Publishing; 1990.

Haimovici M, Reis EG. Determinação de idade e crescimento da castanha *Umbrina canosai* (Pisces, Sciaeinidae) do Sul do Brasil. Revista Atlântica. 1984; 7: 25-46.

Hamilton SK, Sippel SJ, Melack JM. Seasonal inundation patterns in two large savanna floodplains of South America: the Llanos de Moxos (Bolivia) and the Llanos del Orinoco (Venezuela and Colombia). Hydrol. Process. 2004; 18: 2103-2116.

He F, Zarfl C, Bremerich V, Henshaw A, Darwall W, Tockner K, Jähnig SC. Disappearing giants: a review of threats to freshwater megafauna. WIREs Water. 2017; 4:e1208. doi: 101002/wat21208.

Hegg JC, Giarrizzo T, Kennedy BP. Diverse early life-history strategies in migratory Amazonian catfish: implications for conservation and management. PLoS ONE. 2015; 10 (7): e0129697 doi: 101371/journalpone0129697.

Hermann TW, Stewart DJ, Limburg KE, Castello L. (2016) Unravelling the life history of Amazonian fishes through otolith microchemistry. Royal Soc. Open Sci. 2016; 3(6): 160206 doi: 101098/rsos160206.

Hutchinson CE, TenBrink TT. Age determination of the Yellow Irish Lord: management implications as a result of new estimates of maximum age North American. Journal of Fisheries Management. 2011; 31(6): 1116–1122.

Junk WJ, Bayley PB, Sparks RE. The flood pulse concept in river-floodplain-systems. In: Dodge. editor. Proceedings of International Large River Symposium. Can Spec Publ Fish Aquat Sci. 1989; 106: 110-127.

Junk WJ. The Central Amazon floodplains Ecology of pulsing system. Berlin: Springer; 1997.

Kimura DK. (1980) Likelihood methods for the von Bertalanffy growth curve. Fishery Bulletin. 1980; 77(4): 765-776.

Latrubesse EM, Stevaux JC, Sinha R. Tropical rivers. Geomorphology. 2005; 70(3): 187-206.

Latrubesse EM, Arima EY, Dunne T, Park E, Baker VR, d'Horta FM, Wight C, Wittmann F, Zuanon J, Baker PA *et al*. Damming the rivers of the Amazon basin. Nature. 2017; 546(7658): 363-369.

Lees AC, Peres CA, Fearnside PM, Schneider M, Zuanon JAS. Hydropower and the future of Amazonian biodiversity. Biodiversity and Conservation. 2016; 25(3): 451-466.

Loubens G, Panfili J. Estimation de l'âge individuel de *Prochilodus nigricans* (Teleostei: Prochilodidae) dans le Béni (Bolivie): protocole d'étude et application. Aquat. Living Resour.1992; 5: 41-56.

Loubens G, Panfili J. Biologie de *Colossoma macropomum* (Teleostei: Serrasalmidae) dans le bassin du Mamoré (Amazonie bolivienne). Ichthyol Explor Freshwaters. 1997; 8(1): 1–22.

Loubens G, Panfili J. Biologie de *Pseudoplatystoma fasciatum* et *P. tigrinum* (Teleostei: Pimelodidae) dans le bassin du Mamoré. Ichthyol Explor Freshwaters. 2000; 11(1): 13-34.

Loubens G, Panfili J. (2001) Biologie de *Piaractus brachypomus* (Teleostei: Serrasalmidae) dans le bassin du Mamoré (Amazonie bolivienne). Ichthyol Explor Freshwaters. 2001; 12(1): 51–64.

Loubens G. Biologie de *Plagioscion squamosissimus* (Teleostei: Scianidae) dans le bassin du Mamoré (Amazonie bolivienne) Ichthyol Explor Freshwaters. 2003; 14(4): 335-352.

Lowe-McConnel RH. Estudos ecológicos de comunidades de peixes tropicais: introdução e diversidade: sua manutenção e evolução. São Paulo: EDUSP; 1999.

Lupo AR, Nocera JJ, Bosart LF, Hoffman EG, Knight DJ. South American Cold Surges: Types, Composites, and Case Studies. Monthly Weather Review. 2001; 129:1021-1041.

Mazur CF, Tillapaugh D, Brett JR, Iwama GK. (1993) The effect of feeding level and rearing density on growth Feed conversion and survival in Chinook salmon (*Oncorhynchus tshawytscha*) reared in salt water. Aquaculture. 1993; 117: 129-140.

Odum EP. Fundamentos de ecologia. 4th ed. Lisboa: Fundação Calouste Gulbenkian; 1998.

Oliveira BI. Determinação de idade e aspectos da dinâmica populacional do curimatã *Prochilodus nigricans* (Pisces: Prochilodontidae) da Amazônia Central. [Master Thesis]. Manaus, AM: Instituto Nacional de Pesquisas da Amazônia; 1996.

Pelicice FM, Pompeu PS, Agostinho AA. Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. Fish Fish. 2015; 16(4): 697-715.

Paine RT. Food Web Complexity and Species Diversity. Am. Nat. 1966; 100 (910): 65-75.

Paine RT. (1980) Food Webs: Linkage, Interaction Strength and Community Insfrasctruture J. Animal Ecol.1980; 49 (3): 666-685.

Pérez A, Fabré NN. Seasonal growth and life history of the catfish *Calophysus macropterus* (Lichtenstein, 1819) (Siluriformes: Pimelodidae) from the Amazon floodplain. J Appl Ichthyol. 2009; 25(3): 343-349.

Puffer M, Berg OK, Huusko A, Vehanen T, Elnum S. Effects of intra- and interspecific competition and hydropeaking on growth of juvenile Atlantic salmon (*Salmo salar*). Ecol Freshw Fish. 2015; 26(1): 99-107.

Rochet MJ, Trenkel VM. Which community indicators can measure the impact of fishing? A review and proposals. Can J Fish Aquat Sci. 2003; 60(1): 86-99

Ronchail J. Advections polaires en Bolivie: mise en évidence et caractérisation des effets climatiques. Hydrologie Continentale. 1989; 4(1): 49-56.

Santos GM, Ferreira EJG, Zuanon JAS. Peixes Comerciais de Manaus. Manaus: Ibama/ProVárzea; 2006.

Silva EA, Stewart DJ. Age structure, growth and survival rates of the commercial fish *Prochilodus nigricans* (bocachico) in North-eastern Ecuador. Environ. Biol. Fish. 2006 ; 77(1): 63-77

Silva VMF, Goulding M, Barthem R. Golfinhos da Amazônia. Manaus: Editora INPA; 2008.

Taniguchi Y, Nakano S. Condition-Specific competition: Implications for the altitudinal distribution of stream fishes. Ecology. 2000; 81(7): 2027-2039.

Tomassone R, Dervin C, Masson JP. Biométrie: Modélisation de Phénomènes biologiques. Paris: Masson; 1993.

Val AL, Almeida-Val VMF, Randal DJ. The Physiology of Tropical Fishes. Academic Press; *2005*

Van Damme PA, Carvajal-Vallejos FM, Molina-Carpio J. Los peces y delfines de la Amazonía boliviana: hábitats, potencialidades y amenazas. Cochabamba: INIA; 2011.

Vieira EF. Determinação da idade e crescimento do jaraqui-de-escamagrossa (*Semaprochilodus insignis*) na Amazônia. [Master Thesis]. Manaus, AM: Instituto Nacional de Pesquisas da Amazônia; 1999.

Villacorta-Correa MA. Estudo de idade e crescimento do Tambaqui *Colossoma macropomum* (Characiformes: Characidae) no Amazonas central, pela analise de marcas sazonais nas estructuras mineralizadas e microestructuras nos otolitos. [PhD Thesis]. Manaus, AM: Instituto Nacional de Pesquisas da Amazônia; 1997.

Vismara MR, Benedito-Cecilio E, Faria ACEA. Efeito da maturação gonadal sobre o conteúdo calórico e condição geral de peixes da planície de inundação do alto rio Paraná. Acta Sci Biol Sci. 2004; 26(2): 189-199.

Vøllestad LA, Olsen EM, Forseth T. Growth-rate variation in brown trout in small neighbouring streams: evidence for density-dependence? J Fish Biol. 2002; 61(6): 1513-1527.

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

CAPÍTULO II

Desvendando o *homing* natal em um bagre gigante na Amazônia

Redigido no formato de artigo científico visando breve submissão ao periódico Journal Applied Ecology sob o título “Unmasking natal homing in a goliath catfish in the Amazon”.

Unmasking natal homing in a goliath catfish in the Amazon

ABSTRACT

point 1 sets the context and need for the work; point 2 indicates the approach and methods used; the next 2-3 points outline the main results; and the last point identifies the wider implications and relevance to management or policy. The final point is the most important of all in maximising the impact of the paper. It should synthesise the paper's key messages and should be generic, seminal and accessible to non-specialists, and must carry one of the following subheadings: 'Synthesis and applications' for articles that identify recommendations for management practices. 'Policy implications' for articles that are less directly tied to on-the-ground management and include discussion on conservation implications or links to policy.

1. The giant Amazonian catfish is largely spread in the Amazon Basin. Recently, otolith ^{87}Sr:^{86}Sr analyses using LA-MC-ICPMS revealed a > 8,000 km trans-Amazonian natal homing in *B. rousseauxii* among fish caught and hatched in the largest Amazon River tributary in the upper Madeira basin. Although also suspected for fish caught and hatched in the upper Amazon, homing could not be demonstrated owing to lower environmental ^{87}Sr:^{86}Sr gradients along the Amazon mainstem. Using SXFM, another study provided evidence that Se:Ca is a useful marker for identifying migration into or out of Andean headwaters and Sr:Ca for incursions into the estuarine environment. (100)

2. We analysed otoliths of known ^{87}Sr:^{86}Sr profiles using SXFM mapping to test if Sr:Ca and Se:Ca patterns could confirm natal homing for three fish caught in the upper Amazon, using as a reference four individuals from the upper Madeira River: two presenting natal homing and two forced residents hatched after construction of hydroelectric dams on the Madeira River. (58)

3. As hypothesised, although the Sr isotope profiles of the upper Amazon individuals were uninformative, two of them presented similar alternating mirror patterns of Sr:Ca and Se:Ca to those of the upper Madeira natal homers, indicating migrations out of the Andean region and into the estuary area. Both were therefore natal homers from the upper Amazon. (55)

4. The third individual from the upper Amazon presented similar Sr:Ca and Se:Ca patterns to those of the upper Madeira residents, suggesting it was a natural resident from the upper Amazon. (30)

5. '*Synthesis and applications*' By combining the results of ^{87}Sr:^{86}Sr analyses (LA-MC-ICPMS) and Sr:Ca and Se:Ca mappings (SXFM), we demonstrated that *B. rousseauxii* also performs natal homing in the upper Amazon. Our results indicate that the life cycle of *B. rousseauxii* is more complex than anticipated, with the existence of homers, strayers and

resident fish, even in absence of physical barriers to migrations. Quantifying the relative importance of these different life history strategies will have important implications for fisheries management. Our results also lay ground for conservation efforts in the context of hydropower development in the Amazon basin and set testable hypotheses of the potential impacts of the Madeira River dams. (110)

Key words: *Brachyplatystoma rousseauxii*, otolith, microchemistry, LA-MC-ICPMS, SXFM, Sr isotopiques, dam impacts.

INTRODUCTION

Natal philopatry or natal homing is the behaviour exhibited by individuals returning to their area of origin to breed. It is known in several animal groups, from invertebrates such as microcrustaceans and insects, to vertebrates such as mammals, birds, reptiles and fish (Weyer & Schmitt, 2013; Rooker et al., 2008; Brothers & Lohmann, 2015; Miller & Smallwood, 1997; Hoffman & Forcada, 2012). Among vertebrates, homing behaviour is well documented in diadromous fish species, which travel between freshwater and the sea, such as the classic case of salmonids that reproduce in freshwater, grow in the sea and then perform natal homing in north America (Mills, 1986; Dittman & Quinn, 1996).

Knowledge about these migratory processes quickly improved in recent years with advances in otolith microchemistry (Campana, 2005; Elsdon & Gillanders, 2003; Elsdon et al., 2008; Secor, 2010; Walther & Limburg, 2012; 2017). Among the available chemical markers, Sr:Ca and Ba:Ca have proved to be optimal indicators of movements between marine and freshwater environments (Gillanders, 2005; Walther & Thorrold, 2006; Bath et al., 2000; Lord, Tabouret, Claverie, Pécheyran & Keith, 2011; Webb, Woodcock & Gillanders, 2012).

However, studies on the migratory behaviour of potamodromous species are less documented in characterize natal homing (Northcote, 1997; Saiget, Sloat & Reeves, 2007; Sammons, 2015; Tyus, 1990; Lucas & Baras, 2001) due a difficulty of uncover chemical elements proper to reveal diadromous migrations (Walther & Limburg, 2012). By contrast, strontium (Sr) isotopic ratios in otoliths, which depend almost exclusively on the age and bedrock geological composition of watersheds, and thus barely vary across years, has been represented accurate habitat signatures in freshwaters (Kennedy, Folt, Blum & Chamberlain, 1997; Kennedy, Blum, Folt & Nislow, 2000; Walther & Limburg, 2012). Recently, the use of

$^{87}Sr:^{86}Sr$ has proved efficient in determining migratory patterns of freshwater fishes in river basin systems as complex and extensive as those of the Amazon basin (Pouilly, Point, Sondag, Henry & Santos, 2014; Garcez, Humston, Harbor & Freitas, 2015; Duponchelle et al., 2016; Sousa, Humston & Freitas, 2016).

In the Amazon, *Brachyplatystoma rousseauxii* are known to perform extensive transnational migrations in white-water rivers between their breeding areas in the Andean piedmont of Bolivia, Ecuador, Peru and Colombia, and their nurseries in the lower Amazon estuary, in Brazil (Barthem & Goulding, 1997; Duponchelle et al., 2016; Barthem et al., 2017). Recently, otolith $^{87}Sr:^{86}Sr$ analyses using laser ablation–multicollector–inductively coupled plasma mass spectrometry (LA-MC-ICPMS) have confirmed a > 8,000-km migration and revealed natal philopatry in populations of *B. rousseauxii* from the largest white-waters' Amazon River tributary – the Madeira River (Duponchelle et al., 2016; see chapter III; Fig. 1). The Madeira River has high environmental $^{87}Sr:^{86}Sr$ gradients unlike the Amazon River where low environmental $^{87}Sr:^{86}Sr$ gradients along the Amazon mainstem are not able to trace migratory routes and detect natal homing for *B. rousseauxii* (Duponchelle et al., 2016; see chapter III).

However, Hermann, Stewart, Limburg & Castello (2016) employed a multi-method, multi-elemental approach to elucidate patterns of migration of five Amazonian fish species. Their study provided further insights into the complex life cycle of two *Brachyplatystoma* species, particularly regarding the use of the estuary as a nursery by *B. rousseauxii* with strontium to calcium ratio (Sr:Ca), for incursions into the estuarine environment, and selenium to calcium ratio (Se:Ca), as a useful marker for identifying migration into or out of Andean headwaters. Such discovery could be done by using complementary techniques scanning X-ray fluorescence microscopy (SXFM) to produce 2-D element:Ca maps, and because in the Amazon Se is an element exclusive from Andean region, and not occur downstream rivers or estuary areas (Yee, Measures & Edmond, 1987). Therefore, the complementarity of both approaches ($^{87}Sr:^{86}Sr$ by LA-MC-ICPMS and Se:Ca, Sr:Ca by SXFM) suggests useful to verify if the natal homing pattern observed in the Madeira also exists along the Amazon mainstem, which would have important consequence for fisheries and conservation management.

The genus *Brachyplatystoma* encompass most important exploited Amazon commercial species supporting annual landings above 40,000 tons·year^{-1} considering only the Brazilian portion, whereas *B. rousseauxii* represents about 14,486 t (MPA, 2013; Batista, Alonso, Ladle & Fabré, 2018). The sustainability of these populations and the fisheries they support are widely threatened by at least 334 new Amazon dams proposed by Brazilian government (Winemiller et al., 2016) disrupting migratory routes of these goliath catfishes (Finer & Jenkins, 2012; Castello et al., 2013; Duponchelle et al., 2016; Fearnside, 2014; Castello & Macedo, 2016; Lees, Peres, Fearnside, Schneider & Zuanon, 2016; Winemiller et al., 2016; Latrubesse et al., 2017; Hauser et al., 2018) independent of the extension of each species migration.

Our work hypothesized that if *B. rousseauxii* performs natal philopatry in the main Amazon River we should to detect it by using complementary techniques scanning X-ray fluorescence microscopy (SXFM) to produce 2-D element:Ca maps where we expect to find: i) selenium in the core of the otolith corresponding to birth in the Andes, ii), strontium up to 2-3 years old as juvenile due young phase in the estuary; iii) selenium in the border again, when the adult returns to the breeding area to confirm homing, following the schematic in Figure 2. Otoliths with known ^{87}Sr:^{86}Sr profiles (LA-MC-ICPMS) from Upper Madeira guide us to patterns expected for the Upper Amazon River (see chapter III). The upper Madeira River was blocked to take place for Jirau and Santo Antônio run-of-river dams built in cascade, in 2011 (Cella-Ribeiro et al., 2017). Specimens sampled in this area after the dams construction were evaluated highlighting *B. rousseauxii* migratory behaviour with river fragmentation too. Tropical rivers are, currently, the primary frontier for dam construction due to their predominantly free-flowing natural conditions and high hydroelectric potential (Fearnside, 2016; Finer & Jenkins, 2012; Latrubesse et al., 2017; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016; Winemiller et al., 2016). Our results highlight the potential of SXFM techniques to investigate natal phylopatry for migratory fish species, and the ineffectiveness of fishpass proposed to maintain *B.rousseauxii* life cycle faced to those several promises of dams in the Amazon River Basins.

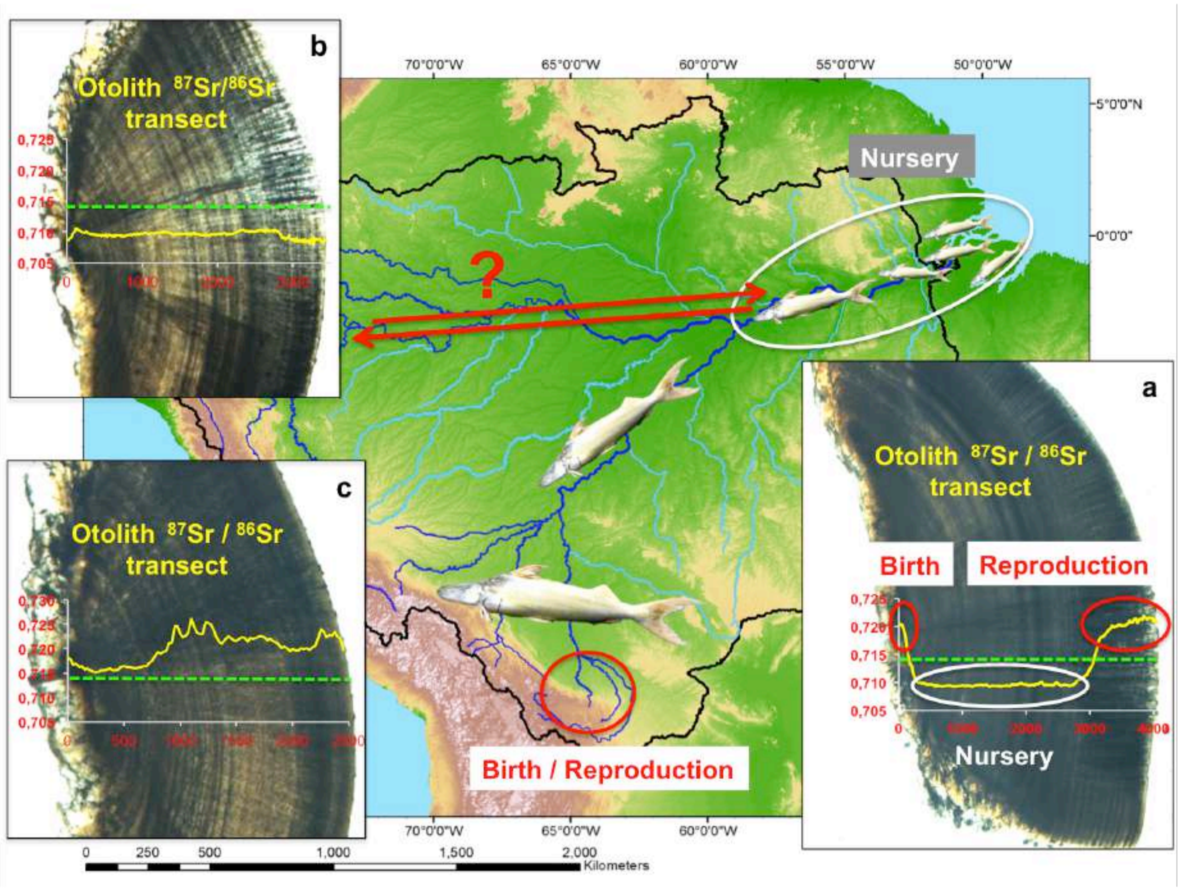

Figure 1. Illustration of the migratory patterns of *B. rousseauxii* in the Amazon basin, as revealed by otoliths ^{87}Sr:^{86}Sr profiles (based on Duponchelle et al., 2016, and Hauser, 2018). For a better visualisation, a dashed green line represents the 0.714 ^{87}Sr:^{86}Sr value. **a**- Natal homing behaviour of a fish hatched and caught in the Upper Madeira sub-basin (Bolivia), after a prolonged migration down to the lower Amazon River: on the otolith's transverse section, the hatching signature (~0.721), characteristic of the upper Madeira waters (0.714–0.726), quickly drops to a lower value typical of the lower Amazon River (~0.710), when the larvae is flushed down to the lower Amazon by the current at a mean size of ~3.4 cm (Duponchelle et al., 2016). The juvenile then stays in the lower Amazon waters for a few years (see Hauser et al., 2018, for age validation). The ^{87}Sr:^{86}Sr profile then starts rising again to come back approximately to the hatching value at the moment of the fish's capture in the upper Madeira sub-basin (in the Ichilo River). **b**- Given the lack of water ^{87}Sr:^{86}Sr contrast along the Amazon River mainstem, natal homing, although also likely in the upper Amazon, could not be demonstrated using Sr isotopes only. **c**- otolith ^{87}Sr:^{86}Sr profile of a fish hatched and caught in the upper Madeira after the dams' completion (= forced residents): unlike the pattern observed before the dams (see **a**), the isotopic values remain within the range of Madeira water vales (0.714–0.7126) throughout the fish's life (see chapter III).

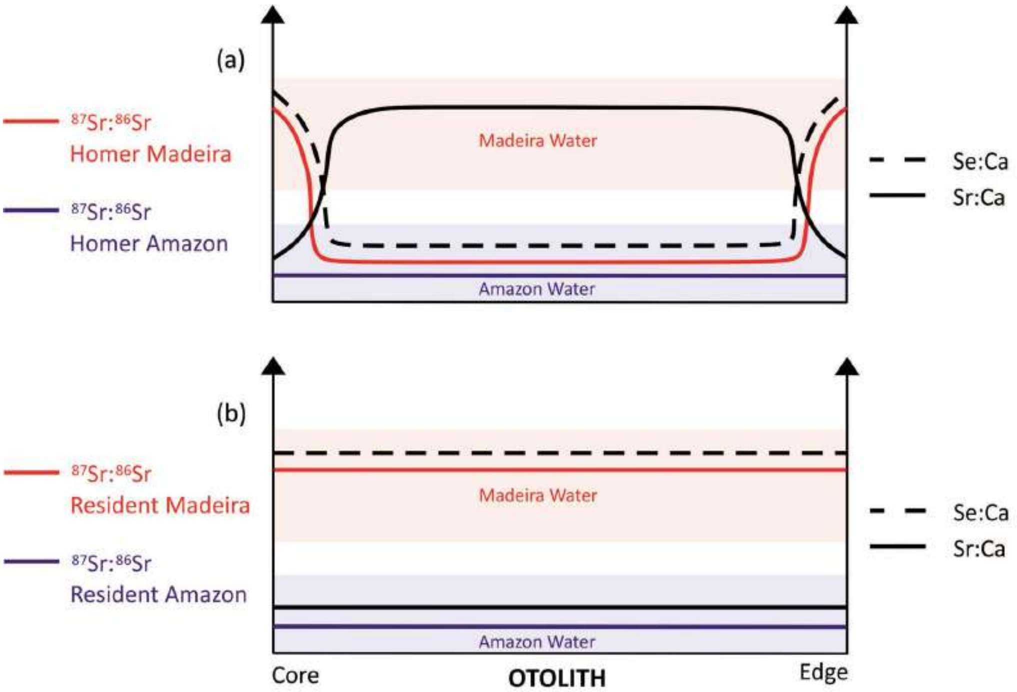

Figure 2. **a**- Schematic patterns of ^{87}Sr:^{86}Sr profiles in homers from the upper Madeira and alleged homers from the upper Amazon (based on Duponchelle et al., 2016) and their expected similar Se:Ca and Sr:Ca mapping patterns (based on Herman, Stewart, Limburg & Castello, 2016). Here, we used the classification of Duponchelle et al. (2016) for distinguishing the ^{87}Sr:^{86}Sr signatures of the Amazon mainstem (0.705–0.712) and Madeira (0.714–0.726) drainage. As Se concentration is higher close to the Andes and diminishes away from the Andes, the Se:Ca pattern from the core to the edge of the otolith is expected to follow that of ^{87}Sr:^{86}Sr profile for the upper Madeira homers (a high Se concentration around the core, when the fish hatches close to the Andean piedmont, then a strong decrease in Se concentration when the fish migrates down the lower Amazon or to the estuary and an increased Se concentration when the fish migrates back to the upper Madeira, close to the Andes). By contrast, Sr:Ca is expected to follow an inverse trend, as Sr concentration is higher close to the estuary (Angino et al., 1996; Palmer & Edmond, 1992). If, as hypothesised, the fish caught and hatched in the upper Amazon also perform natal homing, the Se:Ca and Sr:Ca distributions from the core to the edge of their otolith is expected to follow the same pattern as the upper Madeira homers, whereas the ^{87}Sr:^{86}Sr profile remains flat. **b**- Schematic patterns of ^{87}Sr:^{86}Sr profiles in forced residents from the upper Madeira, alleged residents from the upper Amazon, and their expected similar Se:Ca and Sr:Ca mapping patterns. For residents of the upper Madeira or upper Amazon, we expect to observe relatively high and more homogeneously distributed Se concentration across the otolith, whereas Sr concentration should remain low throughout the otolith.

MATERIALS AND METHODS

We selected fish that had previously been analysed for $^{87}Sr:^{86}Sr$ profiles using LA-MC-ICPMS (see chapter III): i) two known natal homers (fish hatched in the upper Madeira and caught in the Mamoré River - BR 56 and in the Béni River -CE 20); ii) two forced resident (fish hatched in the upper Madeira and caught after the dams completion around Puerto Maldonado, Madre de Dios River in Peru - BR 224 and BR 234); iii) and three fish caught in the upper Amazon around Iquitos, Peru (BR 004, BR 008 in the Ucayali River and BR 130 in the Marañon River) which we could not confirm the homing natal behaviour from only the $^{87}Sr:\ ^{86}Sr$ profiles. Then, we analysed the same otoliths using SXFM mapping in order to test whether Sr:Ca and Se:Ca could shed some light on the hypothesized natal homing behaviour of fish caught in the upper Amazon, using as a reference the individuals from the upper Madeira River presenting natal homing and resident behaviours. Here, we used the classification of Duponchelle *et al.* (2016) (see chapter III, too) for distinguishing the $^{87}Sr:^{86}Sr$ signatures of the Amazon (0.705-0.712) and Madeira (0.714-0.726) basins.

For each specimen, SL had been measured (nearest cm) and otoliths (lapilli) extracted, rinsed in clear water, dried and stored for later examination (Table I).

Table 1. Detailed information about the *Brachyplatystoma rousseauxii* specimens used in this study: geographical origin of capture, period of capture (before or after the dams), standard length (SL), sex, age and migratory behaviour determined by $^{87}Sr:^{86}Sr$ analyses.

Fish	Basin	River	Country	Dams	Date	SL (cm)	Sex	Growth rings	Age (year)	Behaviour
BR56	upper Madeira	Mamoré	Bolivia	Before	03/18/05	98	M	14	7	Homer
CE20	upper Madeira	Beni	Bolivia	Before	02/15/07	103	F	7	3,5	Homer
BR224	upper Madeira	Madre de Dios	Peru	After	04/01/15	92	M	6	3	Resident
BR234	upper Madeira	Madre de Dios	Peru	After	07/01/15	73		4	2	Resident
BR004	upper Amazon	Ucayali	Peru	After	09/23/14	94		4	2	?
BR008	upper Amazon	Ucayali	Peru	After	01/27/16	92		4	2	?
BR130	upper Amazon	Marañon	Peru	After	04/26/15	116	F	13	6,5	?

OTOLITH PREPARATION AND ANALYSIS

Otoliths were mounted in Araldite epoxy resin and a frontal section of approximately 0.7 mm thickness was made with a low-speed Isomet saw (Buehler, Düsseldorf, Germany) to obtain a dorso-ventral slice including the otolith core. The section was then ground and polished using polishing papers (1,200 and 2,400 μm) and ultra-pure water until the core was visible on one side, as detailed in Duponchelle et al. (2016). The age of every individual was estimated assuming biannual growth rings (Hauser et al., 2018). LA-MC-ICPMS analyses (^{87}Sr:^{86}Sr profiles) were carried out at the Laboratoire de Chimie Analytique Bio-inorganique et Environnement (LABCIE) in Pau and at the Laboratoire Cycles Géochimiques et Ressources of IFREMER in Brest (for details see Duponchelle et al., 2016; Hauser, 2018). SXFM analyses were performed at the Synchrotron in CHESS (for details see Hermann, Stewart, Limburg & Castello, 2016; and Limburg & Elfman, 2017). All samples were analyzed with SXFM at the F3 Beamline Station at the Cornell High Energy Synchrotron Source (CHESS). Briefly, sample sections were fixed to cardboard slide frames with tape and secured with clips prior sampling. A 16.1-keV X-ray beam is produced by a double-bounce multilayer monochromator (0.6% bandpass) and focused by a single-bounce glass capillary[1,2] focused onto a 25–50-μm spot on the sample with a photon flux of approximately 4×10^{10} counts s^{-1}. The fluorescence spectrum was collected with a vortex energy-dispersive silicon drift quad (4-in-1) detector fitted with an aluminium foil attenuator to increase sensitivity to trace elements and reduce high-intensity calcium fluorescence. Dwelling times of 0.25–1 s were used during the two-dimensional fly scans of fluorescence mapping. Initial spectral processing consisted of screening for a suite of 25 trace elements. The instrument calibrations were made using an in-house standard[3]. Relative elemental abundances are reported in ratio to Ca abundance (Bilderback et al., 2003; Cornaby, 2008; Limburg et al., 2011, Hermann, Stewart, Limburg & Castello, 2016; Limburg & Elfman 2017).

RESULTS

KNOWN NATAL HOMERS FROM THE UPPER MADEIRA BEFORE THE CONSTRUCTION OF DAMS

Otoliths from the Madeira natal homers (BR 56, CE 20) showed a clear inverse relationship between Se:Ca and Sr:Ca concentrations (Fig. 3). As indicated by their ^{87}Sr:^{86}Sr profiles, these individuals were hatched in the upper Madeira (hence close to the Andes) and travelled down to the lower Amazon at approximately 33 and 40 days after born for BR 56 and CE 20, respectively, and back to the upper Madeira close to the Andean region at approximately 3.5 and 2.5 years old for BR 56 and CE 20, respectively (Fig. 3a, d). Both had a high concentration of Se:Ca around the core, then almost none until the end of life when Se:Ca concentration rose again (Fig. 3c, f).

Also, there was a clear inverse relationship between ^{87}Sr:^{86}Sr profiles and bulk Sr:Ca concentrations in these two natal homers from the Madeira: the Sr:Ca concentration was low around the core, increased when the fish left the Madeira waters and entered the Amazon (i.e., when the ^{87}Sr:^{86}Sr profile dropped) in the first part of their lives, and decreased when they returned to the Madeira (i.e., when the ^{87}Sr:^{86}Sr profile rose again; Fig. 3b, e).

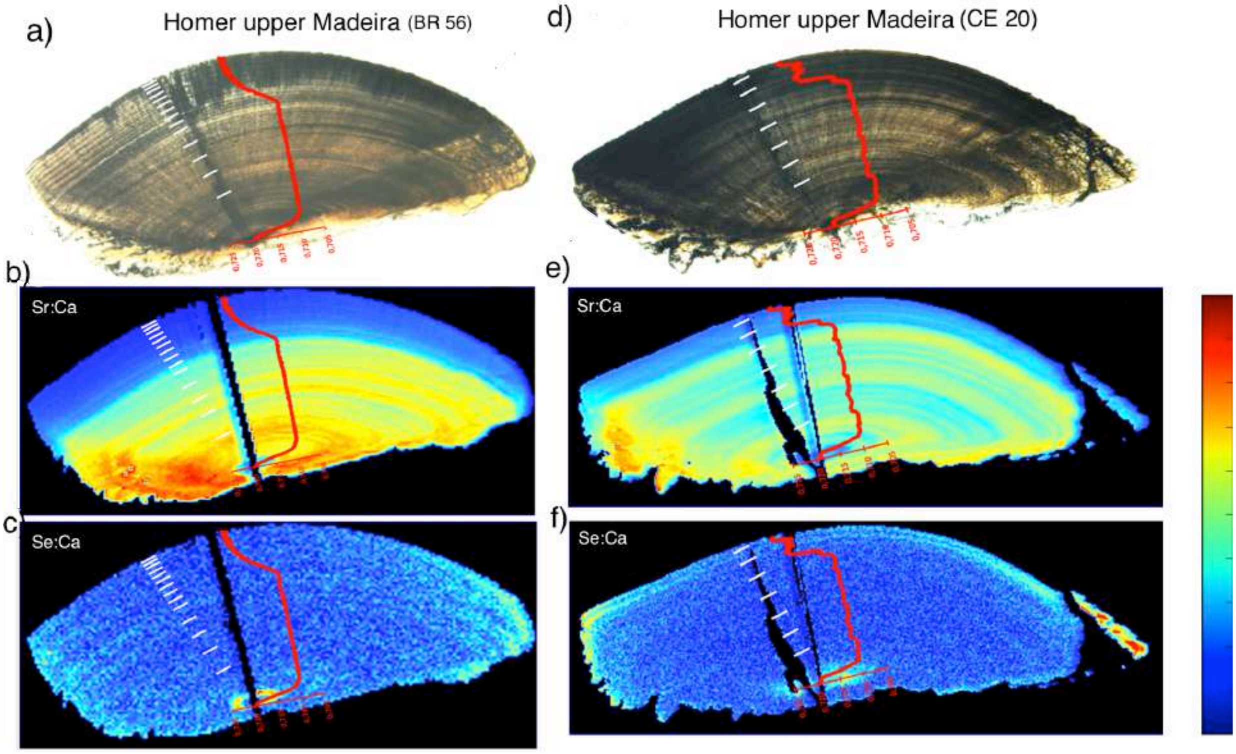

Figure 3. Otoliths ^{87}Sr:^{86}Sr profiles (red), and Se:Ca and Sr:Ca maps of *B. rousseauxii* performing regional natal homing in the upper Madeira River (hatched and caught before the construction of dams): **a**- BR 56 and **b**- CE 20. Scale bar = 1 mm. Ratios of Sr:Ca and Se:Ca are scaled 0 to 8 and 0 to 0.01, from blue to red, respectively. Each white line corresponds to a growth ring.

KNOWN RESIDENTS FROM THE UPPER MADEIRA AFTER THE CONSTRUCTION OF DAMS (UPSTREAM FROM THE DAMS)

The two fish caught in the upper Madeira in January 2015 (BR 224 and BR 234) were 3 and 2 years old, respectively (Table 1, Fig. 4) and were therefore hatched after the dams' completion in 2011. Both presented ^{87}Sr:^{86}Sr profiles different from those of the Madeira natal homers, without a single value below 0.715, indicating they remained all their lives within the upper Madeira above the dams (= forced residents). The inverse relationship of increasing/decreasing Sr and Se concentration observed in the upper Madeira natal homers was completely absent in the otoliths of these two forced-residents (Fig. 4). Contrary to the natal homers, they had a larger Se band around the core, intermediate Se bands and almost no variation in Sr:Ca throughout the otolith (Fig. 4).

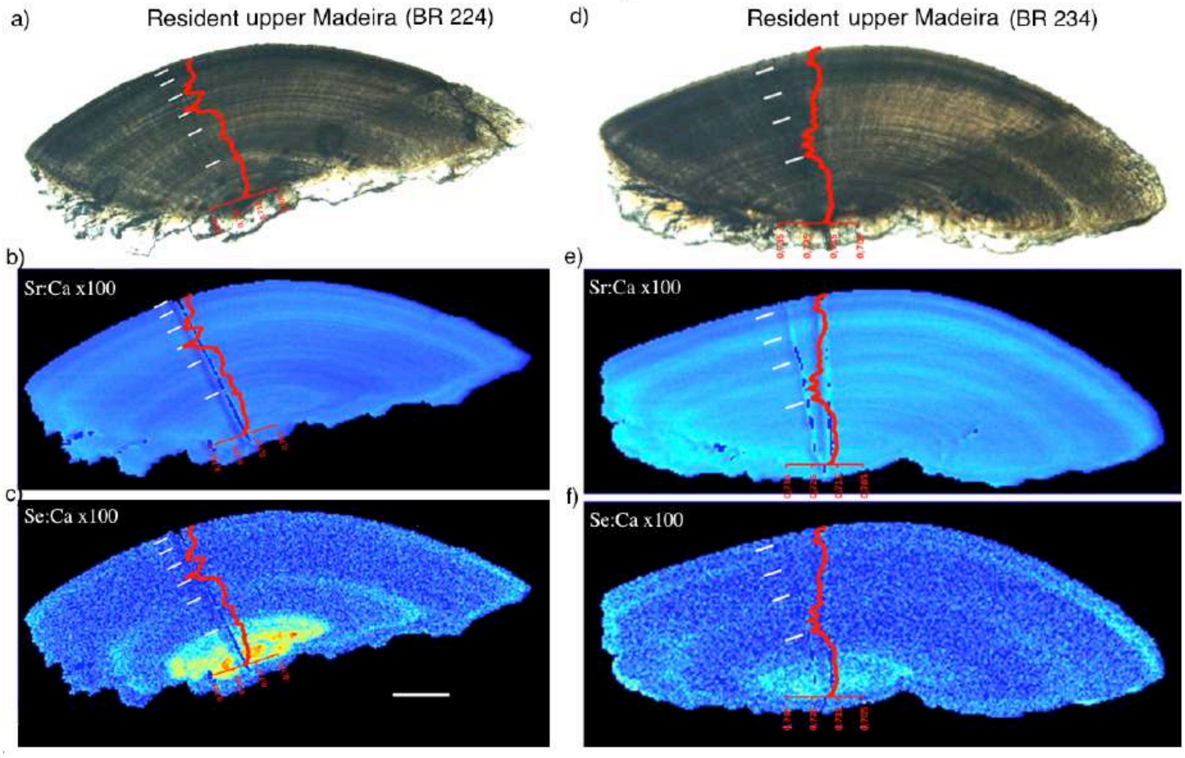

Figure 4. Otoliths ^{87}Sr:^{86}Sr profiles (red) and Se:Ca and Sr:Ca maps of *B. rousseauxii* performing forced-resident behaviour (hatched and caught after the construction of dams) in the upper Madeira (upstream of the dams): **a**- BR 224 and **b**- BR 234. Scale bar = 1 mm. Ratios of Sr:Ca and Se:Ca are scaled 0 to 8 and 0 to 0.01, from blue to red, respectively. Each white line corresponds to a growth ring.

FISH FROM THE UPPER AMAZON

Two of the fish caught in the upper Amazon, BR 130 and BR 004, despite their relatively flat ^{87}Sr:^{86}Sr profiles (Fig. 5), had similar Sr:Ca and Se:Ca patterns to those of the two homers from the upper Madeira (Fig. 3). The same pattern of increasing / decreasing Sr concentration was also observed, albeit weaker than in the upper Madeira fish. BR 130 had low Sr:Ca and high Se:Ca around the core, then Sr:Ca rapidly increased and remained relatively high whereas Se:Ca followed an opposite trend (Fig. 5b, c). Sr:Ca progressively decreased and reached the lowest values when Se:Ca started to peak again in the last two years of life. BR 004, a younger fish (Table 1, Fig. 5d), had a slightly different pattern as

Sr:Ca remained low until after one year old, peaked for a few months and started decreasing again to reach the lowest value close to the otolith edge (Fig. 5e). On the other hand, Se:Ca remained high for over half a year from hatching before strongly decreasing until it started to increase again at the edge of the otolith (Fig. 5f).

BR 008, the youngest of the three fish caught in the upper Amazon, presented a completely different pattern (Fig. 5g-i) that resembled that of the resident from the upper Madeira (Fig. 4), with low Sr:Ca and relatively high Se:Ca throughout the otolith, apart for a decrease in Se:Ca for about one year (Fig. 5h, i).

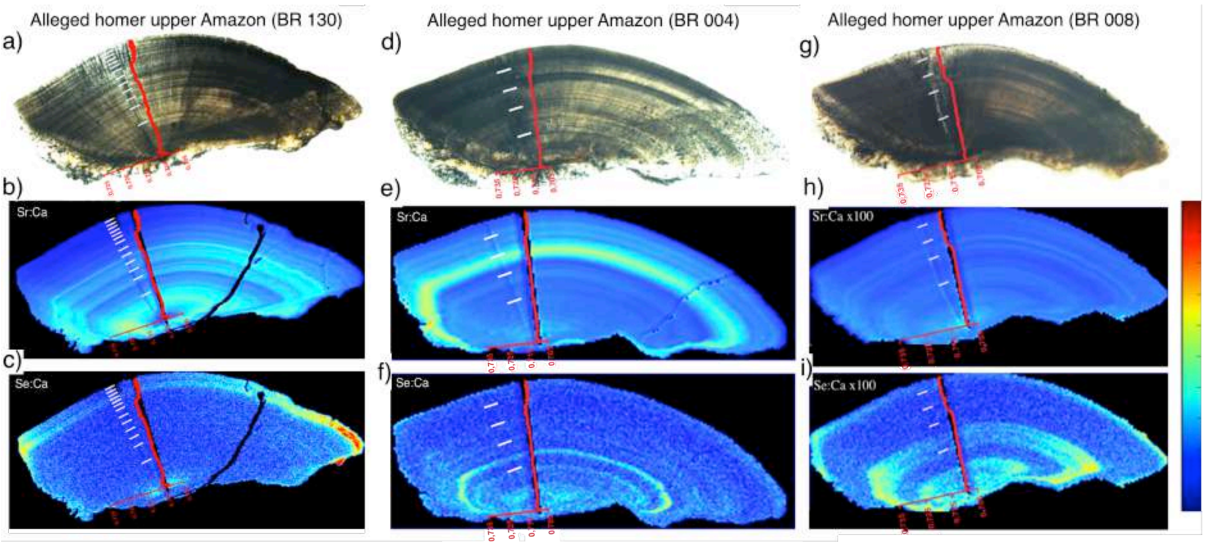

Figure 5. Otoliths ^{87}Sr:^{86}Sr profiles (red) and Se:Ca and Sr:Ca maps of *B. rousseauxii* performing alleged natal homing in the upper Amazon River based on ^{87}Sr:^{86}Sr profiles: **a**- BR 130, **b**- BR 004 and **c**- BR 008. Scale bar = 1 mm. Ratios of Sr:Ca and Se:Ca are scaled 0 to 8 and 0 to 0.01, from blue to red, respectively. Each white line corresponds to a growth ring.

DISCUSSION

The analyses presented here are based on completely different physical principles. Strontium isotopic ratio analysis quantifies small differences in isotopic mass, which in the case of strontium depends largely on the age of bedrock from which the isotopes derive (Kennedy, Folt, Blum & Chamberlain, 1997; Kennedy, Blum, Folt & Nislow, 2000; Walther & Limburg, 2012). In contrast, the analyses of bulk Ca, Se, and Sr, from which Se:Ca and Sr:Ca ratios are calculated, are quantified by fluorescence counts of photons emitted when the otolith samples are excited by X-ray beams (Limburg *et al*. 2007). The relative ratios of Se:Ca and Sr:Ca derive from concentrations in river water flowing over bedrock and soil.

