


Unmasking continental natal homing in goliath catfish from the upper Amazon

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Abstract

1. Amazonian goliath catfishes are widespread in the Amazon Basin. Recently, otolith $^{87}\text{Sr}:$ ^{86}Sr analyses using laser ablation–multi-collector–inductively coupled plasma mass spectrometry (LA-MC-ICPMS) revealed a >8,000 km trans-Amazonian natal homing in *Brachyplatystoma rousseauxii* among fish caught and hatched in the largest Amazon River tributary, the upper Madeira basin. Although also suspected for fish in the upper Amazon, homing could not be demonstrated owing to less distinct environmental $^{87}\text{Sr}:$ ^{86}Sr gradients along the Amazon mainstem. Using scanning X-ray fluorescence microscopy (SXFM), a separate study provided evidence that Se:Ca and Sr:Ca are useful markers for identifying migration into Andean headwaters and the estuarine environment.
2. We analysed otoliths of known $^{87}\text{Sr}:$ ^{86}Sr profiles using SXFM mapping to test if Sr:Ca and Se:Ca patterns could demonstrate natal homing for three fish caught in the upper Amazon, using as reference two individuals that were natal homers and two forced residents (hatched after the construction of hydroelectric dams on the Madeira River) from the upper Madeira River.

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.
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.
5. By combining the results of $^{87}\text{Sr}:^{86}\text{Sr}$ analyses (LA-MC-ICPMS) and Sr:Ca and Se:Ca mappings (SXFEM) that are completely independent of one another, 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 previous literature hypothesised, with the existence of partial migration, even in absence of physical barriers. Quantifying the relative importance of these different life-history strategies will have important implications for fisheries management. Our results also lay the groundwork 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.

KEYWORDS

Brachyplatystoma rousseauxii, dam impacts, microchemistry, otolith

1 | INTRODUCTION

Natal homing or natal philopatry 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 fishes (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). Homing among diadromous fishes is increasingly important to understand given the population declines that have been caused in rivers of Europe and North America, which have been fragmented largely by construction of dams (Limburg & Waldman, 2009). River fragmentation from damming is now widespread and increasing in tropical rivers (Winemiller et al., 2016), posing clear problems for fishes.

A case in point concerns the Amazonian goliath catfishes of the genus *Brachyplatystoma* in the Amazon Basin, undertaking the largest known freshwater migrations between breeding areas in the Andean piedmont of Bolivia, Colombia, Ecuador, and Peru, and their nurseries in the lower Amazon and estuary in Brazil (Barthem & Goulding, 1997; Duponchelle et al., 2016; Barthem et al., 2017). As migrations of goliath catfishes can span over several international

boundaries, addressing fisheries management and conservation challenges requires understanding their homing behaviour.

As apex consumers performing large-scale migrations, goliath catfishes have key ecological functions in the Amazon basin (Barthem & Goulding, 1997; Angelini, Fabr e, & Silva 2006). They also rank among the most economically important exploited fishes, supporting annual landings above 40,000 tons/year (MPA, 2013; Batista, Alonso, Ladle &, Fabr e 2018), leading to documented or suspected overexploitation in some species (Petrere et al., 2004; Alonso & Pirker, 2005; Garc a-Vasquez et al., 2009; Agudelo et al., 2013). The sustainability of these populations is threatened by current and planned hydropower development projects in the Amazon Basin, with >100 dams being planned for future construction (Finer & Jenkins, 2012; Castello et al., 2013; Duponchelle et al., 2016; Lees, Peres, Fearnside, Schneider, & Zuanon 2016; Anderson et al., 2018).

Knowledge of fish migratory processes quickly improved in recent years with advances in microchemistry of otoliths, the calcareous *ear-stones* in the hearing/balance system of teleost fishes (Campana, 2005; Elsdon et al., 2008; Secor, 2010; Walther & Limburg, 2012; Walther et al., 2017). Among the available chemical markers, Sr:Ca and Ba:Ca have proved to be indicators of movements between marine and freshwater environments (Gillanders, 2005; Lord, Tabouret, Claverie, P echeyran, & Keith 2011; Webb, Woodcock & Gillanders, 2012). Despite these methodological advances, studies of migratory behaviour in potamodromous species, which complete

their entire life cycle within fluvial fresh waters, are less documented (Northcote, 1997; Saiget, Sloat, & Reeves 2007; Sammons, 2015; Tyus, 1990; Lucas & Baras, 2001). This may reflect the difficulty in differentiating freshwater environments with the chemical elements widely used in studies of 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, represent accurate habitat signatures in freshwaters (Kennedy, Folt, Blum, & Chamberlain 1997; Kennedy, Blum, Folt, & Nislow 2000; Barnett-Johnson, Pearson, Ramos, Grimes, & MacFarlane 2008). Recently, the use of $^{87}\text{Sr}:^{86}\text{Sr}$ has proved effective in determining migratory

patterns of freshwater fishes in complex and extensive river systems, such as the Amazon Basin (Pouilly, Point, Sondag, Henry, & Santos 2014; Garcez, Humston, Harbor, & Freitas 2015; Souza, Humston, & Freitas 2016), including in goliath catfishes (Hegg, Giarrizzo, & Kennedy 2015; Duponchelle et al., 2016). Otolith $^{87}\text{Sr}:^{86}\text{Sr}$ analyses using laser ablation–multi-collector–inductively coupled plasma mass spectrometry (LA-MC-ICPMS) have confirmed a >8,000-km migration and revealed natal homing in populations of *B. rousseauxii* from the largest white-water Amazon River tributary—the Madeira River (Duponchelle et al., 2016; Figure 1). Although also suspected for fish caught and hatched in the upper Amazon, this migratory pattern has not been demonstrated owing to less distinct environmental