Nevertheless, these two methods produce highly complementary results and inform each other.

As hypothesised (Fig. 2), although the Sr isotope profiles of the upper Amazon individuals (BR 130 and BR 004) were homogeneous (relatively flat), they presented similar alternating mirror patterns of Sr:Ca and Se:Ca to those of the upper Madeira natal homers (BR 56 and CE 20), indicating both were natal homers from the upper Amazon: they hatched in the upper Amazon, then travelled down the lower Amazon-estuary area before returning to the upper Amazon where they were caught. Similar to the natal homers from the upper Madeira, BR 130 also returned at about 3 years old to the upper Amazon, when Se and Sr concentrations increased and decreased, respectively (Fig. 5b, c). Specimen BR 004 on the other hand, delayed its downstream migration to the lower Amazon to ~ 1.5 years old, and returned to the upper Amazon only about six months later (Fig. 5-e, f). The third fish sampled in the upper Amazon (BR 008), on the contrary, did not display alternating patterns of high and low Se:Ca and Sr:Ca. Instead, it presented Se:Ca and Sr:Ca patterns similar to those of the forced resident from the upper Madeira (BR 224 and BR 234, Figure 4): low Sr:Ca and relatively high Se:Ca throughout the otolith, indicating it had remained in the upper Amazon all its life and was therefore a natural resident.

These results demonstrate that the seemingly dominant natal homing behaviour observed for this species in the upper Madeira (Duponchelle *et al.* 2016), also exists in the upper Amazon. And they also emphasize the usefulness of combining MC-ICPMS and SXFM (Limburg *et al.* 2007; Hermann *et al.* 2016) to unravel the migratory patterns of Amazonian fish species. These results still indicate that the life cycle of *B. rousseauxii* is probably more complex than previously thought, with the existence of a resident behaviour in the upper Amazon (BR 008), even without barrier to the downriver migration.

Apart from extreme examples, not all individuals in a migratory population do migrate, a phenomenon known as partial migration (Secor & Kerr 2009; Chapman *et al.* 2011; 2012; Kendal *et al.* 2015). What determines whether an individual will migrate or not is the result of a complex interaction among the fish's genotype, individual condition and environment (Sloat *et al.* 2014; Kendal *et al.* 2015), which aims to maximize individual fitness (Arai *et al.* 2006). Although resident behaviour was not observed on the eighteen *B. rousseauxii* from the upper Madeira analysed in Duponchelle *et al.* (2016), it is likely that further sampling would evidence it as well. Indeed, this species is known to spawn both during the highest river discharge - high water season and during the receding waters - dry season, including within the same river basin (García-Vasquez *et al.* 2009; Cañas & Pine

2011; Van Damme *et al.* 2011; Agudelo *et al.* 2013; Cella-Ribeiro *et al.* 2015; García-Dávila *et al.* 2015; Barthem *et al.* 2017). Reproducing during the receding water period, when the river returns to its natural bed, probably reduces the risk of eggs and larvae being lost in the adjacent floodplains and therefore maximizes their chances to reach the nursery area of the estuary thousands of km downstream (García-Vasquez *et al.* 2009). On the other hand, breeding during the high water periods increases this risk and lost juveniles that survive the floodplain may become residents.

Another way to become resident is to have the downstream migration disrupted by some barrier, such as the two hydroelectric dams erected since 2011 on the Brazilian portion of the Madeira River, upstream of Porto Velho. The two fish caught in January 2015 in the upper Madeira (BR 224 and BR 234), hence after the dams' construction, had remained all their lives within the upper Madeira, as attested by both their ^{87}Sr:^{86}Sr profiles and Se:Ca and Sr:Ca mappings, indicating they were forced-residents. This apparent departure from the expected migratory pattern for fish caught in the upper Madeira (Duponchelle *et al.* 2016) will need to be confirmed and quantified by further studies on a larger number of fish. It can nevertheless be hypothesized to be a consequence of the hydroelectric dams and that it has become the more frequent pattern. This hypothesis, amenable to testing with the technics used in this study, is very likely given that only one of the two hydroelectric impoundments, Santo Antonio Energy, has a fish pass, and that it was found ineffective for accommodating the upstream run of returning pre-adults goliath catfishes, including *B. rousseauxii* (Fearnside 2014). The probability of observing, in the upper Madeira, *B. rousseauxii* that have travelled down the lower Amazon and returned, except for old individuals hatched and returned before the dams, is therefore almost null.

It will also be important to assess whether the disruption of the seemingly compulsory passage through the lower Amazon-estuary alters growth and reproductive patterns of resident fish. The geographic separation between the breeding and nursery areas for *B. rousseauxii* was hypothesized to be an advantageous adaptive response, improving growth and survival of individuals in the early stages of development (Barthem & Goulding 1997). Reduced growth is a common phenomenon observed in resident salmonids when compared with the individuals performing anadromy (Waples *et al.* 2008; Kendal *et al.* 2015). As smaller individuals have lower fecundity, reduced growth also reflects negatively on the recruitment's rate of the population, with direct effects on fisheries production. It can therefore be hypothesized that forced resident in the upper Madeira will have slower growth, smaller sizes, hence reduced fecundity.

The confirmation of a natal homing in the upper Amazon also has profound implications for the conservation and fisheries management of *B rousseauxii* at the Amazon basin scale. As the proportions of homers, residents and strayers directly influence the abundance, intra and inter-population diversity, resilience, structure, and productivity of populations (Waples *et al*. 2008), the relative proportions of these migratory behaviours will have to be quantified for *B. rousseauxii*.

This study, combining the results of LA-MC-ICPMS and SXFM mappings, provides a significant step in the knowledge of *B. rousseauxii*'s life cycle and opens the way for future studies aiming at estimating the impacts of current and planned hydropower development scenario in the Amazon.

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REFERENCES

Agudelo, E., Joven León, Á.V., Bonilla Castillo, C.A., Petrere Jr, M., Peláez, M. & Duponchelle, F. (2013) Breeding, growth and exploitation of *Brachyplatystoma rousseauxii* in the Caqueta River, Colombia. *Neotropical Ichthyology,* **11,** 637-647.

Angelini, R., Fabré, N. N., & Silva-JR, U. L. (2006). Trophic analysis and fishing simulation of the biggest Amazonian catfish. *African Journal Of Agricultural Research*, **55**, 151-158.

Angino EE, Billings GK, Andersen N. (1966). Observed variations in the strontium concentration of sea water. *Chemical Geology*, **1,** 145–153.

Arai T, Yang J, Miyazaki N (2006) Migration flexibility between freshwater and marine habitats of the pond smelt Hypomesus nipponensis. *Journal* of *Fish Biology*, **68**, 1388–1398

Batista, V., Alonso, J. C., Ladle, R. J., & Fabré, N. N. (2018). Drivers of the upper River Amazon giant catfish fishery. *Fisheries Management* and *Ecology*, 1–11. DOI: 10.1111/fme.12270

Barthem, R. B., & Goulding, M. (1997). *The Catfish Connection: Ecology, Migration, and Conservation of Amazon Predators*. New York, EUA: Columbia University Press.

Barthem, R.B., Goulding, M., Leite, R.G., Cañas, C., Forsberg, B., Venticinque, E., Petry, P., Ribeiro, M.L.d.B., Junior, C. & Mercado, A. (2017) Goliath catfish spawning in the far western Amazon confirmed by the distribution of mature adults, drifting larvae and migrating juveniles. *Scientific reports,* **7**, 41784.

Bath G, Thorrold S, Jones C, Campana S, McLaren J, Lam J (2000) Strontium and barium uptake in ara- gonitic otoliths of marine fish. *Geochimica et Cosmochimica Acta*, **64**, 1705–1714.

Bilderback D, Huang R, Kazimiro A, Kriksunov I, Limburg K, Fontes E. 2003 Monocapillary optics developments and applications. Adv. X-Ray Anal. **46**, 320–325

Brothers JR, Lohmann KJ. (2015). Evidence for geomagnetic imprinting and magnetic navigation in the natal homing of sea turtles. *Current Biology,* **25**, 392–396. doi:10.1016/j.cub.2014.12.035

Campana SE. (2005). Otolith science entering the 21st century. Marine and *Freshwater Research,* **56**:485–495.

Castello , L., McGrath, D. G., Hess, L. L, Coe, M. T., Lefebvrel, P. A., Petry, P., … Arantes, C. C. The vulnerability of Amazon freshwater ecosystems. (2013). *Conservation Letters*, **6**, 217–229.

Castello, L., & Macedo, M. N. (2016). Large-scale degradation of Amazonian freshwater ecosystems. *Global Change Biology*, **22**, 990-1007.

Cella-Ribeiro, A., Assakawa, L.F., Torrente-Vilara, G., Zuanon, J., Leite, R.G., Doria, C. & Duponchelle, F. (2015) Temporal and spatial distribution of young Brachyplatystoma spp. (Siluriformes: Pimelodidae) along the rapids stretch of the Madeira River (Brazil) before the construction of two hydroelectric dams. *Journal of Fish Biology,* **86,** 1429-1437.

Cañas, C.M. & Pine, W.E. (2011) Documentation of the temporal and spa- tial patterns of Pimelodidae catfish spawning and larvae dispersion in the Madre de Dios River (Peru): insights for conservation in the Andean- Amazon headwaters. *River Research and Application*s, **27**, 602–611.

Carolsfeld, J., Harvey, B., Ross, C. & Baer, A. (eds) (2003) *Migratory fishes of South America: Biology, Fisheries and Conservation Status*. IDRC, World Bank, Washington, DC, USA

Chapman, B. B., Brönmark, C. , Nilsson, J-A., & Hansson, L.-A. (2011). The ecology and evolution of partial migration. *Oikos,* **120**, 1764–1775, 2011 doi: 10.1111/j.1600-0706.2011.20131.x

Chapman, B. B., Hulthén, K., Brodersen, J., Nilsson, P. A., Skov, C., Hansson, L. A., & Brönmark, C. (2012). Partial migration in fishes: Causes and consequences. *Journal of Fish Biology*, **81**, 456–478. https://doi. org/10.1111/j.1095-8649.2012.03342.x

Cornaby SW. 2008 The handbook of X-ray single-bounce monocapillary optics, including optical design and synchrotron applications. Doctoral dissertation. Cornell University, Ithaca, NY, USA.

Dittman, A. H. & Quinn, T. P. (1996). Homing in Pacific salmon: mechanisms and ecological basis. *Journal of Experimental Biology*, **199**, 83–91.

Duponchelle, F., Pouilly, M., Pécheyran, C., Hauser, M., Renno, J. F., Panfili, ... Baras, E. (2016). Trans-Amazonian natal homing in giant catfish. *Journal of Applied Ecology*, **53**, 1511-1520.

Elsdon, T. S., & Gillanders, B. M. (2003). Reconstructing migratory patterns of fish based on environmental influences on otolith chemistry. *Reviews in Fish Biology and Fisheries,* **13**, 219–235.

Elsdon TS, Wells BK, Campana SE, Gillanders BM, Jones CM, Limburg KE, Secor DH, Thorrold SR, Walther BD (2008) Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences using five methods. *Oceanography* and *marine biology*, **46**, 207–330.

Fearnside, P. M. (2014). Brazil's Madeira River dams: A setback for environmental policy in Amazonian development. *Water Alternatives*, **7**, 154-167.

Fearnside, P. M. (2015) *Hidrelétricas na Amazônia: impactos ambientais e sociais na tomada de decisões sobre grandes obras-Vol* 1. Manaus, Brazil: Editora do INPA.

Finer, M., & Jenkins, C. N. (2012). Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PLoS ONE*, **7**, e35126.

Garcez, R.C.S., Humston, R., Harbor, D. & Freitas, C.E.C. (2015) Otolith geochemistry in young-of-the-year peacock bass Cichla temensis for investigating natal dispersal in the Rio Negro (Amazon – Brazil) river system. *Ecology of Freshwater Fish*, **24**, 242–251

García Dávila, C., Castro-Ruiz, D., Renno, J.F., Chota-Macuyama, W., Carvajal-Vallejos, F.M., Sanchez, H., Angulo, C., Nolorbe, C., Alvarado, J., Estivals, G., Núñez-Rodríguez, J. & Duponchelle, F. (2015) Using barcoding of larvae for investigating the breeding seasons of pimelodid catfishes from the Marañon, Napo and Ucayali rivers in the Peruvian Amazon. *Journal of Applied Ichthyology,* **31,** 40-51.

García Vasquez, A., Alonso, J.C., Carvajal, F., Moreau, J., Nuñez, J., Renno, J.F., Tello, S., Montreuil, V. & Duponchelle, F. (2009) Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. *Journal of Fish Biology,* **75,** 2527-2551.

Gillanders, B. M. (2005). Otolith chemistry to determine movements of diadromous and freshwater fish. *Aquatic Living Resources*, **18**, 291–300. DOI: 10.1051/alr:2005033

Hauser, M., Doria, C. R. C., Melo, L. C. R., Santos, A. R, Ayala, D. M., Nogueira, L. D., Amadio, S., Fabré, N., Torrente-Vilara, G., García-Vásquez, A., Renno, J-F., Carvajal-Vallejos, F. M., Alonso, J. C., Nuñez, J. & Duponchelle, F. (2018). Age and Growth of Amazonian migratotory catfish *Brachyplatystoma rousseauxii* in the Madeira River basin before the construction of dams. *Neotropical Ichthyology*, **16**, e170130. DOI: 10.1590/1982-0224-20170130

Hermann, T. W., Stewart, D. J., Limburg, K. E., & Castello, L. (2016). Unravelling the life history of Amazonian fishes through otolith microchemistry. *Royal Society Open Science*, **3**, 160206. DOI: 10.1098/rsos.160206

Hoffman J.I., Forcada J. (2012). Extreme natal philopatry in female Antarctic fur seals (*Arctocephalus gazella*). *Mammalian Biology*, **77**, 71–73.

Kendal, N. W., McMillan, J. R., Sloat, M. R., Buehrens, T. W., Quinn, T.P., Pess, G. R., … Zabel, R. W. (2015). Anadromy and residency in steelhead and rainbow trout (Oncorhynchus mykiss): a review of the processes and patterns. *Canadian Journal* of *Fisheries and Aquatic* Sciences, **72**, 319–342.

Kennedy, B.P., Folt, C.L., Blum, J.D. & Chamberlain, C.P. (1997) Natu- ral isotope markers in salmon. *Nature*, **387**, 766–767.

Kennedy, B.P., Blum, J.D., Folt, C.L. & Nislow, K.H. (2000) Using natu- ral strontium isotopic signatures as fish markers: methodology and application. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2280–2292.

Latrubesse, E. M., Arima, E. Y, Dunne, T., Park, E., Baker, V. R., d'Horta, F. M., …. Stevaux, J. C. (2017). Damming the rivers of the Amazon basin. *Nature*, **546**, 363-369.

Lees, A. C., Peres, C. A., Fearnside, P. M., Schneider, M., & Zuanon, J. A. S. (2016). Hydropower and the future of Amazonian biodiversity. *Biodiversity and Conservation*, **25**, 451-466.

Limburg KE, Huang R, Bilderback DH. (2007). Fish otolith trace elementmaps: new approaches with synchrotronmicrobeam X-ray fluorescence. *X-Ray Spectrom*, **36**, 336–342. (doi:10.1002/xrs.980)

Limburg KE,Olson C,WaltherY,DaleD,Slomp CP, Høie H. 2011 Tracking Baltic hypoxia and cod migration overmillenniawith natural tags. Proc. Natl Acad.Sci.USA **108**, E177–E182. (doi:10.1073/pnas.1100684108)

Limburg, K. E, & Elfman, M. (2017). Insights from two-dimensionalmapping of otolith chem- istry. *Journal of Fish Biology*, **90**, 480–491. doi: 10.1111/jfb.13048).

Lord, C., Tabouret, H., Claverie, F., Pécheyran, C. & Keith, P. (2011). Femtosecond laser abla- tion ICP-MS measurement of otolith Sr:Ca and Ba:Ca composition reveal differential use of freshwater habitats for three amphidromous *Sicyopterus* (Teleostei: Gobioidei: Sicydiinae) species. *Journal of Fish Biology*, **79**, 1304–1321.

Lucas, M.C. & Baras, E. (2001) *Migration of Freshwater Fishes*. Blackwell Science Ltd., Oxford.

Miller, K. E., & Smallwood, J. A. (1997). Natal dispersal and philopatry of southeastern American Kestrels in Florida. *Wilson Bulletin*, **109,** 226-232)

Mills, D.H. (1986). Threats to the Atlantic salmon (*salmo salar)* at various stages of its life-history. *Environmental Conservation*, **13**, 257–260. DOI:10.1017/ S0376892900036316

MPA (2013). *Boletim estatístico de pesca e aquicultura do Brasil 2011*. Brasília: Ministério da Pesca e Aquicultura.

Northcote T. G. (1997). Potamodromy in Salmonidae - living and mov- ing in the fast lane. *North American Journal of Fisheries Management*, **17**, 1029-1045.

Palmer, M. R., & Edmond, J. M. (1992) Controls over the strontium isotope composition of river water. *Geochimica et Cosmochimica Acta*, **56**, 2099–2111.

Pouilly M., Point D., Sondag F., Henry M. & Santos R.V. (2014) Geographical origin of Amazonian Freshwater Fishes Fingerprinted by 87Sr/86Sr Ratios on Fish Otoliths and Scales. *Environmental Science & Technology*, **48**, 8980–8987.

Rooker, J. R., Secor,D. H., DeMetrio, G., Schloesser, R., Block, B. A. & Neilson, J. D. (2008). Natal homing and connectivity in Atlantic bluefin tuna populations. *Science*, **322**, 742–744

Saiget, D. A., M. R. Sloat & G. H. Reeves (2007). Spawning and movement behavior of migratory coastal cutthroat trout on the western Copper River Delta, Alaska. *North American Journal of Fisheries Management*, **27**, 1029–1040.

Sammons, S. M. (2015). First evidence of potadromy and partial migration in black basses: shoal bass *Micropterus cataractae* (Actinopterygii , Centrarchidae) in the Upper Flint River , USA. *Hydrobiologia*, **751**, 135–146. DOI 10.1007/s10750-015-2182-8

Secor DH, Kerr LA (2009) A lexicon of life cycle diversity in diadromous and other fishes. American Fisheries Society Symppsium Series, **69**, 537–556.

Secor, D. H. (2010). Is otolith science transformative? New views on fish migration. *Environmental Biology of Fishes*, **89**, 209–220. DOI 10.1007/s10641-010-9683-0

Sloat, M.R., Fraser, D.J., Dunham, J.B., Falke, J.A., Jordan, C.E., McMillan, J.R. & Ohms, H.A. (2014). Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. *Reviews in Fish Biology and Fisheries*, **24**, 689–707.

Souza, R . G . C, Humston, R., & Freitas, C. (2016). Movement patterns of adult peacock bass *Cichla temensis* between tributaries of the middle Negro River basin (Amazonas – Brazil): an otolithgeochemical analysis. *Fisheries Management and Ecology*, 23, 76–87.

Tyus, H. M. (1990). Potamodromy and reproduction of Colorado squawfish in the Green River Basin, Colorado and Utah. *Transactions of the American Fisheries Society*, **119**, 1035–1047.

Van Damme, P.A., Carvajal-Vallejos, F., Camacho, J., Muñoz , H. & Coronel, J.S. (2011) Peces migratorios de la Amazonía Boliviana. *Los peces y delfines de la Amazonía Boliviana - Hábitats, potencialidades y amenazas* (eds P.A. Van Damme, F. Carvajal-Vallejos & J. Molina Carpio), pp. 149-200. Editorial INIA, Cochabamba, Bolivia.

Walther B, Thorrold S (2006). Water, not food, contributes the majority of strontium and barium deosited in the otoliths of a marine fish. *Marine Ecology Progress Series*, **311**, 125–130.

Walther, B. D. & Limburg, K. E. (2012). The use of otolith chemistry to characterize diadromous migrations. *Journal of Fish Biology*, **81**, 796–825

Walther, B. D., & Limburg, K. E. (2017) Frontiers in otolith chemistry: insights, advances and applications. *Journal of Fish Biology*, **90**, 473–479 doi:10.1111/jfb.13266.

Waples, R.S., Zabel, R.W., Scheuerell, M.D., and Sanderson, B.L. (2008). Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. *Molecular Ecology*, **17**, 84–96. doi:10.1111/j.1365-294X.2007.03510.x.

Webb SD, Woodcock SH, Gillanders BM (2012) Sources of otolith barium and strontium in estuarine fish and the influence of salinity and temperature. *Marine Ecology Progress Series*, **453**, 189–199.

Weyer, J., & Schmitt, T. (2013). Knowing the way home: strong philopatry of a highly mobile insect species, *Brenthis ino*. *Journal of Insect Conservation,* **17**, 1197–1208. DOI 10.1007/s10841-013-9601-9

Winemiller, K. O., McIntyre, P. B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., … Sáenz, L. (2016). Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, **351**, 128–129.

Yee H,Measures C, Edmond J. 1987 Selenium in the tributaries of the Orinoco in Venezuela. Nature **326,** 686–689. (doi:10.1038/326686a0)

CAPÍTULO III

História de vida de *Brachyplatystoma rousseauxii* sob a perspectiva dos empreendimentos hidrelétricos na Amazônia

1 – INTRODUÇÃO

A migração é a história da vida em movimento. Anualmente bilhões de animais migram em uma incrível variedade de escalas espaciais e temporais, comportamentos estes que fascinam os cientistas desde a antiguidade (Aristóteles 350 A.C.) e atualmente vêm somando cada vez mais esforços para a compreensão de seus diferentes padrões (DINGLE, 1996; LUCAS; BARAS 2001; CHAPMAN et al., 2011; BAUER; HOYE, 2014). Os processos migratórios além de moldarem a história de vida dos indivíduos e o destino das populações, também determinam as estruturas da comunidade e do ecossitema, influenciando diretamente os processos e padrões evolutivos da biodiversidade local e global (NATHAN et al., 2008). Essa importância dos animais migratórios é bem exemplificada pelo papel que eles desempenham na ligação e estruturação das teias tróficas das diferentes comunidades residentes, ao longo de suas rotas migratórias, refletindo no melhor funcionamento e maior resiliência dos ecossistemas (WILCOVE; WIKELSKI, 2008; BAUER; HOYE, 2014).

Desse modo, a compreensão da ecologia da migração animal torna-se ainda mais pungente nos dias atuais, considerando as diversas e intensas perturbações antropogênicas na rota migratória desses indivíduos (CHAPMAN et al., 2011). Neste tocante, notabiliza-se a bacia Amazônica, reconhecida pela sua extraordinária diversidade de peixes a qual vem sendo categoricamente ameaçada pela construção de inúmeras usinas hidrelétricas nesse sistema (FINER; JENKINS, 2012; CASTELLO et al., 2013; CASTELLO; MACEDO 2016; LEES et al., 2016; WINEMILLER et al., 2016; FORSBERG et al., 2017; LATRUBESSE et al., 2017; ANDERSON et al., 2018). Esses empreedimentos hidrelétricos além de impactarem diretamente o ciclo de vida das espécies ictiícas, pelo bloqueio de suas rotas migratórias, também afetam os pescadores que dependem da atividade pesqueira, tanto financeiramente como para subsistência familiar (FEARNSIDE, 2014; 2015).

Dentre os recursos pesqueiros de grande importância econômica na Amazônia ameaçados pelos barramentos hidrelétricos está *Brachyplatystoma rousseauxii*, popularmente conhecida como dourada. Esse bagre é reponsável por uma produção superior a 14 mil toneladas considerando apenas estatísticas da amazônia brasileira (MPA, 2013). E recentemente ganhou o status da espécie com a maior migração já descrita inteiramente dentro de água doce, percorrendo mais de onze mil quilômetros entre sua área de nascimento nos andes, crescimento na região estuarina do rio Amazonas, e retorno aos andes no período reprodutivo (DUPONCHELLE et al., 2016; BARTHEM et al., 2017).

Assim, quando consideramos *B. rousseauxii,* em particular, os impactos dos barramentos tomam uma proporção de escala multinacional, visto que as áreas reprodutivas estão localizadas na Bolívia, Colômbia, Equador e Peru, ao passo que as regiões de berçário e crescimento estão situadas dentro do Brasil (BARTHEM; GOULDING, 1997; DUPONCHELLE et al., 2016; BARTHEM et al., 2017). Nessa perspectiva, já se observa os efeitos dos barramentos das usinas hidrelétricas de Santo Antônio Energia (SAE) e Energia sustentável do Brasil (ESBR), construídas na porção brasileira do rio Madeira entre 2009 e 2013, sobre a produção pesqueira de *B. rousseauxii* (CARVAJAL-VALLEJOS, 2013; LIMA, 2017; VAN DAMME dados não publicados). Em relação a porção brasileira do rio Madeira, Lima (2017) observou um declínio de 74% nas capturas dessa espécie no principal mercado pesqueiro de Rondônia, após o início da construção dos barramentos em 2009, ao passo que para a porção boliviana a representatividade desse bagre decaiu de 2,3 - 8,8% para 0,65% (VAN DAMME dados não publicados). Ainda considerando a Bolívia e o Peru, a intensificação da pesca dos indivíduos reprodutores deve piorar o panorama de produção de *B. rousseauxii* nesses países, com a manutenção da população dependendo sobretudo dos juvenis coletados acima das cachoeiras (CARVAJAL-VALLEJOS, 2013; DUPONCHELLE et al., 2016). E a partir desse contexto, um outro agravante que deve ser avaliado, é o fato de que peixes residentes comumente crescem menos em comparação àqueles que realizam amplas migrações (e separam geograficamente as áreas reprodutivas daquelas de berçário e crescimento) (WAPLES et al., 2008; KENDAL et al., 2015), podendo refletir diretamente no menor recrutamento de indivíduos no Alto Madeira.

Apesar de menos discutido, mas tão importante quanto os impactos no aporte rio acima das espécies migradoras, está a interferência na rota de deriva de ovos, larvas e juvenis rio abaixo. Possivelmente o aporte dessas fases iniciais de desenvolvimento será comprometido nas áreas do Baixo rio Madeira e até em outras porções da bacia amazônica (CELLA-RIBEIRO et al., 2015). Nessa perspectiva, esse trabalho objetivou investigar os diferentes comportamentos migratórios de *B. rousseauxii* ao longo de toda a bacia amazônica e as possíveis diferenças de crescimento associadas a tais comportamentos, bem como avaliar os impactos das usinas hidrelétricas do rio Madeira sobre essa migração, a partir da razão isotópica de ^{87}Sr: ^{86}Sr dos otólitos.

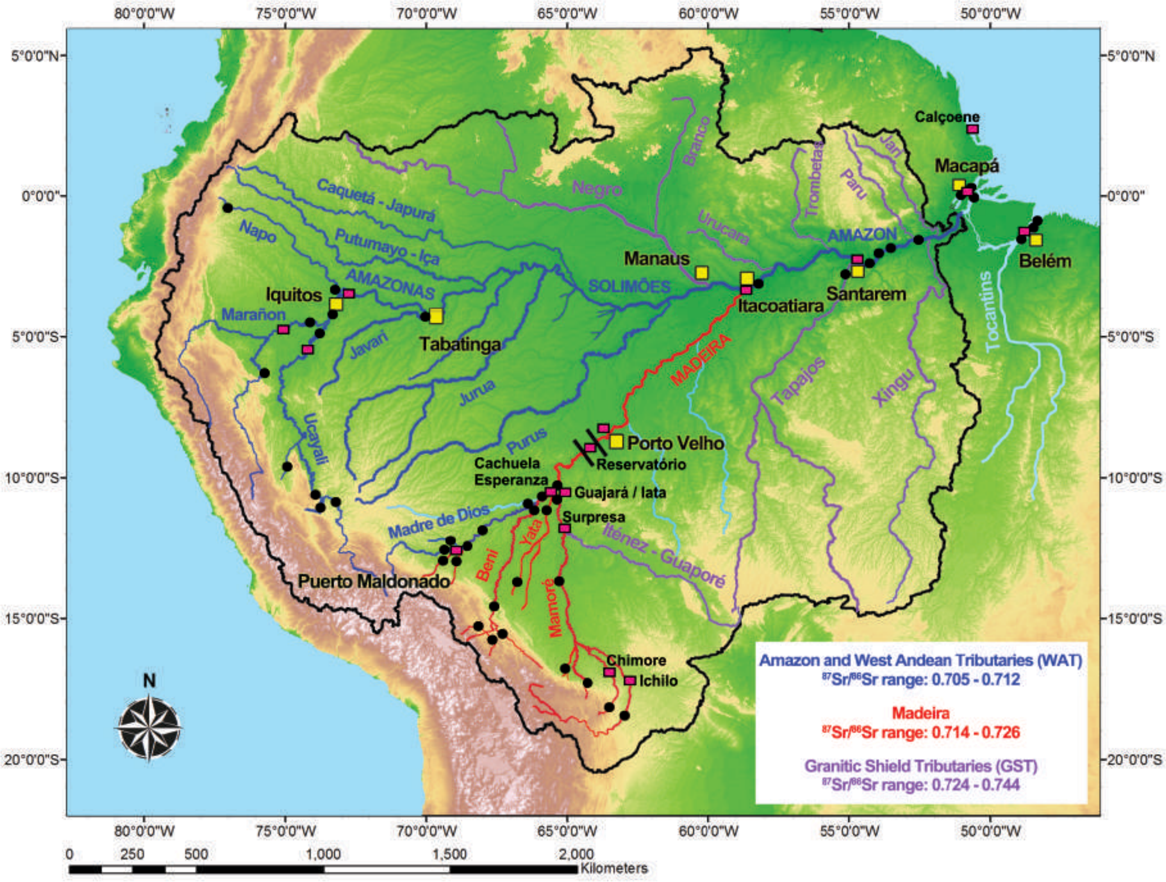
2 - MATERIAL E MÉTODOS

2.1 - *ÁREA DE ESTUDOS*

A bacia Amazônica possui área estimada em 6.300.000 km^2, com aproximadamente 5 milhões em território brasileiro, e o restante distribuído entre os demais países da América do Sul (Peru, Bolívia, Colômbia, Equador, Venezuela e Guiana). Este complexo sistema hídrico é limitado: a oeste pela Cordilheira dos Andes (com elevações de até 6000 m, onde ocorre a nascente do leito principal do rio Amazonas, no sopé dos Andes peruanos); ao norte pelo Planalto das Guianas (com picos montanhosos de até 3000 m); ao sul pelo Planalto Central (altitudes típicas de 1200 m) e à leste pelo Oceano Atlântico, onde toda a água captada na bacia (proveniente de cerca de 7 mil rios) escoa para o mar, despejando cerca de 3 milhões de toneladas de sedimentos por dia (FIORAVANTI, 2008).

Com tamanha magnitude, este complexo sistema hídrico é formado por grande diversidade de formações geológicas, com diferentes razões isotópicas de estrôncio (^{87}Sr:^{86}Sr), as quais refletem diretamente nos valores isotópicos de seus corpos de águas, permitindo distinguir a bacia amazônica em pelo menos 3 grandes sub-bacias: 1- Tributários andinos ocidentais (WAT), calha principal do rio Amazonas e seus tributários da planície de inundação, e o rio Madre de Dios (0,705-0,712); 2- Sub-bacia do rio Madeira e Baixo rio Negro (0,714-0,726); e 3- Tributários que drenam os Escudos Graníticos da Guiana (GST) (0,724-0,744) (PALMER & EDMOND, 1992; GAILLARDET et al., 1997; QUEIROZ et al., 2009; POUILLY et al., 2014, SANTOS et al. 2015; DUPONCHELLE et al., 2016). A pequena variabilidade anual e sazonal destas razões isotópicas permite a reconstrução verossímel de padrões migratórios dos peixes que realizam grandes deslocamentos como *B. rousseauxii*. Nessa perspectiva, a área de estudo compreendeu 65 pontos amostrais de água e 16 de peixes, ao longo de toda bacia amazônica, englobando toda a área de ciclo de vida dessa espécie, desde a porção andina até o estuário (Figura 1).

Figura 1 - Área de estudo.



Quadrados amarelos referem-se às principais cidades ao longo da bacia amazônica; quadrados rosa referem-se aos locais de amostragem de peixes; círculos negros referem-se às estações de amostragem de água com os seguintes códigos de cores: azul para os afluentes andinos ocidentais do Amazonas (WAT), calha principal do rio Amazonas e seus tributários da planície de inundação, e o rio Madre de Dios; vermelho para o rio Madeira e Baixo Negro; e roxo para os afluentes de escudo granítico com águas negras ou límpidas (GST). As duas barras pretas transversais no rio Madeira, a montante de Porto Velho, representam as usinas de Jirau e Santo Antônio construídas desde 2011. Fonte: Hauser (2018)

2.3 – *COLETA DE DADOS*.

2.3.1 – Amostragem das águas.

Como na região tropical o pulso de inundação é o principal fator determinante nas características ambientais e biológicas, as coletas dos 65 pontos de amostragem de águas, distribuídos entre Brasil, Bolívia e Peru, foram realizadas durante a cheia e vazante dos rios, entre outubro de 2014 e março de 2017. Os dados geoquímicos dos rios Marañon, Napo e Ucayali foram cedidos pelo Observatório de Pesquisa Ambiental/ Controle Geodinâmico, Hidrológico e Biogeoquímico da Erosão/Alteração e Transporte de Material da Bacia Amazônica (ORE/HYBAM) (http://www.ore-hybam.org/).

As amostras foram coletadas próximas a superfície (cerca de 40 cm de profundidade) da porção média dos rios (na proa da voadeira com o motor da mesma desligado, para evitar contaminação com os gases da queima do combustível) em frascos plásticos de polietileno lavados com ácido nítrico 5%, e acondicionadas em caixas térmicas com gelo.

Na região de Macapá, considerando a influência da maré do oceano Atlântico sobre a foz do rio Amazonas, foram realizadas duas coletas por dia em cada ponto de amostragem: uma durante a vazante e outra na cheia do rio. Por sua vez, afim de determinar possível estratificação da coluna de água na região estuariana de Belém (visto a influência da salinidade da maré oceânica), além da superfície também foram tomadas amostras próximas ao fundo do rio Amazonas, com o auxílio de uma *Garrafa de Van Dorn* vertical (Figura 2).

Nas proximidades de Itacoatiara, com intuito de verificar como o valor isotópico se comportava na região de confluência com o rio Madeira, além de amostragens na superfície também foram realizadas coletas no fundo da coluna de água, tanto para o centro do canal do rio Amazonas, como para suas margens direita e esquerda.

Para assegurar que as características físico-químicas fossem mantidas, todas as amostras foram filtradas em até no máximo 12 horas após a coleta, com membranas 0,47-µm Millipore DURAPORE®, e estocadas em frascos com ácido HNO_3 supra puro bidestilado (Figura 2).

Figura 2 - Coleta das amostras de água.

Tomada dos parâmetros limnológicos (A); Coleta de amostras de fundo com *Garrafa de Van Dorn* (B); Sistemas de filtração em polietileno (C) ; Filtragem das águas com o auxílio de bomba manual (D). Fonte: Araújo (2015).

2.3.2 – Amostragem dos peixes.

Exemplares de *B. rousseauxii* (Figura 3) foram amostrados entre fevereiro de 2005 e junho de 2017 nos principais portos pesqueiros da Bolívia (rios Beni e Mamoré) e Peru (rios Madre de Dios, Marañon e Ucayali). Na porção brasileira, os peixes analisados foram obtidos juntos ao Programa de Monitoramento e Apoio à Atividade Pesqueira do rio Madeira, desenvolvido pelo Laboratório de Ictiologia e Pesca (LIP), da Universidade Federal de Rondônia (UNIR). O referido programa acompanhou a pescaria artesanal realizada por pescadores profissionais, ao longo do rio Madeira, no trecho compreendido entre Surpresa e Humaitá (AM), entre abril de 2009 e junho de 2012 (antes e após a implantação do complexo hidrelétrico do rio Madeira). Entre janeiro 2015 e junho de 2017 também foram amostrados exemplares em Guajará-Mirim, São Sebastião, na região estuarina de Belém (peixes comercializados no Mercado Ver-o-peso provenientes da baía do Marajó) e de Macapá (na peixes pescados na Ilha da Pedreira e na comunidade pesqueira de Calçoene), e na confluência dos rios Madeira e Amazonas (peixes comercializados no Mercado Pesqueiro de Itacoatiara) (Figura 4).

Figura 3 - Exemplar de *B. rousseauxii*.

Indivíduo amostrado no rio Madeira com 60 cm de comprimento padrão. Fonte : LIP /UNIR (2013).

De cada exemplar amostrado foram tomados os dados biométricos de comprimento padrão (cm) e peso total (g). Em seguida, as cabeças coletadas foram identificadas com códigos de campo (local, data e número de registro) e armazenadas em caixas térmicas com gelo (Figura 4).

Figura 4 - Coleta dos peixes.

Pesca com malhadeira descaída (A); Pesca nas burras da extinta cachoeira de Teotônio (B); coleta de peixes no Mercado Ver-o-Peso em Belém (C); tomada dos dados biométricos dos exemplares (D), retirada da cabeça (E). Fontes: A) Lima (2011); B) Torrente-Vilara (2009); C) Hauser (2015) ; D e E) LIP/UNIR (2012).

2.4 – *ANÁLISE DOS DADOS*

2.4.1 - Razão de ^{87}Sr:^{86}Sr das Águas

Todas as amostras de água foram analisadas no Laboratório de Estudos Geocronológicos, Geodinâmicos e Ambientais da Universidade de Brasília (UnB). Os processos de separação e digestão foram realizados em sala limpa de ISO classe 2. Para cada amostra analisada foram evaporados 500 ml de água (filtrados e acidificados), obtendo-se cerca de 50ng de Sr (equivalente a 15 ou 20 ml da amostra de água). Em seguida, este resíduo foi dissolvido em 1 ml de ácido nítrico 2N, e os isótopos de Sr foram separados através de resinas de troca iônica (Eichrom Sr-Spec®). As razões isotópicas foram medidas no espectrômetro de massa por termo-ionização (N-TIMS) THERMO SCIENTIFIC TRITON. A acurácia das análises foi controlada pela análise de padrão internacional NBS987 (com valor médio de 0,71027 ±1).

2.4.2 - Preparação dos otólitos

A extração dos otólitos *Lapillus* foi realizada por meio de cortes transversais no centro dos ossos basio-supraoccipital, com auxílio de serra de mão e pinça, segundo metodologia de

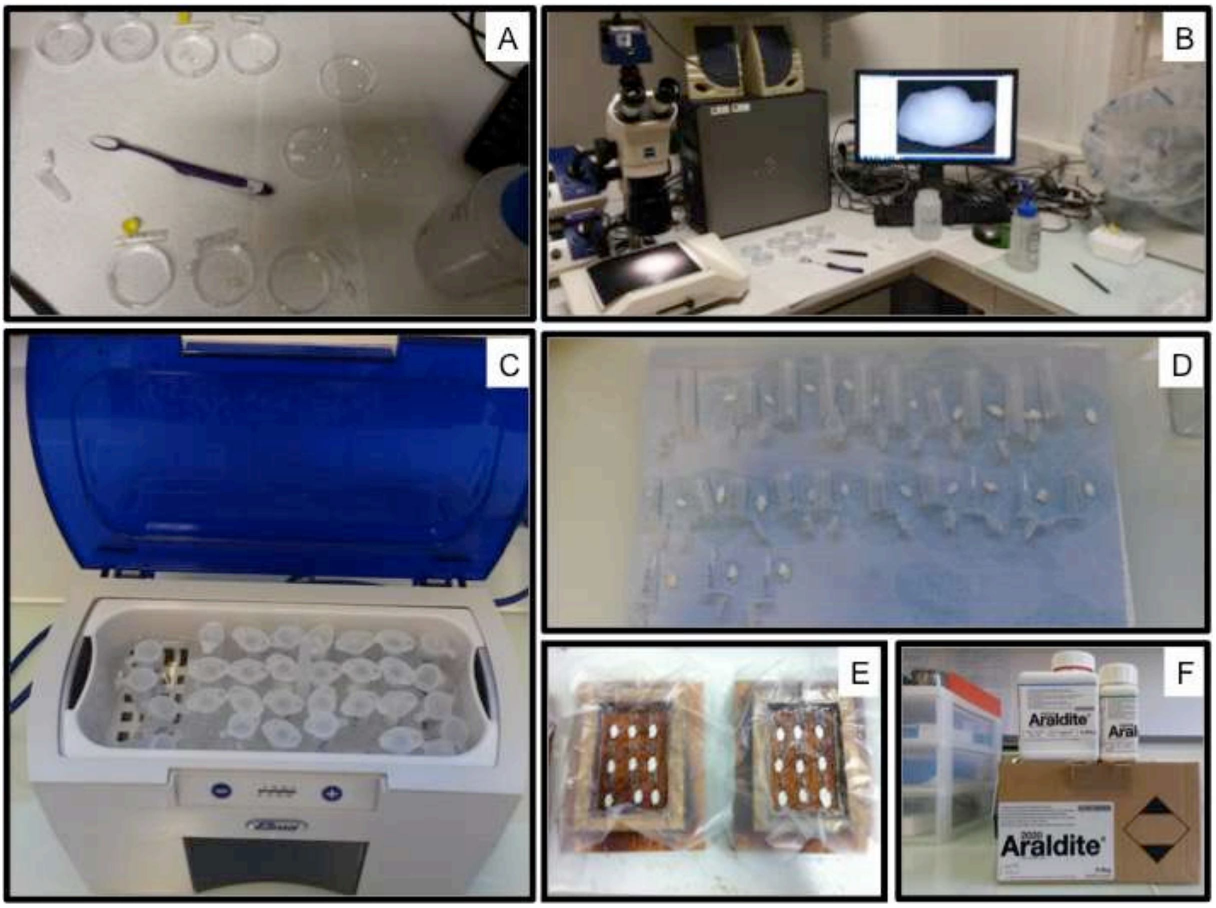
Valeruz-Rêgo e colaboradores (1998). Posteriormente foram limpos, secos e armazenados em envelopes contendo todos os dados dos respectivos exemplares (Figura 5).

Figura 5 - Retirada dos otólitos.

Corte das cabeças com o auxílio de morsa e serra de mão (A, B, C); extração dos otólitos com auxílio de pinça (D e E); pares de otólitos *Lapilli* e *Asterici* com os dados do exemplar (F). Fontes: A, B, D, E e F) Hungria (2011); C) Araújo (2015).

Todos os otólitos foram processados no laboratório *Marine Biodiversity Exploitation and Conservation* (MARBEC), na Universidade de Montpellier (França). Com o intuito de evitar contaminação, antes das análises microquímicas, os otólitos foram acondicionados em tubos de *eppendorf* com água destilada por 24 horas, lavados com auxílio de escova, e enxaguados novamente com água destilada. Para auxiliar a localização do núcleo no momento do corte, os otólitos foram fotografados em estereomicroscópio com câmera AxioCam Zeiss acoplada. Em seguida, os otólitos foram lavados em banheira ultrassônica por 5 minutos e secos em estufa de circulação a 60^0 C, por 48 horas. Após a secagem os otólitos foram emblocados em resina epóxica Araldite 2020 (com a parte dorsal voltada para cima) e acondicionados novamente em estufa a 60^0 C, por 24 horas, até a obtenção de placas resistentes (Figura 6).

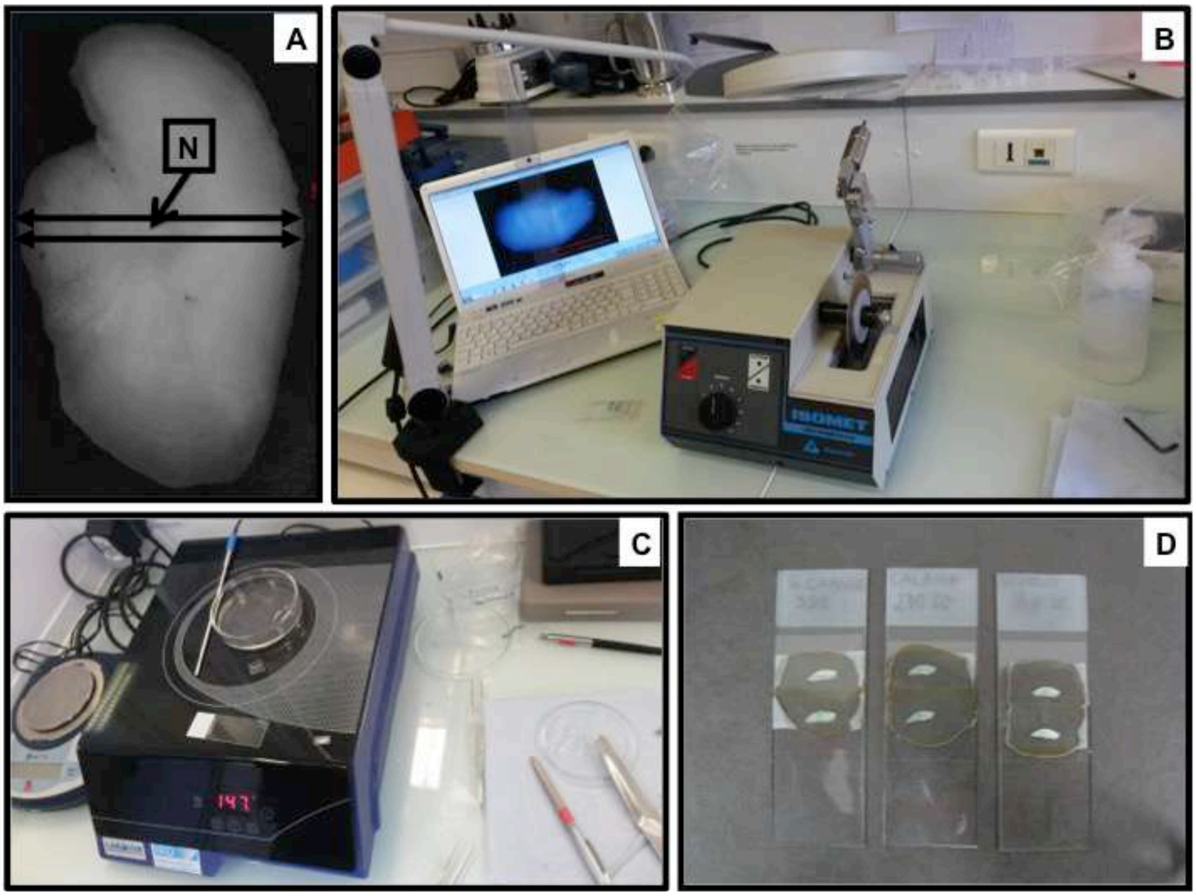
Figura 6 - Processamento dos otólitos.



Limpeza dos otólitos (A); fotografia dos otólitos em estereomicroscópio (B); limpeza dos otólitos em banheira ultrassônica (C); secagem dos otólitos em papel absorvente (D); emblocamento dos otólitos com resina epóxi (E e F). Fonte: Hauser (2016).

Com o auxílio de uma lupa de bancada os blocos de otólitos resinados foram cortados dorso-ventralmente com um micrótomo digital de baixa velocidade (ISOMET, BUEHLER, LTDA, 2009, D€usseldorf- Germany), processo que gerou finos cortes (com espessura entre 0,7 e 0,9 mm) os quais continham o núcleo. Estes cortes foram polidos com discos de polimento (1200 e 2400 micras) e água ultrapura até a visualização do núcleo em um de seus lados. Posteriormente foram colados em pequenas lâminas de vidro, com o auxílio de placa aquecedora e cola *Cristal Bond*, e polidos novamente até a perfeita visualização do núcleo. Em seguida estas placas de vidro contendo os cortes foram levadas à banheira ultrassônica por 5 minutos, secas com papel absorvente e acondicionadas em sacos plásticos herméticos (Figura 7). Para auxiliar a localização do núcleo durante o processo de ablação a laser, as lâminas foram fotografadas em estereomicroscópio com câmera AxioCam Zeiss acoplada (Figura 8 A).

Figura 7 - Preparação do otólitos para as análises microquímicas.



Preparação dos otólitos: localização do núcleo (A); corte dos otólitos no micrótomo digital com o auxílio de lupa de bancada (B); colagem dos cortes de otólitos em lâminas de vidro com o auxílio da placa aquecedora e cola *Cristal Bond* (C); lâminas prontas (D). Fonte: Hauser (2018).

2.4.3 - Razão de $^{87}Sr:^{86}Sr$ dos otólitos

As análises isotópicas de estrôncio ($^{87}Sr:^{86}Sr$) dos otólitos foram realizadas por ablação a laser em espectrômetro de massa com multicoletor no *Laboratoire de Chimie Analytique Bio-inorganique et Environnement* (LCABIE) do *Institut Pluridisciplinaire de Recherche sur l'Environnement et les Matériaux* (IPREM), na *Université de Pau et des Pays de l'Adour*, e no *Laboratoire Cycles Géochimiques et ressources, Département Ressources physiques et Écosystèmes de fond de Mer* (REM), do *Institut Français de Recherche pour l'Exploitation de la Mer* (IFREMER) em Brest, ambos na França. A ablação a laser ocorreu ao longo de um transecto dos otólitos, partindo do núcleo (momento de eclosão do peixe) em direção ao bordo (momento de captura do peixe), perpendicular às marcas de crescimento, permitindo refinada reconstrução do uso do hábitat durante todo o ciclo de vida de cada indivíduo analisado. A fim de evitar o efeito de explosão no núcleo, iniciou-se a ablação 200 μm antes deste. As características do espectrômetro de massa com multicoletor e do laser, utilizados em cada laboratório, estão resumidas na tabela 1.

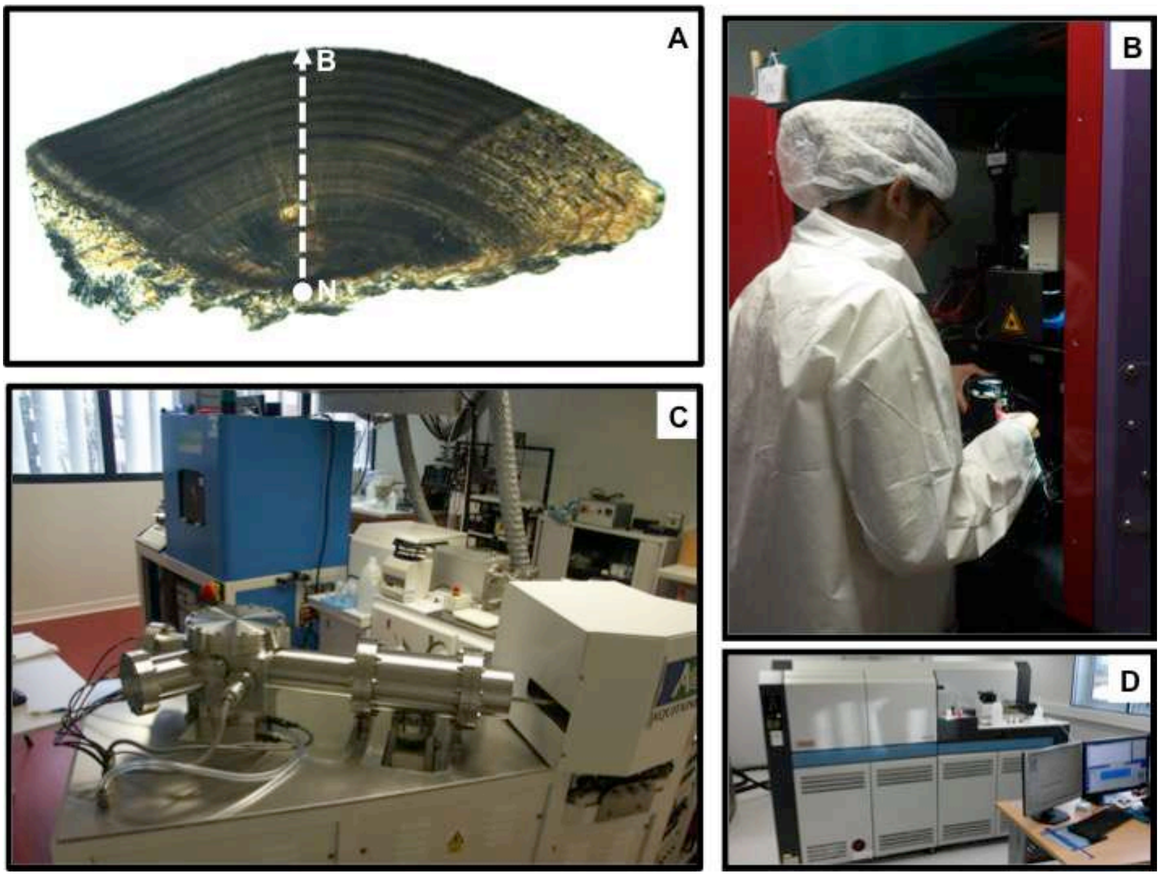
Tabela 1 – Propriedades do espectrômetro de massa com multicoletor e do laser, utilizados em cada laboratório

Parâmetro	LCABIE-IPREM - Pau	PSO-IFREMER - Brest
ICP-MS		
Espectrômetro de massa	Nu Plasma HR (Nu instruments)	MC-ICP-MS Thermo Neptune
Potência do plasma (W)	1300 (wet)	1200 (wet)
Gás frio (L/min)	13	16
Gás auxiliar (L/min)	0.8	0,8
Gás Nebulizador (L/min)	24	0,6
Gás adicional (L/min)	He = 0.5	0,5
Nebulizador	vidro microconcêntrico 200μL/min	PFA 50uL/min
Câmara de pulverização	ciclônica	Entrada dupla
Tempo de aquisição	5s	n x2s
Gás branco	10s	30s
Correção de pico	Sim	Sim
Método de validação	NIST-987	NIST-987
Modelo de correção de discriminação de massa	Exponencial	Exponencial
Correção de interferência	87Rb, 86Kr	87Rb, 86Kr
LASER		
Sistema	Lambda 3 Nexeya	213LSX CETAC
Fonte	UV-257 nm	Nd-YAG UV
Tamanho do ponto (um)	50-150	50-150
Velocidade da Ablação (um/s)	5	5
Energia (mJ)	10	4
Frequência (Hz)	2000	20
Fluxo do He (L/min)	0,35	0,6
Pré-ablação	No	No
Método de validação	NIES-22	NIES-22

Fonte: Hauser (2018).

Para verificar a confiabilidade das medidas de ^{87}Sr:^{86}Sr obtidas durante as análises, foi analisado um pélete em pó de ^{87}Sr:^{86}Sr para otólitos, certificado em laboratório (NIES22, material de referência certificado produzido pelo Instituto Nacional para Estudos Ambientais, Japão), duas vezes por dia. Para todas as análises, os valores FS-LA-MC-ICPMS ^{87}Sr:^{86}Sr corresponderam satisfatoriamente aqueles certificados em laboratório (Figura 8).

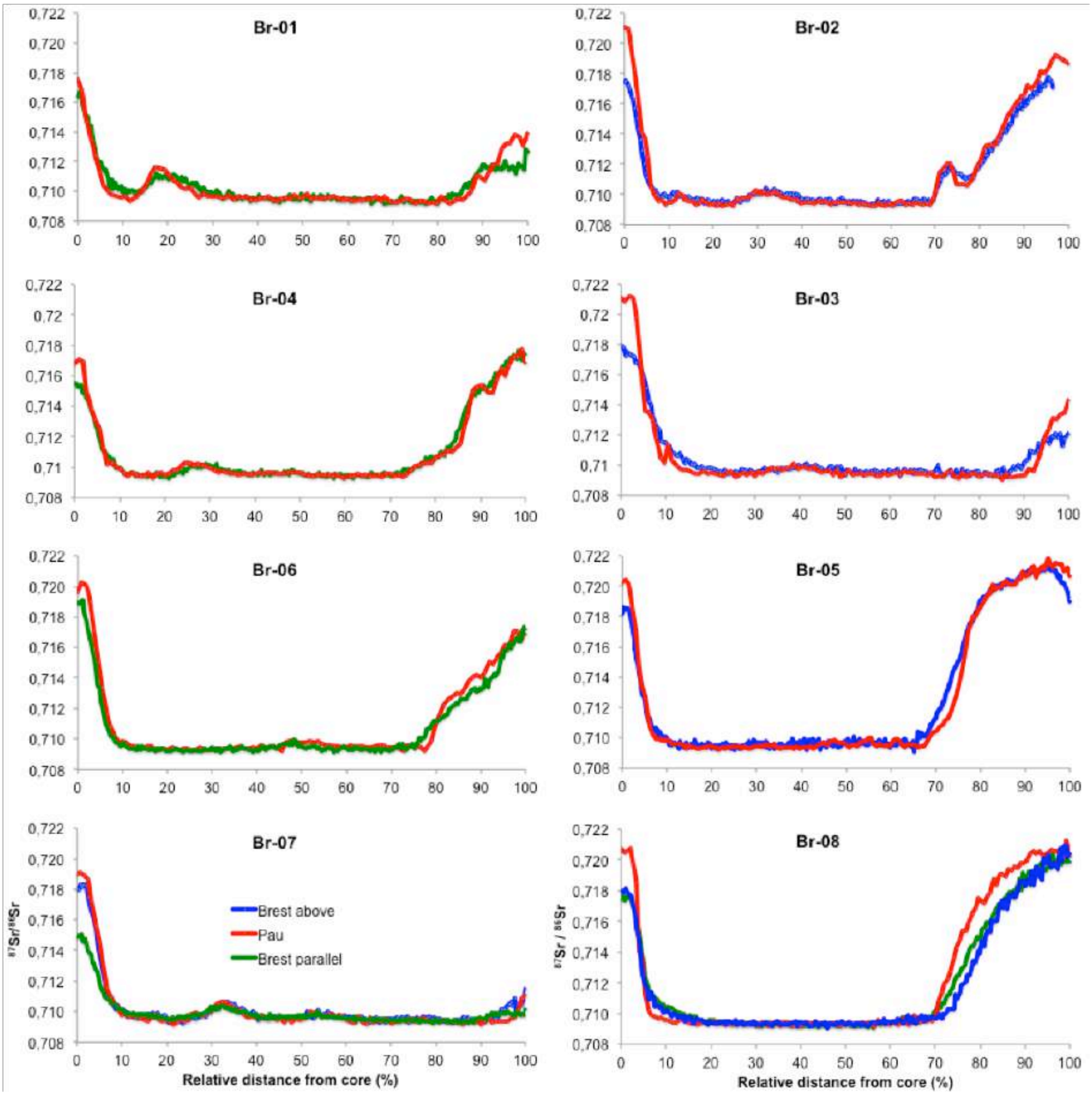
Figura 8 - Análise isotópica dos otólitos.



Corte transversal do otólito ilustrando o sentido do laser saindo do núcleo em direção ao bordo (A); espectrômetro de massa de ablação a laser com multicoletor do IPREM-Pau (B e C) e do IFREMER-Brest (D). Fontes: (A, C e D) Hauser (2016); B) Barbotin (2016).

Com o intuito de confirmar se os perfis de ^{87}Sr: ^{86}Sr dos otólitos trabalhados em Pau e Brest eram verossivelmente comparáveis, em virtude das diferenças de cada equipamento, oito indivíduos tiveram seus perfis isotópicos analisados em ambos os laboratórios (Figura 8). Os perfis de Brest foram realizados sobre (exatamente dentro) os *rasters* obtidos em Pau (curvas azuis; Br-02, 03, 05) ou paralelos e o mais próximo possível a estes *rasters* (curvas verdes; Br-01, 04, 06). Em alguns otólitos, as comparações foram realizadas tanto sobre cima quanto paralelamente aos *rasters* feitos em Pau (Br-07 e Br-08) (Figura 8). Os perfis realizados em ambos os laboratórios, usando diferentes *lasers* e MC-ICP-MS (ver Tabela 1 para detalhes), foram muito semelhantes, exceto para a região nuclear e do bordo de alguns otólitos, onde os *rasters* feitos em Brest exibiram valores um pouco menor do que àqueles de Pau. Estes resultados eram esperados, visto que a região nuclear é perdida durante a varredura do primeiro *raster*, ao passo que a borda normalmente tende a ser mais fina em alguns indivíduos, devido a diferenças de polimento ao longo do otólito durante a preparação dos mesmos. Confirmou-se assim a confiabilidade da comparação dos perfis isotópicos realizados em ambos os laboratórios.

Figura 9 - Comparação dos perfis de ^{87}Sr: ^{86}Sr dos otólitos de *B. rousseauxii* analisados em Pau e posteriormente em Brest.



Curvas vermelhas correspondem aos *rasters* analisados em Pau; curvas azuis correspondem aos *rasters* analisados em Brest sobre o *rasters* de Pau; curvas verdes correspondem aos *rasters* analisados em Brest paralelo e próximo aos *rasters* de Pau. Fonte: Hauser (2018)

2.4.4 – Cronologia das migrações

O tamanho mínimo, médio e máximo com a qual os juvenis de *B. rousseauxii* saíram do rio Madeira, após o nascimento na região de cabeceiras, e nos quais os indivíduos retornaram quando adultos, foram estimados a partir das regressão entre o raio transversal do otólito (R) e o comprimento padrão (Cp) dos indivíduos. Essas regressões foram estimadas por Duponchelle e colaboradores (2016), onde: $Cp = 0{,}030845^{\cdot *} R - 0{,}000093$ foi utilizada para indivíduos $\leq$ 45 cm; e $Cp = 70{,}545 * \mathrm{Ln}(R) - 469{,}65$ para indivíduos > 45 cm.

Então, a partir dos comprimentos obtidos por meio das regressões acima, determinou-se a idade desses indivíduos segundo a equação: $I_n = \{-\ln[1 - (Cp * Cp_{\infty} - 1)]K - 1\} + t_0$, onde: Cp é o comprimento padrão estimado pelo raio total do otólito; $Cp_{\infty =}102.84$ cm, é o comprimento assintótico; K= 0,57 é o coeficiente de crescimento do peixe; e $t_0 = 0{,}021$ é a idade teórica na qual o comprimento é zero. Esses três últimos parâmetros foram obtidos da curva VBGF estimada para *B. rousseauxii* por Hauser e colaboradores (2018) (ver capítulo 1). Apenas as idades nas quais o menor e maior indivíduo retornaram ao rio Madeira, foram determinadas pela contagem direta dos anéis de crescimento nos otólitos.

2.4.5 – Taxa de crescimento dos diferentes comportamentos migratórios

Com intuito de verificar possíveis diferenças na taxa de crescimento entre indivíduos *homers* e residentes do Alto rio Madeira (com estes últimos sendo subdividos em antes e após os represamentos dessa bacia), foi realizada uma análise de variância *one way* e um test T, a partir do comprimento padrão dos indivíduos dos diferentes comportamentos migratórios para as classes etárias de 2,5-3,4 e 3,5-4,4 respectivamente.

3 – RESULTADOS

3.1 – ^{87}*Sr:*^{86}*Sr DAS ÁGUAS*

Nos dois ciclos anuais estudados (entre outubro de 2014 e Março de 2017) foram coletadas 87 amostras de água em 65 pontos de coletas distribuídos entre Brasil (31) Bolívia (21) e Peru (13) (Tabela 2). A partir dessa amostragem foi possível diferenciar isotopicamente o rio Madeira, em pelo menos 4 principais grupos de corpos de água: 1- Madre de Dios; 2- Madeira, Tambopata, Inambari e Beni, 3- Mamoré, 4- Yata e; 5- Iténez-Gauporé (Figura 10). Embora o rio Amazonas seja mais homogêneo quando comparado ao Madeira, pode-se diferenciar dois padrões: 1) Afluentes andinos ocidentais do Amazonas até a confluência com o rio Negro (0,705-0,710); e 2) e calha principal do rio Amazonas a partir da confluência com o rio Negro até a região estuarina (0,710-0,712). Segundo os dados estuarinos de Vigia e Ilha do Sol, também foi possível observar dois padrões distintos: 1) em Maio de 2015, quando os valores de 0,716-0,717 sugerem que essa área sofreu grande influência do rio Tocantins; e 2) em Setembro de 2015, quando os valores foram semelhantes ao da calha principal do rio Amazonas (0,709-0,710). Ainda nessa região, o ponto de amostragem na Ilha do Sirituba (0,717-0,719) parece ser influenciado ao longo de todo o ano pelo rio Guamá (um afluente do GST), refletindo a proximidade com este tributário. Por sua vez, a área estuarina de Macapá exibiu valores semelhantes aos da calha principal do rio Amazonas para região (0,711), em ambos os períodos de coleta (Figura 10).

Tabela 2 - Valores da ^{87}Sr :^{86}Sr das águas da bacia amazônica.

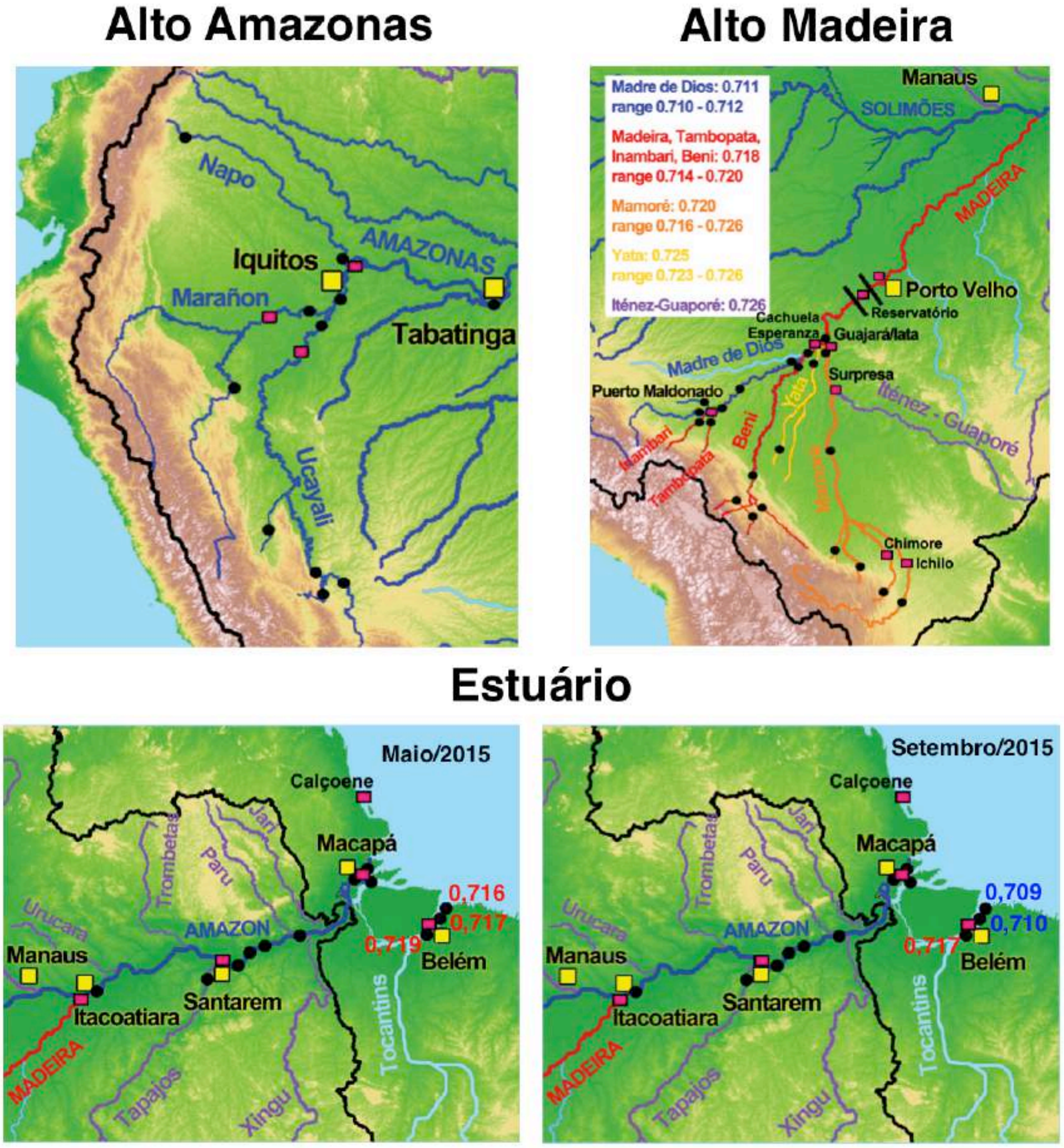
	Ponto Amostral	^{87}Sr:^{86}Sr± 2SE	Latitude	Longitude	Data
BRASIL	Almeirim Superfície	0,71150+/-1	S01°31.893'	W052°34.596'	02/10/15
	Almeirim Superfície	0,71184+/-1	S01°31.872'	W052°33.331'	29/05/15
	Amazonas 2 Superficie	0,71086+/-1	S01°01.964'	W051°41.271'	02/10/15
	Amazonas 2 Superficie	0,71168+/-1	S00°27.333'	W051°26.061'	29/05/15
	Amazonas 1 Superfície	0,71073+/-1	S02°23.663'	W054°43.468'	01/10/15
	Amazonas 1 Superfície	0,71114+/-1	S02°23.850'	W054°43.046'	28/05/15
	Baía Do Sol Fundo	0,71738+/-2	S01°00.287'	W048°19.558'	23/05/15
	Baía Do Sol Fundo	0,71034+/-1	S01°00.287'	W048°19.558'	26/09/15
	Baia Do Sol Superfície	0,71036+/-1	S01°00.287'	W048°19.558'	26/09/15
	Baía Do Sol Superfície	0,71742+/-1	S01°00.287'	W048°19.558'	23/05/15
	Canal Sul Vazante	0,71215+/-1	S00°05.998'	W050°36.411'	02/06/15
	Canal Sul Cheia	0,71103+/-1	S00°05.998'	W050°36.411'	06/10/15
	Canal Sul Cheia	0,71176+/-1	S00°05.998'	W050°36.411'	02/06/15
	Canal Sul Vazante	0,71112+/-1	S00°05.998'	W050°36.411'	06/10/15
	Foz Uatumã Fundo	0,70998+/-1	S02°40.638'	W057°43.507'	10/08/15
	Foz Uatumã Superficie	0,71001+/-1	S02°40.638'	W057°43.507'	10/08/15
	Ilha Da Pedreira Vazante	0,71156+/-1	N00°17.281'	W050°35.297'	03/06/15

	Ilha Da Pedreira Cheia	0,71162+/-1	N00°17.281'	W050°35.297'	03/06/15
	Ilha Da Pedreira Vazante	0,71098+/-1	S00°17.281'	W050°35.297'	07/10/15
	Ilha Da Pedreira Cheia	0,71098+/-1	S00°17.281'	W050°35.297'	07/10/15
	Ilha Do Sirituba Fundo	0,71944+/-1	S01°42.516'	W048°55.731'	24/05/15
	Ilha Do Sirituba Fundo	0,71747+/-1	S01°42.217'	W048°54.827'	28/09/15
	Ilha Sirituba Superfície	0,71947+/-1	S01°42.516'	W048°55.731'	24/05/15
	Ilha Sirituba Superfície	0,71756+/-1	S01°42.217'	W048°54.827'	28/09/15
	Itacoatiara CF 01	0,71004+/-1	S03°09.655'	W058°23.611'	10/08/15
	Itacoatiara CS 01	0,70994+/-1	S03°09.655'	W058°23.611'	10/08/15
	Itacoatiara MD 01	0,71031+/-1	S03°11.495'	W058°22.595'	10/08/15
	Itacoatiara MD 02	0,71055+/-1	S02°49.533'	W057°55.352'	10/08/15
	Itacoatiara ME 02	0,71001+/-1	S02°47.510'	W057°56.638'	10/08/15
	Itacoatiara CF 02	0,71027+/-1	S02°48.115'	W057°56.085'	10/08/15
	Itacoatiara CS 02	0,71018+/-1	S02°48.115'	W057°56.085'	10/08/15
	Itacoatiara ME 01	0,70994+/-1	S03°09.000'	W058°23.944'	10/08/15
	Macapá Cheia	0,71154+/-1	S00°02.502'	W051°01.685'	02/06/15
	Macapá Cheia	0,71093+/-1	S00°02.502'	W051°01.685'	06/10/15
	Macapá Vazante	0,71170+/-1	S00°02.502'	W051°01.685'	02/06/15
	Macapá Vazante	0,71092+/-1	S00°02.502'	W051°01.685'	06/10/15
	Monte Alegre Superfície	0,71119+/-1	S02°00.436'	W054°04.189'	01/10/15
	Monte Alegre Superfície	0,71213+/-1	S02°00.601'	W054°04.221'	28/05/15
	Prainha Superfície	0,71083+/-1	S02°00.436'	W054°04.189'	02/10/15
	Prainha Superfície	0,71174+/-1	S01°48.541'	W053°28.855'	29/05/15
	Tapajós Superfície	0,73369+/-2	S02°24.500'	W054°43.260'	28/05/15
	Tapajós Superfície	0,72999+/-3	S02°24.171'	W054°43.662'	01/10/15
	Vigia De Nazaré Fundo	0,71608+/-5	S00°46.826'	W048°13.392'	23/05/15
	Vigia De Nazaré Fundo	0,70927+/-1	S00°49.048'	W048°13.349'	26/09/15
	Vigia De Nazaré Superfície	0,70940+/-1	S00°49.048'	W048°13.349'	26/09/15
	Vigia De Nazaré Superfície	0,71520+/-1	S00°46.826'	W048°13.392'	23/05/15
BOLIVIA	Abapó	0,71838+/-1	S18°54.626'	W063°24.075'	03/09/15
	Beni	0,71903+/-1	S11°01.276'	W066°06.462'	07/07/15
	Chaparé	0,72042+/-1	S16°58.376'	W065°23.914'	04/09/15
	Chaparé	0,72075+/-1	S16°58.361'	W065°24.016'	10/07/15
	Chimoré	0,72486+/-1	S16°59.821'	W065°08.135'	04/09/15
	Chimoré	0,72580+/-1	S16°59.826'	W065°08.177'	10/07/15
	Chipiriri	0,71713+/-1	S16°53.726'	W065°24.663'	10/07/15
	Confluência Beni - Madre Dios	0,71310+/-1	S10°59.191'	W066°03.440'	07/07/15
	Ibaré	0,72273+/-1	S15°05.973'	W064°40.990'	05/07/15
	Ibaré	0,7223+/-1	S14°52.134’	W64°58.260’	28/04/15
	Ichilo	0,71768+/-1	S16°50.228'	W064°47.496'	03/09/15
	Ichilo	0,72144+/-1	S17°15.751'	W064°20.430'	09/07/15
	Madidi	0,71729+/-1	S13°14.375'	W068°19.510'	15/07/15
	Madre De Dios	0,71192+/-1	S10°58.201'	W066°05.500'	07/07/15
	Mamoré 1	0,72010+/-1	S15°20.410'	W064°51.319'	05/07/15
	Mamoré 2	0,72135+/-1	S14°52.982'	W065°01.963'	06/07/15
	Mamoré (acima Conf. Yata)	0,72191+/-1	S10°50.570'	W065°41.247'	04/03/17
	Mamoré (abaixo Conf. Yata)	0,72196+/-1	S10°47.920'	W065°42.912'	04/03/17
	Pojige	0,72103+/-1	S15°26.132'	W064°52.771'	05/07/15
	Porto Siles	0,72026+/-1	S12°48.350’	W65°0.259’	30/04/15
	Quiquibey	0,71608+/-1	S14°37.682'	W067°31.851'	13/07/15
	Sena	0,71159+/-1	S11°28.173'	W067°14.302'	06/07/15
	Sena	0,71214+/-1	S11°28.173'	W067°14.302'	30/09/15
	Sapechó	0,71792+/-1	S15°33.432'	W067°22.470'	27/09/15
	Securé	0,71887+/-1	S15°14.451'	W064°57.420'	05/07/15
	Tuichi	0,71956+/-1	S14°35.460'	W067°32.549'	13/07/15
	Yata	0,72572+/-1	S13°26.937'	W066°36.003'	29/09/15
	Yata	0,72728+/-1	S10°48.781'	W065°43.805'	04/03/17
	Yapacani	0,71890+/-1	S17°24.446'	W063°50.886'	09/07/15
	Yapacani	0,71591+/-1	S17°24.319'	W063°50.777'	03/09/15

PERU	Huallaga	0,70891+/-1	S 6°34'13.64"	W 76°07'09.35"	14/08/15
	Inambari	0,71635+/-1	S12°45'09.01"	W069°49'29.03"	25/06/15
	Las Piedras	0,71020+/-1	S12°30'47.19"	W069°14'35.51"	24/06/15
	Madre De Dios Arriba C.Iram.	0,71099+/-1	S12°41'06.94"	W069°48' 12.98"	25/06/15
	Madre De Dios Bajo C. Iram.	0,71094+/-1	S12°42'52.02"	W069°40'13.83"	25/06/15
	Madre De Dios Bajo PM	0,71097+/-1	S12°36'05.37"	W069°04'36.96"	24/06/15
	Napo	0,70594+/-1	S 3°28'49.57"	W 73°04'29.74"	25/07/15
	Puerto Inca (Pachitela)	0,70862+/-1	S 9°22'42,17"	W 74°58'08.63"	10/08/15
	Requena	0,70930+/-1	S 5°01'48.18"	W 73°49'59.52"	22/07/15
	San Regis	0,70812+/-1	S 4°30',56.18"	W 73°54'31.44"	21/07/15
	Tambopata	0,71719+/-1	S12°43'37.40"	W069°12'57.42"	24/06/15
	Tambo	0,70877+/-1	S 10°44'46.78"	W 73°44'51.77"	05/08/15
	Tamshiyacu	0,70868+/-1	S 4°00'18.89"	W 73°09'53.13"	25/07/15
	Urubamba	0,70926+/-1	S 10°44'10.47"	W 73°43'14.06"	06/08/15
	Total				**87**

Fonte: Hauser (2018).

Figura 10 - Mapeamento da ^{87}Sr:^{86}Sr da bacia Amazônica.



Para detalhes ver apêndice 2. Fonte: Hauser (2018).

3.2 – *^{87}Sr:^{86}Sr EM OTÓLITOS DE B. rousseauxii*

Durante este estudo foram analisados um total 265 indivíduos de *B. rousseauxii* ao longo da bacia amazônica, considerando o período anterior (n= 105) e posterior (n=160) à construção do complexo hidrelétrico da bacia do rio Madeira, os quais exibiram entre 26 e 142 cm de comprimento padrão, e diferentes comportamentos migratórios (Tabela 3).

Tabela 3 - Indivíduos de *B. rousseauxii* analisados ao longo da bacia Amazônica.

UHE	Bacia	Rio/Local	Comportamento	n	%
Antes	Alto Madeira (n=86)	Mamoré	Homer	37	78%
		Beni*		26	
		Madre de Dios		4	
		Mamoré	Residente	1	14%
		Beni*		11	
		Mamoré	Strayer (receptor-Madeira)	2	8%
		Madeira		1	
		Beni		4	
	Alto Amazonas (n=19)	Ucayali/ Marañon/ Napo	Homer	5	?
			Homer e Residente*	10	?
			Strayer (receptor-Amazonas)	4	21%
Depois	Alto Madeira (n=23)	Madre de Dios	Residente	16	100%
		Mamoré		7	
	Reservatório UHE Santo Antônio (n=29)	Madeira	Residente	29	100%
	Abaixo UHE Santo Antônio (n=8)	Madeira	Homer	5	62,5%
			Residente	3	37,5%
	Alto Amazonas (n=13)	Ucayali/ Marañon	Homer	6	?
			Residente	1	?
			Strayer (receptor-Amazonas)	1	8%
			Homer e Residente*	5	?
	Confluência Madeira/Amazonas (n=8)	Itacoatiara	Nascimento Amazonas	5	62,5%
			Nascimento Madeira	3	37,5%
	Estuário (n=79)	Belém	Nascimento Amazonas	51	84%
		Macapá		15	
		Belém	Nascimento Madeira	9	16%
		Macapá		4	

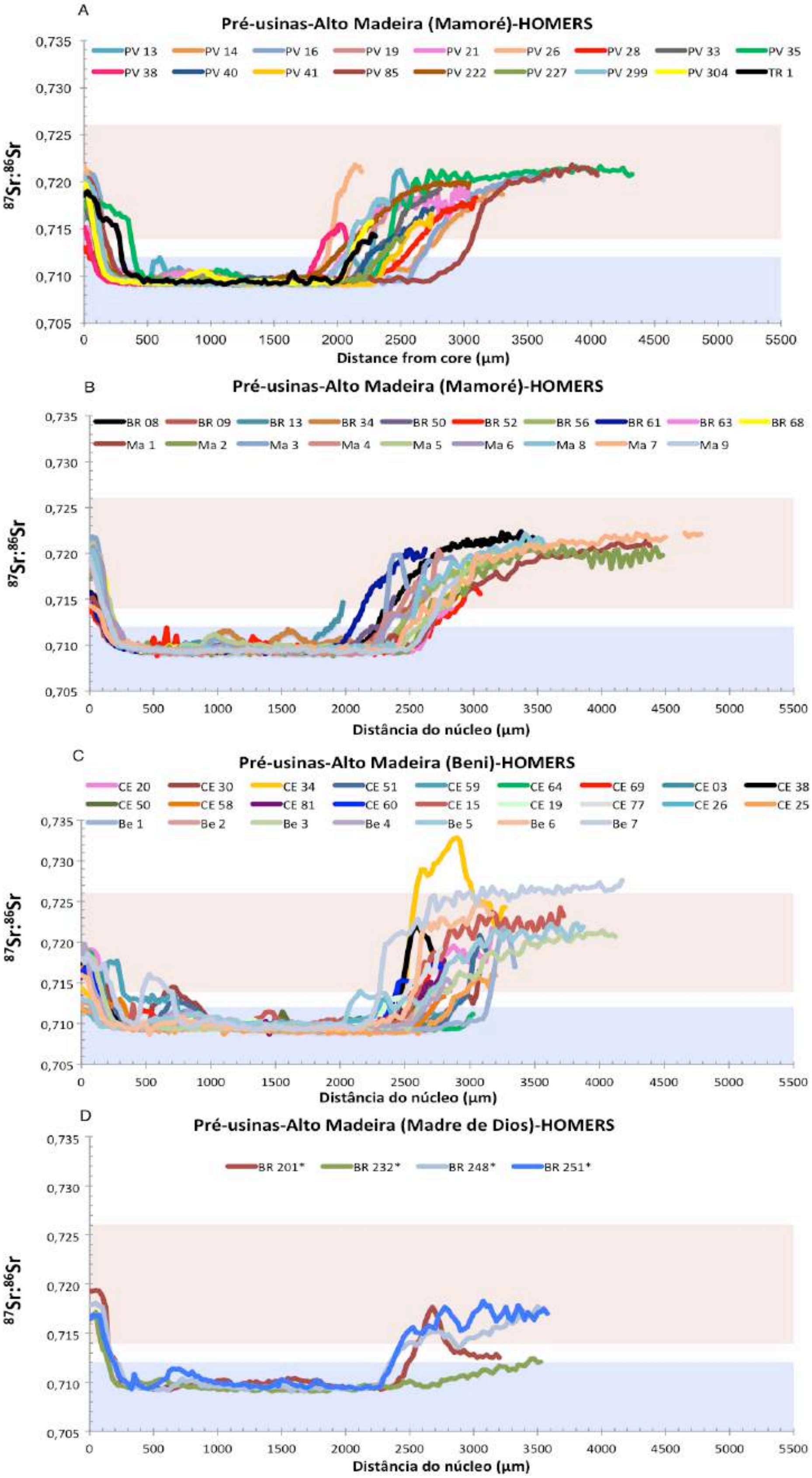
* Impossível confirmar se o indivíduo era *homer* ou residente. Fonte: Hauser (2018).

3.2.1 - Peixes amostrados no rio Madeira antes do barramento

Dos 86 peixes amostrados no Alto Madeira, antes da construção do complexo hidrelétrico, 78% (67/86) exibiram comportamento de *homing* natal, com migração entre as bacias dos rios Madeira e Amazonas. (Figura 11, Tabela 3). Suas assinaturas da ^{87}Sr:^{86}Sr da região nuclear foram típicas das águas dos rios Beni e Mamoré (0,715-0,726), os quais então migraram rio abaixo e após cerca de 39 dias, entraram em águas com assinaturas do rio Amazonas (0,709-0,712) (Tabela 4). Uma vez dentro do Amazonas, estes indivíduos permaneceram nesse rio por no mínimo 2 e no máximo 4,5 anos (Tabela 4), quando retornaram para a bacia do Madeira, onde foram capturados com assinatura isotópica desse rio (0,714-0,726) (Figuras 11 A, B e C; Figuras 12 A e B). Quatro desses indivíduos (BR 201, 232, 248 e 251) foram amostrados em Madre de Dios após a construção das usinas hidrelétricas (junho 2015). Entretanto, todos tinham mais de seis anos de idade no momento da captura, os quais ingressaram no Alto Madeira por volta de 2,5 anos (com aproximadamente 2200 μm de distância em relação ao núcleo), que coincide com o ano de 2011, período em que o rio ainda não havia sido totalmente barrado (Figura 11 D e Figura 12 C).

Aproximadamente 14% (12/86) dos indivíduos foram residentes do Alto Madeira, com perfis da ^{87}Sr:^{86}Sr indicando migrações apenas entre as suas principais sub-bacias (Figuras 13 A). Semelhante aos *homers*, os residentes também nasceram nos rios Beni ou Mamoré, migraram para áreas menos radiogênicas dentro do Alto Madeira, e depois realizaram migrações entre as sub-bacias dessa área. Três desses indivíduos (CE 83, SUR 373 e CE13) se deslocaram para águas altamente radiogências do Iata ou Guaporé, inclusive, com CE 83 exibindo valores acima daqueles observados para a bacia do Madeira (0,735) (Figura 12 A, Tabela 3). Os outros 8% (07/86) foram *strayers* do rio Amazonas, ou seja, nasceram e se desenvolveram em águas típicas desse rio, e quando adultos entraram no rio Madeira provavelmente para se reproduzirem (Figura 13 B, Tabela 3).

Figura 11 - Perfil isotópico de *homers* de *B. rousseauxii* no Alto Madeira antes do barramento.



Cada curva corresponde a ablação a laser (MC-ICP-MS) da ^{87} Sr:^{86}Sr, ao longo de secção transversal do otólito (do núcleo ao bordo), de um indivíduo amostrado nos rios Mamoré (A e B), Beni (C) e Madre de Dios (D). Fonte: Hauser (2018).

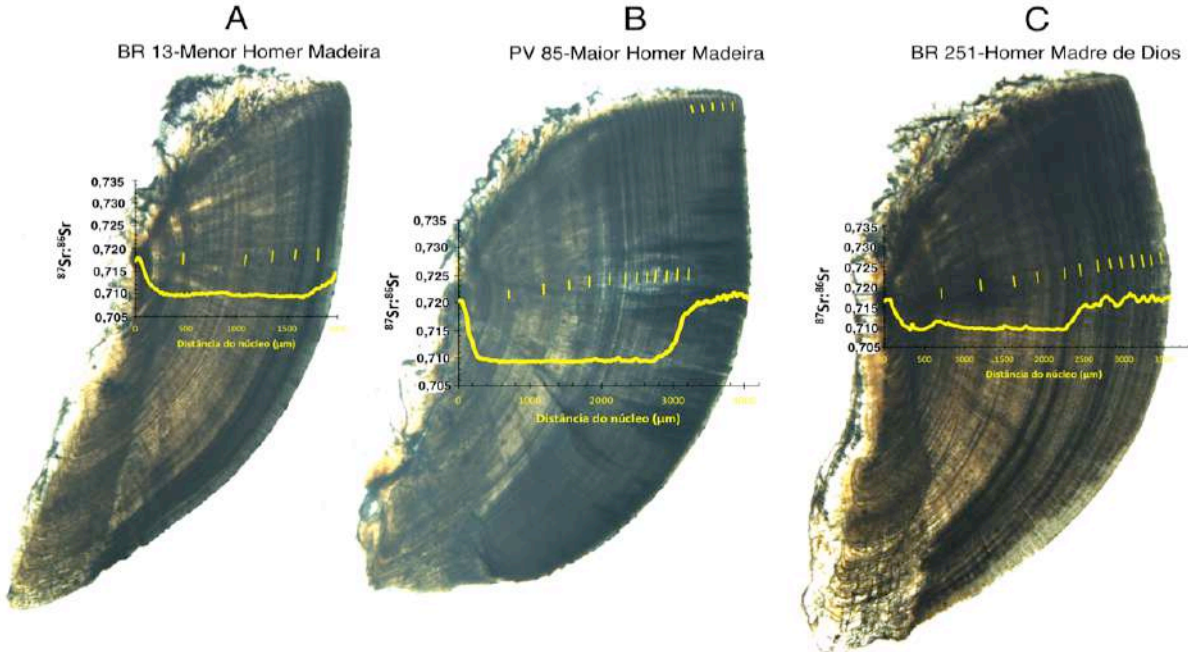
Tabela 4 - Comprimento e idade de saída dos jovens, e retorno dos adultos, de *B. rousseauxii* na bacia do rio Madeira.