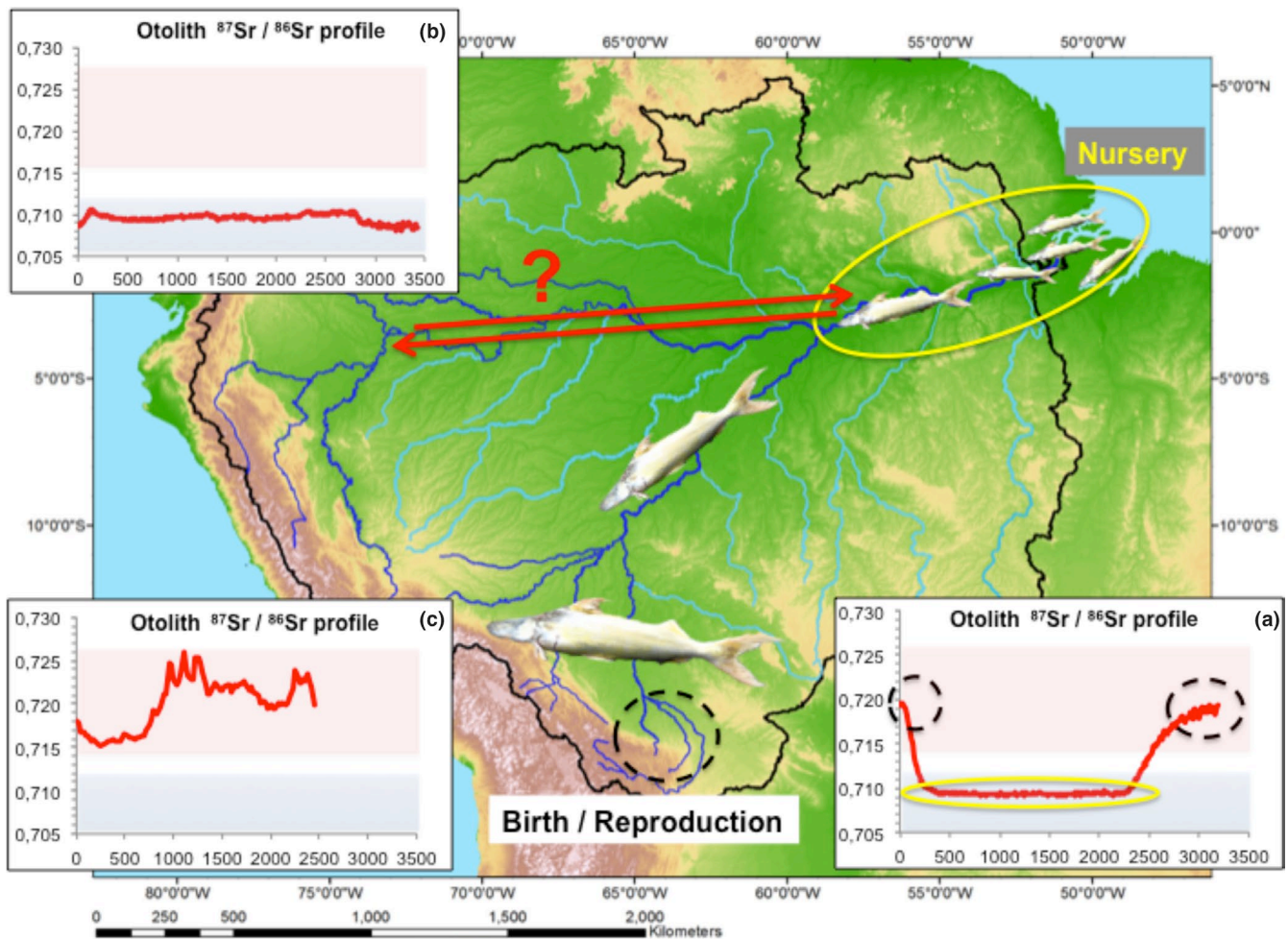


FIGURE 1 Illustration of the migratory patterns of *Brachyplatystoma rousseauxii* in the Amazon basin, as revealed by otoliths $^{87}\text{Sr}:^{86}\text{Sr}$ profiles, in red on the graphs (based on Duponchelle et al., 2016, and Hauser, 2018). The light blue and light pink rectangles correspond to the range of $^{87}\text{Sr}:^{86}\text{Sr}$ values in waters of the Amazon (0.705–0.712) and Madeira (0.714–0.726), respectively. (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 (c. 0.721), characteristic of the upper Madeira waters, quickly drops to a lower value typical of the lower Amazon River (c. 0.710), when the larvae are flushed down to the lower Amazon by the current at a mean size of c. 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 $^{87}\text{Sr}:^{86}\text{Sr}$ 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 $^{87}\text{Sr}:^{86}\text{Sr}$ 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 $^{87}\text{Sr}:^{86}\text{Sr}$ profile of a fish hatched and caught in the upper Madeira after completion of the dams (= forced residents); unlike the pattern observed before the dams (see a), the isotopic values remain within the range of Madeira water vales throughout the fish's life (Hauser, 2018)

$^{87}\text{Sr}:$ ^{86}Sr gradients along the Amazon mainstem (Duponchelle et al., 2016).

Using a different, complementary technique of scanning X-ray fluorescence microscopy (SXF) to produce 2-D element:Ca maps, Hermann, Stewart, Limburg, & Castello (2016) provided further insights into the complex life cycle of *Brachyplatystoma* species. These authors showed that *Brachyplatystoma* use of the estuary as a nursery, with elevated Sr to calcium ratio (Sr:Ca) for incursions into the estuarine environment and elevated selenium to calcium ratio (Se:Ca) as a useful marker for identifying migration into or out of Andean headwaters. We therefore test here the complementarity of both approaches ($^{87}\text{Sr}:$ ^{86}Sr by LA-MC-ICPMS and Se:Ca, Sr:Ca by SXFM) to

investigate if the natal homing behaviour observed for *B. rousseauxii* in the Madeira also exists along the Amazon mainstem, which would enhance our knowledge of the complex ecology of this species. Such knowledge would have direct application for decision-making processes, as more hydroelectric dams are built in the Amazon basin.