Saída dos juvenis do Madeira			
	Rádio do otólito (µm)	CP peixe (cm)	Idade (dias)
Menor	110,0	3,4	21,5
Médio (n = 67)	196,5 ± 94	6,0 ±2,9	39,0
Maior	750,0	23,1	162, 2

Retorno dos adultos ao Madeira			
	Rádio do otólito (µm)	CP peixe (cm)	Idade (anos)
Menor	1840	60,7	2*
Médio (n=67)	2422,6 ± 270,7	80,0 ± 8,3	2,6
Maior	2975	94,6	4,5*

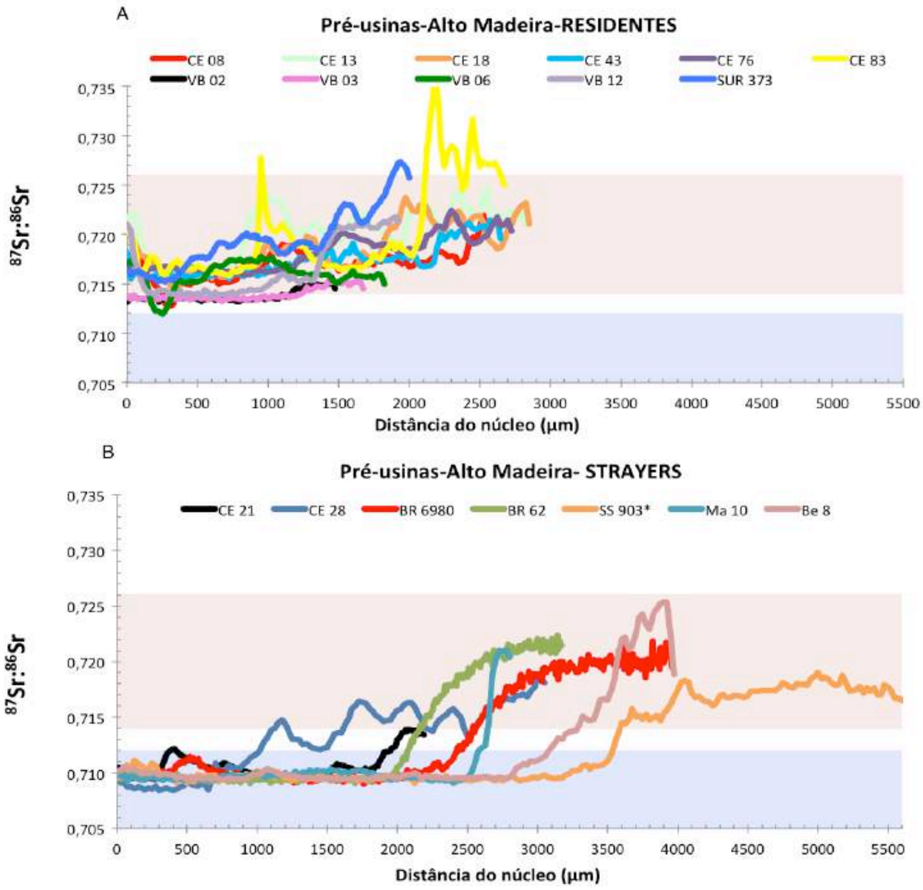
Dados determinados a partir de indivíduos capturados antes do barramento. *Estimado a partir da contagem dos anéis de crescimento. Fonte: Hauser (2018)

Figura 12 - Perfil isotópico em função da idade dos *homers* de *B. rousseauxii* no Alto Madeira.



As curvas amarelas correspondem a ablação a laser (MC-ICP-MS) da ^{87} Sr:^{86}Sr, ao longo de secção transversal dos otólitos (do núcleo ao bordo), dos *homers*: mais jovem (A) e mais velho (B), ao retornar ao rio Mamoré, e um com a idade média (C) de retorno, capturado no Madre de Dios. Cada pequena linha amarela corresponde a um anel de crescimento, e a cada dois anéis a um ano de idade (ver HAUSER et al., 2018). Fonte: Hauser (2018).

Figura 13. Perfil isotópico dos residentes e *strayers* de *B. rousseauxii* no Alto Madeira antes do barramento.

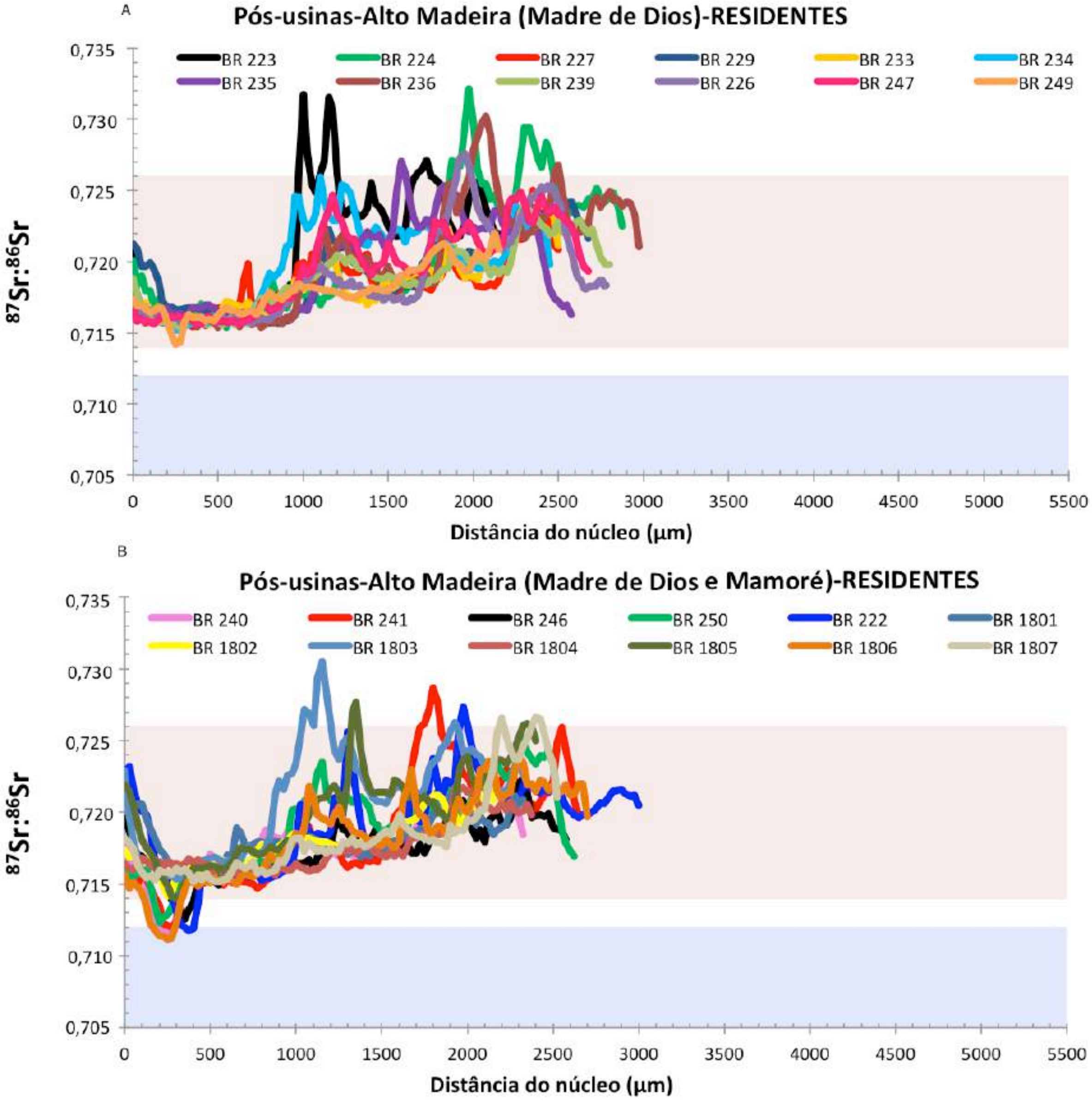


Cada curva corresponde a ablação a laser (MC-ICP-MS) da ^{87} Sr:^{86}Sr, ao longo de secção transversal do otólito (do núcleo ao bordo), de um indivíduo residente (A) e *strayer* (B). Fonte: Hauser (2018).

3.2.2 - Peixes amostrados no rio Madeira após o barramento

Todos os peixes amostrados no Alto Madeira (nos rios Madre de Dios e Mamoré), após a construção das usinas hidrelétricas, exibiram comportamento residente nessa área. Seguindo o padrão observado para os *homers*, a maioria nasceu nos rios Beni ou Mamoré, e realizaram migrações entre águas mais e menos radiogênicas dessa região, inclusive, com alguns indivíduos exibindo valores isotópicos maiores do aqueles reportados para o rio Madeira (>0,726) (Figuras 14 A e B, Tabela 3).

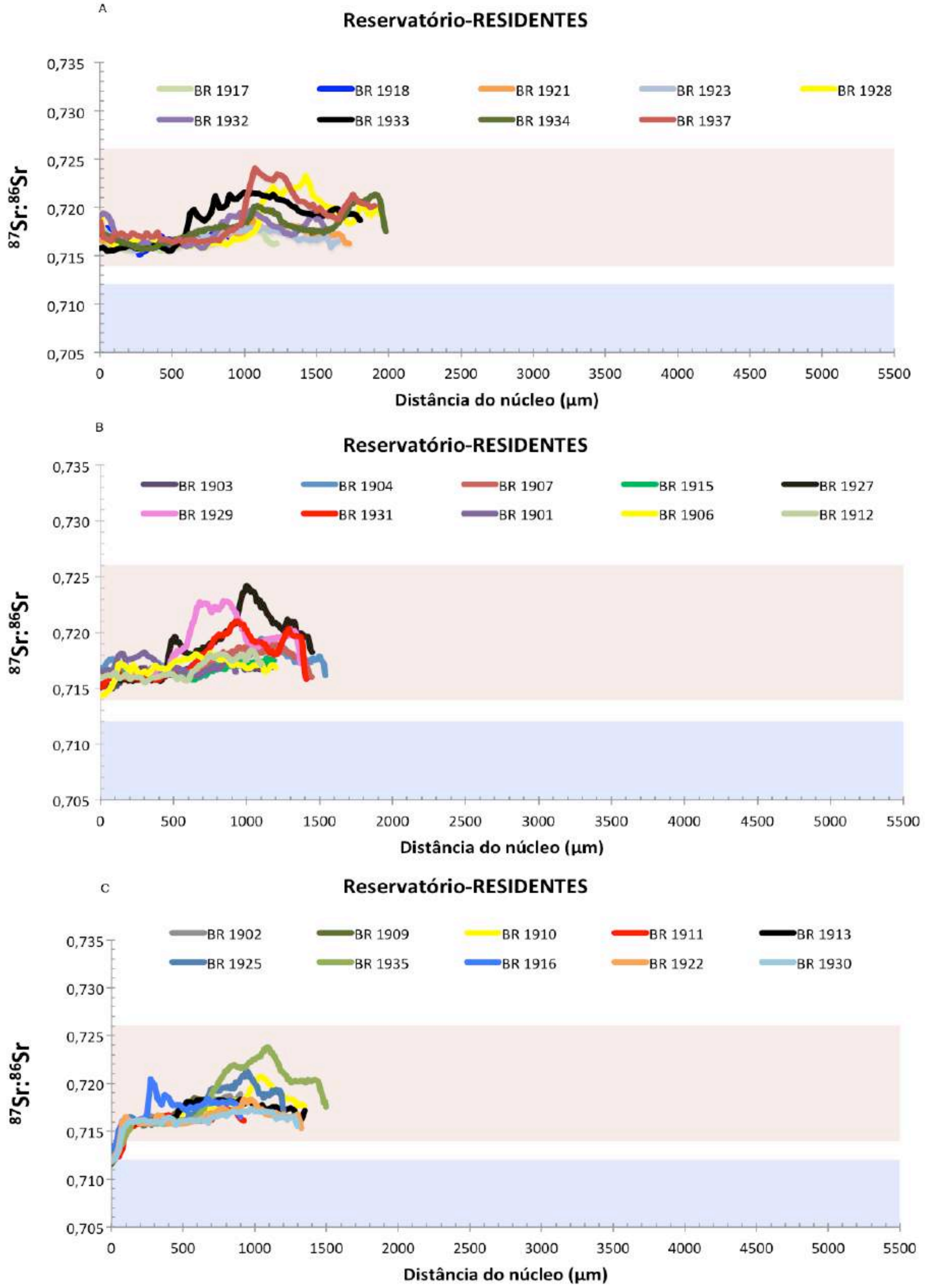
Figura 14 - Perfil isotópico dos residentes de *B. rousseauxii* no Alto Madeira após o barramento.



Cada curva corresponde a ablação a laser (MC-ICP-MS) da ^{87} Sr:^{86}Sr, ao longo de secção transversal do otólito (do núcleo ao bordo), de um indivíduo amostrado nos rios Madre de Dios (A e B) e Mamoré (B). Os indivíduos com códigos numerados entre BR 1801 e BR 1807 foram amostrados em Guajará-Mirim, no rio Mamoré. Fonte: Hauser (2018).

Seguindo o mesmo padrão, todos os indivíduos amostrados no reservatório jamais saíram do Alto e Médio Madeira, com a maioria desses nascendo nos rios Beni ou Mamoré (Figuras 15 A e B; Tabela 3), e uma menor quantidade no Madre de Dios (0,710-0,712) (Figura 15 C; Tabela 3).

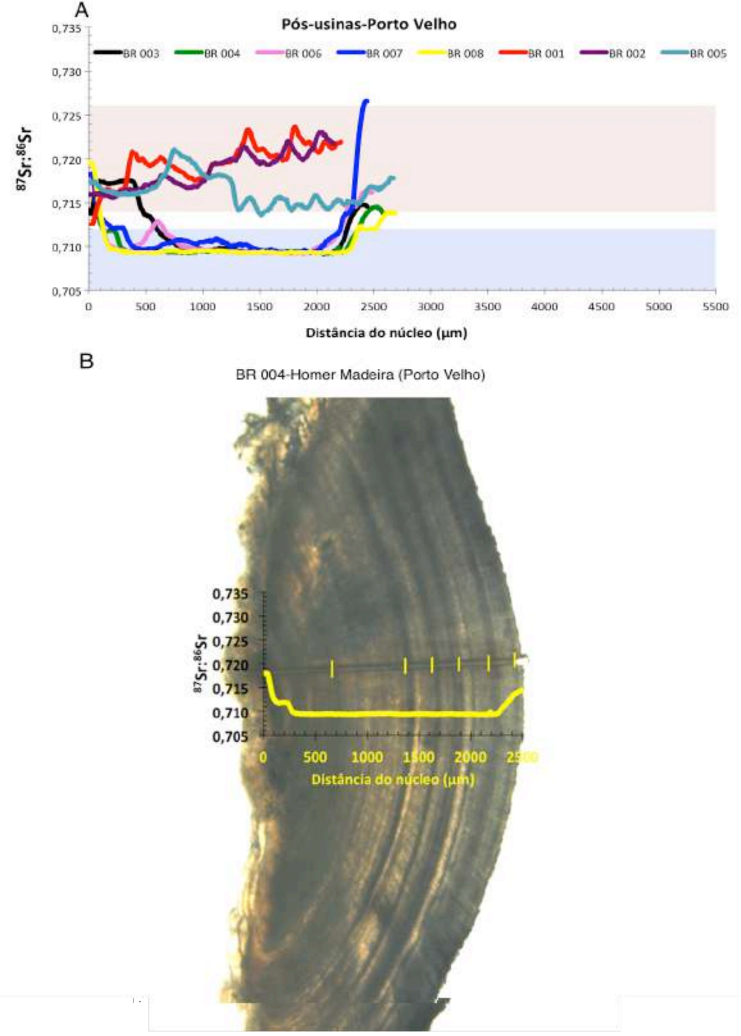
Figura 15 - Perfil isotópico dos residentes de *B. rousseauxii* no reservatório da UHE-SAE.



Cada curva corresponde a ablação a laser (MC-ICP-MS) da ^{87} Sr:^{86}Sr, ao longo de secção transversal do otólito (do núcleo ao bordo), de um indivíduo amostrado no reservatório da usina hidrelétrica de Santo Antônio Energia, entre 2012 e 2013. Fonte: Hauser (2018).

Todos os oito indivíduos amostrados logo abaixo da usina hidrelétrica de Santo Antônio Energia (em frente a comunidade de São Sebastião), em junho de 2017, nasceram no Alto Madeira (Figura 16 A), com cinco deles (BR 003, 004, 006, 007 e 008) exibindo comportamento clássico de *homing* natal (interrompido). Após o nascimento nos rios Beni ou Mamoré (por volta de 2014) esses peixes passaram pelas turbinas das usinas hidrelétricas e chegaram até o rio Amazonas, onde cresceram por volta de até 2,5 anos (2200 µm de distância do núcleo), e em seguida retornaram para o rio Madeira, onde permaceram bloqueados abaixo da usina. Os outros três peixes (BR 001, 002 e 005) exibiram comportamento residente dessa bacia, os quais também atravessaram as turbinas em algum momento do ciclo de vida, chegando até a parte média do rio Madeira, onde foram capturados (Figura 16 A e B; Tabela 3).

Figura 16 - Perfil isotópico dos *homers* e residentes de *B. rousseauxii* em Porto Velho após o barramento.

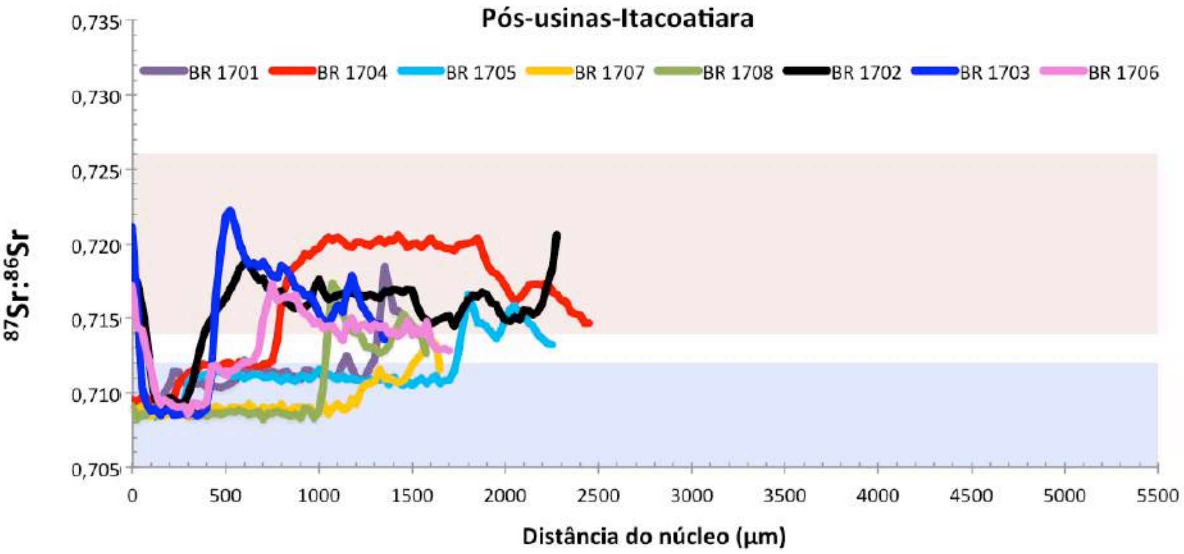


Na figura A, cada curva corresponde a ablação a laser (MC-ICP-MS) da ^{87} Sr:^{86}Sr, ao longo de secção transversal do otólito (do núcleo ao bordo) de um indivíduo amostrado abaixo da usina de SAE. A figura B refere-se ao perfil isotópico de um *homer* em função da idade. Cada pequena linha amarela corresponde a um anel de crescimento, e a cada dois anéis a um ano de idade (ver HAUSER et al., 2018). Fonte: Hauser (2018).

3.2.3 - Peixes amostrados na região da confluência dos rios Madeira e Amazonas após o barramento

Em relação à Itacoatiara, foram amostrados peixes que nasceram tanto no rio Madeira, como no rio Amazonas, os quais realizaram migrações entre ambas as bacias (Figura 17; 32).

Figura 17- Perfil isotópico de *B. rousseauxii* em Itacoatiara após o barramento.

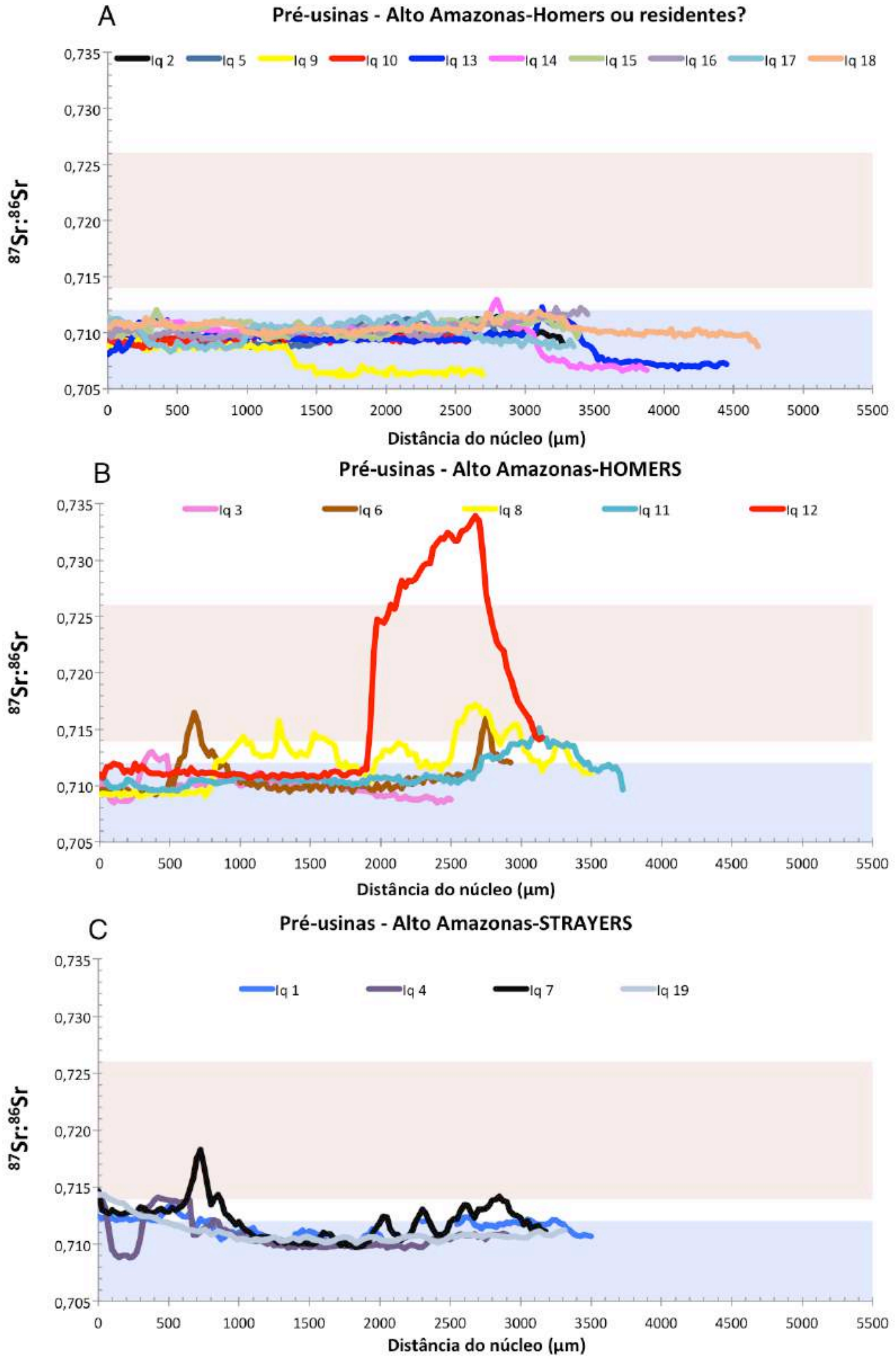


Cada curva corresponde a ablação a laser (MC-ICP-MS) da ^{87}Sr:^{86}Sr, ao longo de secção transversal do otólito (do núcleo ao bordo), de um indivíduo. Fonte: Hauser (2018).

3.2.4 - Peixes amostrados no Alto Amazonas, antes e após o barramento

Dos 19 indivíduos capturados no Alto Amazonas, antes da implantação do complexo hidrelétrico do rio Madeira, 10 exibiram perfis da ^{87}Sr:^{86}Sr relativamente planos, indicando que permaneceram no eixo principal do rio Amazonas todo seu ciclo de vida. Entretanto, visto a homogeneidade das águas deste sistema, não foi possível determinar se esses indivíduos exibiram comportamentos residentes do Alto Amazonas ou se migraram até as porções baixas desse rio (Figura 18 A, Tabela 3). Pelo menos três desses indivíduos permaneceram boa parte do ciclo de vida no rio Napo (0,705-0,707) (Iq 9, Iq13 e Iq14), onde provavelmente foram capturados (Tabela 3). Cinco indivíduos exibiram provável comportamento de *homing* natal, os quais nasceram em águas com assinatura isotópica do Alto Amazonas, se deslocaram para águas mais radiogênicas (Iq12), ou para zonas de confluências com valores próximos daqueles encontrados na bacia do Madeira, ou de tributários do escudo granítico brasileiro, no Baixo Amazonas, retornando novamente para o Alto Amazonas no momento da captura (Figura 18 B). Os outros quatro peixes foram *strayers* do Madeira, os quais nasceram nessa bacia e posteriormente migraram para o Amazonas onde foram capturados (Figura 18 C).

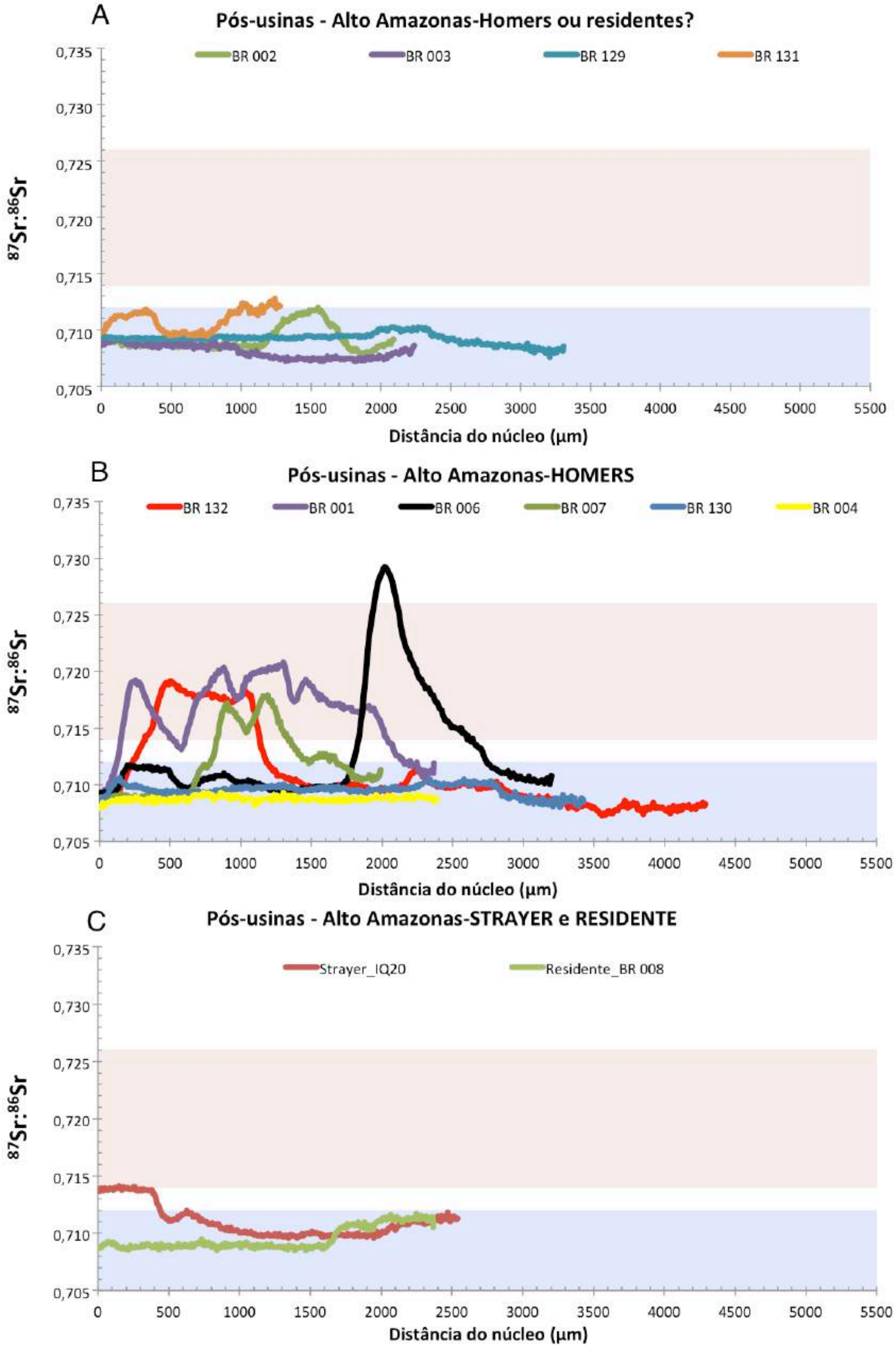
Figura 18 - Perfil isotópico dos *homers*, residentes e *strayers*de *B. rousseauxii* no Alto Amazonas antes do barramento.



Cada curva corresponde a ablação a laser (MC-ICP-MS) da ^{87} Sr:^{86}Sr, ao longo de secção transversal do otólito (do núcleo ao bordo), de um indivíduo *homer* ou residente (indeterminado) (A), *homer* confirmado (B) e *strayer* (C). Fonte: Hauser (2018).

Dos 12 indivíduos capturados no Alto Amazonas, após a implantação do complexo hidrelétrico do rio Madeira, 07 exibiram perfis da ^{87}Sr:^{86}Sr relativamente planos, indicando que permaneceram no eixo principal do rio Amazonas todo seu ciclo de vida (Figura 19). Visto a homogeneidade das águas deste sistema, para quatro desses indivíduos não foi possível confirmar se eles exibiram comportamento residente do Alto Amazonas, ou se migraram até as porções baixas desse rio (Figura 19 A). Por sua vez, a partir de análise de microscopia eletrônica de varredura de raio X, foi possível confirmar para os outros três peixes, tanto a presença de comportamento de *homing* natal (BR 004 e BR 130, Figura 19 B) como de residência (BR 008, Figura 19 C) (para detalhes ver capítulo II). Quatro outros indivíduos também exibiram provável comportamento de *homing* natal, mas diferentemente, após nasceram em águas com assinatura isotópica do Alto Amazonas, se deslocaram para águas mais radiogênicas, com valores próximos aqueles encontrados na bacia do Madeira, ou de tributários do escudo granítico brasileiro, retornando novamente para o Alto Amazonas no momento da captura (Figura 19 B). Apenas um indivíduo foi *strayer* do Madeira, o qual nasceu nessa bacia (0,714) e posteriormente se deslocou para o Amazonas onde foi capturado (Figura 19 C).

Figura 19 - Perfil isotópico dos *homers*, residente e *strayer* de *B. rousseauxii* no Alto Amazonas após o barramento.

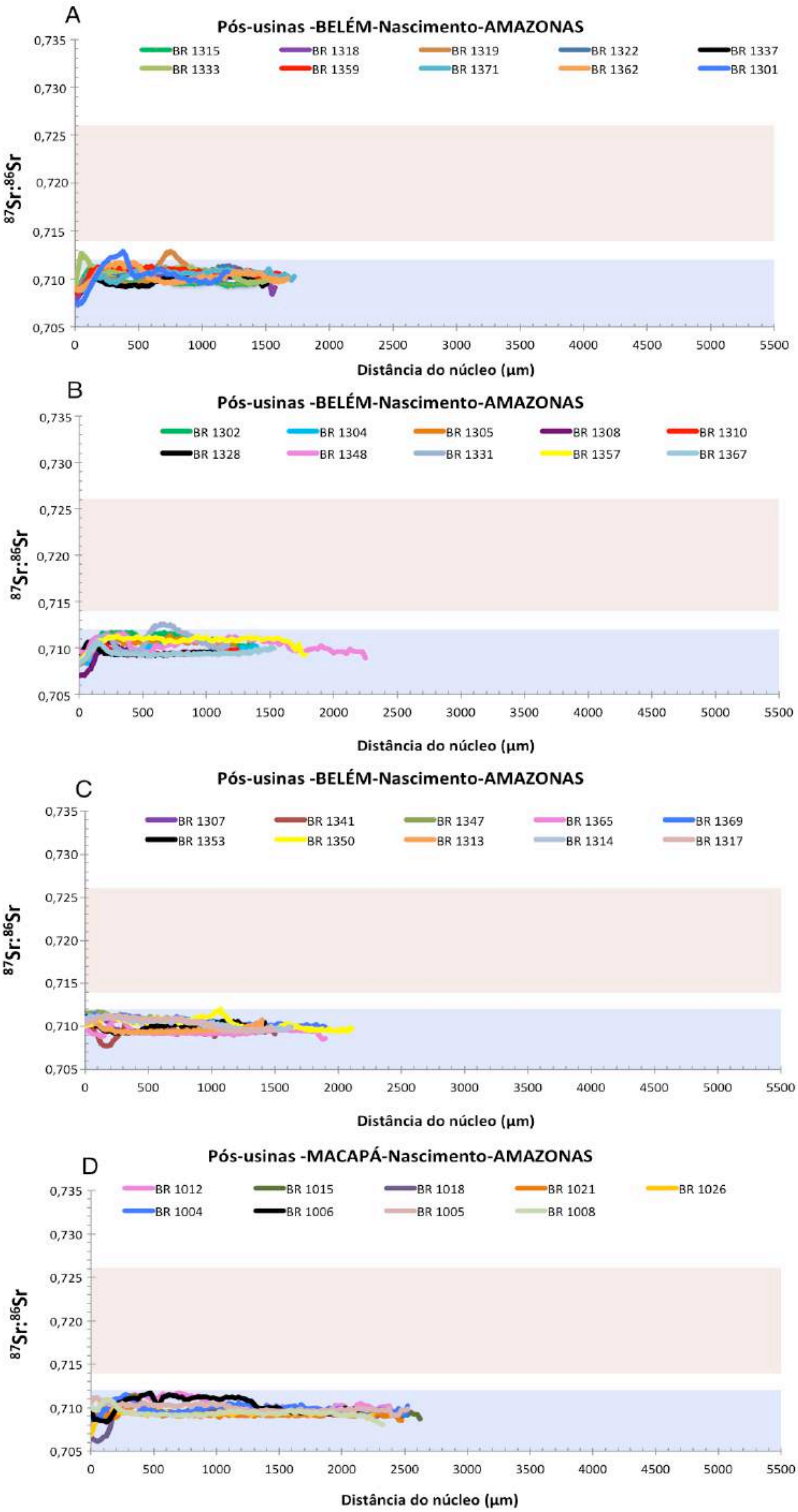


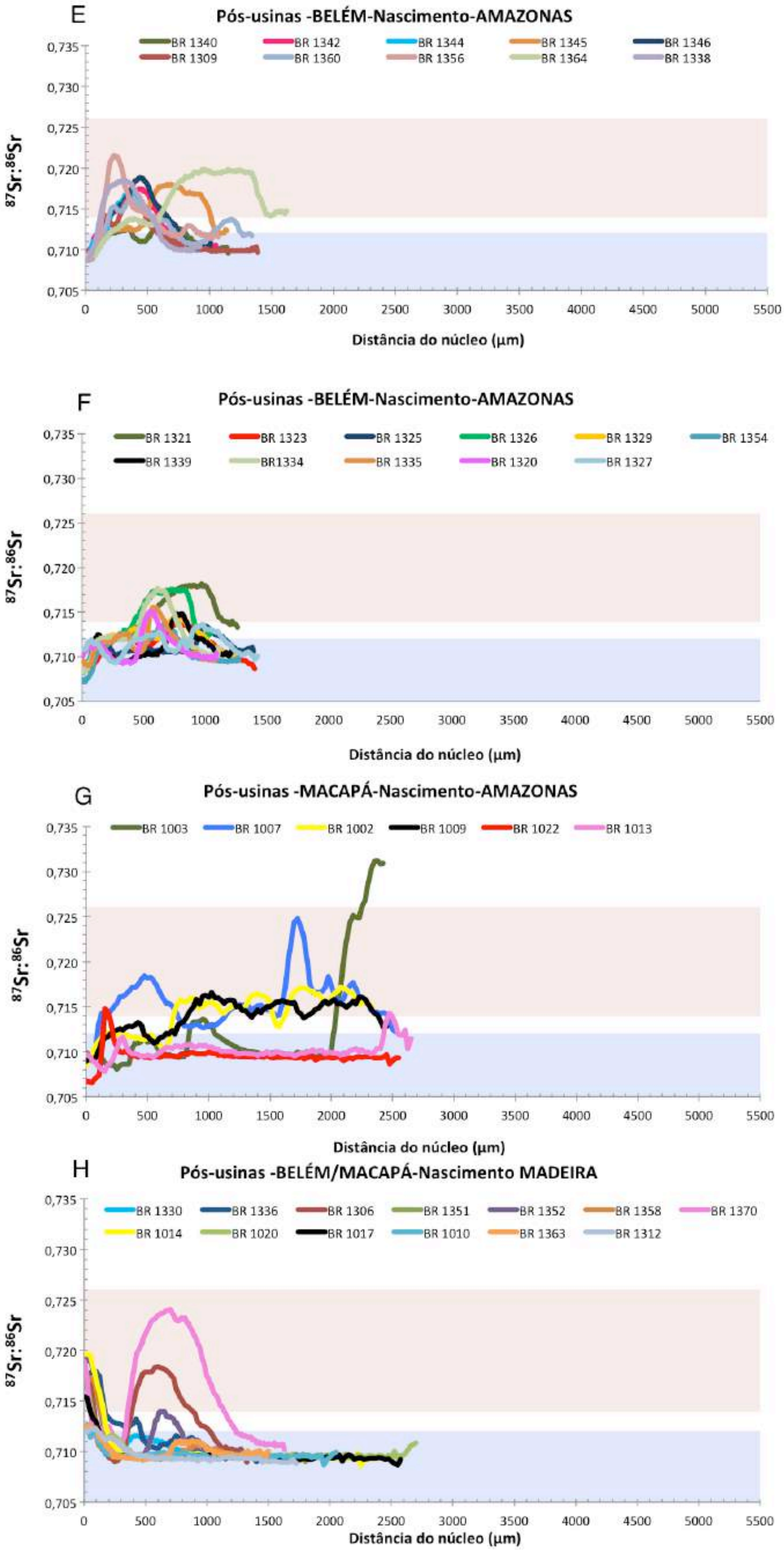
Cada curva corresponde a ablação a laser (MC-ICP-MS) da ^{87} Sr:^{86}Sr, ao longo de secção transversal do otólito (do núcleo ao bordo), de um indivíduo *homer* ou residente (indeterminado) (A), *homer* confirmado (B), e *strayer* e residente confirmado (C). Fonte: Hauser (2018).

3.2.5 - Peixes amostrados no estuário após o barramento

Aproximadamente 84% dos indivíduos amostrados em Belém e Macapá nasceram no Alto Amazonas, com cinco destes indivíduos oriundos do rio Napo (BR 1018, 1022, 1301, 1308, 1354) (0,705-0,707) (Figuras 20 A, B, F e H). Dentre esses peixes observaram-se dois padrões distintos de perfis isotópicos: 1) indivíduos com perfis planos, indicando que permaneceram no eixo principal do rio Amazonas todo seu ciclo de vida (Figura 20 A, B, C e D); e 2) indivíduos com perfis com valores tanto do Amazonas, como de águas mais radiogênicas como aquelas encontradas - i) no rio Madeira, ii) nas de zonas de confluência com rios do escudo granítico (GST), iii) nos próprios adluentes do GST localizados próximos a região estuarina, como observado para dois indivíduos (BR1003 e BR 1007) coletados no rio Calçoene, em Amapá (Figura 20 G; Tabela 3), iv) na própria região estuarina de Belém (Vigia-0,717), no período de influência do rio Tocantins (Figura 20 E, F e G).

Figura 20 - Perfil isotópico de *B. rousseauxii* amostrada no estuário.



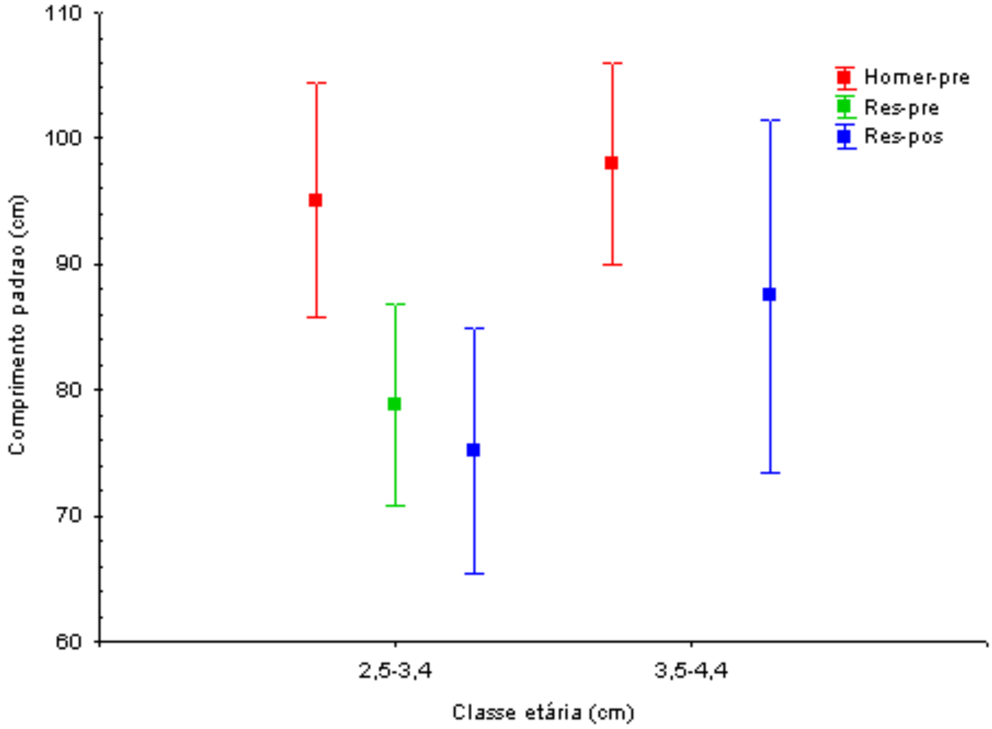


Cada curva corresponde a ablação a laser (MC-ICP-MS) da ^{87} Sr:^{86}Sr, ao longo de secção transversal do otólito (do núcleo ao bordo), de um indivíduo amostrado em Belém (A, B, C, E, F e H) e Macapá (D, G e H). Fonte: Hauser (2018).

3.2.6 – Diferença de crescimento entre *homers* e residents do Alto Madeira

Os indivíduos *homers* foram significativamente maiores que os residentes, tanto para a classe etária de 2,5-3,4 ($F_{2,\ 28}$=15,4; p<0,005) quanto para a de 3,5-4,4 (T=2,1; p=0,047; df=18) (Figura 21).

Figura 21 – Diferença de crescimento entre *homers* e residentes de *B. rousseauxii* do Alto Madeira.



Diferença do comprimento entre *Homers* pré (vermelho) e residentes, pré (verde) e pós (azul) barramento, amostrados no Alto Madeira, em diferentes classes etárias. n=média ; I= desvio padrão. Fonte: Hauser (2018).

4 – DISCUSSÃO

O estudo da ecologia da migração de *B. rousseauxii*, além de representar uma oportunidade para entender os processos ecossistêmicos em larga escala dos deslocamentos aquáticos, também constitui um desafio internacional de conservação, visto que os movimentos dessa espécie se estendem através de múltiplas fronteiras nacionais. Nesse contexto, este trabalho é o primeiro a realizar uma reconstrução robusta em larga escala *B. rousseauxii*, com mais de 260 otólitos analisados entre a área de nascimento nos Andes e o berçário no estuário, antes e após a construção das usinas hidrelétricas do rio Madeira, o qual permitiu de maneira irrefutável confirmar os impactos desses empreendimentos sobre a migração dessa espécie.

O predominante perfil isotópico da ^{87}Sr:^{86}Sr observado nos otólitos de *B. rousseauxii* do Alto Madeira (~ 80%), antes da implementação do complexo hidrelétrico, indicou três fases distintas do ciclo de vida dessa espécie, confirmando assim, que o comportamento de *homing* natal era o padrão migratório dominante, exibido por esse bagre no rio Madeira (DUPONCHELLE et al., 2016). Ainda, com base na relação entre o raio transversal do otólito, o comprimento padrão dos peixes (ver DUPONCHELLE et al., 2016), e a equação de Von bertallanfy dessa espécie (ver HAUSER et al., 2018), este trabalho permitiu pela primeira vez estimar a duração de cada uma dessas fases, determinando de forma precisa a idade em que os juvenis saíram do rio Madeira, e a idade na qual os adultos retornaram a esse rio.

A primeira fase foi marcada pelo alto valor da ^{87}Sr:^{86}Sr (0,714-0,726) da região nuclear do otólito, que corresponde ao nascimento dos indivíduos nas cabeceiras do Alto Madeira, os quais permaneceram em média 39 dias nessa bacia, quando então entraram no rio Amazonas, com aproximademente 6 cm de comprimento padrão, valores maiores que aqueles reportados na literatura (3,7 cm por DUPONCHELLE et al., 2016; e 2 cm por BARTHEM et al., 2017). Embora Duponchelle e colaboradores (2016) tenham utilizado a mesma metodologia para determinar o tamanho em que os juvenis de *B. rousseauxii* saem do rio Madeira, a análise dos respectivos autores foi baseada em apenas 12 indivíduos, o que provavelmente refletiu no tamanho subestimado encontrado por eles, o qual todavia, ainda se enquadra dentro da variação de comprimentos observados nesta tese.

Por sua vez, Barthem e colaboradores (2017) realizaram essas estimativas, a partir do tamanho dos indivíduos amostrados em redes de ictioplâncton e de arrasto bentônico, ao longo da bacia do rio Madeira. Como o último ponto de amostragem avaliado pelos autores foi o município de Humaitá, o qual se encontra ainda a aproximadamente 1000 km de distância do Amazonas, este fator possivelmente subestimou a estimativa de tamanho de saída dos juvenis do rio Madeira, observado no respectivo trabalho. Ademais, a partir de Humaitá o rio Madeira torna-se menos encaixado dando origem a sua planície de inundação (QUEIROZ et al., 2013), e diminuindo a velocidade da corrente da água, o que consequentemente deve refletir em uma migração mais lenta dos juvenis rio abaixo. Essa suposição é sustentada pelos dados de velocidade média da água, ao longo da calha principal do rio Madeira, onde se observa uma variação de 5,71 a 0,60 m/s, entre o rio Mamoré (abaixo da confluência com o rio Guaporé) e a região de foz do rio Madeira com o Amazonas (Nova Olinda), respectivamente (dados não publicados LIP/UNIR).

Além disso, a partir de 2 cm de comprimento os indivíduos de *B. rousseauxii* perdem os órgãos embrionários e larvais, e começam a desenvolver a nadadeira caudal (LEITE et al., 2007; CELLA-RIBEIRO et al., 2015). Essas mudanças ontogenéticas propiciam maior capacidade de movimento autônomo e de resistência à corrente, bem como um comportamento mais ativo na busca de alimento, permitindo maior crescimento durante este último trajeto. Estas suposições ratificam, portanto, o maior tamanho de juvenis observados na respectica tese, e a provável subestimação de comprimento desses indivíduos reportadas por Barthem e colaboradores (2017).

Por sua vez, a ampla variação da idade com que esses juvenis entraram no Amazonas, entre 21 dias (3,1 cm) e 5 meses (23 cm), encontradas nessa tese, reflete o extenso período reprodutivo da *B. rousseauxii* no Alto Madeira (CELLA-RIBEIRO et al., 2015). Como a velocidade da corrente do rio varia de acordo com o período hidrológico, sendo maior na enchente/cheia do que na vazante/seca, a época em que os juvenis nascem influencia diretamente a velocidade com que eles são carreados rio abaixo. É interessante destacar também, que o tempo de permanência dos juvenis no rio Madeira aqui encontrados, ratificam a eficiência da ^{87}Sr:^{86}Sr como marcadora de origem para os indivíduos nascidos no Alto Madeira. Embora não exista na literatura estimativas acerca do tempo que os peixes levam para assimilar a ^{87}Sr:^{86}Sr da água circundante, como esses isótopos não sofrem fracionamento, é admissível aceitar que eles necessitam de um período semelhante aquele observado para o metal elementar estrôncio, o qual é estimado entre 10 e 30 dias (YOKOUCHI et al., 2011).

A segunda fase do ciclo de vida foi caracterizada pelos baixos valores isotópicos (0,709-0,711), que corresponderam a passagem obrigatória dos indivíduos pela calha principal do rio Amazonas, onde permaneceram se desenvolvendo em média até 2,6 anos de vida (quando possuem cerca de 80 cm), coincidindo ao postulado na literatura para essa espécie (BARTHEM; GOULDING, 1997; ALONSO, 2002; DUPONCHELLE et al., 2016; HERMANN et al., 2016). A partir dessa idade começou a terceira etapa do ciclo de vida desses indivíduos, marcada pelo retorno dos altos valores da ^{87}Sr:^{86}Sr (0,714-0,726), característicos do rio Madeira. Segundo Hauser e colaboradores (2018) a partir de 2,2 anos de idade as douradas do rio Madeira já estão sexualmente maduras, resultado que ratifica o retorno dos indivíduos a essa bacia por volta de 2,6 anos, visando posteriormente a reprodução nas cabeceiras. É interessante notar que alguns desses adultos ao retornarem ao rio Madeira exibiram valores da ^{87}Sr:^{86}Sr maiores (0,735) que aqueles conhecidos na literatura (e amostrados durante o desenvolvimento dessa tese), para a calha dos principais afluentes dessa bacia. Embora *B. rousseauxii* seja uma espécie adaptada a desenvolver seu ciclo de vida marjoritariamente na calha principal dos rios, esse resultado sugere que esses indivíduos possam ter passado algum tempo em lagoas marginais adjacentes, conforme já foi observado maiores valores da ^{87}Sr:^{86}Sr (de até 0,01 magnitude) em otólitos de peixes de lagoas do rio Beni, quando comparados aos da calha principal desse afluente (POUILLY et al., 2014). Alternativamente estes apontamentos sugerem ainda que possam existir tributários do Alto Madeira com valores > 0,726, os quais todavia não foram amostrados, ratificando inclusive, a necessidade de um maior refinamento da ^{87}Sr:^{86}Sr da malha hídrica dessa bacia.

A separação geográfica entre as áreas de reprodução e de crescimento é uma resposta evolutiva direcionada à diminuição da competição, entre a prole e seus genitores (HAMILTON; MAY, 1977). Para *B. rousseauxii* a migração de juvenis para o estuário e Baixo Amazonas, além de evitar a competição com seus pais, também deve reduzir a pressão competitiva exercida pelos jovens das outras espécies, que crescem próximo à área de reprodução (BARTHEM; GOULDING, 1997). Estas características, associadas à alta produtividade e disponibilidade de recursos alimentares no estuário, tornam este comportamento muito vantajoso para *B. rousseauxii*. Essa vantagem foi claramente demonstrada neste trabalho, pelo maior comprimento dos indivíduos *homers* quando comparados aos residentes em uma mesma classe etária no Alto Madeira.

Por sua vez, o retorno aos locais natais também é altamente adaptativo, proporcionando benefícios de condicionamento físico e contribuindo para a evolução de populações localmente adaptadas (TAYLOR 1991; CURY, 1994; HENDRY et al., 2000; McDOWALL, 2001; WAPLES et al., 2004). A familiaridade com o espaço físico, além de aumentar a probabilidade dos peixes em idade reprodutiva encontrarem parceiros, também permite a localização de habitats favoráveis à desova adulta e à sobrevivência juvenil (CURY, 1994; KEEFER; CAULDILL, 2014). Portanto, o predominante comportamento de *homing* natal observado para *B. rousseauxii* no Alto Madeira, antes do represamento dessa bacia, reflete o quão adaptativo esse comportamento é para essa espécie na bacia amazônica.

Embora a homogeneidade das águas da calha principal do rio Amazonas não tenha permitido estimar precisamente a parcela de indivíduos de *B.rousseauxii* que realizaram *homing* natal nessa sub-bacia, também se espera que este seja o comportamento predominante para o rio Amazonas. Essa hipótese é sustentada, tanto pelo comportamento marjoritário de *homers* (80%) observado no rio Madeira, como pela presença de *homers* confirmados na calha principal do rio Amazonas, com migração até o estuário (ver capítulo II), ou pelo menos até a Amazônia central (onde estão localizados os tributários com águas radiogênicas do escudo granítico), antes de retornarem ao Alto Amazonas, onde foram capturados (Figura 18 A e Figura 19 A).

Dentre os mecanismos que permitem os peixes anádromos realizarem com sucesso, o comportamento de *homing* natal descrito acima, estão: a capacidade dos juvenis de registrarem olfativamente substâncias químicas únicas (ou seja, odores ambientais), da água de seus locais de nascimento (durante a migração rio abaixo), e a habilidade dos adultos de retornar a esses locais utilizando tais odores (CURY, 1994; DITTMAN; QUINN, 1996; HINO et al*.,* 2009; UEDA, 2011; 2012). No entanto, a assimilação incompleta desses odores em função de taxas hormonais insuficientes, para estimular as memórias olfativas dos juvenis, ou mesmo a interrupção desse processo por intervenção humana, bem como a falha do sistema sensorial ou da memória dos adultos, podem refletir na falha de reconhecimento das áreas natais no momento da migração reprodutiva (DITTMAN; QUINN 1996; KEEFER; CAULDILL, 2014). No caso de *B. rousseauxii,* em especial, a grande velocidade da corrente de água quando os indivíduos se reproduzem durante o pico das cheias (CAÑAS; PINE, 2011), também pode ser outro fator que induz a assimilação incompleta desses odores.

Para os salmonídeos, uma pequena proporção desses indivíduos, conhecidos como *strayers*, costuma ter pouco efeito sobre as populações doadoras, visto que esses peixes possuem alta fecundidade (McCLURE et al., 2003), como é o caso de *B. rousseauxii* (GARCÍA-VASQUEZ et al., 2009). Por outro lado, uma pequena taxa de *strayers* costuma ser um ganho demográfico para a população receptora, sobretudo quando contribuem para a reprodução, visto que aumentam a resiliência geral e a estabilidade genética da mesma (ARAKI et al., 2007; WALTER et al., 2009). Embora não seja possível afirmar qual a porcentagem média de *strayers* esperada dentro de populações naturais, visto a dificuldade de estimar esses valores em populações sem interferência humana, bem como compará-los entre os diferentes estudos (KEEFER; CAULDILL, 2014), a ocorrência desses indivíduos nas áreas reprodutivas de *B. rousseauxii* no Alto Madeira e Alto Amazonas, ressaltam a importância da manutenção e monitoramento de suas taxas nas sub-bacias amazônicas.

Mas, a despeito de exemplos extremos, em nenhuma população migratória, 100% dos indivíduos migram (CURY, 1994; SECOR; KERR, 2009; CHAPMAN et al., 2011, KENDAL et al., 2015). Normalmente, os indivíduos de uma população mostram diferenças no comportamento migratório. Alguns se deslocam entre habitats enquanto outros permanecem residentes em um único local, fenômeno conhecido como migração parcial (CHAPMAN et al., 2011; 2012; KENDAL et al., 2015). O quê determina se um indivíduo migrará ou não, é o resultado de uma complexa interação entre o genótipo, a condição individual e o ambiente do peixe (SLOAT et al., 2014, KENDAL et al., 2015), que visa maximizar a aptidão de cada indivíduo (ARAI et al., 2006). Nessa perspectiva, a presença de exemplares residentes de *B. rousseauxii* no Alto Madeira, antes da construção do complexo hidrelétrico, e após o barramento no Alto Amazonas, refletem essa complexa interação de fatores. Ademais, considerando o componente genético fortemente associado aos comportamentos de *homing* e residência, a ocorrência desses diferentes padrões migratórios contribuem para a estabilidade genética das populações (KENDAL et al., 2015).

Além disso, esta espécie é conhecida por desovar tanto nas águas altas como nas águas baixas, dentro de uma mesma bacia (GARCÍA-VASQUEZ et al., 2009; CAÑAS; PINE, 2011; VAN DAMME et al., 2011; AGUDELO et al., 2013; CELLA-RIBEIRO et al., 2015; GARCÍA-DÁVILA et al., 2015; BARTHEM et al., 2017). A reprodução durante o período de vazante, quando o rio retorna ao leito natural, provavelmente reduz o risco de perda de ovos e larvas nas várzeas adjacentes, e portanto, maximiza as chances desses indivíduos atingirem a área de berçário no estuário, a milhares de quilômetros a jusante (GARCÍA-VASQUEZ et al., 2009). Por sua vez, a reprodução durante os períodos de cheia e enchente aumenta esse risco, e os juvenis perdidos que sobrevivem na planície de inundação podem se tornar residentes dessas áreas de cabeceira.

Por outro lado, o comportamento residente exibido por todos os peixes capturados, após a construção do complexo hidrelétrico no Alto Madeira, foi um claro efeito do barramento sobre a migração dessa espécie. Este apontamento é suportado, tanto pelo predominante número de *homers* observado para *B. rousseauxii* no alto Madeira, antes da construção das hidrelétricas, quanto pela completa ausência desses indivíduos e de *strayers*, após o barramento. Ademais, a recente amostragem (junho de 2017) de indivíduos *homers* bloqueados abaixo da usina hidrelétrica de Santo Antônio Energia, foi outra evidência dos impactos das barragens sobre o ciclo de vida dessa espécie. Estes resultados confirmaram a ineficácia dos sistemas de transposição na passagem a montante dessa espécie, ratificando as previsões de impactos sobre a atividade econômica pesqueira na bacia do rio Madeira (FEARNSIDE 2014; 2015; CARVAJAL et al., 2014; DUPONCHELLE et al., 2016).

Ainda que existam peixes residentes no Alto Madeira, ou que os descendentes dos *homers* retidos nessa região possam se estabelecer, como discutido acima, a separação geográfica entre as áreas de reprodução e berçário é uma resposta adaptativamente vantajosa para *B. rousseauxii*, a qual proporciona crescimento significativo maior em relação ao indivíduos que são residentes. Considerando que peixes menores possuem menor fecundidade (KING, 1995), o comportamento residente obrigatório afetará diretamente o recrutamento de *B. rousseauxii* na bacia do rio Madeira. Inclusive, redução na taxa de fecundidade de salmonídeos residentes quando comparados àqueles que realizaram anadromia já foram reportadas na literatura (WAPLES et al., 2008; KENDAL et al., 2015)

O comportamento residente exclusivo reportado acima somado à ocorrência de vários jovens de um ano de idade no reservatório de Santo Antônio Energia, entre 2012 e 2013 (neste período a hidrelétrica de Jirau ainda estava sendo construída), à pequena taxa de *strayers* provenientes do rio Madeira no Alto Amazonas, e à diminuição do desembarque de douradas no mercado pesqueiro de Porto velho (LIMA, 2017) (responsável pela comercialização de grande parte da produção pesqueira a jusante das usinas hidrelétricas), também apontam para os impactos dos reservatórios na passagem a jusante das larvas e juvenis de *B. rousseauxii* (ver DUPONCHELLE et al., 2016).

Por outro lado, a ocorrência de juvenis oriundos do rio Madeira na região estuarina, indicam que pelo menos uma parcela desses indivíduos conseguiram passar pelas turbinas das hidrelétricas. Fato este que corroborou a presença de larvas e juvenis amostradas abaixo desse complexo em 2014 (LIMA, 2015). Embora não tenha sido possível determinar se a contribuição atual do rio Madeira (16%), no recrutamento do estuário, é menor do que aquela anterior à instalação das usinas hidrelétricas, mediante às considerações discutidas acima, é provável que essa bacia esteja aportando menos juvenis ao estuário. Nessa perspectiva, estimativas da contribuição dos diferentes afluentes no recrutamento de *B. rousseauxii* no estuário, antes da implementação do complexo hidrelétrico do rio Madeira, seria uma ótima forma de quantificar o impacto desses empreendimentos nessa região de berçário da espécie. Para tanto, as análises microquímicas de otólitos de indivíduos coletados anteriormente a esse período (ferramenta que teve sua aplicabilidade robustamente confirmada ao longo desse trabalho), seria uma ótima alternativa para mensurar essas perturbações.

A despeito de que a confirmação de *homing* natal de *B. rousseauxii* na bacia amazônica, com movimentos transfronteiriços entre Peru, Bolívia e Brasil, tenha desdobramentos importantes sobre a produção e manejo dessa espécie, considerando o atual e previsto plano de matriz energética da bacia amazônica (com mais de 154 grandes hidrelétricas em operação, 14 sobre construção e 221 planejadas, CASTELO; MACEDO, 2016), a presença pretérita de *homers*, *strayers* e residentes nas áreas de cabeceiras, torna esse cenário um pouco mais otimista. Conforme discutido acima, a ocorrência de indivíduos com padrões migratórios distintos dentro de uma mesma área reprodutiva aumentam a resiliência geral e a estabilidade genética das populações, tornando a espécie mais adaptada às alterações ambientais.

Outro ponto positivo foi a passagem (ainda que pequena) de juvenis pelas turbinas, o que demonstrou possível atividade reprodutiva nas cabeceiras. Uma terceira característica favorável de *B. rousseauxii*, pelo menos para o rio Madeira, é que uma vez que os adultos retornam para se reproduzirem nas área de cabeceiras, eles permanecem nesta região todo o resto do ciclo de vida, não realizando migrações rio abaixo em direção ao Amazonas (DUPONCHELLE et al., 2016; HAUSER et al., 2018). Assim, os deletérios efeitos dos reservatórios sobre a migração rio abaixo dos adultos (AGOSTINHO et al., 2008; PELICICE et al., 2015) não é um problema para *B rousseauxi*, considerando a escala do Alto Madeira. Entretanto, é importante salientar que apesar dessas migrações dos *homers* e *strayers* adultos, e dos residentes ao longo de todo o ciclo de vida, serem restritas ao Alto Madeira, esses indivíduos ainda assim realizam extensos deslocamentos entre as sub-bacias dessa área de cabeceira. Ressalta-se assim, o quão imprescindível é a manutenção de conectividade desse trecho e o quão deletério será a implementação de novas hidrelétricas já previstas para o Alto Madeira, sugerindo veemente a reavaliação do plano de matriz energética da bacia amazônica (DUPONCHELLE et al., 2016; ANDERSON et al., 2018).

Ademais, o fato de atualmente 100 % dos indivíduos amostrados no Alto Madeira serem residentes, os quais possuem menor taxa de crescimento que os *homers*, com prováveis efeitos negativos sobre a fecundidade e recrutamento populacional, recomenda-se categoricamente a necessidade do funcionamento efetivo dos sistemas de transposição de peixes das usinas hidrelétricas de Santo Antônio e Jirau. É essencial que os *homers* e *strayers* continuem tendo acesso as áreas reprodutivas de cabeceira, para a garantir a manutenção de populações viáveis de *B. rousseauxii* no Alto Madeira, bem como sua contribuição aos estoques genéticos da bacia amazônica como um todo.

5– REFERÊNCIAS

AGOSTINHO, A. A.; PELICICE, F. M.; GOMES, L. C. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. **Brazilian Journal of Biology**, v. 68, s. 4, p. 1119–1132, 2008.

AGUDELO, E.; JOVEN-LEÓN, A. V.; BONILLA-CASTILLO, C. A.; PETRERE, M. JR.; PELÁEZ, M.; DUPONCHELLE, F. Breeding, growth and exploitatinon of *Brachyplatystoma rousseauxii* in the Caqueta River, Colombia. **Neotropical Ichthyology**, v. 11, n. 3, p. 637–647, 2013.

ALONSO, J. C. **Padrão espaço-temporal da estrutura populacional e estado atual da exploração pesqueira da dourada *Brachyplatystoma flavicans*, Castelnau, 1855 (Siluriformes: Pimelodidae), no sistema Estuário- Amazonas- Solimões.** Tese de doutorado do Instituto Nacional de Pesquisa da Amazônia/ Fundação Universidade do Amazonas. Manaus, Amazonas, p. 217, 2002.

ANDERSON, E. P.; JENKINS, C. N.; HEILPERN, S.; MALDONADO-OCAMPO, J. A.; CARVAJAL-VALLEJOS, F. M.; ENCALADA, A. C.; RIVADENEIRA, J. F.; HIDALGO, M.; CAÑAS, C. M.; ORTEGA, H.; SALCEDO, N.; MALDONADO, M.; TEDESCO, P. A. Fragmentation of Andes-to-Amazon connectivity by hydropower dams. **Science Advances**, v. 4, eaao1642., 2018.

ARAI, T.; YANG, J.; MIYAZAKI, N. Migration flexibility between freshwater and marine habitats of the pond smelt *Hypomesus nipponensis*. **Journal of Fish Biology**, v. 68, p. 1388−1398, 2006.

ARAKI, H.; WAPLES, R. S.; ARDREN, W. R.; COOPER, B.; BLOUIN, M. S. Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life-history forms. **Molecular Ecology**, v. 16, p. 953–966, 2007.

BARTHEM, R. B.; GOULDING, M. **Os bagres balizadores: ecologia, migração e conservação de peixes amazônicos.** Sociedade Civil Mamirauá/MCT/CNPQ: Brasília, p. 130, 1997.

BARTHEM, R.; GOULDING, M; LEITE, R. G.; CAÑAS, C.; FORSBERG, E. V.; PETRY, P.; RIBEIRO, M. L. B.; CHUCTAYA, J.; MERCADO, A. Goliath catfish spawning in the far western Amazon confirmed by the distribution of mature adults, drifting larvae and migrating juveniles. **Scientific Reports**, v.7, p. 41784, 2017. DOI: 101038/srep41784.

BAUER, S.; HOYE, B. J. Migratory animals couple biodiversity and ecosystem functioning worldwide. **Science,** v. 344, 1242552, 2014.

CAÑAS, C. M.; PINE, W. E. Documentation of the temporal and spatial patterns of Pimelodidae catfish spawning and larvae dispersion in the Madre de Dios River (Peru): insights for conservation in the Andean-Amazon headwaters. **River Research and Applications**, v. 27, p. 602–611, 2011.

CARVAJAL-VALLEJOS, F. M. **Phylogeny and population genetics of the fish performing the largest migration known in freshwater, the amazonian catfish *Brachyplatystoma rousseauxii*: revelations from the Upper Madera basin**. Tese de doutoramento da Université Montpellier II Sciences et Techniques du Languedoc. Paris, França, p. 174, 2013.

CARVAJAL-VALLEJOS, F. M.; DUPONCHELLE, F.; DESMARAIS, E.; CERQUEIRA, F.; QUEROUIL, S.; NUÑEZ, J.; GARCÍA, C.; RENNO, J. F. Genetic structure in the Amazonian catfish *Brachyplatystoma rousseauxii:* influence of life history strategies. **Genetica**, v. 142, p. 323-336, 2014.

CASTELLO, L.; MCGRATH D. G.; HESS, L. L.; COE, M. T.; LEFEBVREL, P. A.; PETRY. P.; MACEDO, M. M.; RENÓ, V. F.; ARANTES, C. C. The vulnerability of Amazon freshwater ecosystems. **Conservation Letters**, v. 6, n. 4, p. 217–229, 2013.

CASTELLO L.; MACEDO, M. N. Large-scale degradation of Amazonian freshwater ecosystems. **Global Change Biology**, v. 22, n. 3, p. 990-1007, 2016.

CELLA-RIBEIRO, A.; ASSAKAWA, L. F.; TORRENTE-VILARA, G.; ZUANON, J.; LEITE, R. G.; DORIA, C.; DUPONCHELLE, F. Temporal and spatial distribution of young *Brachyplatystoma* spp. (Siluriformes: Pimelodidae) along the rapids stretch of the Madeira River (Brazil) before the construction of two hydroelectric dams. **Journal of Fish Biology**, v. 86, p.1429-1437, 2015.

CHAPMAN, B. B.; BRÖNMARK, C.; NILSSON, J-A.; HANSSON, L. A. The ecology and evolution of partial migration. **Oikos**, n. 120, p. 1764–1775, 2011.

CHAPMAN, B. B.; HULTHÉN, K.; BRODERSEN, J.; NILSSON, P. A.; SKOV, C.; HANSSON, L. A.; BRÖNMARK, C. (2012). Partial migration in fishes: Causes and consequences. **Journal of Fish Biology**, v. 81, p. 456–478, 2012.

CURY, P. Obstinate nature: an ecology of individuals. Thoughts on reproductive behavior and biodiversity. **Canadian Journal of Fisheries and Aquatic Sciences,** n. 51, p. 1664–1673, 1994. DOI:10.1139/F94-167

DINGLE, H. **Migration: the biology of life on the move**. – Oxford Univ. Press, p. 326, 1996.

DITTMAN, A. H.; QUINN, T. P. Homing in Pacific salmon: mechanisms and ecological basis. **Journal of Experimental Biology**, v. 199, p. 83–91, 1996.

DUPONCHELLE, F.; POUILLY, M.; PECHEYRAN, C.; HAUSER, M.; RENNO, J.F.; PANFILI, J.; DARNAUDE, A. M.; GARCÍA-VASQUEZ, A.; CARVAJAL-VALLEJOS, F.; GARCIÍA-DÁVILA, C.; DORIA, C.; BERAIL, S.; DONARD, A.; SONDAG, F.; SANTOS, R.V.; NUÑEZ, J.; POINT, D.; LABONNE, M.; BARAS, E. Trans-Amazonian natal homing in giant catfish. **Journal of Applied Ecology**, v. 53, p. 1511-1520, 2016.

FEARNSIDE, P. M. Brazil's Madeira River dams: A setback for environmental policy in Amazonian development. **Water Alternatives**, v. 7, n. 1, p. 154-167, 2014.

FEARNSIDE, P. M. **Hidrelétricas na Amazônia: impactos ambientais e sociais na tomada de decisões sobre grandes obras-Vol 1**. Manaus: Editora do INPA, p. 296, 2015.

FINER, M.; JENKINS, C. N. Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. **PLoS ONE**, v. 7, n. 4, e35126, 2012.

FIORAVANTI, C. As primeiras águas de um rio. **Revista Pesquisa FAPESP [online].** 2008, n150 [viewed 10 Novembro 2016]. Available from: http://revistapesquisa.fapesp.br/2008/08/01/as-primeiras-aguas-de-um-rio/

FORSBERG, B. R.; MELACK, J. M.; DUNNE, T.; BARTHEM, R. B.; GOULDING, M.; PAIVA, R. C. D.; WEISSER, S. The potential impact of new Andean dams on Amazon fluvial ecosystems. **PLoS ONE**, v. 12**,** e0182254, 2017.

GAILLARDET, J.; DUPRE, B.; ALLEGRE, C. J.; NEGREL, P. Chemical and physical denudation in the Amazon River Basin. **Chemical Geology,** v. 142, p. 141–173, 1997.

GARCÍA-DAVILA, C.; CASTRO-RUIZ, D.; RENNO, J.F.; CHOTA-MACUYAMA, W.; CARVAJAL-VALLEJOS, F. M.; SANCHEZ, H.; ANGULO, C.; NOLORBE, C.; ALVARADO, J.; ESTIVALS, G.; NUÑEZ-RODRIGUEZ, J.; DUPONCHELLE, F. Using barcoding of larvae for investigating the breeding seasons of pimelodid catfishes from the Marañon, Napo and Ucayali rivers in the Peruvian Amazon. **Journal of Applied Ichthyology***,* v. 31, p. 40-51, 2015.

GARCÍA-VASQUEZ, A.; ALONSO, J.C.; CARVAJAL, F.; MOREAU, J.; NUÑEZ, J.; RENNO, J. F.; TELLO, S.; MONTREUIL, V.; DUPONCHELLE, F. Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. **Journal of Fish Biology***,* v. **75,** p. 2527-2551, 2009.

HAMILTON, M. D.; MAY, R. M. Dispersal in stable strategies. **Nature**, n. 269, p. 578-581, 1977.

HAUSER, M.; DORIA, C. R. C.; MELO, L. C. R.; SANTOS, A. R.; AYALA, D. M.; NOGUEIRA, L. D.; AMADIO, S.; FABRE, N.; TORRENTE-VILARA, G.; GARCÍA-VASQUEZ, A.; RENNO, J. F.; CARVAJAL-VALLEJOS, F. M.; ALONSO, J. C.; NUÑEZ, J.; DUPONCHELLE, F. Age and Growth of Amazonian migratotory catfish *Brachyplatystoma rousseauxii* in the Madeira River basin before the construction of dams. **Neotropical Ichthyology**, v. 16, n. 1, e170130, 2018. DOI: 10.1590/1982-0224-20170130

HENDRY, A. P.; WENBURG, J. K.; BENTZEN, P.; VOLK, E. C.; QUINN, T. P. Rapid evolution of reproductive isolation in the wild: evi- dence from introduced salmon. Science 290:516–518, 2000.

HERMANN, T. W.; STEWART, D. J.; LIMBURG, K. E.; CASTELLO, L. Unravelling the life history of Amazonian fishes through otolith microchemistry. **Royal Society Open Science**, v. 3, p. 160206, 2016. DOI: 10.1098/rsos.160206

KEEFER, M. L.; CAULDILL, C. C. Homing and straying by anadromous salmonids: a review of mechanisms and rates. **Reviews in Fish Biology and Fisheries**, v. 24, p. 333–368, 2014. DOI 10.1007/s11160-013-9334-6

HINO, H; MILES, N. G.; BANDOH, H.; UEDA, H. Molecular bio- logical research on olfactory chemoreception in fishes. **Journal of Fish Biology**, v. 75, p. 945–959, 2009.

KING, M. **Fisheries biology, assessment and management**. Oxford: Osney Mead. Fishing New Books, p.341, 1995.

KENDAL, N. W.; MCMILLAN, J. R.; SLOAT, M. R.; BUEHRENS, T. W.; QUINN, T. P.; PESS, G. R.; KUZISHCHIN, K. V.; McCLURE, M. M.; ZABEL, R. W. Anadromy and residency in steelhead and rainbow trout (*Oncorhynchus mykiss*): a review of the processes and patterns. **Canadian Journal of Fisherie*s* and Aquatic Sciences**, v. 72, p. 319–342, 2015.

LEITE, R. G.; CAÑAS, C.; FORSBERG, B.; BARTHEM, R. B.; GOULDING, M. **Larvas dos Grandes Bagres Migradores.** Lima, Peru, p. 127, 2007.

LATRUBESSE, E. M. ; ARIMA, E. Y.; DUNNE, T.; PARK, E.; BAKER, V. R.; D'HORTA, F. M.; WIGHT, C.; WITTMANN, F.; ZUANON, J.; BAKER, P. A.; RIBAS, C. C.; NORGAARD, R. B.; FILIZOLA, N.; ANSAR, A.; FLYVBJERG, B.; STEVAUX, J. C. Damming the rivers of the Amazon basin. **Nature,** v. 546, p. 363-369, 2017.

LEES, A. C.; PERES, C. A.; FEARNSIDE, P. M.; SCHNEIDER, M.; ZUANON, J. A. S. Hydropower and the future of Amazonian biodiversity. **Biodiversity and Conservation**, v. 25, p. 451-466, 2016.

LIMA, P. A. **Influência da construção da usina hidrelétrica de Santo Antônio sobre a passagem de larvas e juvenis de pimelodidae, de montante a jusante da barragem no rio Madeira, Porto Velho-RO, Brasil**. Dissertação de mestrado do Programa de Pós-Graduação Em Desenvolvimento Regional e Meio Ambiente, Universidade Federal de Rondonia, Porto Velo, RO, p. 46, 2015.

LIMA, M. A. L. **História do ecossistema e dos recursos pesqueiros frente a implementação de hidrelétricas na bacia do rio Madeira**. Tese de doutorado do Programa de Pós-Graduação Em Desenvolvimento Regional e Meio Ambiente, Universidade Federal de Rondonia, Porto Velo, RO, p. 138, 2017.

LUCAS, M.C.; BARAS, E. **Migration of Freshwater Fishes**. Blackwell Science Ltd., Oxford, p. 420, 2001.

McCLURE, M. M; HOLMES, E. E; SANDERSON, B. L.; JORDAN, C. E. A large-scale, multispecies status, assessment: anadromous salmonids in the Columbia River Basin. **Ecological Applications**, v. 13, p. 964–989, 2003.

McDOWALL, R. M. Anadromy and homing: two life-history traits with adaptive synergies in salmonid fishes? **Fish and Fisheries**, v. 2, p. 78–85, 2001.

MPA. **Boletim estatístico de pesca e aquicultura do Brasil 2011**. Brasília: Ministério da Pesca e Aquicultura, 2013.

NATHAN, R.; GETZ, W. M.; REVILLA, E.; HOLYOAK, M.; KADMON, R.; SALTZ, D.; SMOUSE , P. E. A movement ecology paradigm for unifying organismal movement research. **Proceedings of the National Academy *of* Sciences of the United States of America**, v.105, n. 49, p. 19052 – 19059, 2008.

PALMER, M. R.; EDMOND, J. M. Controls over the strontium isotope composition of river water. **Geochimica et Cosmochimica Acta,** v. 56, p. 2099–2111, 1992.

PELICICE, F. M.; POMPEU, P. S.; AGOSTINHO, A. A. Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. **Fish and Fisheries**, v. 16, p. 697–715, 2015.

POUILLY, M.; POINT, D.; SONDAG, F.; HENRY, M.; SANTOS, R. V. Geographical origin of Amazonian freshwater fishes fingerprinted by ^{87}Sr/^{86}Sr ratios on fish otoliths and scales. **Environmental Science & Technology**, v. 48, p. 8980-8987, 2014.

QUEIROZ, M. M. A.; HORBE, A. M. C.; SEYLER, P.; MOURA, C. A. V. Hidroquímica do rio Solimões na região entre Manacapuru e Alvarães: Amazonas—Brasil. **Acta Amazonica**, v. 39, p. 943–952, 2009.

QUEIROZ, L. J.; TORRENTE-VILARA, G.; OHARA, W. M.; PIRES, T. H. S.; ZUANON, J.; DORIA, C. R. C. **Peixes do Rio Madeira**. 1. ed. São Paulo: Dialeto, 2013. v. 3. 1163p.

SECOR, D. H,; KERR, L. A. A lexicon of life cycle diversity in diadromous and other fishes. **American Fisheries Society Symppsium Series**, v. 69, p. 537–556, 2009.

SANTOS, R.V.; SONDAG, F.; COCHONNEAU, G.; LAGANE, C.; BRUNET, P.; HATTINGH, K.; CHAVES, J. G. S. Source area and seasonal ^{87}Sr/^{86}Sr variations in rivers of the Amazon basin. **Hydrological Processes**, v. 29, p. 187–197, 2015.

SLOAT, M. R.; FRASER, D. J.; DUNHAM, J. B.; FALKE, J. A.; JORDAN, C. E.; MCMILLAN, J. R.; OHMS, H. A. Ecological and evolutionary patterns of freshwater maturation in Pacific and Atlantic salmonines. **Reviews in Fish Biology and Fisheries**, v. 24, p. 689–707, 2014.

TAYLOR, E. B. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. **Aquaculture**, v. 98, p. 185–207, 1991.

UEDA, H. Physiological mechanism of homing migration in Pacific salmon from behavioral to molecular to biological approaches. **General and Comparative Endocrinology,** v. 170, p. 222–232, 2011.

UEDA, H. Physiological mechanisms of imprinting and homing migration in Pacific salmon *Oncorhynchus* spp. **Journal of Fish Biology**, v. 81, p. 543–558, 2012.

VAN DAMME, P. A.; CARVAJAL-VALLEJOS, F.; CAMACHO, J.; MUÑOZ, H.; CORONEL, J. S. **Los peces y delfines de la Amazonía Boliviana - Hábitats, potencialidades y amenazas.** Editorial INIA, Cochabamba, Bolivia, p. 490, 2011.

WALTER, R. P.; AYKANAT, T.; KELLY, D. W.; SHRIMPTON, J. M.; HEATH, D. D. Gene flow increases temporal stability of Chinook salmon (*Oncorhynchus tshawytscha*) populations in the Upper Fraser River, British Columbia, Canada. **Canadian Journal of Fisheries and Aquatic Sciences**, v. 66, p. 167–176, 2009.

WAPLES, R. S.; TEEL, D. J.; MEYER, J. M.; MARSHALL, A. R. Life-his- tory divergence in Chinook salmon: historic contingency and parallel evolution. **Evolution**, v. 58, p. 386–403, 2004.

WAPLES, R. S.; ZABEL, R. W.; SCHEUERELL, M. D.; SANDERSON, B. L. Evolutionary responses by native species to major anthropogenic changes to their ecosystems: Pacific salmon in the Columbia River hydropower system. **Molecular Ecology**, v,17, p. 84–96, 2008. DOI:10.1111/j.1365-294X.2007.03510.x

WILCOVE, D. S.; WIKELSKI, M. Going, going, gone: is animal migra- tion disappearing? **PLoS Biology**, v. 6, e188, 2008.

WINEMILLER, K. O.; MCINTYRE, P. B.; CASTELLO, L.; FLUET- CHOUINARD, E.; GIARRIZZO, T.; NAM, S.; BAIRD, I. G.; DARWALL, W.; LUJAN, N. K.; HARRISON, I.; STIASSNY, M. L. J.; SILVANO, R. A. M.; FITZGERALD, D. B.; PELICICE, F. M.; AGOSTINHO, A. A.; GOMES, L. C.; ALBERT, J. S.; BARAN, E.; PETRERE Jr., M.; ZARFL, C.; MULLIGAN, M.; SULLIVAN, J. P.; ARANTES, C. C.; SOUSA, L. M.; KONING, A. A.; HOEINGHAUS, D. J.; SABAJ, M.; LUNDBERG, J. G.; ARMBRUSTER, J.; THIEME, M. L.; PETRY, P.; ZUANON, J.; TORRENTE-VILARA, G.; SNOEKS, J.; OU, C.; RAINBOTH, W.; PAVANELLI, C. S.; AKAMA, A.; VAN SOESBERGEN, T A.; SÁENZ, L. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. **Science.** v. 351(6269), p.128–129, 2016.

YOKOUCHI, K.; FUKUDA, N.; SHIRAI, K.; AOYAMA, J.; DAVERAT, F.; TSUKAMOTO, K. Time lag of the response on the otolith strontium/calcium ratios of the Japanese eel, *Anguilla japonica* to changes in strontium/calcium ratios of ambient water. **Environmental Biology of Fishes**, v. 92, p. 469−478, 2011.

CAPÍTULO IV

Desvendando os padrões migratórios do grande bagre amazônico *Brachyplatystoma platynemum*, usando análises da ^{87}Sr:^{86}Sr dos otólitos

Aceito para Publicação em Aquatic Conservation Marine and Freshwater Ecosystem sob o título Shedding light on the migratory patterns of the Amazonian goliath catfish, *Brachyplatystoma platynemum*, using otolith ^{87}Sr:^{86}Sr analyses.

Shedding light on the migratory patterns of the Amazonian goliath catfish, *Brachyplatystoma platynemum*, using otolith ^{87}Sr:^{86}Sr analyses

ABSTRACT

1. In the Amazon, migratory catfishes of the genus *Brachyplatystoma* are apex predators of considerable interest for fisheries and conservation. The life cycle of *Brachyplatystoma platynemum* is poorly known, although it has been hypothesized to be very similar to that of *B. rousseauxii*, which uses the entire length of the Amazon basin to complete its life cycle (from the Andes to the estuary). This study provides the first data on the migratory patterns of *B. platynemum* at the individual level using otolith microchemistry.
2. A total of 94 individuals were sampled close to major breeding areas in the Amazon basin (78 fish from the middle and upper Madeira and 14 from the upper Amazon rivers) and assessed their lifetime movements by measuring variations in ^{87}Sr:^{86}Sr along transverse sections of their otoliths (ear stones), using laser ablation multicollector mass spectrometry (LA-MC-ICP-MS).
3. The migrations of *B. platynemum* are not as extensive as those of *B. rousseauxii*, and do not involve natal homing. Furthermore, the estuary is not a nursery area, at least for fish hatched in the Madeira. Nevertheless *B. platynemum* migrates several thousand kilometres within the Amazon basin, with transboundary displacements between at least Bolivia, Brazil and Peru.
4. Current and planned hydroelectric development in the Amazon basin will severely disrupt the migrations and access to the breeding grounds, ultimately impacting the recruitment and population dynamics of these apex predators.
5. Their conservation is crucial for the stability of the Amazonian aquatic food webs. This requires building effective fish passage on the two existing Madeira dams and consider alternative options to the large-scale hydropower development in the Amazon basin.

Key words: river, catchment, migration, conservation evaluation, fish, fishing, hydroelectric dams.

1 INTRODUCTION

Migration is an important feature of the life cycle of most freshwater and marine fishes (Harden-Jones, 1968; Miles, West, & Norman, 2009) that strongly influences ecosystems dynamics through large-scale flows of energy, nutrients and processes (Flecker, McIntyre, Moore, & Hall, 2010; Bauer & Hoye, 2014). Understanding spatial and temporal patterns of fish movements is fundamental for management and conservation strategy of these important resources (Elsdon & Gillanders, 2003; Wilcove & Wikelski, 2008; Bauer & Hoye, 2014), especially in large international river basins (Carolsfeld, Harvey, Ross, & Baer, 2003; McIntyre et al., 2016). The lack of knowledge about the migratory behaviour of tropical freshwater fishes, associated with the level of fragmentation of their ecosystems (>50% fragmented by dams, Nilsson et al*.,* 2005), emphasize the need for such information, particularly for species that are a key source of protein to millions of people, such as goliath catfishes in the Amazon basin (Barthem & Goulding 1997; and 2007; Batista, Alonso, Ladle, & Fabré, 2018).

The pimelodid genus *Brachyplatystoma* includes the commercially important goliath catfishes. Official statistics of Brazilian fisheries authorities estimated that three species of this genius (*B. rousseauxii, B. vaillantii* and *B. filamentosum*) alone accounted for a production of more than 40,000 tonnes per year (MPA, 2013). Among these goliath catfishes, *B. platynemum* (Boulenger, 1898), popularly known as babão in Brazil and as baboso, tabla barba or mota flemosa in other South American countries, was considered, until recently, of little commercial interest in total landings of the Amazon basin (Ochoa et al., 2015). Declines in the landings of the other large *Brachyplatystoma* species, however, have contributed to increased catches of *B. platynemum* in recent years (Petrere Jr, Barthem, Córdoba, & Gomez, 2004: Ochoa et al., 2015). On the other hand, this species has long been important in the Madeira basin, where it represented between 1 and 3.6% of total landings before the construction of two hydroelectric dams in the Brazilian portion of the basin (Doria et al., 2018).

Along with river dolphins, goliath catfishes are the apex predators of the main river channels in the Amazon (Barthem & Goulding, 1997; Petrere Jr, Barthem, Córdoba, & Gomez, 2004). As such, they hold particularly important ecological roles for the stability of the aquatic food chains. The role of top predators on ecosystem structure, functioning and resilience is so important that modifying their abundance frequently leads to profound ecosystem alterations through cascading effects (Pace, Cole, Carpenter, & Kitchell, 1999; Myers, Baum, Shepherd, Powers, & Peterson, 2007; Baum & Worm, 2009; Estes et al., 2001). Goliath catfishes are therefore particularly important for conservation strategies and have been suggested as umbrella species (Agostinho, Thomaz, & Gomes, 2005).