2 | METHODS

Our approach was to use SXFM (Se:Ca and Sr:Ca mappings) to compare fish from the upper Madeira and upper Amazon that had been previously analysed for $^{87}\text{Sr}:$ ^{86}Sr profiles (Hauser, 2018; Figure 1). We

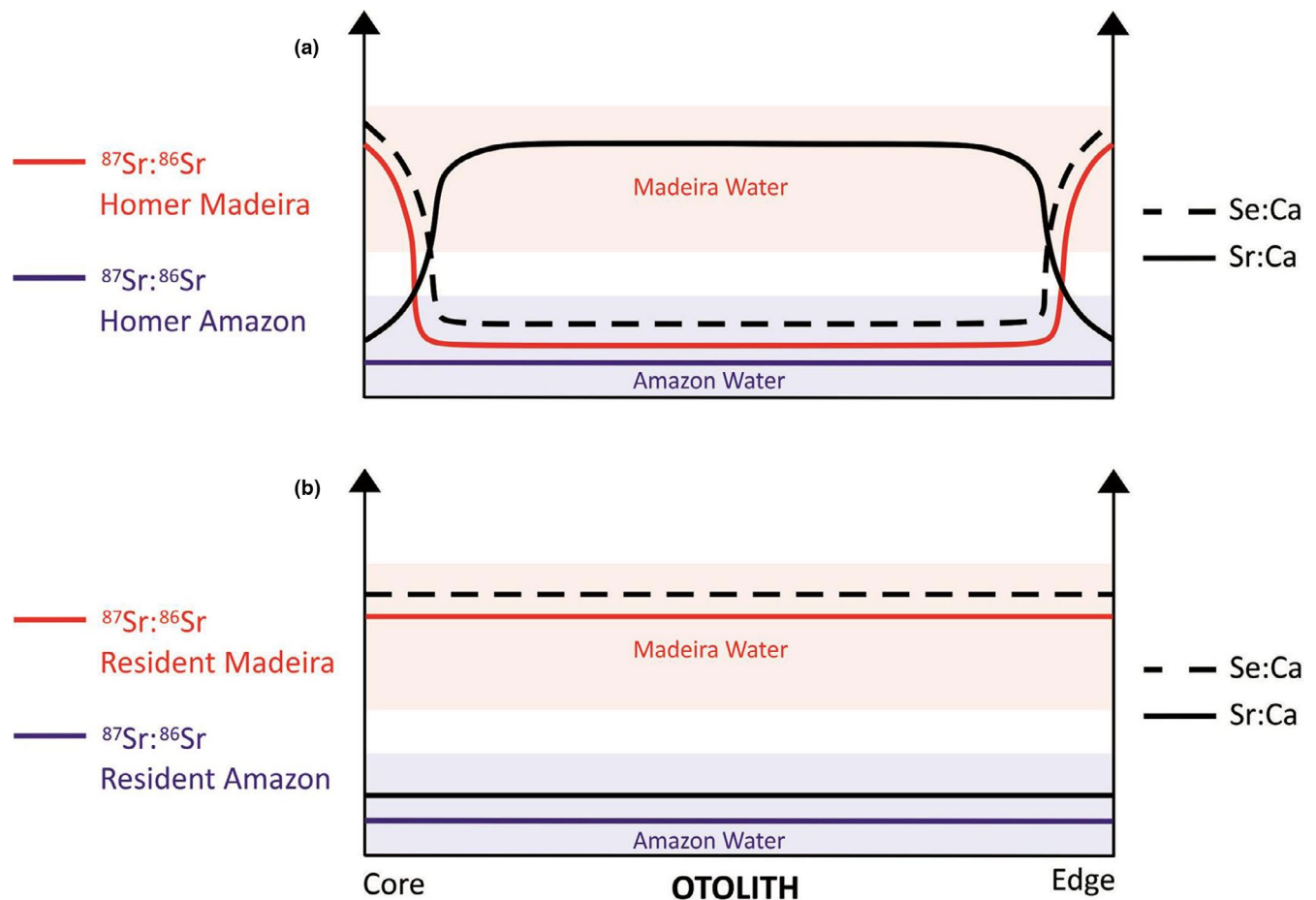


FIGURE 2 (a) Schematic patterns of $^{87}\text{Sr}:$ ^{86}Sr profiles in homers from the upper Madeira and alleged homers from the upper Amazon (based on Duponchelle et al., 2016) and their expected similar Se:Ca and Sr:Ca mapping patterns (based on Herman, Stewart, Limburg & Castello, 2016). Here, we used the classification of Duponchelle et al. (2016) for distinguishing the $^{87}\text{Sr}:$ ^{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 $^{87}\text{Sr}:$ ^{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. 1966; 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 $^{87}\text{Sr}:$ ^{86}Sr profile remains flat. (b) Schematic patterns of $^{87}\text{Sr}:$ ^{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

selected: (1) two known natal homers from the upper Madeira (fish hatched in the upper Madeira and caught in the Mamoré River—BR 56—and in the Béni River—CE 20); (2) two forced residents from the upper Madeira (fish hatched and caught in the upper Madeira after Santo Antônio and Jirau dams' completion, and therefore performed their complete life cycle in the upper Madeira, BR 224 and BR 234); and (3) three fish caught in the upper Amazon around Iquitos in Peru (BR 004, BR 008 in the Ucayali River and BR 130 in the Marañon River) for which precise movement patterns could not be appraised using Sr isotopes alone. We analysed the same otoliths using SXFM mapping. Based on both Duponchelle et al. (2016) and Hermann et al. (2016), we tested the hypotheses: (1) that fish from the upper Amazon would display similar Se:Ca and Sr:Ca mappings to those of proven homers from the upper Madeira, demonstrating homing also in the upper Amazon; and (2) that forced residents from the upper Madeira would display different patterns, following the schematic in Figure 2.

The analyses were based on completely different physical principles. Strontium isotopic ratio analysis quantifies small differences in isotopic mass, whereas 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, Huang, & Bilderback 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.

Here, we used the classification of Duponchelle et al. (2016) and Hauser (2018) for distinguishing the $^{87}\text{Sr}:^{86}\text{Sr}$ signatures of the Amazon (0.705–0.712) and Madeira (0.714–0.726) basins. For each specimen, standard length (SL) was measured (nearest cm) and otoliths (lapilli) were extracted, rinsed in clear water, dried, and stored for later examination (Table 1).

2.1 | 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). Photos of the prepared otoliths before microchemical analyses, as well as their respective growth marks, are presented in supporting information (Figure S1). Analyses using LA-MC-ICPMS ($^{87}\text{Sr}:^{86}\text{Sr}$ profiles) were conducted at the Laboratoire de Chimie Analytique Bio-inorganique et Environnement in Pau and at the Laboratoire Cycles Géo-chimiques et Ressources of IFREMER in Brest (for details see Duponchelle et al., 2016; Hauser, 2018; Hauser et al., 2019). All samples were re-analysed with SXFM at the F3 Beamline Station at the Cornell High Energy Synchrotron Source (CHESS), Cornell University, Ithaca, NY, USA, following methods described in Hermann et al. (2016). Sample sections were fixed to cardboard slide frames with tape and secured with clips prior to 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 onto a 30–40- μm spot on the sample with a photon flux of approximately 4×10^{10} counts/s (Limburg et al., 2007). 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. Dwell times of 0.33–0.45 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 made of crushed otoliths pressed into a pellet (Limburg et al., 2011). Relative elemental abundances are reported in ratio to Ca abundance.

For an easier visualisation of the SXFM data presented on 2D maps, we also produced Sr:Ca and Se:Ca profiles that could be directly compared to respective $^{87}\text{Sr}:^{86}\text{Sr}$ profiles. Ideally, the profiles should have been extracted parallel to the transects used for $^{87}\text{Sr}:^{86}\text{Sr}$ profiles, approximately in the centre of the otolith. However, Se:Ca concentrations, which were relatively uniformly distributed along the lateral edges of the otoliths, were much lower or null in the centre edge of most otoliths. We therefore ran transects from the core to the outer lateral edge, perpendicular to the major

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 (see Figure S1), and migratory behaviour determined by $^{87}\text{Sr}:^{86}\text{Sr}$ analyses

Fish	Basin	River	Country	Dams	Date	SL (cm)	Sex	Growth rings	Age (years)	Behaviour
BR 56	Upper Madeira	Mamoré	Bolivia	Before	20050318	98	M	14	7	Homer
CE 20	Upper Madeira	Beni	Bolivia	Before	20070215	103	F	7	3.5	Homer
BR 224	Upper Madeira	Madre de Dios	Peru	After	20150401	92	M	6	3	Resident
BR 234	Upper Madeira	Madre de Dios	Peru	After	20150701	73		4	2	Resident
BR 004	Upper Amazon	Ucayali	Peru	After	20140923	94		4	2	?
BR 008	Upper Amazon	Ucayali	Peru	After	20160127	92		4	2	?
BR 130	Upper Amazon	Marañon	Peru	After	20150426	116	F	13	6.5	?