Yet, apart from information on its population dynamics (Sant'Anna, Doria, & Freitas, 2014), very little is known about the ecology and migration patterns of *B. platynemum*. It has been hypothesised to perform the same Amazon basin-wide migration as *B. rousseauxii* (Barthem & Goulding, 2007). The life cycle of *B. rousseauxii* indeed involves the largest known migration in freshwaters, with a round trip of over 11,000 km between the breeding grounds in the Andean piedmont of Bolivia, Colombia, Ecuador and Peru, and the nurseries in the lower Amazon and estuary areas (Barthem & Goulding, 1997; Duponchelle et al., 2016; Hermann, Stewart, Limburg, & Castello, 2016; Barthem et al., 2017). A recent basin wide analysis of larval sizes and distribution of *Brachyplatystoma* species suggested, however, that the migration pattern of *B. platynemum*, would be more restricted than that of *B. rousseauxii* (Barthem et al., 2017). This later hypothesis is consistent with molecular studies that indicate stronger geographic genetic structure in *B. platynemum* (Ochoa et al., 2015) than in *B. rousseauxii* (Carvajal-Vallejos et al., 2014). As a mixed distribution of larvae and juveniles across the Amazon basin was observed for *B. platynemum*, Barthem et al. (2017) suggested that, contrary to *B. rousseauxii*, their spawning areas might not be exclusively in the far western Amazon nor their nurseries only in the eastern Amazon. A four year (2009-2012) monitoring of fish reproductive activity in the Brazilian portion of the Madeira yielded no *B. platynemum* with ripe gonads, indicating that their breeding areas are likely located in the upper Madeira (Cella-Ribeiro, Torrente-Vilara, Lima-Filho, & Doria, 2016), within Bolivian and Peruvian territories. Available evidence regarding the Amazon mainstem also indicates that reproduction of *B. platynemum* occurs in the upper Amazon in white water rivers of Colombia, Peru and Ecuador (Córdoba et al., 2000; A. García-Vasquez, pers. comm., March 2018), if not as far upstream as *B. rousseauxii* (Barthem et al., 2017).

Planned and current hydroelectric development in the Amazon basin will likely have several critical impacts on the Amazonian ecosystem and its exceptional biodiversity (Agostinho, Pelicice, & Gomes, 2008; Finer & Jenkins, 2012; Castello et al., 2013; Castello & Macedo 2016; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016; Winemiller et al., 2016; Forsberg et al., 2017; Latrubesse et al., 2017; Anderson et al., 2018). Regarding fish and migratory species in particular, one of the major threats undoubtedly lies in disruption or interruption of connectivity (Agostinho, Pelicice, & Gomes, 2008; Castello et al., 2013; Pelicice, Pompeu, & Agostinho, 2015; Duponchelle et al., 2016; Barthem et al., 2017;

Anderson et al., 2018). The recent construction of two run-of-river hydroelectric dams in the Brazilian portion of the Madeira River has already led to modifications of fish assemblages, particularly of bottom dwelling species (Cella-Ribeiro, Doria, Dutka-Gianelli, Alves, & Torrente-Vilara, 2017), such as *Brachyplatystoma* spp. These two dams, and the absence of fish passage in one of them (Jirau), have a great potential to disrupt fish migrations and affect their populations, which further emphasizes the importance of carrying out ecological studies better to understand spatial and temporal patterns of goliath catfish movements.

In the last decades, otolith (ear bones) microchemistry has been increasingly used in migration studies (Campana, 1999; Walther, Limburg, Jones, & Schaffler, 2017). In the calcium carbonate matrix of otoliths, Ca is progressively substituted by chemical elements (or their isotopes), usually in proportion of their ambient concentrations in the natural environment of fishes or of their food. As fish otoliths grow proportionally with the fish, forming seasonal growth rings, they act as an airplane's black box of the environmental conditions of the waters the fish have lived in during its life. The quantitative analysis of otoliths can thus be used as a proxy of the fish's habitat at a particular age or size. The potential of otolith ^{87}Sr:^{86}Sr ratio for studying the migrations of fish species in the Amazon basin has recently been demonstrated (Pouilly, Point, Sondag, Henry, & Santos, 2014; Garcez, Humston, Harbor, & Freitas, 2015; Sousa, Humston, & Freitas, 2016), including for *Brachyplatsytoma* species (Hegg, Giarrizzo, & Kennedy, 2015; Duponchelle et al., 2016), along with a trans-Amazonian natal homing behaviour in *B. rousseauxii* (Duponchelle et al., 2016). By correlating the ^{87}Sr:^{86}Sr ratio in the fish otoliths and in the main tributaries of the Amazon basin, the present work (1) tests whether the migratory pattern of *B. platynemum* is similar to that of *B. rousseauxii*, (2) examines whether the run-of-river dams erected on the Madeira disrupt its migrations, and (3) discusses the implications for management and conservation strategies. Based on the strong genetic structure observed between the Madeira and the Amazon mainstem (Ochoa et al., 2015) and the presence of both larvae and juveniles in most sampling points (Barthem et al., 2017), we hypothesize that both the extent of migrations performed by *B. platynemum* and its inter-basin movements between the Madeira and the Amazon mainstem will be more restricted than that of *B. rousseauxii*.

2 MATERIALS AND METHODS

2.1 STUDY AREA

The Amazon basin encompasses 6.300.000 km^2, of which approximately five millions are in Brazilian territory and the rest is distributed between Bolivia, Colombia, Ecuador, Guyana Peru and Venezuela. This complex hydrological network is bordered, to the West, by the Andean cordillera (with elevations over 6,000 m), where the source of the Amazon lies in the Peruvian Andes; to the North, by the Guyanese shield uplands (with elevation of over 3,000 m); to the South, by the Brazilian shield uplands (with elevation of ~1200 m) and to the East, by the Atlantic ocean, where waters channelled through ~7,000 rivers into the Amazon mainstem drain ~3 million tons of sediments per day (Fioravanti, 2008).

The Madeira River is largest tributary of the Amazon basin with a length of approximately 3,250 km. It is subdivided into a lower stretch with by a steep-walled channel and a very narrow floodplain, and an upper basin, delineated by rapids and waterfalls just upstream of Porto Velho, Brazil. The upper basin drains many large rivers, the principal of which are the Guaporé (or Itenez in Bolivia), Mamoré, Madre de Dios and Béni. The vast inundation area of the upper basin includes a high number of floodplain lakes (Crespo & Van Damme, 2011). The abrupt elevation change in the transition from the Brazilian Central highlands to the Amazon lowlands results in a long stretch of muddy water rapids, unique in the Amazon. The rapids start 3,300 km upstream from the confluence of the Madeira and Amazon Rivers (near Itacoatiara), and the steepest and most important falls were situated in a 300 km river stretch between the cities of Guajará-Mirim and Porto Velho in the State of Rondônia at the border between Brazil and Bolivia. Eighteen rapids occurred in this 300 km stretch, totalling a fall of 60 m, the most famous being Jirau and Teotônio falls (Cella-Ribeiro et al., 2013). Recently, the construction of two large run-of-river hydroelectric dams, Jirau with 50 bulb turbines of 75 MW each (3,750 MW total) and Santo Antônio with 50 bulb turbines of 71.6 MW each (3,568 MW total), permanently flooded Jirau and Teotônio falls, in 2011 and 2012 respectively (Figure 1).

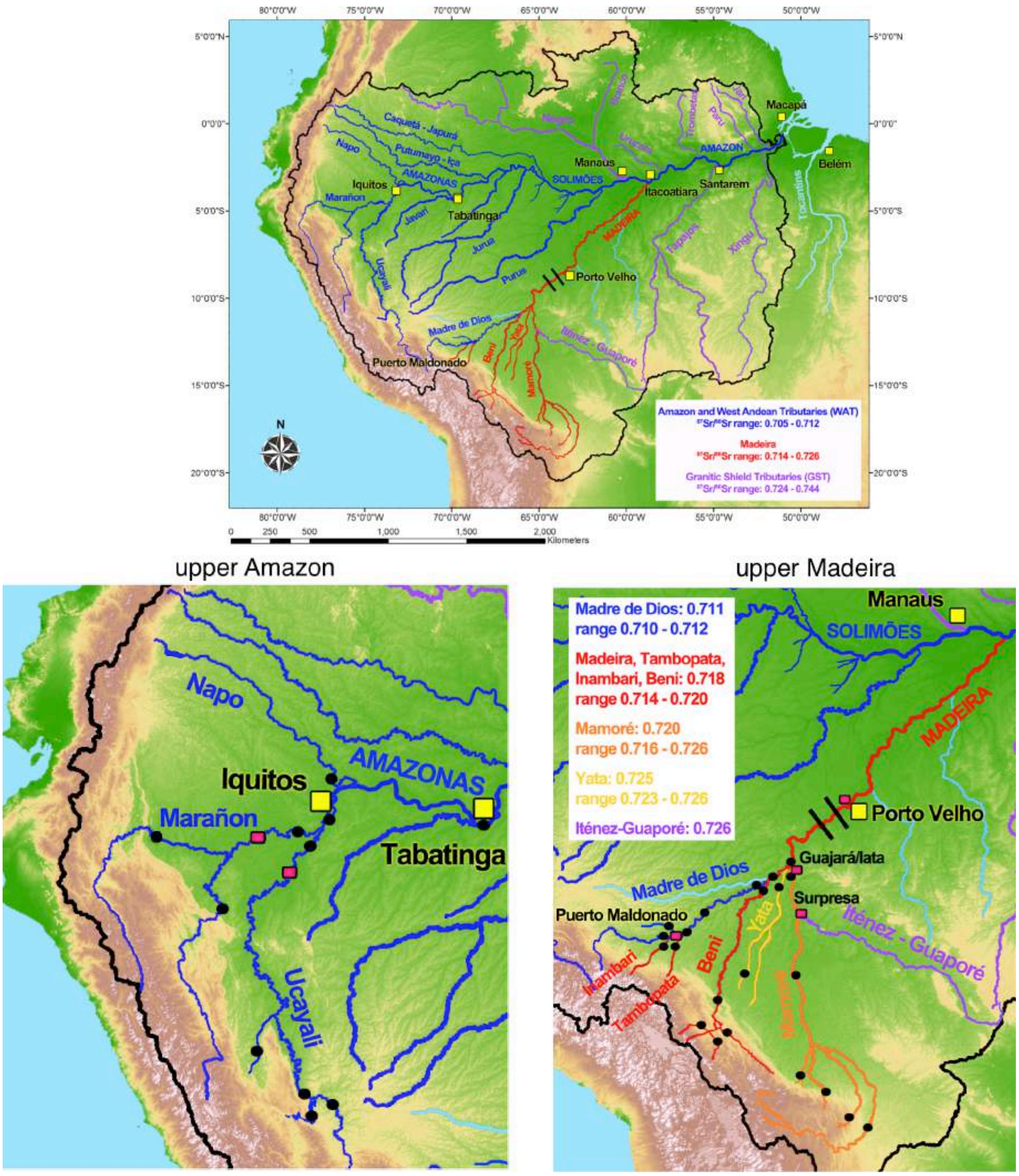


Fig. 1. Map of the reference water ^{87}Sr:^{86}Sr values in the Amazon basin (Table S1). Yellow squares refer to some of the cities mentioned in the text, pink squares to fish sampling localities and black dots refer to water sampling stations in this study, with the following colour code; blue for the Western Andean tributaries of the Amazon (WAT) (until the confluence with the Negro River: 0.705-0.710), the Amazon mainstem and floodplain tributaries (from the confluence with the Negro River to the Óbidos) and Madre de Dios River (0.710-0.712); red for the Madeira and Lower Negro; and purple for the granitic shield tributaries with black or clear waters (GST). The two transverse black bars on the Madeira River upstream of Porto Velho represent two large hydroelectric dams erected since 2011 (Jirau and Santo Antônio).

The Peruvian Amazon represents over 300,000 km^2 and encompasses the major part of the upper Amazon, which corresponds to the Eastern slope of the Andes of Colombia, Ecuador and Peru. It is sub-divided into several sub-basins: the Ucayali, Marañon, Napo, Putumayo (shared with Colombia), Yavari and Purus (both shared with Brazil) and the Madre de Dios, which is part of the Madeira basin (Ortega et al., 2012). The upper Napo sub-basin is located in Ecuador and some affluent of the Marañon (such as the Pastaza) also have their source in Ecuador. The largest sub-basins of the Peruvian Amazon are the Marañon and Ucayali, where most *B. platynemum* were sampled. With respective lengths of > 1600 km and >1500 km, the Marañon and Ucayali both hold a multitude of affluent originating in the Andes or in lowlands. These two major sub-basins join in the largest floodplain and most productive area of the Peruvian Amazon (Tello & Bayley, 2001) to form the Amazonas, known as the Solimões in Brazil.

2.2 WATER SAMPLING AND ANALYSIS

In order to complete our database of $^{87}Sr:^{86}Sr$ water sources of the Amazon basin, compiled from: i) SO-HYBAm (Geodynamical, hydrological and biogeochemical control of erosion/alteration and material transport in the Amazon, Orinoco and Congo basins, http://www.ore-hybam.org/); ii) Palmer & Edmond (1992); iii) Gaillardet, Dupré, Allègre, & Négrel (1997); iv) Pouilly, Point, Sondag, Henry, & Santos (2014); and v) Santos et al. (2015) (see Duponchelle et al., 2016 for details), water samples were collected between October 2014 and February 2017 at 34 sites distributed among the main sub-basin of the upper Madeira basin (Madre de Dios, Mamore, Beni, Yata) and upper Amazon basin (Marañon, Ucayali and Napo) (Fig. 1). Detailed $^{87}Sr:^{86}Sr$ values of these sites are given in Table S1 in Supplementary information.

Samples of near-surface water from the middle of the river were collected in acid-washed HD polyethylene containers for geochemical analysis of dissolved solids. These water samples were filtered through 0.47-µm Millipore DURAPORE® filters and stored in acid-washed HD polyethylene bottles. Samples were acidified with concentrated supra-pure HNO_3. The analyses of $^{87}Sr:^{86}Sr$ were carried out in the laboratory of Geochronological, Geodynamic and Environmental Studies of the University of Brasília (UnB). A quantity of sample sufficient to obtain 500 ng of Sr (typically around 500 ml of sample water) was evaporated, and the residue was dissolved in 1ml of 2N nitric acid. The chemical separation of Sr isotopes was then performed using ion exchange resins (Eichrom Sr-Spec®). The isotopic ratios were measured using a thermo-ionization mass spectrometer (N-TIMS) THERMO SCIENTIFIC TRITON (GGA/UnB)(for details see Santo et al., 2015).

2.3 FISH SAMPLING

Eighty-three fish (66–103 cm total length, LT) were sampled between April 2009 and June 2015 in the upper Madeira River on three fish-landing sites along the Brazilian portion (Surpresa, Guajará Mirim, Iata, all on the Mamoré River), in Puerto Maldonado (Madre de Dios River) in Peru and in the middle Madeira River (Porto Velho). Fourteen other fish (62–86 cm LT) were sampled in upper Amazon basin in the Ucayali and Marañon rivers, between September 2014 and July 2015 (Figure 1 and Table 1). Each specimen was processed at the Ichthyology and fishing laboratory (LIP/UNIR), Porto Velho (Brazil). The total length (TL) was measured (nearest cm) and otoliths (lapilli) were extracted, rinsed in clear water, dried and stored for later examination.

Table 1. Information about individuals of *B. platynemum* sampled throughout the Amazon basin, including their locality of capture, standard length (SL) and whether they were caught before or after the construction of the hydroelectric dams of the Madeira.

Basin	River	Country	Locality	Date	n	Individual codes	Dams	SL (cm) ± SD
middle Madeira	Madeira	Brazil	Porto Velho	Dec/09-May/10	3	BP SS 052, 329 and 399	Before	81 ± 1.4
upper Madeira	Mamoré	Bolivia / Brazil	Iata	Apr/10-Nov/11	19	BP IATA 003 tc BP IATA 533	Before	85 ± 8
upper Madeira	Mamoré	Bolivia / Brazil	Surpresa	Sep/12-Oct/12	8	BP SUR 376 to BP SUR 456	Before	88 ± 3
upper Madeir	Madre de Dios	Peru	Puerto Maldonado	Jun/15	20	BP 202 to BP 225	Before	89 ± 10.4
middle Madeira	Madeira	Brazil	Porto Velho	Jan/12-Oct/12	13	BP SS 20715 to BP SS 20888	After	80 ± 8
upper Madeir	Mamoré	Bolivia / Brazil	Guajará-Mirim	Aug/15-Oct/15	26	BP1833 to BP 1861	After	90 ± 21
upper Amazon	Marañon	Peru	Marañon	Set/14-Apr/15	2	BP 105 and 135	After	62.4 ±
upper Amazon	Ucayali	Peru	Pucallpa	Set/14-Jul/15	12	BP 001 to BP 012	After	74.5 ± 7.64

2.4 OTOLITH ANALYSIS

Every collected otolith was processed at the MARBEC laboratory, Montpellier (France). They were mounted in Araldite epoxy resin and a transverse section to a thickness of approximately 0.7 mm was made with a low-speed Isomet saw (Buehler, Düsseldorf, Germany) to obtain a dorso-ventral slice including the otolith core. The section was then ground and polished using polishing papers (1200 and 2400 µm) and ultra-pure water until seeing the core on one side, as detailed in Duponchelle et al. (2016).

Analyses of Sr isotopes in fish otoliths were carried out in the laboratory LCABIE-IPREM (Université de Pau et des Pays de l'Adour, Pau - France) and in the laboratory PSO-IFREMER (Pole Spectrometrie Océan, Brest - France). Material characteristics of both laboratories are presented in Table 2. In each laboratory, the laser ablated a transect from the core (hatching of the fish) to the edge (death of the fish) of the otolith (i.e. perpendicular to the growth marks). At each opening of the ablation cell for the exchange of otoliths, we analysed an in-lab ^{87}Sr:^{86}Sr certified otolith powder pellet (NIES22, certified Reference Material produced by the National Institute for Environmental Studies, Japan) to check the reliability of ^{87}Sr:^{86}Sr measurements (Yoshinaga, Nakama, Morita, & Edmonds, 2000; Bareille et al., 2005; Allègre et al., 2010). In all cases fs-LA-MC-ICP-MS ^{87}Sr:^{86}Sr measured values (mean ± 2 SD; LCABIE-IPREM-Pau = 0.709214 ± 0.000786; PSO-IFREMER-Brest =0,709137 ± 0.000145) corresponded to certified values.

In order to ensure repeatability and comparability of the analyses performed in LCABIE-IPREM and PSO-IFREMER, several otoliths were analysed in both laboratories (Fig. S1).

Table 2. Characteristics and parameters of the ICP-MS (Inductively Coupled-Mass Spectrometry) and lasers in Pau and Brest laboratories.

Parameter	**LCABIE-IPREM - Pau**	**PSO - Brest**
ICP-MS		
Mass spectrometer	Nu Plasma HR (Nu instruments)	MC-ICP-MS Thermo Neptune
Plasma power (W)	1300 (wet)	1200 (wet)
Cool gas (L/min)	13	16
Auxiliary gas (L/min)	0.8	0.8
Nebulizer gas (L/min)	24	0.6
Additional gas (L/min)	He = 0.5	0.5
Nebulizer	Glass micro-concentric 200μL/min	PFA 50uL/min
Spray chamber	Cyclonic	Dual inlet
Acquisition time	5s	n x2s
Gas blank	10s	30s
On Peak Zero correction	Yes	Yes
Method validation	NIST-987	NIST-987
Mass discrimination correction model	Exponential	Exponential
Interference correction	87Rb, 86Kr	87Rb, 86Kr
LASER		
System	Lambda 3 Nexeya	213LSX CETAC
Source	UV-257 nm	Nd-YAG UV
Spot size (um)	50-150	50-150
Ablation speed (um/s)	5	5
Energy (mJ)	10	4
Frequency (Hz)	2000	20
He flow (L/min)	0.35	0.6
Preablation	No	No
Method validation	NIES-22	NIES-22

LCABIE (Laboratoire de Chimie Analytique Bio-inorganique et Environnement), IPREM (Institut Pluridisciplinaire de Recherche sur l'Environnement et les Matériaux), PSO (Pole Spectrometrie Océan)

3 RESULTS

3.1 WATER CHEMISTRY

The Madre de Dios sub-basin holds a particular position within the Madeira basin. Some of its tributaries have Sr isotopic signatures falling within the range of previously known Madeira values (0.714 to 0.726), such as the Tambopata and the Inambari rivers (Figure 1, Table S1), whereas the Madre de Dios itself displays values typical of the West Andean Tributaries (WAT) and Amazon mainstem (0.710-0.712, Santos et al., 2015; Duponchelle et al., 2016). This should not, however, hamper the interpretation of migratory patterns and the discrimination between fish hatched in the Madre de Dios from those hatched in the Upper Amazon. Indeed, in order to access the lower Amazon or the estuary from the Madre de Dios, fish would have to pass through the Beni and the Madeira and would therefore retain an Upper Madeira signature with values ~ 0.718-720.

3.2 FISH SAMPLED BEFORE THE CONSTRUCTION OF DAMS IN THE MADEIRA RIVER

Most of the 27 fish caught in the upper Madeira, before the dams' completion (Figure 2), never went to the Amazon, because no single value below 0.7129 was observed in any fish. All were hatched in Andean tributaries of the Madeira River, either in the upper Mamoré (> 0.720), in the upper Beni or in the Inambari and Tambopata from the Madre de Dios sub-basin (~ 0.714-0.720).

All fish from Surpresa (Figure 2a) and Iata community (Fig. 2b, c), were caught in the lower Mamoré River. Most were hatched in waters with signatures between 0.715 and 0.718, potentially corresponding to the Beni or Madre de Dios (Inambari or Tambopata) sub-basins. Four specimens were hatched in water signatures > 0.720 (Fig. 2b: BP IATA 184, 421, 432 and 520), hence probably in the Mamoré. Most fish migrated relatively early in their lives into more radiogenic waters (> 0.722), either in the Mamoré, Yata or Itenez sub-basins, until the moment of their capture (Fig. 2a, b). Only a few specimens remained in waters with signatures < 0.720 during the major part of their lives (Fig. 2b: BP IATA 005, 014, 475). One specimen (BP IATA 527), instead of migrating to more radiogenic waters like most other fish, first migrated to less radiogenic waters (down to 0.713, probably in the Madre de Dios sub-basin), before moving also to radiogenic waters (values of up to 0.727) and coming back to the Mamoré, where it was caught.

Only two fishes (BP IATA 184 and BP IATA 005) remained in waters with approximately the same isotopic signature from their birth until their capture (Fig. 2b). Five specimens (BP IATA 410, 413, 433 and 509) hatched in the Béni-Madre de Dios system quickly entered water bodies with exceptionally radiogenic waters (up to > 0.80 for two of them) (Fig 2c). One of them, BP SUR 456 (Fig. 2a), retained the signature of the waters in which it had spent the last part of its life (~ 0.735).

The three individuals sampled in the middle Madeira River (Porto Velho) exhibited different migratory patterns (Fig. 2d). BP SS 399 hatched in the upper Madeira (Beni or Mamoré rivers) and migrated to waters with exceptionally radiogenic signatures for the latter system (> 0.750) before ultimately migrating to the vicinity of Porto Velho. With a hatching signature at 0.7116, specimen BP SS 52 probably hatched in the Madre de Dios (0.710-0.712) and migrated downstream to Porto Velho where it was caught. With a hatching signature at 0.7096, specimen BP SS 329 could have hatched in Madre de Dios itself (0.710-0.712) and migrated to waters with exceptionally radiogenic values before migrating to the middle Madeira River (around Porto Velho), where it was caught.

Alternatively, specimen BP SS 329 could also have hatched in one of the WAT in the upper Amazon basin (0.705-0.710) and entered a highly radiogenic river in the Central or lower Amazon, such as the Negro River, before quickly migrating to the middle Madeira (Fig. 2d). In either case, its final isotopic signature did not correspond to that of the middle Madeira were it was sampled.

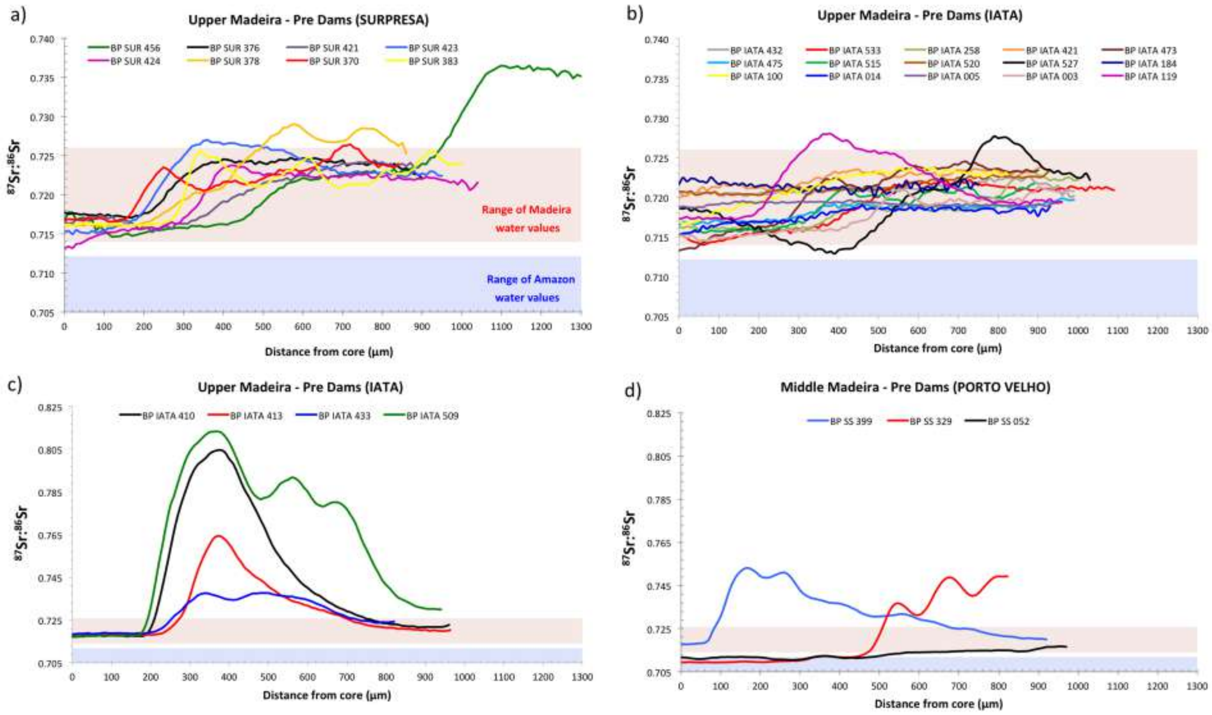


Fig. 2. Laser ablation-MC-ICPMS transects of $^{87}Sr:^{86}Sr$ along otolith transverse sections (from the core to the edge) of *B. platynemum*. Each curve corresponds to one individual caught either in the upper (a, b, c) and middle (d) Madeira River, before the construction of the Madeira dams.

3.3 FISH SAMPLED FOLLOWING DAMS CONSTRUCTION IN THE MADEIRA

As observed for most fish sampled before the construction of the dams, none of the 46 fish caught within the upper Madeira (26 in Guajará-Mirim in Brazil and 20 around Puerto Maldonado in Peru), after the dams' completion, ever entered the Amazon (Fig. 3). Of all the fish caught in the Madre de Dios sub-basin (Fig. 3a), only one fish had a hatching signature corresponding to the Madre de Dios River itself (BP 220, with a value of 0.7112). The other fish were either hatched in the Inambari, Tambopata or Béni sub-basins (0.714-0.716) or in waters with intermediate isotopic signatures (0.7125-0.714), which might correspond to confluence areas between the Madre de Dios and the Tambopata or Inambari. Only two specimens (BP 210, 213) stayed close to their hatching locality (probably the Inambari or Tambopata rivers) for most of their lives (Fig. 3a). Most other fish apparently migrated to other upper Madeira sub-basins with more radiogenic waters (between 0.717 and 0.730). Surprisingly, none of these fish had registered the signature of the Madre de Dios (0.710 – 0.712), into which they had to travel to reach the area of Puerto Maldonado where they were caught.

Most fish sampled in Guajará Mirim_(Figs. 3b, c) hatched in the Mamoré (hatching signature > 0.720), apart from two specimens (BP 1832 - Fig. 3b and BP 1861 - Fig. 3c), which had hatching signatures corresponding to the Madre de Dios River (0.712). Their movement patterns were similar to those of the fish caught before the dams' completion, with inter-sub-basin migrations between the hatching rivers and more radiogenic waters either within the Mamoré, Yata or Itenez-Guaporé sub-basins. Two specimens (BP 1834, 1858), probably hatched in the Beni or Inambari-Tambopata (Madre de Dios sub-basin), progressively travelled to the Mamoré, where they were caught (Fig. 3b).

Fish sampled at Porto Velho (Figure 3d) were all fished just below the dams between January and October 2012. Three fish probably hatched in the upper WAT in the Amazon River (BP SS 20814, 20818 and 20888, with hatching values of 0.7099, 0.7094 and 0.7082, respectively) and then later entered the Madeira River. All other fish had hatching signatures (0.7155 – 0.7175) corresponding to the Beni or Madre de Dios sub-basins. As these fish were caught between two and ten months after the completion of Santo Antônio dam, they might have migrated downstream before the dam's completion, or alternatively have survived the reservoir and the turbines. As already observed for specimens sampled in the Madeira before the dams' completion, several fish migrated to waters with exceptionally high radiogenic values for the Madeira basin (~0.740-0.765: BP SS 20777, 20868, 20715, 20834, 20829) before they were caught below Porto Velho, whereas others remained most of their lives in waters with signatures typical of the Madeira.

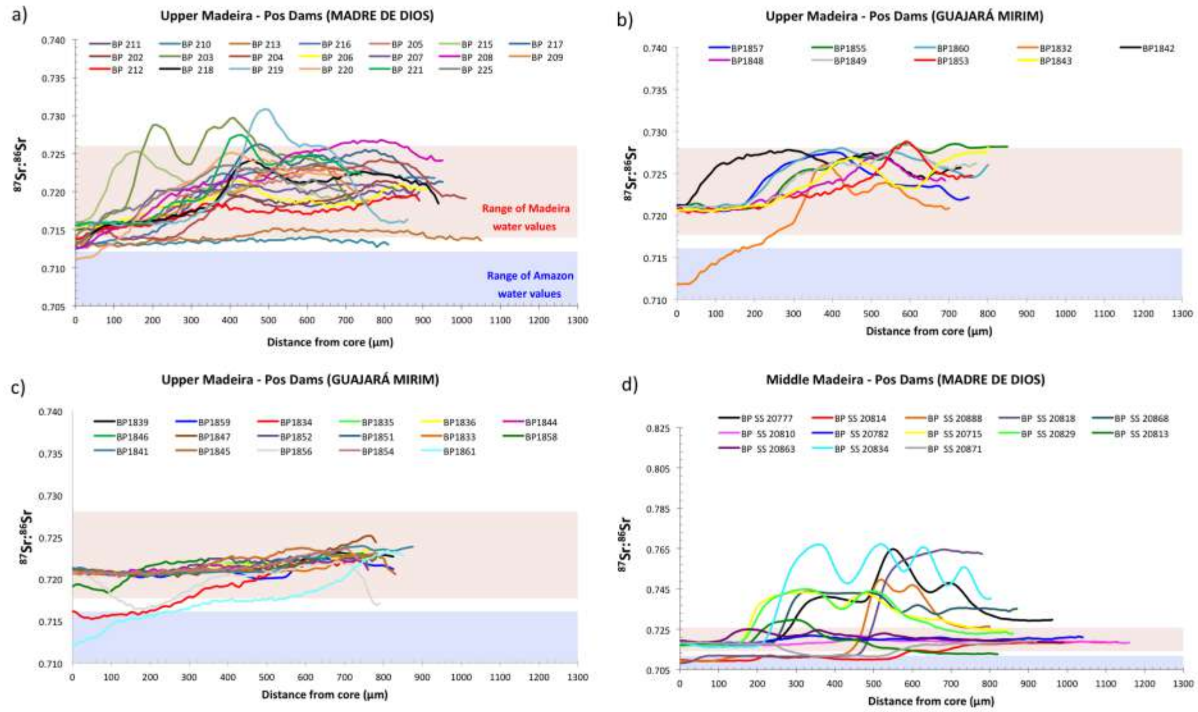


Fig. 3. Laser ablation-MC-ICPMS transects of $^{87}Sr:^{86}Sr$ along otolith transverse sections (from the core to the edge) of *B. platynemum*. Each curve corresponds to one individual caught either in the upper (a, b, c) and middle (d) Madeira River, after the construction of the Madeira dams.

3.4 FISH SAMPLED IN THE UPPER AMAZON

All fourteen specimens sampled in the upper Amazon River (12 from the Ucayali and 2 from the Marañon rivers) hatched in water with signatures of this region (~ 0.709) (Fig. 4). Most specimens had flat profiles, seemingly remaining in the same waters, or at least in the main channel of the Amazon and western Andean tributaries, which do not present such contrasts as the Madeira basin, during all their lives (BP 001, 002, 007, 009, 010, 012, 135). Two individuals (BP 008, 105) migrated to very radiogenic waters > 0.725. Some other fish (BP003, 004, 005, 011) moved to waters with signatures up to 0.712-0.713, supposedly in the lower Amazon (or the Madre de Dios in the upper Madeira basin, but fish would have first had to go through the more radiogenic Madeira waters, which would show on their isotopic profile), before migrating progressively back to the upper Amazon where they were caught. One fish, BP006, spent a considerable part of its life in the Napo River, the only known source of water signatures between 0.705 and 0.706.

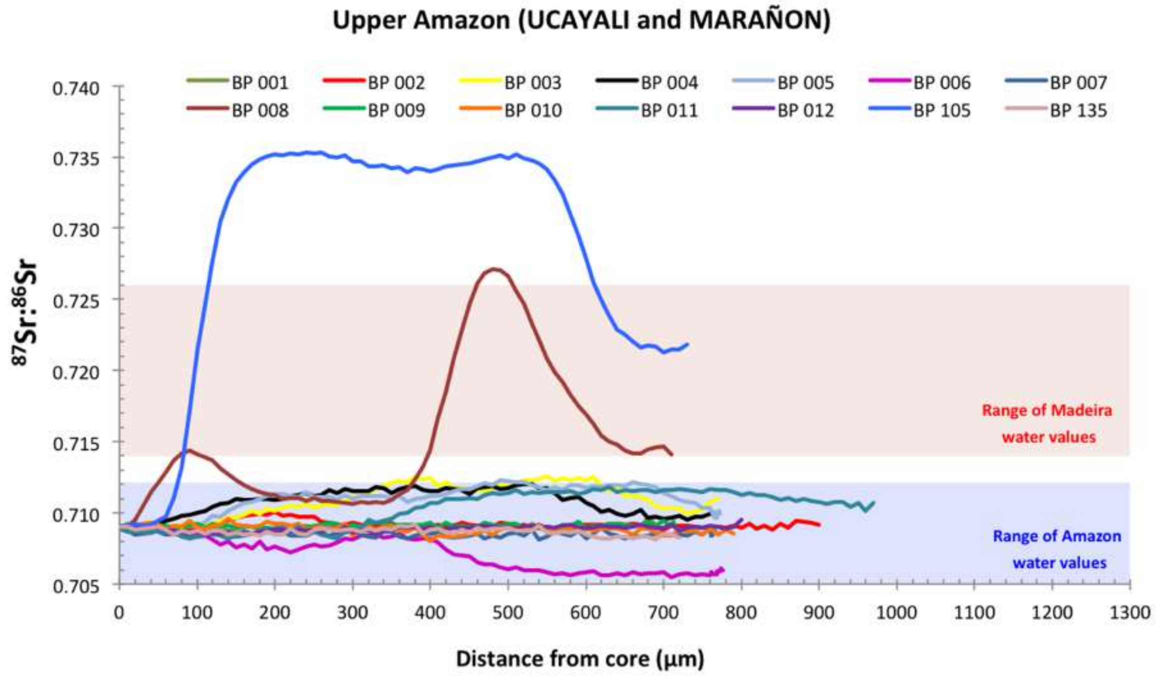


Fig. 4. Laser ablation-MC-ICPMS transects of ^{87}Sr:^{86}Sr along otolith transverse sections (from the core to the edge) of *B. platynemum*. Each curve corresponds to one individual caught either in the upper Amazon River.

4 DISCUSSION

Comparative studies of fish movements using pre- and post-impoundment data are scarce in the Neotropics, particularly in the Amazon basin. The present study further provides the very first information on the migratory behaviour of *B. platynemum* at the individual level. Contrary to what was first hypothesized (Barthem & Goulding, 2007), our results demonstrate that migration patterns of *B. platynemum* are clearly different from that of *B. rousseauxii* (Duponchelle et al., 2016) in that they are not so extensive and do not involve a compulsory passage through the lower Amazon-estuary area, nor natal homing behaviour. Our results emphasize the importance of carrying out species-specific studies on these large migratory species and demonstrate that generalisations drawn from better-studied species may proved to be oversimplifying and erroneous for designing adequate conservation strategies.

Most fish caught in the upper Madeira before the construction of dams were hatched in this sub-basin and never entered the Amazon, indicating that contrary to *B. rousseauxii*, nursery areas for *B. platynemum* must be located within the Madeira sub-basin for fish hatched in the Madeira and not in the estuary or the Lower Amazon. These results are consistent with the existence of two distinct genetic populations of *B. platynemum* in the

Amazon basin: one in the Amazon mainstem and another in the Madeira River (Ochoa et al., 2015). They also are consistent with the lack of relationship between the size of larvae and juveniles and the distance from the estuary to the headwaters of the Madeira River (Barthem et al., 2017). Despite the movement patterns we observed between the Madeira and the Amazon, the strong genetic structure described between these two basins (Ochoa et al., 2015) suggests that these movements did not involve regular reproductive exchanges and that the two populations should be considered as independent management and conservation units.

Differences in movement patterns between fish caught before and after the run-of-river dams' completion were observed in the upper Madeira River. Five out of the twenty-seven (18.5%) specimens caught in the upper Madeira before the dam's completion exhibited surprisingly high otolith ^{87}Sr:^{86}Sr ratios (> 0.735, with two otoliths > 0.80), whereas this was not observed in any of the 46 fish (0%) caught after the dam's completion. On the other hand, for fish caught in the middle Madeira (below the dam's locations), such high isotopic values were observed in similar proportions before (2 out of 3 fish, 66.7%) and after (8 out of 13 fish, 61.5%) the dam's completion. A few of these specimens had a final signature higher than that of the locality where they were caught, suggesting that the sources of highly radiogenic signatures could be very close to the fishing grounds. It is possible that, contrary to *B. rousseauxii*, for which otolith values above 0.735 were not observed (Duponchelle et al., 2016; Hauser, 2018), *B. platynemum* might spend some time in adjacent oxbow lakes or lagunas, which have been shown to have higher Sr isotopic signatures than the river they are connected to (Pouilly, Point, Sondag, Henry, & Santos, 2014). This hypothesis could hold for the fish that exhibited signatures 0.005 to 0.01 above their site of capture, hence up to 0.735 (see Pouilly, Point, Sondag, Henry, & Santos, 2014). It cannot explain, however, otolith Sr isotopic values above 0.750 or as high as 0.813 (Fig. 2c). Although ^{87}Sr:^{86}Sr water values as high as 0.92 were reported in the Orinoco basin (Palmer & Edmond, 1992), the highest known values for the Amazon basin, around 0.780, were reported in the otoliths (not in water) of *Cichla temensis* caught in the Negro River system (Garcez, Humston, Harbor, & Freitas, 2015; Sousa, Humston, & Freitas, 2016). The Orinoco and Negro rivers both drain the same granitic shield and it is likely that the Negro sub-basin could also hold ^{87}Sr:^{86}Sr water values as high as those observed in the Orinoco. It is possible that the fish exhibiting exceptionally high isotopic values (>0.740) might have travelled quickly into the Negro River for some time before coming back to the Madeira where they were caught. The proximity between the Madeira and the Negro (~ 130 km) is such that fish could potentially pass from one to the other quickly enough without registering the lower isotopic signature of the Amazon in between. The fact that none of the several fish caught within the upper Madeira after the dams exhibited these exceptionally high isotopic values and that such values were only observed after the dams in fish caught in the lower Madeira, below the dams (Fig. 3d), tend to support this hypothesis. It fails, however, to explain why some of these fish, after migrating up the Madeira for ~ a thousand kilometres (to Porto Velho, Fig. 2d, 3d) or more to the upper Madeira fishing grounds of the Mamoré (Fig. 2c), had not yet acquired the isotopic signature of the waters where they were caught. Alternatively, the tributaries where *Brachyplatystoma* could potentially venture within the Madeira basin have not all been sampled, far from that, and we cannot rule out the possibility that yet unknown sources of highly radiogenic waters might exist in the tributaries draining the Brazilian granitic shield (Itenez-Guapore River; see Hegg, Giarrizzo, & Kennedy, 2015; and Santos et al., 2015) or the Yata River. These hypotheses are not mutually exclusive.

Brachyplatystoma platynemum is relatively abundant year round in the landings of Puerto Maldonado in Peru, where it is regularly fished including in the Madre de Dios itself (Barthem et al., 2017). The upper Madre de Dios is also known to be an important breeding area for *Brachyplatystoma* species (Cañas & Pine, 2011), including *B. platynemum* (Barthem et al., 2017). Yet, surprisingly, except for three fish (BP 220, 1832 e 1861) that may have hatched in this river, no other fish captured in the upper Madeira, before or after the dam's construction, seem to have hatched or spent any significant time in waters with signatures typical of the Madre de Dios River (0.710-0.712). Regarding the hatching signature, the breeding period for *Brachyplatystoma* species in the Madre de Dios corresponds to the highest flows (Cañas & Pine, 2011) and most larvae hatched in the Madre de Dios might be flushed out in the Beni or the Madeira within a few days, which might not be enough to register the Madre de Dios signature. Also surprising is the fact that none of the fish caught around Puerto Maldonado in the Madre de Dios had registered its isotopic signature (0.710 - 0.712) at the moment of their capture. As it is unlikely that they would all have migrated over 600 km up the Madre de Dios without a single one registering its signature, an alternative explanation is that all these fish would have remained all their lives within the Madre de Dios sub-basin, in the Tampopata or Inambari or in yet un-sampled tributaries with isotopic signature between 0.718 and 0.725. As already suggested earlier, they could also spend a significant amount of their time in adjacent oxbow lakes or lagunas with higher Sr isotopic signatures than the river they are connected to (Pouilly, Point, Sondag, Henry, & Santos, 2014).

Despite the fact that fewer fish from the Amazon were analysed, fish hatched in the upper Amazon seem to have more diverse migratory patterns, some involving longer migrations, than fish hatched in the Madeira, which usually stayed within the Madeira. Indeed, some fish hatched in the upper Amazon migrated a long way downstream and either entered the Madeira where they were caught (Fig. 3d, BP SS 20814, SS 20818, SS 20888), or highly radiogenic tributaries in the lower Amazon (Fig. 4, BP 105, 008). As observed for some specimens caught in the upper Madeira, BP 105 and BP 008 retained the signature of the granitic tributaries they migrated into at the moment of their capture in the Upper Amazon (in the Marañon and Ucayali, respectively). An explanation could potentially be rapid upstream migrations to the areas of capture, but it seems unlikely that fish could travel up over 2000 km from the closest known highly radiogenic tributary (the Negro River) without registering the Amazon mainstem signature. Again, an alternative explanation is the possible existence of highly radiogenic tributaries or floodplains in the upper Amazon, within the Ucayali, Marañon or Amazonas sub-basins. One fish (BP 006) stayed a notable part of its life in waters characteristic of the Napo River (0.705-0.706), including at the moment of its capture, suggesting it probably travelled very recently into the Ucayali, where it was caught. Other fish also migrated downstream into waters with signatures up to 0.712-0.713, supposedly in the lower Amazon, as so far such values were only observed below Santarém-Óbidos or at the confluence between the Amazon mainstem and granitic shield tributaries. These fish could theoretically have migrated to the Madre de Dios in the upper Madeira basin, but it is unlikely, as they would have had to go a long way (~2000 km) through the more radiogenic Madeira waters, which would show on their isotopic profile. Some others had almost completely flat profiles, suggesting they stayed within the upper Amazon.

Although this study provides crucial information about the migratory patterns of *B. platynemum*, it also emphasizes how our ability to interpreting these migratory patterns is hampered by the limited amount of water sources for which geochemical information is available. Despite these limitations, our results clearly demonstrate that migrations of *B. platynemum* are not as extensive as those observed for *B. rousseauxii* (Duponchelle et al., 2016; Barthem et al., 2017). The species nevertheless performs long-distance movements of several thousand kilometres within the Amazon basin. Our study suggests highly individualistic migratory behaviours in *B. platynemum*, with a higher behavioural diversity in the Amazon mainstem, which might be related with the highest genetic diversity observed in the Amazon population (Ochoa et al., 2015).

Our results also provide evidence of transboundary displacements between at least Bolivia, Brazil and Peru, valuable information for the fisheries management and conservation strategies of this ecologically (apex predator) and economically important goliath catfish. Although the two run-of-river dams now installed in the middle Madeira River will not have such an important impact on the migration of this species as that expected on its congener *B. rousseauxii* (see Duponchelle et al., 2016; and Hauser, 2018), they could nevertheless prevent, or disrupt, former migrations of *B. platynemum* from the upper Madeira River toward the Amazon sub-basin and the Negro River in particular.

The Madeira dams and the associated modifications of river characteristics, such as the presence of lentic waters (reservoirs) where series of rapids formerly existed could also alter the behaviour and distribution of these species. In the Brazilian portion of the Madeira upstream of the dams up to the Bolivian border, large migratory catfishes, which accounted for > 50% of total fish landings before the construction of the dams (Doria, Ruffino, Hijazi, & da Cruz, 2012), have now almost disappeared from the catches (C. Doria, pers. comm., March 2018). As witnessed in terrestrial, marine and freshwater ecosystems, the depletion of top predators can have profound consequences on food chains via trophic cascades (Pace, Cole, Carpenter, & Kitchell, 1999; Myers, Baum, Shepherd, Powers, & Peterson, 2007; Baum & Worm, 2009; Estes et al., 2001). Until recently, the fish passage of Santo Antônio dam was found ineffective in accommodating the upstream migrations of the goliath catfish species, apart from a few *B. vaillantii* (Fearnside, 2014).

The conservation of "migratory fishes is a global challenge that requires balancing numerous biological, social and economic factors" and that also requires preserving breeding and feeding habitat as well as the migratory corridors that connect these distant habitat (McIntyre et al., 2016). In the Amazon basin, the situation is further complicated by the sheer size of the basin shared by five main countries (Bolivia, Brazil, Colombia, Ecuador and Peru) with different environmental, exploitation and conservation policies (Castello et al., 2013; Castello & Macedo, 2016). Nevertheless, a first step in the conservation of goliath catfishes would be that proper modifications of the fish transposition system of Santo Antônio dam be implemented to ensure effective passage of these species. A second step would be for the upstream dam (Jirau) to build an effective fish passage, which is currently not contemplated (Cella-Ribeiro, Doria, Dutka-Gianelli, Alves, & Torrente-Vilara, 2017). Such measures would likely be beneficial to the conservation of goliath catfishes, but also of most other migratory fish species.

Although the two existing dams on the Madeira probably already pose a threat to the populations of *B. platynemum* and other goliath catfishes, the conservation of these species could be far more complicated if the other hydroelectric impoundments planned in the Amazon basin (Finer & Jenkins, 2012; Castello et al., 2013; Castello & Macedo 2016; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016; Winemiller et al., 2016; Forsberg et al., 2017; Latrubesse et al., 2017; Anderson et al., 2018) were to be carried out. Many of these projects involve lowland dams that will further alter connectivity and disrupt goliath catfish migrations. However, even more projects are planned in the Andean piedmont, where these species reproduce (Barthem & Goulding, 1997; García-Vasquez et al., 2009; Cañas & Pine, 2011; Córdoba et al., 2000; Córdoba et al., 2013; Barthem et al., 2017). These latter dams will disrupt the access to the breeding grounds. Even dams planned upstream of the breeding grounds will alter hydrology, sediments and nutrient supplies downstream (Forsberg et al., 2017), ultimately impacting the recruitment and population dynamics of these apex predators, with expected consequences on the food webs via trophic cascades.

Populations of goliath catfishes might adapt to a few dams along their migratory routes, although it remains to be demonstrated, providing effective fish passage be implemented. However, the multiplications of complete barriers or strong filters to both passive and active movements imposed by hydroelectric impoundments in between their nursery and breeding grounds will likely be an insurmountable challenge to the long-term persistence of these crucial Amazonian resources. The conservation of goliath catfishes and associated aquatic food webs requires urgent manager's recognition of hydrological connectivity as a priority in the Amazon basin (but see Castello et al., 2013; Castello & Macedo, 2016). This in turn, probably requires re-considering the real pros and cons of large-scale hydropower development in the Amazon basin, which hosts the world's richest biodiversity, and for which cheaper, greener and more effective solutions exist (Stickler et al., 2013; Kahn, Freitas, & Petrere; 2014).

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REFERENCES

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

Agostinho, A. A., Pelicice, F. M. &, Gomes, L. C. (2008). Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Brazilian Journal of Biology, 68, 1119-1132.

Córdoba, E. A., Salinas, Y., Sanchez, C. L., Munoz-Sosa, D. L., Alonso, J. C., Arteaga, M. E., … Valdes, H. (2000) *Bagres de la Amazonia Colombiana: un Recurso sin Fronteras,* Santa Fé de Bogota D.C., Colombia: SINCHI. Programa de Ecosistema Acuaticos. Editorial Scipto Ltda.

Córdoba, E. A., Léo, A .V. J., Bonilla-Castillo, C. A., Petrere Jr, M., Peláez, M., & Duponchelle, F. (2013) Breeding, growth and exploitation of *Brachyplatystoma rousseauxii* in the Caqueta River, Colombia. *Neotropical Ichthyology,* 11, 637–647.

Allègre, C. J., Louvat, P., Gaillardet, J., Meynadier, L., Rad, S., & Capmas, F. (2010). The fundamental role of island arc weathering in the oceanic Sr isotope budget. *Earth and Planetary Science Letters*, 292, 51-56.

Anderson, E. P., Jenkins, C. N., Heilpern, S., Maldonado-Ocampo, J. A., Carvajal-Vallejos, F. M., Encalada, A. C., ... Tedesco, P. A. (2018). Fragmentation of Andes-to-Amazon connectivity by hydropower dams. *Science Advances*, 4, eaao1642.

Bareille, G., Sasal, P., Mary, N., Meunier, F. J., Deschamps, M. H., Berail, S., & Lecomte-Finiger, R. (2005). Are elemental and strontium isotopic microchemistry of otolith and histomorphometrical characteristics of vertebral bone useful to resolve the eel Anguilla obscura status in Lalolalo lake in Wallis Island? *Vie et Milieu / Life and Environment*, 65, 29-39.

Barthem, R. B., & Goulding, M. (1997). *The Catfish Connection: Ecology, Migration, and Conservation of Amazon Predators*. New York, EUA: Columbia University Press.

Barthem, R. B., & Goulding, M. (2007). *Um ecossistema inesperado: A Amazônia revelada pela pesca***.** Belém, Brazil: Amazon Conservation Association (ACA) & Sociedade Civil Mamirauá.

Barthem, R. B., Goulding, M., Leite. R. G., Cañas. C., Forsberg, E. V., Petry, P., ... Mercado, A. (2017). Goliath catfish spawning in the far western Amazon confirmed by the distribution of mature adults, drifting larvae and migrating juveniles. *Scientific Reports 7* DOI: 10.1038/srep41784

Batista, V. S., Alonso, J. C., Ladle, R. J., & Fabré, N. N. (2018). Drivers of the upper River Amazon giant catfish fishery. *Fisheries Management and Ecology*, 25, 116-126.

Bauer, S., & Hoye, B. J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, 344, 1242552.

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology,* 78, 699-714.

Campana, S.E. (1999). Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series,* 188, 263-297.

Cañas, C. M., & Pine, W. E. III. (2011). Documentation of the temporal and spatial patterns of Pimelodidae catfish spawning and larvae dispersion in the Madre de Dios River (Peru): insights for conservation in the Andean-Amazon headwaters. *River Research and Applications*, 27, 602–611.

Carolsfeld, J., Harvey, B., Ross, C., & Baer, A. (2003). *Migratory fishes of South America: Biology, Fisheries and Conservation Status*. Washington, DC, USA: IDRC, World Bank.

Carvajal-Vallejos, F. M., Duponchelle, F., Desmarais, E., Cerqueira, F., Querouil, S., Nuñez, J., ... Renno, J. F. (2014) Genetic structure in the Amazonian catfish *Brachyplatystoma rousseauxii*: influence of life history strategies. *Genetica*, 142, 323-336.

Castello , L., McGrath, D. G., Hess, L. L, Coe, M. T., Lefebvrel, P. A., Petry, P., … Arantes, C. C. The vulnerability of Amazon freshwater ecosystems. (2013). *Conservation Letters*, 6, 217–229.

Castello, L., & Macedo, M. N. (2016). Large-scale degradation of Amazonian freshwater ecosystems. *Global Change Biology*, 22, 990-1007.

Cella-Ribeiro, A., Torrente-Vilara, G., Hungria, D. B., & Oliveira, M. (2013). As corredeiras do rio Madeira. In Queiroz, L. J., Torrente-Vilara, G., Ohara, W. M., Pires, T., Zuanon, J. A., & Doria, C. R. C. (Eds.), *Peixes do rio Madeira* (pp. 56‑63), São Paulo, SP: Dialeto.

Cella-Ribeiro, A., Torrente-Vilara, G., Lima-Filho, J. A., & Doria, C. R. C. (2016). *Ecologia e Biologia de Peixes do Rio Madeira*. Porto Velho, Brazil: EDUFRO.

Cella-Ribeiro, A., Doria, C. R. C., Dutka-Gianelli, J., Alves, H., & Torrente-Vilara, G. (2017). Temporal fish community responses to two cascade run-of-river dams in the Madeira River, Amazon basin. *Ecohydrology,* 10, e1889-n/a.

Crespo, A., & Van Damme, P. A. (2011). Patrones espaciales de inundación en la cuena Amazónica de Bolivia. In: Van Damme, P. A., Carvaval-Vallejos, F. M., & Molina Carpio, J. (Eds.), *Los peces y delfines de la Amazonia boliviana: Habitats, potencialidades y amenazas* (pp. 15–27), Cochabamba: INIA.

Doria, C. R. C., Ruffino, M. L., Hijazi, N. C., & da Cruz, R. L. (2012). A pesca comercial na bacia do rio Madeira no estado de Rondônia, Amazônia brasileira. *Acta Amazonica,* 42, 9–40.

Doria, C. R. C., Duponchelle, F., Lima, M. A. L., García, A., Carvajal-Vallejos, F. M., Mendez, C. C., … Van Damme, P.A. (2018). Review of fisheries resource use and status in the Madeira River basin (Brazil, Bolivia, and Peru) before hydroelectric dam completion.

Reviews in Fisheries Science & Aquaculture, 26, 494-514.

Duponchelle, F., Pouilly, M., Pécheyran, C., Hauser, M., Renno, J. F., Panfili, ... Baras, E. (2016). Trans-Amazonian natal homing in giant catfish. *Journal of Applied Ecology***,** 53, 1511-1520.

Elsdon, T. S., & Gillanders, B. M. (2003). Reconstructing migratory patterns of fish based on environmental influences on otolith chemistry. *Reviews in Fish Biology and Fisheries,* 13, 219–235.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., … Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science,* 333, 301-306.

Fearnside, P. M. (2014). Brazil's Madeira River dams: A setback for environmental policy in Amazonian development. *Water Alternatives***,** 7, 154-167.

Finer, M., & Jenkins, C. N. (2012). Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PLoS ONE.*, 7, e35126.

Fioravanti, C. (2018). As primeiras águas de um rio. *Revista Pesquisa FAPESP*, n. 150.

Flecker, A. S., McIntyre, P. B., Moore, J. W., & Hall, R. O. (2010). Migratory fishes as material and process subsidies in riverine ecosystems. *American Fisheries Society Symposium*, 73, 559 -592.

Forsberg, B. R., Melack, J. M., Dunne, T., Barthem, R. B., Goulding, M., Paiva, R. C. D., & Weisser, S. (2017). The potential impact of new Andean dams on Amazon fluvial ecosystems. *PLoS ONE,* 12**,** e0182254.

Gaillardet, J., Dupre, B., Allegre, C. J., & Négrel, P. (1997). Chemical and physical denudation in the Amazon River Basin. *Chemical Geology*, 142, 141-173.

Garcez, R. C. S., Humston, R., Harbor, D., & Freitas, C. E. C. (2015). Otolith geochemistry in young-of-the-year peacock bass *Cichla temensis* for investigating natal dispersal in the Rio Negro (Amazon – Brazil) river system. *Ecology of Freshwater Fish*, 24, 242–251.

García-Vasquez, A., Alonso, J. C., Carvajal, F., Moreau, J., Nuñez, J., Renno, J. F., … Duponchelle, F. (2009). Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. *Journal of Fish Biology,* 75, 2527-2551.

Harden Jones, F. R. (1968). *Fish migration*. London, UK: Edward Arnold Press.

Hauser, M. (2018). Migração dos grandes bagres Amazônicos pela perspectiva dos isótopos de Estrôncio em otólitos (PhD Thesis). University Federal of Rondônia, Brazil.

Hegg, J. C., Giarrizzo, T., & Kennedy, B. P. (2015). Diverse early life-history strategies in migratory Amazonian catfish: implications for conservation and management. *PLoS ONE*, 10, e0129697. DOI: 10.1371/journal.pone.0129697

Hermann, T. W., Stewart, D. J., Limburg, K. E., & Castello, L. (2016). Unravelling the life history of Amazonian fishes through otolith microchemistry. *Royal Society Open Science*, 3, 160206. DOI: 10.1098/rsos.160206

Kahn, J. R., Freitas, C. E., & Petrere Jr., M. (2014). False shades of green: the case of Brazilian Amazonian hydropower. *Energies,* 7, 6063-6082.

Latrubesse, E. M., Arima, E. Y, Dunne, T., Park, E., Baker, V. R., D'Horta, F. M., …. Stevaux, J. C. (2017). Damming the rivers of the Amazon basin. *Nature*, 546, 363-369.

Lees, A. C., Peres, C. A., Fearnside, P. M., Schneider, M., & Zuanon, J. A. S. (2016). Hydropower and the future of Amazonian biodiversity. *Biodiversity and Conservation*, 25, 451-466.

McIntyre, P. B., Reidy Liermann, C., Childress, E., Hamann, E., Hogan, D., Januchowski-Hartley, S., ... Pracheil, B. (2016). Conservation of migratory fishes in freshwater ecosystems. In: Closs, G. P., Krkosek, M., &. Olden, J. D (Eds.), *Conservation of Freshwater Fishes* (pp. 324–360), Cambridge: Cambridge University Press.

Miles N. G., West, R. J., & Norman, M. D. (2009). Does otolith chemistry indicate diadromous life cycles for five Australian riverine fishes? *Marine and Freshwater Research*, 60, 904–911.

MPA. Boletim estatístico de pesca e aquicultura do Brasil 2011. Brasília: Ministério da Pesca e Aquicultura, 2013.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading Effects of the Loss of Apex Predatory Sharks from a Coastal Ocean. *Science,* 315, 1846-1850.

Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science*, 308, 405-408.

Ochoa, L. E, Pereira, L. H. G., Costa-Silva, G. J., Roxo, F. F., Batista, J. S, Formiga, K., … Oliveira, C. (2015). Genetic structure and historical diversification of catfish *Brachyplatystoma platynemum* (Siluriformes: Pimelodidae) in the Amazon basin with implications for its conservation. *Ecology and Evolution,* 5, 2005–2020.

Ortega, H., Hidalgo, M., Trevejo, G., Correa, E., Cortijo, A. M., Meza, V., & Espino, J. (2012). Lista anotada de los peces de aguas continentales del Perú: Estado actual del conocimiento, distribución, usos y aspectos de conservación. Ministerio del Ambiente, Dirección General de Diversidad Biológica - Museo de Historia Natural, UNMSM., Lima, Peru.

Pace, M. L., Cole, J. J., Carpenter, S. R., & Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution,* 14, 483-488.

Palmer, M. R., & Edmond, J. M. (1992) Controls over the strontium isotope composition of river water. *Geochimica et Cosmochimica Acta*, 56, 2099–2111.

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

Petrere Jr., M., Barthem, R. B., Córdoba, E. A., & Gomez, B. C. (2004). Review of the large catfish fisheries in the upper Amazon and the stock depletion of piraiba (*Brachyplatystoma filamentosum* Lichtenstein). *Reviews in Fish Biology and Fisheries*, 14, 403-414.

Pouilly, M., Point, D., Sondag, F., Henry, M. & Santos, R. V. (2014). Geographical origin of Amazonian freshwater fishes fingerprinted by ^{87}Sr/^{86}Sr ratios on fish otoliths and scales. *Environmental Science & Technology* 48, 8980-8987.

Sant'Anna, I. R., Doria, C. R. C., & Freitas, C. E. C. (2014). Pre-impoundment stock assessment of two Pimelodidae species caught by small-scale fisheries in the Madeira River (Amazon Basin – Brazil). *Fisheries Management and Ecology*, 21, 322–329.

Santos, R.V., Sondag, F., Cochonneau, G., Lagane, C., Brunet, P., Hat- tingh, K., & Chaves, J. G. S. (2015). Source area and seasonal ^{87}Sr/^{86}Sr variations in rivers of the Amazon basin. *Hydrological Processes*, 29, 187–197.

Sousa, R . G . C, Humston, R., & Freitas, C. (2016). Movement patterns of adult peacock bass *Cichla temensis* between tributaries of the middle Negro River basin (Amazonas – Brazil): an otolithgeochemical analysis. *Fisheries Management and Ecology*, 23, 76–87.

Stickler, C. M., Coe, M. T., Costa, M. H., Nepstad, D. C., McGrath, D. G., Dias, L. C. P., … Soares-Filho, B. S. (2013). Dependence of hydropower energy generation on forests in the Amazon Basin at local and regional scales. *Proceedings of the National Academy of Science, USA,* 110, 9601-9606.

Tello, S., & Bayley, P. B. (2001). La pesquería comercial de Loreto con énfasis en el análisis de la relación entre captura y esfuerzo pesquero de la flota comercial de Iquitos, cuenca del Amazonas (Perú). *Folia Amazonica,* 12, 123-139.

Walther, B. D., Limburg, K. E., Jones, C. M., & Schaffler, J. J. (2017). Frontiers in otolith chemistry: insights, advances and applications. *Journal of Fish Biology,* 90, 473-479.

Wilcove, D. S., & Wikelski, M. (2008) Going, going, gone: is animal migration disappearing? *PLoS Biology*, 6, e188.

Winemiller, K. O., McIntyre, P. B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., … Sáenz, L. (2016). Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, 351, 128–129.

Yoshinaga, J., Nakama, A., Morita, M., & Edmonds, J. S. (2000). Fish otolith reference material for quality assurance of chemical analyses. *Marine Chemistry*, 69, 91-97.

CONSIDERAÇÕES FINAIS

A presente tese de doutorado, com base em uma combinação de geoquímica ambiental de águas e de otólitos (^{87}Sr: ^{86}Sr), ao longo de toda a bacia amazônica, incluindo amostras antes e após o barramento do rio Madeira, fornece o maior conjunto de informações acerca dos padrões migratórios dos grandes bagres amazônicos do gênero *Brachyplatystoma*, já descritos na literatura a nível de indivíduos. Ademais, o expressivo conjunto de fontes de água levantados ao longo desse trabalho, inclusive aportando os primeiros dados referente ao estuário amazônico, proporciona um mapeamento isotópico de ^{87}Sr:^{86}Sr da bacia amazônica em grande escala, que além de ter permitido o refinamento dos processos migratórios das espécies investigadas no presente estudo, também servirá de base para futuras investigações, inclusive de outros grupos ictiícos.

Em relação a *B. rousseauxii* este foi o primeiro trabalho a estimar a idade e crescimento da espécie, a partir da contagem direta de marcas de crescimento em estruturas rígidas, para a bacia do rio Madeira. Essas informações permitiram a determinação precisa da idade em que ocorre os diferentes processos migratórios da dourada ao longo de toda bacia amazônica. Esse estudo também confirmou o *homing* natal de *B. rousseauxii* na bacia do rio Madeira, além de ter comprovado pioneiramente este comportamento para a calha principal do rio Amazonas, corroborando a hipótese central do trabalho. Esses dados ratificaram, portanto, a ampla área que essa espécie utiliza para desenvolver seu ciclo de vida. Ainda, sob a luz da comparação entre os resultados obtidos antes e após a construção das usinas hidrelétricas do rio Madeira, foi comprovado de maneira irrefutável o impacto desses empreendimentos sobre a migração de *B. rousseauxii*.

Esta tese também permitiu, pela primeira vez, estimar a contribuição atual (após o barramento) dos rios Madeira e Amazonas no recrutamento de *B. rousseauxii* no estuário. Esses dados mostraram que ao menos uma parcela das larvas e juvenis sobreviveram às turbinas e reservatórios de Jirau e Santo Antônio, conseguindo chegar até a região estuarina. Entretanto, quando esses indivíduos retornaram ao rio Madeira para alcançar as zonas de reprodução foram bloqueados pelos sistemas de transposição ineficientes. Demonstrou-se portanto, a necessidade de modificações que tornem os respectivos sistemas efetivos no aporte dos indivíduos adultos às porções altas do rio Madeira, permitindo assim, a continuidade de seus ciclos de vida.

Em relação a *B. platynemum*, embora tenha sido observado que sua migração não foi tão extensa quanto a de *B. rousseauxii*, e não envolveu o comportamento de *homing* natal, refutando a hipótese central da tese, esse bagre também apresentou processos migratórios singulares. Os indivíduos analisados chegaram a percorrer milhares de quilômetros ao longo de seus ciclos de vida, com deslocamentos transfronteiriços entre Brasil, Bolívia e Peru.

Mediante às informações aqui levantadas demonstrou-se claramente a importância da manutenção da conectividade do sistema fluvial amazônico para o desenvolvimento do ciclo de vida dessas espécies. Consequentemente, salienta-se o quão deletério se revela o plano de matriz energética dessa bacia, com a previsão de construção de inúmeras usinas hidrelétricas, as quais terão desdobramentos negativos tanto sobre a biodiversidade, como em relação a produção pesqueira. Enfatiza-se assim, a necessidade de planos de conservação e manejo que englobem toda área de ciclo de vida dessas espécies, independente dos limites geopolíticos, de país ou mesmo estado.

APÊNDICES

Tabela atualizada de Duponchelle et al. (2016) com os novos valores de ^{87}Sr:^{86}Sr das amostras de águas amostradas neste estudo. Fontes de referência:1) Palmer; Edmond (1992); 2) Gaillardet et al. (1997); 3): Queiroz et al. (2009); 4) Pouilly et al. (2014); 5) Santos et al. (2015). Por uma questão de consistência, esta tabela é deliberadamente restrita aos valores de água mensurados.

Original name	Sub-basin	Code Fig. 1	Category	Sampling dates	^{87}Sr/^{86}Sr	N	Mean	SD	Range	latitude	Longitude	Ref
BPA11 Ucayali	Ucayali	1	Western Andean tributaries	nov/78	0.7092	1						1
A-01 Mantaro	Tambo	1a	Western Andean tributaries	may-77	0.7075	1	0.7087	0.0017				1
A-03 Higueras	Tambo	1a	Western Andean tributaries	may-77	0.7099	1						1
Tambo	Tambo		Western Andean tributaries	aug-2015	0.7088	1				S 10°44'46.78"	W 73°44'51.77"	This study
BPAOB Urubamba	Urubamba	1b	Western Andean tributaries	nov/78	0.7095	1						1
Urubamba	Urubamba		Western Andean tributaries	aug-2015	0.7093	1				S 10°44'10.47"	W 73°43'14.06"	This study
Puerto Inca	Ucayali		Western Andean tributaries	aug-2015	0.7086	1				S 9°22'42,17"	W 74°58'08.63"	This study
Requena	Ucayali		Western Andean tributaries	jul/15	0.7093	1				S 5°01'48.18"	W 73°49'59.52"	This study
Atalaya	Ucayali	1c	Western Andean tributaries	jun/04	0.7089	1						5
BPA10 Marañon	Marañon	2	Western Andean tributaries	nov/78	0.7079	1						1
San Regis	Marañon		Western Andean tributaries	jul/15	0.7081	1				S 4°30',56.18"	W 73°54'31.44"	This study
A-11 Tocache	Huallaga	2a	Western Andean tributaries	may-77	0.7103	1	0.7096	0.0010				1
A-14 Huallabamba	Huallaga	2a	Western Andean tributaries	may-77	0.7089	1						1
Chazuta	Huallaga		Western Andean tributaries	aug-2015	0.7089	1				S 6°34'13.64"	W 76°07'09.35"	This study
Borja	Marañon	2b	Western Andean tributaries	03/2004 - 02/2010		26	0.7085	0.0002	0.70813 - 0.70894			5
S304 Napo	Napo	3	Western Andean tributaries	may-77	0.7059	1						1
Francisco de Orellana	Napo	3a	Western Andean tributaries	03/2004 -10/2010		26	0.7059	0.0004	0.70555 - 0.70721			5
Bella Vista	Napo		Western Andean tributaries	jul/15	0.7093					S 5°01'48.18"	W 73°49'59.52"	This study
S302 Amazon	Amazonas	4	Western Andean tributaries	may-77	0.7086	1						1
Tabatinga	Solimoes	5	Western Andean tributaries	06/2003 - 06/2010		9	0.7088	0.0003	0.70841 - 0.70922			5
S242 Javari	Javari	6	Amazon and floodplain tributaries	jun/76	0.7115	1						1
S238 Iça	Iça	7	Western Andean tributaries	jun/76	0.7075	1						1
S233 Jurua	Jurua	8	Amazon and floodplain tributaries	jun/76	0.7096	1						1
S231 Japura	Japura	9	Western Andean tributaries	jun/76	0.7088	1						1
S230 Tefe	Tefe	10	Amazon and floodplain tributaries	jun/76	0.7108	1	0.7106	0.0002				1
Tefe 26	Tefe	10	Amazon and floodplain tributaries	nov/04	0.7105	1						3
S225 Coari	Coari	11	Amazon and floodplain tributaries	jun/76	0.7104	1	0.7107	0.0004				1
Coari 20	Coari	11	Amazon and floodplain	nov/04	0.7110	1						3

			tributaries									
Solimoes 22	Solimoes	12	Western Andean tributaries	nov/04	0.7092	1	0.7095	0.0008				3
Solimoes 19	Solimoes	12	Western Andean tributaries	nov/04	0.7107	1						3
Solimoes 18	Solimoes	12	Western Andean tributaries	nov/04	0.7089	1						3
Solimoes 3	Solimoes	12	Western Andean tributaries	nov/04	0.7089	1						3
Solimoes 5	Solimoes	12	Western Andean tributaries	nov/04	0.7107	1						3
Solimoes	Solimoes	12	Western Andean tributaries	may-89	0.7088	1						2
Amazon 6	Solimoes	12	Amazon and floodplain tributaries	may-89	0.7092	1						2
S222 Purus	Purus	13	Amazon and floodplain tributaries	jun/76	0.7096	1	0.7103	0.0008				1
Purus 8	Purus	13	Amazon and floodplain tributaries	nov/04	0.7111	1						3
Labrea	Purus	13	Amazon and floodplain tributaries	sep-04	0.7101	1						5
Manacapuru	Solimoes	14	Western Andean tributaries	06/2003 - 11/2011		38	0.7091	0.0003	0.70879 - 0.70981			5
Serrinha	Negro	15	Granitic shield tributaries	04/2003 - 09/2009		15	0.7318	0.0074	0.72049 - 0.74376			5
UN1 Negro	Negro	15	Granitic shield tributaries	aug-77	0.7378	1						1
Negro	Lower Negro	16	Madeira & Lower Negro	may-89	0.7162	1						2
BR1 Branco	Branco	17	Granitic shield tributaries	aug-77	0.7259	1						1
Caracarai	Branco	17	Granitic shield tributaries	mar/04	0.7224	1						1
M-01 Madeira@Porto Velho	Madeira	18	Madeira & Lower Negro	jun/77	0.7185	1	0.7188	0.0010				1
Borba	Madeira	18	Madeira & Lower Negro	dec-07	0.7176	1						5
Madeira	Madeira	18	Madeira & Lower Negro	may-89	0.7200	1						2
S212 Madeira@Amatari	Madeira	18	Madeira & Lower Negro	jun/76	0.7191	1						1
Above confluence with the Inambari	Madre de Dios		Western Andean tributaries	jun/15	0.70999	1				S12°41’06.94"	W069°48’ 12.98’’	This study
Below confluence with the Inambari	Madre de Dios		Western Andean tributaries	jun/15	0.71024	1				S12°42’52.02"	W069°40’13.83"	This study
Las Piedras	Madre de Dios		Western Andean tributaries	jun/15	0.7102	1				S12°30’47.19"	W069°14’35.51"	This study
Below Puerto Maldonado	Madre de Dios		Western Andean tributaries	jun/15	0.71074	1				S12°36’05.37"	W069°04’36.96"	This study
El Sena	Madre de Dios		Western Andean tributaries	jun/15	0.71159	1				S11°28.173'	W067°14.302'	This study
El Sena	Madre de Dios		Western Andean tributaries	set/15	0.71214	1				S11°28.173'	W067°14.302'	This study
Above confluence with the Beni	Madre de Dios		Western Andean tributaries	jul/15	0.71192	1				S10°58.201'	W066°05.500'	This study
Inambari	Inambari		Madeira & Lower Negro	jun/15	0,7164	1				S12°45’09.01"	W069°49’29.03"	This study
Tambopata	Tambopata		Madeira & Lower Negro	jun/15	0.7172	1				S12°43’37.40"	W069°12’57.42’’	This study
Porto Velho	Madeira	19	Madeira & Lower Negro	03/2004 - 10/2010		9	0.7168	0.0007	0.71542 - 0.71745			5

Rurrenabaque	Béni	20	Madeira & Lower Negro	03/2004 - 09/2011		38	0.7173	0.0013	0.71375 - 0.71938			5
M-03 Béni	Béni	20	Madeira & Lower Negro	jun/77	0.7182	1						1
Above Riberalta	Beni		Madeira & Lower Negro	jul/15	0.7190	1				S11°01.276'	W066°06.462'	This study
Confluence wtih the Madre de Dios	Beni		Madeira & Lower Negro	jul/15	0.7131	1				S10°59.191'	W066°03.440'	This study
Sapecho	Beni		Madeira & Lower Negro	sep-15	0.7179	1				S15°33.432'	W067°22.470'	This study
Madidi	Madidi		Madeira & Lower Negro	jul/15	0.7173	1				S13°14.375'	W068°19.510'	This study
						1						
Tuichi	Tuichi		Madeira & Lower Negro	jul/15	0.7195	1				S14°35.460'	W067°32.549'	This study
Quiquibey	Quiquibey		Madeira & Lower Negro	jul/15	0.7161	1				S14°37.682'	W067°31.851'	This study
M-02 Mamoré	Mamoré	21	Madeira & Lower Negro	jun/77	0.7225	1						1
Above confluence with the Yata	Mamoré		Madeira & Lower Negro	mar/17	0.7219	1				S10°48.985'	W065°42.631'	This study
Below confluence with the Yata	Mamoré		Madeira & Lower Negro	mar/17	0.7219	1				S10°48.219'	W065°42.966'	This study
Porto Siles	Mamoré		Madeira & Lower Negro	april-2014	0.7202	1				S12°48.350’	W65°0.259’	This study
Trinidad	Mamoré		Madeira & Lower Negro	jul/15	0.7201	1				S15°20.410'	W064°51.319'	This study
Trinidad	Mamoré		Madeira & Lower Negro	jul/15	0.7213	1				S14°52.982'	W065°01.963'	This study
Secure			Madeira & Lower Negro	jul/15	0.7189	1				S15°14.451'	W064°57.420'	This study
Pojige			Madeira & Lower Negro	jul/15	0.7210	1				S15°26.132'	W064°52.771'	This study
Ibare	Ibare		Madeira & Lower Negro	apr-2015	0.7223	1				S14°52.134’	W64°58.260’	This study
Ibare	Ibare		Madeira & Lower Negro	jul/15	0.7227	1				S15°05.973'	W064°40.990'	This study
BPAOP San Mateo	Chapare	21a	Madeira & Lower Negro	nov/78	0.7224	1	0.7199	0.0022				1
BPA03 Espiritu Santo	Chapare	21a	Madeira & Lower Negro	nov/78	0.7186	1						1
Espiritu Santo	Chapare	21a	Madeira & Lower Negro	feb-13	0.7186	1						4
Chapare	Chapare		Madeira & Lower Negro	jul/15	0.7207					S16°58.361'	W065°24.016'	This study
Chapare	Chapare		Madeira & Lower Negro	set/15	0.7204	1				S16°58.376'	W065°23.914'	This study
Ichilo	Ichilo	21b	Madeira & Lower Negro	feb-13	0.7219	1	0.7227	0.0012				4
Ichilo	Ichilo	21b	Madeira & Lower Negro	feb-13	0.7222	1						4
Ichilo	Ichilo	21b	Madeira & Lower Negro	feb-13	0.7248	1						4
M-05 Ichilo	Ichilo	21b	Madeira & Lower Negro	jun/77	0.7224	1						1
BPAOl Ichilo	Ichilo	21b	Madeira & Lower Negro	nov/78	0.7223	1						1
Ichilo	Ichilo		Madeira & Lower Negro	jul/15	0.7214	1				S17°15.751'	W064°20.430'	This study
Ichilo	Ichilo		Madeira & Lower Negro	set/15	0.7177	1				S16°50.228'	W064°47.496'	This study
Chimore	Chimore		Madeira & Lower Negro	jul/15	0.7256	1				S16°59.826'	W065°08.177'	This study
Chimore	Chimore		Madeira & Lower Negro	set/15	0.7248	1				S16°59.821'	W065°08.135'	This study
Yapacani	Yapacani		Madeira & Lower Negro	jul/15	0.7190	1				S17°24.446'	W063°50.886'	This study

Yapacani	Yapacani		Madeira & Lower Negro	set/15	0.7159	1				S17°24.319'	W063°50.777'	This study
Chipiriri	Chipiriri		Madeira & Lower Negro	jul/15	0.7171	1				S16°53.726'	W065°24.663'	This study
BPA05 Guapay	Grande	21c	Madeira & Lower Negro	nov/78	0.7195	1						1
Abapo	Grande		Madeira & Lower Negro	sep-2015	0.7184					S18°54.626'	W063°24.075'	This study
Itenez	Itenez	22	Granitic shield tributaries	10/2011 - 10/2012		3	0.7262	0.0010				4
Yata	Yata	23	Madeira & Lower Negro	oct-12	0.7226	1	0.7245	0.0018				4
Yata	Yata	23	Madeira & Lower Negro	oct-12	0.7263	1						4
Yata	Yata	23	Madeira & Lower Negro	oct-12	0.7246	1						4
Yata	Yata		Madeira & Lower Negro	mar/17	0.7273	1				S10°48.6860'	W065°42.966'	This study
Puerto tereza	Yata		Madeira & Lower Negro	sep-15	0.7257	1				S13°26.937'	W066°36.003'	This study
Urucara	Urucara	24	Granitic shield tributaries	may-89	0.7236	1						2
Trombetas	Trombetas	25	Granitic shield tributaries	may-89	0.7323	1						2
S206 Tapajos	Tapajos	26	Granitic shield tributaries	jun/76	0.7322	1						1
Tapajos	Tapajos	26	Granitic shield tributaries	may-89	0.7332	1						2
Itaituba	Tapajos	26	Granitic shield tributaries	09/2004 - 10/2011		27	0.7296	0.0059	0.71516 - 0.7359			5
Amazon 13	Amazon	27	Amazon and floodplain tributaries	may-89	0.7107	1	0.7111	0.0004				2
Amazon 14	Amazon	27	Amazon and floodplain tributaries	may-89	0.7111	1						2
Amazon 20	Amazon	27	Amazon and floodplain tributaries	may-89	0.7115	1						2
S209 Amazon@Obidos	Amazon	28	Amazon and floodplain tributaries	jun/76	0.7109	1						1
S239 Amazon@Obidos	Amazon	28	Amazon and floodplain tributaries	jun/77	0.7108	1						1
Obidos	Amazon	28	Amazon and floodplain tributaries	04/2003 - 01/2012		46	0.7115	0.0005	0.71027 - 0.71233			5
S204 Xingu	Xingu	29	Granitic shield tributaries	jun/76	0.7292	1						1

Fonte: Hauser (2018).

REFERÊNCIAS

DUPONCHELLE, F.; POUILLY, M.; PECHEYRAN, C.; HAUSER, M.; RENNO, J.F.; PANFILI, J.; DARNAUDE, A. M.; GARCIA-VASQUEZ, A.; CARVAJAL-VALLEJOS, F.; GARCIA-DAVILA, C.; DORIA, C.; BERAIL, S.; DONARD, A.; SONDAG, F.; SANTOS, R.V.; NUÑEZ, J.; POINT, D.; LABONNE, M.; BARAS, E. Trans-Amazonian natal homing in giant catfish. **Journal of Applied Ecology**, v. 53, p. 1511-1520, 2016.

GAILLARDET, J.; DUPRE, B.; ALLEGRE, C. J.; NEGREL, P. Chemical and physical denudation in the Amazon River Basin. **Chemical**

Geology, v. 142, p. 141–173, 1997.

PALMER, M. R.; EDMOND, J. M. Controls over the strontium isotope composition of river water. **Geochimica et Cosmochimica Acta,** v. 56, p. 2099–2111, 1992.

POUILLY, M.; POINT, D.; SONDAG, F.; HENRY, M.; SANTOS, R. V. Geographical origin of Amazonian freshwater fishes fingerprinted by $^{87}Sr/^{86}Sr$ ratios on fish otoliths and scales. **Environmental Science & Technology**, v. 48, p. 8980-8987, 2014

QUEIROZ, M. M. A.; HORBE, A. M. C.; SEYLER, P.; MOURA, C. A. V. Hidroquímica do rio Solimões na região entre Manacapuru e Alvarães: Amazonas-Brasil. **Acta Amazonica**, v. 39, p. 943–952, 2009.

SANTOS, R.V.; SONDAG, F.; COCHONNEAU, G.; LAGANE, C.; BRUNET, P.; HAT- TINGH, K.; CHAVES, J. G. S. Source area and seasonal 87Sr/86Sr variations in rivers of the Amazon basin. **Hydrological Processes**, 29, 187–197, 2015.

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Trans-Amazonian natal homing in giant catfish

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Summary

1. Knowledge of fish migration is a prerequisite to sustainable fisheries management and preservation, especially in large international river basins. In particular, understanding whether a migratory lifestyle is compulsory or facultative, and whether adults home to their natal geographic area is paramount to fully appraise disruptions of longitudinal connectivity resulting from damming.

2. In the Amazon, the large migratory catfishes of the *Brachyplatystoma* genus are apex predators of considerable interest for fisheries. They are believed to use the entire length of the basin to perform their life cycle, with hypothesized homing behaviours. Here, we tested these hypotheses, using the emblematic *B. rousseauxii* as a model species.

3. We sampled adults close to major breeding areas in the Amazon basin (upper Madeira and upper Amazonas) and assessed their lifetime movements by measuring variations in ^{87}Sr/^{86}Sr along transverse sections of their otoliths (ear stones) using laser ablation multicollector mass spectrometry (LA-MC-ICPMS).

4. We demonstrate that larvae migrate downstream from the Andean piedmont to the lower Amazon, where they grow over a protracted period before migrating upstream as adults. Contrary to prevailing inferences, not all fish spend their nursery stages in the Amazon estuary. By contrast, the passage in the lower or central Amazon seems an obligate part of the life cycle. We further evidence that most adults home to their natal geographic area within

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the Madeira sub-basin. Such long-distance natal homing is exceptional in purely freshwater fishes.

5. *Synthesis and applications*. By using otolith microchemistry, we were able to demonstrate a seemingly compulsory basin-wide migratory life cycle of large Amazonian catfishes. This makes them the organisms performing the longest migrations (> 8000 km) in fresh waters. This exceptional life history is already jeopardized by two dams recently built in the Madeira River, which block a major migration route and access to a substantial part of their spawning grounds. Major impacts can be anticipated from the current and forthcoming hydroelectric development in the Amazon basin, not only on the populations and fisheries of this apex predator, but also on Amazonian food webs through trophic cascades.

Key-words: ^{87}Sr/^{86}Sr ratios, Amazon, anthropogenic activities, *Brachyplatystoma* spp., freshwater fish, giant catfish, hydroelectric dams, migration, otoliths

Introduction

Inland waters and their biodiversity provide a wealth of goods and services, but are increasingly threatened by anthropogenic activities world-wide (Nilsson *et al.* 2005; Hoeinghaus *et al.* 2009; Vörösmarty *et al.* 2010; Winemiller *et al.* 2016). Although relatively preserved until recently in comparison with other large river systems, the Amazon basin, which holds the most diverse freshwater fish fauna on Earth (Pimm *et al.* 2014), is no longer an exception (Castello *et al.* 2013). Fisheries, one of the most important ecosystem services of Amazonian fresh waters, largely rely on migratory Characiformes and Siluriformes (Lucas & Baras 2001; Carolsfeld *et al.* 2003). The utmost importance of migratory animals in ecosystem functioning and resilience has been stressed in recent studies, emphasizing their major roles in coupling resident communities and shaping food web dynamics along their migration routes (Wilcove & Wikelski 2008; Bauer & Hoye 2014). In-depth knowledge of the movement patterns of these migratory species is required to fully appraise their structuring importance and to implement relevant management policies. Such crucial information is lacking for most migratory Amazonian fishes and in particular for some of the most ecologically and economically important species, the *Brachyplatystoma* spp. (Pimelodidae). These large (up to 3 m) catfishes are apex consumers (Barthem & Goulding 1997). They support the largest fisheries of the Amazon basin and are often overexploited (Petrere *et al.* 2004; García Vasquez *et al.* 2009; Agudelo *et al.* 2013). Based on strong circumstantial evidence, these catfishes – at least *B. rousseauxii* (Castelnau 1855) – were hypothesized to undertake the longest migrations ever described in fresh waters, from the spawning areas in the Andean piedmont to the nursery in the Amazon estuary and back (Barthem & Goulding 1997): small juveniles are caught in the lower Amazon and in the freshwater part of the estuary, body size in fisheries landings increases with distance from the estuary, while ripe adults and newly hatched larvae are exclusively observed in white water tributaries of the Andean piedmont in Bolivia, Colombia, Ecuador and Peru (Barthem & Goulding 1997; García Vasquez *et al.* 2009; Cañas & Pine 2011; Agudelo *et al.* 2013). Recently, using otolith microchemistry Hegg, Giarrizzo & Kennedy (2015) provided evidence that the Amazon estuary might not be the sole nursery area for this species, as was thought originally (Barthem & Goulding 1997). The hypothesis of a single panmictic population of *B. rousseauxii* at the scale of the Amazon basin (Batista & Alves-Gomes 2006) was recently refuted by the existence of several reproductive units, with at least one exclusively found in the Madeira sub-basin (Carvajal-Vallejos *et al.* 2014). This genetic structure can be explained either by a resident lifestyle, with individuals spending their entire life in the Madeira, or by a natal homing behaviour. Natal homing, the return of migratory individuals to reproduce in the geographic area where they originated is widespread among terrestrial and aquatic animals (Papi 1992). Some of the most fascinating examples of this adaptive strategy are found in diadromous and marine fishes (Lucas & Baras 2001), such as salmons (Scheer 1939), eels (Tesch & White 2008) and tunas (Rooker *et al.* 2008). Evidence of long-range natal homing is scarce, however, for purely freshwater fishes (Lucas & Baras 2001). This behaviour has been hypothesized in *B. rousseauxii* (Batista & Alves-Gomes 2006; Carvajal-Vallejos *et al.* 2014) but never demonstrated.

Elucidating the migratory patterns of this large apex predator roaming the rivers of six Amazonian countries with different fisheries policies is paramount for designing adequate conservation and management strategies, especially in view of the current and proposed hydroelectric development throughout the Amazon basin (Finer & Jenkins 2012; Castello *et al.* 2013). In particular, two large dams (Santo Antonio and Jirau) have been erected since 2011 in the Brazilian part of the Madeira River, near Porto Velho (Fearnside 2014; Fig. 1). The impacts of these and other forthcoming dams on *B. rousseauxii* largely depend on their migration patterns: Do these fish actually make basin-wide migrations? Do they make a single or multiple runs? Do they exhibit homing behaviour?