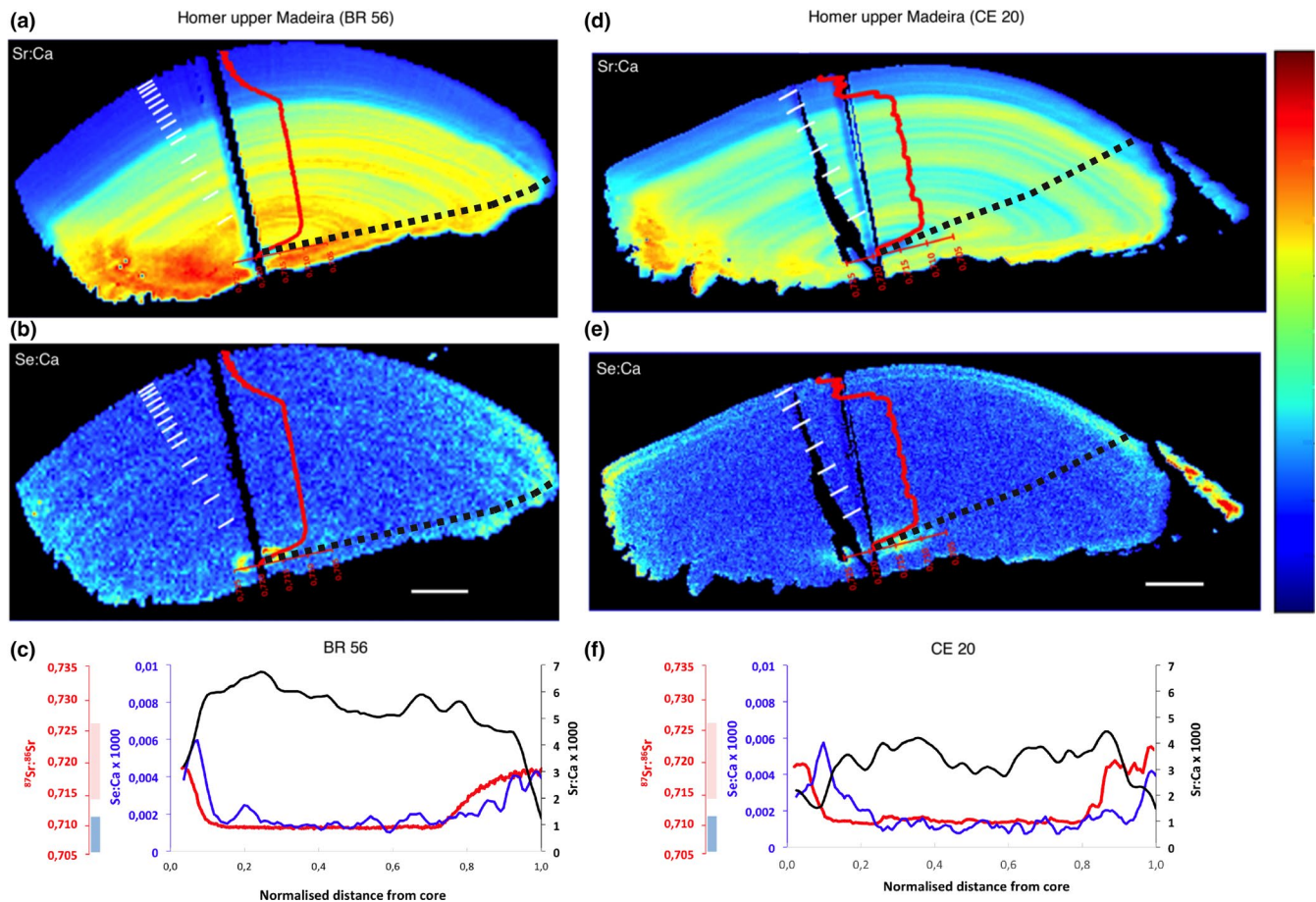


FIGURE 3 Otoliths and corresponding chemical profiles of two *Brachyplatystoma rousseauxii* individuals (BR 56 and CE 20) performing regional natal homing in the upper Madeira River (hatched and caught before the construction of dams). (a, d) Sr:Ca maps. (b, e) Se:Ca maps. On each otolith map, the vertical black band in the centre of the otolith corresponds to the raster from which the $^{87}\text{Sr}:^{86}\text{Sr}$ profile (red) was extracted. 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. (c, f) Sr:Ca (black line) and Se:Ca (blue line) profiles extracted from a core to lateral edge transect (dashed black lines on otolith maps) and $^{87}\text{Sr}:^{86}\text{Sr}$ profiles (red). The light blue and light pink rectangles on the red Y-axis correspond to the range of $^{87}\text{Sr}:^{86}\text{Sr}$ values in waters of the Amazon (0.705–0.712) and Madeira (0.714–0.726), respectively

longitudinal growth axis (represented by dashed black lines in Figures 3–5) for both Sr:Ca and Se:Ca profiles. In the case of individual CE 20 (Figure 3 d,e) we moved the outer part of the transect because the longest edge was broken. In all cases, we used ArcMap 10.7's Stack Profile function to extract data simultaneously from both the Se:Ca and Sr:Ca maps. We then used a 5-point moving-average smoothing function to produce the final profiles.

3 | RESULTS

3.1 | 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 (Figure 3). As indicated by their $^{87}\text{Sr}:^{86}\text{Sr}$ profiles, these individuals were hatched in the upper Madeira, close to the Andes, and had travelled down to the lower Amazon at approximately 33 and

40 days after hatching for BR 56 and CE 20, respectively. These individuals returned to the upper Madeira close to the Andean region at approximately ages 3.5 (BR 56) and 2.5 (CE 20) years (Figure 3). Both had high ratios of Se:Ca around the core, then very low until the end of life when Se:Ca rose again (Figure 3b,c and e,f).