Here, in order to address these questions, we sampled adults of *B. rousseauxii* close to some of their main breeding areas in the Upper Amazonas and Upper Madeira

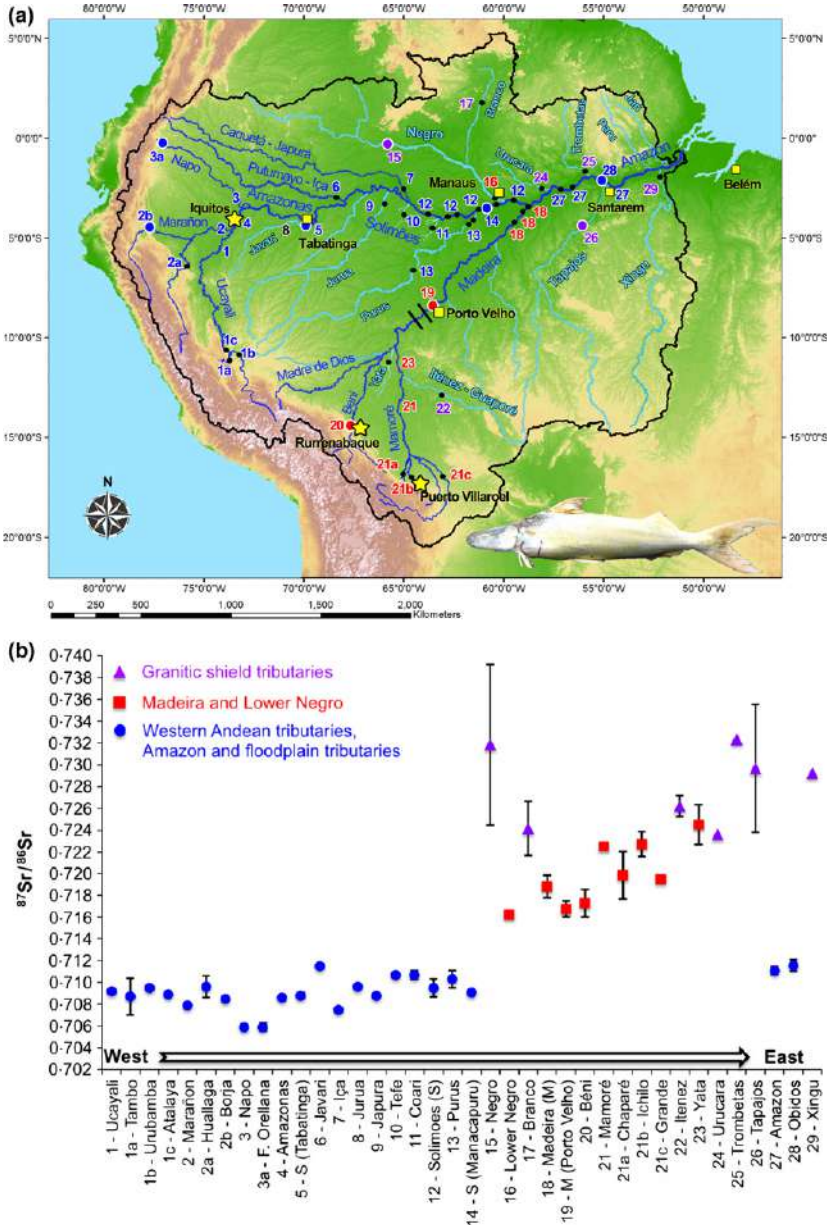

Fig. 1. (a) Map of the reference water ^{87}Sr/^{86}Sr values in the Amazon basin. Yellow squares refer to some of the cities mentioned in the text and yellow stars to fish sampling localities. Black dots refer to water sampling stations, with the following colour code; blue for the Western Andean tributaries, the Amazon and floodplain tributaries; red for the Madeira and Lower Negro; and purple for the granitic shield tributaries with black or clear waters. Coloured circles with a white ring correspond to multiyear samples from SO-HYBAm sampling stations (Table S1). The main Andean white water tributaries are highlighted in dark blue. The two transverse black bars on the Madeira River upstream of Porto Velho represent two large hydroelectric dams erected since 2011 (Santo Antônio and Jirau). (b) Mean isotopic water signatures (±SD) along the Amazon basin following a west-to-east gradient from the Andes to the Amazon mouth. Individual water data are provided in Table S1.

(Fig. 1a), before the construction of the Madeira dams. We measured ^{87}Sr/^{86}Sr ratios in transects along transverse sections of their otoliths, and we compared these observed profiles with those expected from different scenarios of space utilization and migration (Fig. 2).

Materials and methods

STUDY AREA

In Amazonia, the term Amazon is generally restricted to the river stretch between the estuary and the confluence with the Negro River, near Manaus (Fig. 1). Further west, the river is named Solimões until the trifrontier between Peru, Colombia and Brazil near Tabatinga. Further upstream, up to the confluence between the rivers Ucayali and Marañon (upstream of Iquitos, Peru), it is known as Amazonas.

STUDY DESIGN

Most studies of fish migration rely on mark–recapture or biotelemetry (Lucas & Baras 2001). The implementation of these methods, however, is unrealistic for the study of *Brachyplatystoma* spp. migrations, given the small size of their migratory larvae (Cella-Ribeiro *et al.* 2015) and the sheer dimensions of the Amazonian basin. The screening of fish hard body parts for environmental chemicals (such as strontium or barium) or isotopes that naturally substitute for calcium can be used as a proxy to indicate the fish's habitat at a particular age or size (Campana 1999; Kennedy *et al.* 2000; see Appendix S1, Supporting information for details). Methodologies using laser ablation (LA) combined with multicollector (MC) and inductively coupled plasma mass spectrometry (ICPMS) for the measurement of Sr isotopes and their ratio (^{87}Sr/^{86}Sr) along otolith transects enable the fine reconstruction of habitat use during part or the entire fish's life (Outridge *et al.* 2002; Barnett-Johnson *et al.* 2005).

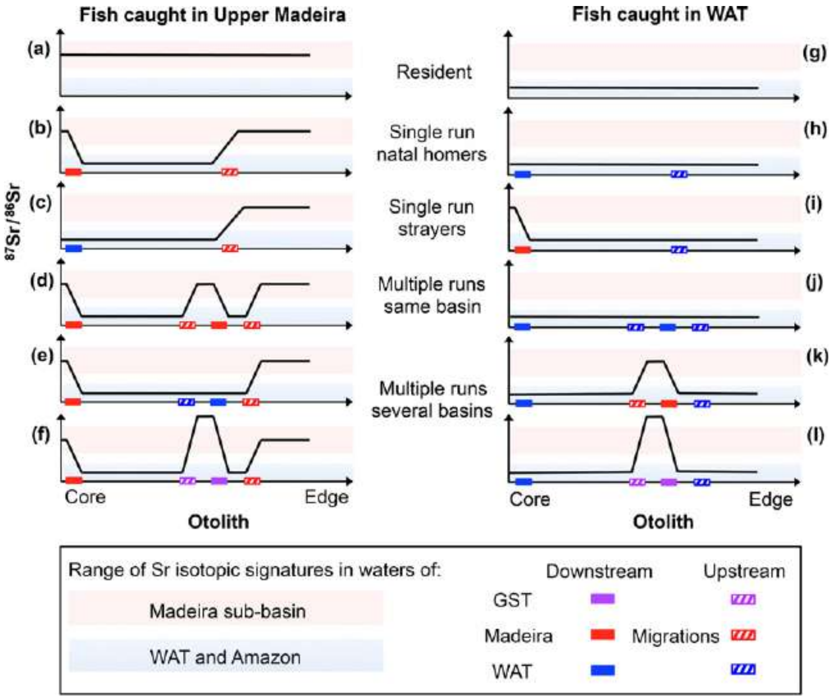

Fig. 2. Isotopic Sr profile patterns corresponding to alternative migration scenarios for *Brachyplatystoma rousseauxii* in the Amazon basin. The light red and blue bands correspond to the ranges of water signatures in the Madeira sub-basin, and in the Amazon and Western Andean tributaries, respectively (see Fig. 1). Rectangles on the horizontal axis of each graph refer to the inferred downstream (closed symbols) and upstream movements (hatched symbols), in the granitic shield tributaries (GST, purple), Madeira (red) or Western Andean tributaries (WAT, blue). The bold black line is the corresponding Sr isotopic ratio in the fish otolith. For the sake of simplicity, only situations for homers were illustrated for scenarios involving multiple runs (d, e, f, j, k, l).

Otoliths are made of relatively inert aragonitic calcium carbonate laid down on an organic matrix, and contrary to other hard body parts, they are not subjected to any resorption process. In contrast to the situation of many other chemicals, strontium (Sr) isotopic ratios in otoliths are unaffected by confounding effects of biotic processes (physiological or dietary dynamics) and abiotic factors (such as temperature) (Kennedy *et al*. 1997, 2000; Walther & Limburg 2012). The diversity of bedrocks with contrasting strontium isotopic ratios (^{87}Sr/^{86}Sr) across the Amazonian Basin, together with the rather limited variability of these ratios across years and seasons (Palmer & Edmond 1992; Gaillardet *et al*. 1997; Queiroz *et al*. 2009; Pouilly *et al*. 2014; Santos *et al*. 2015), provides heuristic opportunities for identifying fish geographic origin or reconstructing their migration patterns (Pouilly *et al*. 2014; Garcez *et al*. 2015; Hegg, Giarrizzo & Kennedy 2015), at least at the scale of large sub-basins. A finer discrimination between tributaries is rendered more difficult or impossible by the similarity of their underlying watershed geology.

Here, we use the classification of Hegg, Giarrizzo & Kennedy (2015), slightly modified in the light of additional data of strontium isotopic ratios in Amazonian waters (Palmer & Edmond 1992). We distinguish three main riverine regions (Fig. 1): (i) the Western Andean tributaries (hereafter, WAT), the Amazon River mainstem and its floodplain tributaries; (ii) the Madeira sub-basin and lower Negro River; and (iii) tributaries draining the Brazilian and Guyanese granitic shields, referred to hereafter as ‘granitic shield tributaries’ (GST). There is some overlap between the Sr isotopic signatures of Madeira waters and those of the lower course of some GST, especially the Tapajos and Lower Negro River (Fig. 1, Table S1). Decades of intensive fisheries and scientific sampling, however, never yielded any ripe adult or larva of *B. rousseauxii* in GST (Barthem & Goulding 1997), in contrast to their routine occurrence in Andean white water tributaries (Barthem & Goulding 1997; García Vasquez *et al*. 2009; Cañas & Pine 2011; Agudelo *et al*. 2013). Therefore, otolith core signatures comprised between 0·715 and 0·726 (range of available ^{87}Sr/^{86}Sr signatures in the Madeira waters, Fig. 1, Table S1) will be considered as evidence of hatching within the Madeira sub-basin. Likewise, otolith core signatures <0·712 will be assigned to fish hatched in WAT waters.

FISH SAMPLING

Fish were sampled between 2005 and 2009, before the construction of the Santo Antonio and Jirau hydroelectric dams on the Madeira River. Eighteen fish (95–120 cm standard length, SL) were obtained directly on the fishing grounds of the Bolivian upper Madeira, near Puerto Villarroel on the Mamoré River, and near Rurrenabaque on the Beni River. Nineteen other fish (89–141 cm SL) were purchased in Iquitos market, Peru, which lands fish caught within ~300 km, including the Amazonas, and the lower parts of the Ucayali, Napo and Marañon river systems. For each specimen, SL was measured (nearest cm) and otoliths (lapilli) were extracted, rinsed in clear water, dried and stored for later examination.

OTOLITH ANALYSIS

Every collected otolith was processed at the MARBEC laboratory, Montpellier (France), mounted in Araldite epoxy resin, and a transverse section was made with a low-speed Isomet saw (Buehler, Düsseldorf, Germany) to obtain a dorso-ventral slice including the otolith core. The section was then ground and polished using polishing papers and ultra-pure water until seeing the core on one side.

Analyses of Sr isotopes in fish otoliths were carried out in the laboratory LCABIE-IPREM (Université de Pau et des Pays de l’Adour, France), using a Nu plasma high-resolution MC-ICPMS (Nu instruments, Wrexham, UK) coupled to an Alfamet femtosecond (fs) laser ablation system (Nexeya SA, Canejan, France). The laser ablated a transect from the core (hatching of the fish) to the edge (death of the fish) of the otolith (i.e. perpendicular to the growth marks) at a speed of 5 μm s^{-1}. The laser was operated at 500 Hz with a pulse energy of 8 μJ to limit the in-depth ablation to no more than 30 μm, while the scanner was doing a permanent 200-μm-wide back-and-forth movement at a speed of 1 mm s^{-1}. In order to prevent blast effect on the nucleus, the ablation was started 200 μm before the core.

Twice a day, we analysed an in-laboratory ^{87}Sr/^{86}Sr-certified otolith powder pellet (NIES22, certified Reference Material produced by the National Institute for Environmental Studies, Japan) to check the reliability of ^{87}Sr/^{86}Sr measurements (Martin *et al.* 2013). In all cases, fs-LA-MC-ICPMS ^{87}Sr/^{86}Sr values (mean ± 2 SD = 0·709289 ± 0·000379, $n = 38$) corresponded well with the in-laboratory-certified values (mean ± 2 SD = 0·709240 ± 0·000021, $n = 54$). Further details about analytical processes are given in Appendix S1.

ESTIMATION OF THE BODY LENGTH OF DOWNSTREAM AND UPSTREAM MIGRANTS IN THE MADEIRA

On the basis of environmental signatures, the limit of ^{87}Sr/^{86}Sr between the Madeira and Amazon waters was set at 0·715 (Fig. 1). We considered that *B. rousseauxii* exited the Madeira when their otolith Sr isotopic ratios were consistently lower than 0·715. Similarly, we assumed that fish had left the Amazon and re-entered the Madeira when their otolith Sr isotopic ratios became anew consistently higher than 0·715. For both events, the distances from the otolith's core were noted (nearest 25 μm). In order to back-calculate the fish SL at these moments, we used a relationship between the otolith dimension along the transverse radius and the fish SL, produced from 351 *B. rousseauxii* caught between 2009 and 2012 by the Laboratory of Ichthyology and Fisheries of the Universidade Federal do Rondônia (UNIR) in the Brazilian stretch of the Madeira River. The relationship is linear in small fish (40–50 cm SL) then becomes curvilinear in larger individuals (Fig. S1), as the otoliths of older fish are thicker. Henceforth, two distinct equations were used for fish ≤and >45 cm SL.

SIZE OF *B. ROUSSEAUXII* AT FIRST SEXUAL MATURITY

The size at first sexual maturity (L_m) is defined as the SL at which 50% of the fish are observed at an advanced maturation stage during the breeding season (Núñez & Duponchelle 2009) (i.e. when oocytes are visible to the naked eye, which means vitellogenesis has started). L_m is estimated by fitting the fraction of mature individuals per 5-cm SL intervals to a logistic function (García Vasquez *et al.* 2009; Agudelo *et al.* 2013), where the contribution of each size class to the model is statistically weighted by the total number of individuals in the same size class:

$$M = 100(1 + e^{(-a(L_i - L_m))})^{-1}$$

where M (%) is the proportion of mature individuals by size class, L_i is the central value of size class i, and a and L_m are the coefficients of the model. Here, the model was adjusted using 152 female *B. rousseauxii* (37–125 cm SL) caught in the Brazilian part of the Madeira sub-basin and for which we histologically determined the stage of gonad maturation. The values of coefficients a and L_m in the model (Fig. S2) were fitted using a nonlinear regression with the quasi-Newton adjustment and were 0·3402 (±0·0141 SE) and 73·33 (±0·14 SE) cm SL, respectively ($P < 0·0001$ in both cases).

Results

As for all migratory fishes, several scenarios can be hypothesized for *B. rousseauxii*, including resident behaviour in the hatching tributary or sub-basin, long-range migration from the hatching tributary to the Amazon mainstem followed by homing or straying, and multiple runs between the Amazon mainstem and the same or different sub-basins. The corresponding theoretical ^{87}Sr/^{86}Sr patterns in the otoliths of fish hatched in the Madeira and WAT are distinct (Fig. 2). Several patterns can be univocal, whereas others may refer to several scenarios. In particular, on the sole basis of Sr isotopic signatures, it is uncertain whether fish ascending the Madeira before their capture did so during their very first upstream run or whether they migrated to WAT in the meanwhile (Fig. 2b, e). Likewise, it is almost impossible to distinguish between fish spending all their life in WAT and those migrating once or several times between these places and the middle or lower Amazon River (Fig. 2g, h, j). It is also difficult to discriminate between fish venturing in the Madeira sub-basin and those entering GST, because of the overlap between the Sr isotopic signatures of these rivers (Fig. 1b). This confusion would only arise for intermediate runs, and exclusively in situations where fish in GST would remain in waters with signatures <0·726, thereby resulting in otolith profiles resembling those illustrated in Fig. 2d or k. Intermediate runs in more radiogenic GST would produce univocal profiles, similar to those illustrated in Fig. 2f or l. Regarding the final upstream run, the interpretation is straightforwardly deduced from the capture location.

INTERPRETATION OF MIGRATION PATTERNS

Twelve of the 18 fish sampled in the Madeira sub-basin could be ranked as natal homers (Figs 2b and 3a). Their core Sr isotopic signatures (0·716–0·722) were typical of Madeira waters, they moved downstream into waters with Amazon and WAT signatures, grew in these waters, then homed to the Madeira sub-basin, where they remained until their capture. As explained above, it is uncertain whether these fish ventured into WAT before returning to the Madeira (Fig. 2b, e). By contrast, it is certain that they did not make any intermediate run in the Madeira or in any GST, as these migratory patterns would have involved a passage in the Amazon on the way back to the Madeira, which would have produced Sr isotopic profiles close to those in Fig. 2d and f, respectively. Likewise, there is no ambiguity for the final upstream run, as these fish were captured in the upper Madeira. Based on the relationship between otolith radius and body length in *B. rousseauxii* (Fig. S1), these fish would have exited the

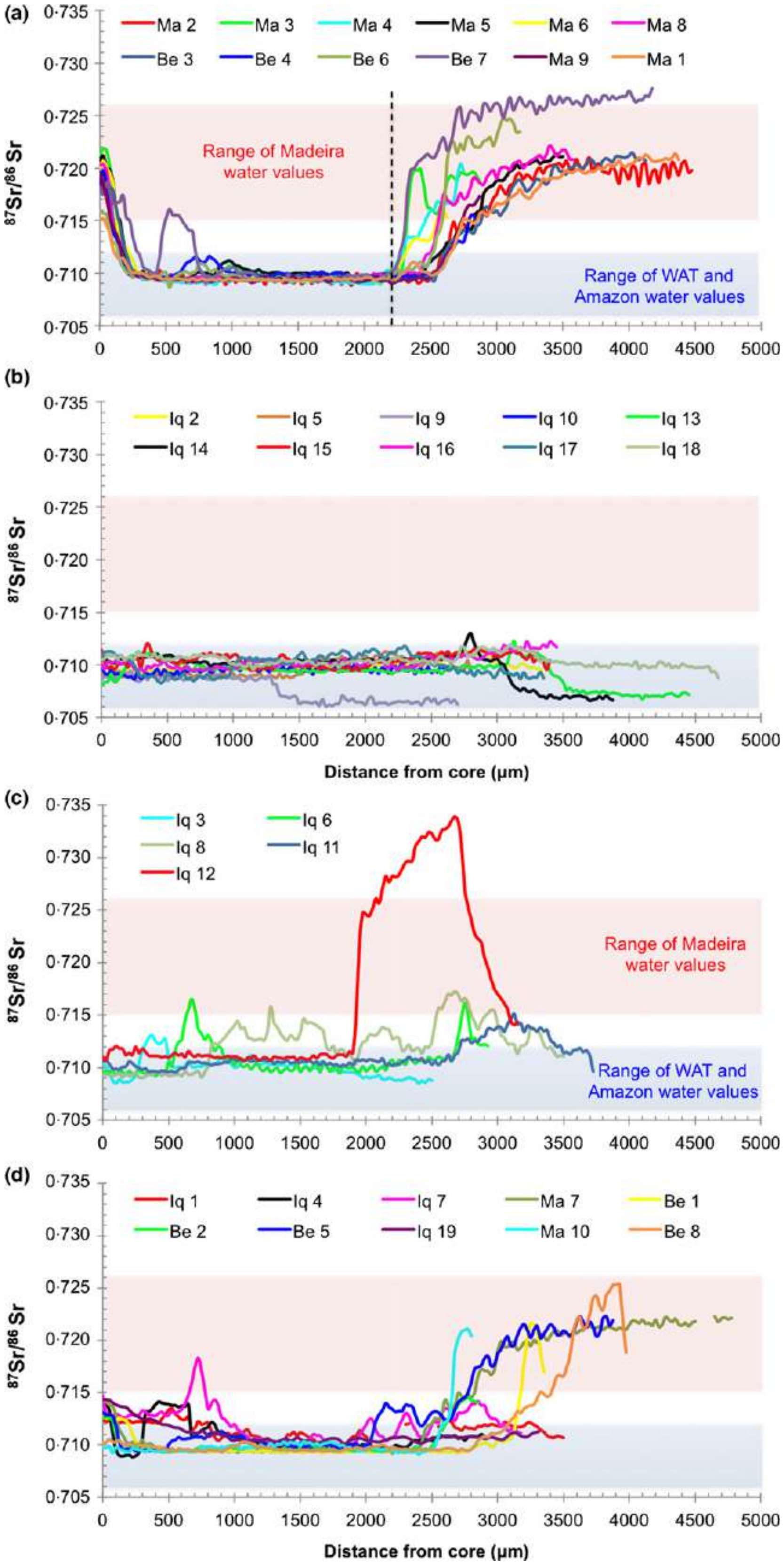

Fig. 3. Laser ablation-MC-ICPMS transects of $^{87/86}$Sr along otolith transverse sections (from the core to the edge) of *Brachyplatystoma rousseauxii*. Each curve corresponds to one individual caught either in the upper Madeira (Mamoré, Ma and Beni, Be rivers) or in the upper Amazon (fish landed in Iquitos, Iq; see Fig. 1). Four migratory patterns were identified among transects (a, b, c, d, see text). The dashed line (a) represents the size at first sexual maturity of *B. rousseauxii* in the Madeira basin (Fig. S2).

Madeira at 3·7 ± 1·6 cm SL (mean ± SD) and returned at 86·0 ± 5·7 cm SL, slightly above the mean size at first sexual maturity (73·3 ± 4·7 cm SL; Fig. S2).

Ten other fish, all collected in Iquitos, exhibited no single Sr isotopic signal >0·713 in their otoliths (Fig. 3b). Therefore, it can be assumed that these fish never entered the Madeira or GST, and they remained in the Amazon or WAT for their entire lives. By contrast, it is uncertain whether these profiles correspond to resident or migratory behaviours, with one or several runs between the Amazon and WAT (scenarios in Fig. 2g, h and j, respectively). Based on existing knowledge, however, it is likely that these fish hatched in WAT, travelled down to the Amazon at a small body size and subsequently returned to WAT. In contrast to the clear-cut situation for fish homing to the Madeira, no information can be obtained here regarding the size of fish during their (presumed) downstream and upstream runs, except that all these fish had passed the size at first sexual maturity when they were captured.

Five other fish also hatched in waters with WAT or Amazon signatures and collected later as adults in Iquitos, showed slightly less typical patterns (Fig. 3c). Four of them (Iq3, Iq6, Iq8 and Iq11) repeatedly moved back and forth in waters with Sr isotopic ratios intermediate between those of the Amazon and Madeira. The fifth fish (Iq12) showed a signature profile matching the scenario of multiple runs in several Amazonian sub-basins (Fig. 2l). This fish, which hatched and lived in waters with WAT and Amazon signatures, thereafter migrated in highly radiogenic waters (^{87}Sr/^{86}Sr > 0·730), which are found exclusively in some GST (probably the Negro or Tapajos rivers, see Fig. 1 and Table S1). It eventually migrated back to the WAT, where it was caught.

For the remaining 10 fish, the edge signatures departed from the core signatures (Fig. 3d). For two of the six fish caught in the Upper Madeira (Ma10 and Be8), the core signatures were typical of WAT, matching the straying scenario illustrated in Fig. 2c. The core signatures of the remaining eight fish (0·7125–0·7147) fell in between the ranges of Madeira and WAT.

Discussion

The migratory patterns of most fish were relatively univocal and indicated long-range migration and natal homing behaviour (Fig. 3a). By contrast, the isotopic profiles of several fish illustrated in Fig. 3c and d were less straightforward and require further discussion. Four fish (Iq3, Iq6, Iq8 and Iq11) apparently moved back and forth in waters with Sr isotopic ratios intermediate between those of the Amazon and Madeira (Fig. 3c). These ratios could correspond to sojourns in non-sampled tributaries or refer to fish movements in confluence areas between waters with highly contrasting signatures (Bouchez *et al.* 2010), as occur in several places in the Amazon River (e.g. confluences with more radiogenic tributaries, such as the Negro, Madeira and Tapajos rivers; Fig. 1). White water tributaries with high sediment loads have a much higher and lasting impact than clear or black water tributaries when mixing with waters of contrasting signatures (Bouchez *et al.* 2010). Hence, it is likely that most profiles depicted in Fig. 3c and d correspond to movements within the confluence area of the Amazon and Madeira or similar situations. Eight fish from Fig. 3d had core signatures (0·7125–0·7147) falling in between the ranges of Madeira and WAT. These atypical signatures might correspond to tributaries for which there is currently no information on Sr isotopic ratios, and in this particular case, all eight fish would be strayers. Alternatively, it is possible that these atypical core signatures originated from fish hatched in the Madeira sub-basin, but moving downstream much faster than others, as can typically happen under higher flows. Several authors have indeed demonstrated that *B. rousseauxii* reproduces during contrasting hydrological periods in the main rivers of the Upper Madeira (Cañas & Pine 2011; Cella-Ribeiro *et al.* 2015). On the basis of hydrological data (SO-HYBAm) upon river discharge, flow and width in the Madeira River, it can be reasonably assumed that fish hatching and drifting during high flows could be flushed down into the Amazon at least three times faster than during periods of low flows. While taking into account the methodological limitations pertaining to the depth of laser ablation for otolith screening, such faster movements would inevitably lead to some degree of integration of the Amazon signature into the core signatures and thus to lower Sr isotopic ratios than expected for fish hatched in Madeira waters. If this hypothesis were valid, then four of the eight fish illustrated in Fig. 3d and that were caught in Iquitos (Iq1, Iq4, Iq7 and Iq19) would be strayers from the Madeira (as illustrated in Fig. 2i) and the remaining four fish caught in the Madeira (Ma7, Be1, Be2 and Be5) would be natal homers.

Our results tend to indicate the absence of multiple upstream and downstream runs of *B. rousseauxii* between the Madeira and the Amazon (Fig. 2d), which had been formerly hypothesized (Barthem & Goulding 1997). The species fine-scale movement patterns cannot be detailed yet, given the limited variability of ^{87}Sr/^{86}Sr ratios along the Amazon and WAT mainstems, and it is uncertain whether fish hatched in the Madeira and WAT share the same nurseries.

There is strong evidence, however, that not all *B. rousseauxii* migrate downstream to the Amazon estuary, as recently suggested by Hegg, Giarrizzo & Kennedy (2015) on the basis of fish caught near Manaus. Indeed, fish hatched in the Madeira or WAT and growing thereafter in the estuary must travel in the meanwhile through the lower Amazon (between the mouth of the Madeira and Santarem, near the estuary), where the contributions of the Madeira River and highly radiogenic GSTs tend to increase significantly the Sr isotopic ratio in the Amazon mainstem to values ranging from 0·7103 to 0·7123 (averaging 0·7115 in Obidos and Santarem, downstream of sampling points 27; Fig. 1, Table S1). Three fish hatched in WAT and later caught in Iquitos (Iq 2, Iq 9 and Iq 10) had no single otolith ^{87}Sr/^{86}Sr value falling within this range, thereby indicating that these fish never entered the Amazon estuary at any life stage. Two other fish hatched in WAT, one caught in Iquitos (Iq 5) and the other one caught in the Upper Madeira (Ma 10), exhibited such Sr isotopic ratios in their otoliths, but only at relatively large body sizes (50 and 47 cm SL, respectively), thereby indicating that they did not move into the estuary during their early juvenile stages. Our results suggest that the nurseries of these five fish were somewhere upstream of the Obidos-Santarem area. No such evidence of an absence of movement into the estuary can be deduced for fish hatched in the Madeira, as these fish always inevitably crossed waters with Sr isotopic ratios between 0·7103 and 0·7123 on their way down to the Amazon. Whatever the exact place of the nurseries and their connections with the spawning areas of *B. rousseauxii*, a protracted period in the lower or central Amazon River at the juvenile stage seems an obligate part of the life cycle of *B. rousseauxii*, thereby refuting the hypothesis of an alternative resident lifestyle (Carvajal-Vallejos *et al.* 2014). This certainly applies to fish hatched in the Madeira, for which evidence is provided here, and presumably to those hatched in the WAT.

Our results provide the very first demonstration of natal homing of *B. rousseauxii* in the Amazon basin, at least for the Madeira sub-basin. This is the longest homing migration ever documented in potamodromous fishes. Once *B. rousseauxii* have homed to the Madeira, at about the size of first sexual maturity, they never return to the Amazon. The database of water isotopic signatures in the Amazon basin is currently too limited to test whether *B. rousseauxii* home precisely to their hatching tributary, although the pelagic nature of their semi-buoyant eggs may suggest that salmon-like precision in homing is unlikely (Papi 1992; Lucas & Baras 2001). Homing is seemingly the predominant behaviour, at least in the Madeira River, but some fish do stray between sub-basins (Fig. 3d). The relatively low number of otolith samples analysed in the present study precludes a reliable estimation of the proportions of different behaviours. The occurrence of both homers and strayers here is nevertheless consistent with molecular analyses indicating at least three reproductive units of *B. rousseauxii* in the Amazon basin, one of which is restricted to the Madeira basin (Carvajal-Vallejos *et al.* 2014).

The movement patterns highlighted here somehow differ from those recently published for the same species by Hegg, Giarrizzo & Kennedy (2015), who did not evidence fish originating from or moving into the Madeira. These differences presumably owe to at least three factors. Their sampling localities were different, lying in the estuary (Belem) or central Amazon (Manaus), and their fish were caught before their upstream spawning runs. Finally, in contrast to the present study, where fish were collected at all seasons over several years, all fish studied by Hegg, Giarrizzo & Kennedy (2015) were caught within less than a month. The latter context is more likely to generate a sampling bias that could account for the absence of fish hatched in the Madeira in their study. Alternatively, it cannot be excluded that fish hatched in the Madeira effectively contribute to the estuarine stock to a lower extent than those hatched in WAT, especially if their main nursery areas were somewhere else. This brief comparison emphasizes the need for further studies to elucidate the migrations of *B. rousseauxii* in the Amazonian basin, in particular to understand the contributions of different sub-basins and tributaries to recruitment and fisheries. In the study by Hegg, Giarrizzo & Kennedy (2015) and in the present study, sample size was limited to a few tens of fish, but in both cases, the method used generated large numbers of samples over the life of individual fish. These observations may be autocorrelated, but they nevertheless provide unprecedented information on the life of this ecologically and economically important species.

In synthesis, the present study demonstrates basin-wide migrations of *B. rousseauxii*, with a downstream migration into the Amazon at a small (<3–4 cm SL) body size, a protracted growth period in the lower or central Amazon at the juvenile stage and a return upstream run as adults. On the basis of fish captured in the Madeira, this long-range migratory lifestyle is seemingly compulsory, with no single specimen exhibiting otolith strontium isotopic profiles characteristic of a resident behaviour. These findings have profound consequences for the management of this ecologically and commercially important species. The now demonstrated existence of transboundary movements in *B. rousseauxii* further advocates for the need of an international fisheries management coordination of this resource across the Amazon basin (Fabré & Barthem 2005). Beyond current issues of overexploitation and complex fisheries management, *B. rousseauxii*, in view of its compulsory basin-wide migrations, might be imperilled to a greater extent than other migratory fishes by disruptions of longitudinal connectivity. Until recently, the Amazon basin had been moderately affected by damming (Nilsson *et al.* 2005; Vörösmarty *et al.* 2010), with no single dam below 400 m a.s.l. (Finer & Jenkins 2012) that could have interfered with the migratory life cycle of *B. rousseauxii*. Since 2011, two large dams were erected in the lower Madeira River. Their fish passage facilities have been found ineffective for accommodating the upstream runs of large catfishes, including *B. rousseauxii* (Fearnside 2014). As *B. rousseauxii* spawns exclusively in the white water tributaries of the Andean piedmont (WAT and upper Madeira), it can be assumed that the access of *B. rousseauxii* to a substantial part of its possible spawning grounds in the Amazon basin is already strongly compromised. This calls for urgent modifications of the fish passages of both Jirau and Santo Antonio dams in order to restore the connectivity between the upper and lower portions of the Madeira. Our results further urge the need to preserve river connectivity in the still undammed parts of the Amazonian lowlands and midlands, while tens of other dams are already planned in these regions (Finer & Jenkins 2012; Castello *et al.* 2013; Fearnside 2014).

The impacts of multiple obstacles on the migration routes of *B. rousseauxii* might just be as dramatic as those suffered in temperate regions by anadromous salmonids, which also undertake basin-wide migrations (Lucas & Baras 2001), or even worse, for two reasons. First, *B. rousseauxii* makes its downstream migrations at a much younger age and smaller body size than salmonids (Cella-Ribeiro *et al.* 2015; present study). Smaller fish have a lower probability to escape predation or adverse physico-chemical conditions in lentic reservoirs upstream of dams, because of their limited swimming capacities, and fish-attracting or deterring devices aiming to facilitate a safe downstream passage are certainly less efficient than for larger fish (Lucas & Baras 2001; Pelicice, Pompeu & Agostinho 2015). Secondly, *B. rousseauxii* is an apex consumer, with key ecological functions (Barthem & Goulding 1997), and its decline could thus have profound top-down effects on the ecosystem through trophic cascades (Estes *et al.* 2011). To our knowledge, it is most infrequent that large piscine predators exhibit long-range migrations in continental ecosystems. As a consequence, damming in the Amazon basin could have more severe impacts on ichthyofauna and food webs than in any other large river system. These issues add to a long list of concerns regarding the sustainability of large-scale hydroelectric development (Nilsson *et al.* 2005; Vörösmarty *et al.* 2010; Ansar *et al.* 2014) and may require re-evaluating the actual pros and cons of large hydropower plants in the Amazon basin (Finer & Jenkins 2012; Stickler *et al.* 2013; Kahn, Freitas & Petrere 2014; Winemiller *et al.* 2016), which hosts the world's richest biodiversity.

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Data accessibility

Source data of fish $^{87}Sr/^{86}Sr$ profiles are available in Table S3.

References

Agudelo, E., Joven León, Á.V., Bonilla Castillo, C.A., Petrere, M. Jr, Peláez, M. & Duponchelle, F. (2013) Breeding, growth and exploitation of *Brachyplatystoma rousseauxii* in the Caqueta River, Colombia. *Neotropical Ichthyology*, **11**, 637–647.

Ansar, A., Flyvbjerg, B., Budzier, A. & Lunn, D. (2014) Should we build more large dams? The actual costs of hydropower megaproject development. *Energy Policy*, **69**, 43–56.

Barnett-Johnson, R., Ramos, F.C., Grimes, C.B. & MacFarlane, R.B. (2005) Validation of Sr isotopes in otoliths by laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICPMS): opening avenues in fisheries science applications. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2425–2430.

Barthem, R. & Goulding, M. (1997) *The Catfish Connection. Ecology, Migration and Conservation of Amazon Predators*. Columbia University Press, New York.

Batista, J.S. & Alves-Gomes, J.A. (2006) Phylogeography of *Brachyplatystoma rousseauxii* (Siluriformes – Pimelodidae) in the Amazon Basin offers preliminary evidence for the first case of "homing" for an Amazonian migratory catfish. *Genetics and Molecular Research*, **5**, 723–740.

Bauer, S. & Hoye, B.J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, **344**, 1242552.

Bouchez, J., Lajeunesse, E., Gaillardet, J., France-Lanord, C., Dutra-Maia, P. & Maurice, L. (2010) Turbulent mixing in the Amazon River: the isotopic memory of confluences. *Earth and Planetary Science Letters*, **290**, 37–43.

Campana, S.E. (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series*, **188**, 263–297.

Cañas, C.M. & Pine, W.E. (2011) Documentation of the temporal and spatial patterns of Pimelodidae catfish spawning and larvae dispersion in the Madre de Dios River (Peru): insights for conservation in the Andean-Amazon headwaters. *River Research and Applications*, **27**, 602–611.

Carolsfeld, J., Harvey, B., Ross, C. & Baer, A. (eds) (2003) *Migratory fishes of South America: Biology, Fisheries and Conservation Status*. IDRC, World Bank, Washington, DC, USA.

Carvajal-Vallejos, F.M., Duponchelle, F., Desmarais, E., Cerqueira, F., Querouil, S., Nuñez, J., García, C. & Renno, J.F. (2014) Genetic structure in the Amazonian catfish *Brachyplatystoma rousseauxii*: influence of life history strategies. *Genetica*, **142**, 323–336.

Castello, L., McGrath, D.G., Hess, L.L., Coe, M.T., Lefebvre, P.A., Petry, P., Macedo, M.N., Renó, V.F. & Arantes, C.C. (2013) The vulnerability of Amazon freshwater ecosystems. *Conservation Letters*, **6**, 217–229.

Cella-Ribeiro, A., Assakawa, L.F., Torrente-Vilara, G., Zuanon, J., Leite, R.G., Doria, C. & Duponchelle, F. (2015) Temporal and spatial distribution of young *Brachyplatystoma* spp. (Siluriformes: Pimelodidae) along the rapids stretch of the Madeira River (Brazil) before the construction of two hydroelectric dams. *Journal of Fish Biology*, **86**, 1429–1437.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.

Fabré, N.N. & Barthem, R. (2005) O manejo da pesca dos grandes bagres migradores: Piramutaba e Dourada no eixo Solimões-Amazonas. *Coleção Documentos Técnicos: Estudos Estrategicos* (eds N.N., Fabré & R., Barthem), pp. 114. Ibama, Provarzea, Manaus.

Fearnside, P.M. (2014) Impacts of Brazil's Madeira River dams: unlearned lessons for hydroelectric development in Amazonia. *Environmental Science & Policy*, **38**, 164–172.

Finer, M. & Jenkins, C.N. (2012) Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PLoS One*, **7**, e35126.

Gaillardet, J., Dupre, B., Allegre, C.J. & Négrel, P. (1997) Chemical and physical denudation in the Amazon River Basin. *Chemical Geology*, **142**, 141–173.

Garcez, R.C.S., Humston, R., Harbor, D. & Freitas, C.E.C. (2015) Otolith geochemistry in young-of-the-year peacock bass *Cichla temensis* for investigating natal dispersal in the Rio Negro (Amazon – Brazil) river system. *Ecology of Freshwater Fish*, **24**, 242–251.

García Vasquez, A., Alonso, J.C., Carvajal, F., Moreau, J., Nuñez, J., Renno, J.F., Tello, S., Montreuil, V. & Duponchelle, F. (2009) Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. *Journal of Fish Biology*, **75**, 2527–2551.

Hegg, J.C., Giarrizzo, T. & Kennedy, B.P. (2015) Diverse early life-history strategies in migratory Amazonian catfish: implications for conservation and management. *PLoS One*, **10**, e0129697.

Hoeinghaus, D.J., Agostinho, A.A., Gomes, L.C., Pelicice, F.M., Okada, E.K., Latini, J.D., Kashiwaqui, E.A.L. & Winemiller, K.O. (2009) Effects of river impoundment on ecosystem services of large tropical rivers: embodied energy and market value of artisanal fisheries. *Conservation Biology*, **23**, 1222–1231.

Kahn, J.R., Freitas, C.E. & Petrere, M. Jr (2014) False shades of green: the case of Brazilian Amazonian hydropower. *Energies*, **7**, 6063–6082.

Kennedy, B.P., Folt, C.L., Blum, J.D. & Chamberlain, C.P. (1997) Natural isotope markers in salmon. *Nature*, **387**, 766–767.

Kennedy, B.P., Blum, J.D., Folt, C.L. & Nislow, K.H. (2000) Using natural strontium isotopic signatures as fish markers: methodology and application. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2280–2292.

Lucas, M.C. & Baras, E. (2001) *Migration of Freshwater Fishes*. Blackwell Science Ltd., Oxford.

Martin, J., Bareille, G., Berail, S., Pécheyran, C., Gueraud, F., Lange, F. *et al.* (2013) Persistence of a southern Atlantic salmon population: diversity of natal origins from otolith elemental and Sr isotopic signatures. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**, 182–197.

Nilsson, C., Reidy, C.A., Dynesius, M. & Revenga, C. (2005) Fragmentation and flow regulation of the world's large river systems. *Science*, **308**, 405–408.

Núñez, J. & Duponchelle, F. (2009) Towards a universal scale to assess sexual maturation and related life history traits in oviparous teleost fishes. *Fish Physiology and Biochemistry*, **35**, 167–180.

Outridge, P.M., Chenery, S.R., Babaluk, J.A. & Reist, J.D. (2002) Analysis of geological Sr isotope markers in fish otoliths with subannual resolution using laser ablation-multicollector-ICP-mass spectrometry. *Environmental Geology*, **42**, 891–899.

Palmer, M.R. & Edmond, J.M. (1992) Controls over the strontium isotope composition of river water. *Geochimica et Cosmochimica Acta*, **56**, 2099–2111.

Papi, F. (1992) *Animal Homing*. Chapman & Hall, London.

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

Petrere, M. Jr, Barthem, R.B., Cordoba, E.A. & Gomez, B.C. (2004) Review of the large catfish fisheries in the upper Amazon and the stock depletion of piraiba (*Brachyplatystoma filamentosum* Lichtenstein). *Reviews in Fish Biology and Fisheries*, **14**, 403–414.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M. & Sexton, J.O. (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, **344**, 1246752.

Pouilly, M., Point, D., Sondag, F., Henry, M. & Santos, R.V. (2014) Geographical origin of Amazonian freshwater fishes fingerprinted by ^{87}Sr/^{86}Sr ratios on fish otoliths and scales. *Environmental Science & Technology*, **48**, 8980–8987.

Queiroz, M.M.A., Horbe, A.M.C., Seyler, P. & Moura, C.A.V. (2009) Hidroquímica do rio Solimões na região entre Manacapuru e Alvarães: Amazonas—Brasil. *Acta Amazonica*, **39**, 943–952.

Rooker, J.R., Secor, D.H., De Metrio, G., Schloesser, R., Block, B.A. & Neilson, J.D. (2008) Natal homing and connectivity in Atlantic bluefin tuna populations. *Science*, **322**, 742–744.

Santos, R.V., Sondag, F., Cochonneau, G., Lagane, C., Brunet, P., Hattingh, K. & Chaves, J.G.S. (2015) Source area and seasonal ^{87}Sr/^{86}Sr variations in rivers of the Amazon basin. *Hydrological Processes*, **29**, 187–197.

Scheer, B.T. (1939) Homing instinct in Salmon. *The Quarterly Review of Biology*, **14**, 408–430.

Stickler, C.M., Coe, M.T., Costa, M.H., Nepstad, D.C., McGrath, D.G., Dias, L.C.P., Rodrigues, H.O. & Soares-Filho, B.S. (2013) Dependence of hydropower energy generation on forests in the Amazon Basin at local and regional scales. *Proceedings of the National Academy of Science of the United States of America*, **110**, 9601–9606.

Tesch, F.W. & White, R.J. (2008) *The Eel*. John Wiley & Sons, Oxford, UK.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P. *et al.* (2010) Global threats to human water security and river biodiversity. *Nature*, **467**, 555–561.

Walther, B.D. & Limburg, K.E. (2012) The use of otolith chemistry to characterize diadromous migrations. *Journal of Fish Biology*, **81**, 796–825.

Wilcove, D.S. & Wikelski, M. (2008) Going, going, gone: is animal migration disappearing? *PLoS Biology*, **6**, e188.

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S. *et al.* (2016) Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, **351**, 128–129.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed methods.

Table S1. Detailed water ^{87}Sr/^{86}Sr data.

Table S2. Laser ablation and multicollector settings.

Table S3. Otolith transect data. Table of raw otolith transect data for each sample analysed (XLSX).

Fig. S1. Relationship between the radius of the otolith transverse section and the standard length of *B. rousseauxii* from the Madeira basin.

Fig. S2. Percentage of mature individuals as a function of standard body length in female *B. rousseauxii* from the Madeira River basin.