Also, there was a clear, inverse relationship between $^{87}\text{Sr}:^{86}\text{Sr}$ profiles and bulk Sr:Ca in these two natal homers from the Madeira: the Sr:Ca ratio was low around the core, increased when the fish left the Madeira waters and entered the Amazon (i.e. when the $^{87}\text{Sr}:^{86}\text{Sr}$ profile dropped) in the first part of their lives, and decreased when they returned to the Madeira (i.e., when the $^{87}\text{Sr}:^{86}\text{Sr}$ profile rose again; Figure 3a,c and d,f). It is worth noting that, in the extracted profiles for BR 56 (Figure 3c), there is a lag between the increasing $^{87}\text{Sr}:^{86}\text{Sr}$ /decreasing Sr:Ca pattern, which usually occurs simultaneously along the transect used for the Sr isotopes (approximately in the otolith centre, Figure 3a); that is, the Sr:Ca profile drops well after $^{87}\text{Sr}:^{86}\text{Sr}$ has started increasing. This is due to the growth pattern of the otolith and the transect selection. BR 56 was the oldest fish and, because otoliths grow more in thickness than in width with age (allometric growth), the

structure of the otolith lateral edge was compressed compared to the centre edge. In addition, we had to use the lateral transect to extract Sr:Ca and Se:Ca profiles because Se:Ca are too low on the centre edge of most otoliths. This artefact, however, was only observed on this older individual (BR 56) and does not concern the other specimens analysed.

3.2 | Known forced 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 aged 3 and 2 years, respectively (Table 1, Figure 4) and were therefore hatched after the completion of the dams in 2011. Both presented $^{87}\text{Sr}:^{86}\text{Sr}$ profiles strikingly different from those of the Madeira natal homers, without a single value below 0.715, indicating that they remained within the upper Madeira above

the dams for their entire lives (= forced residents). The inverse relationship of increasing/decreasing Sr and Se concentrations observed in the upper Madeira natal homers was completely absent in the otoliths of these two forced residents (Figure 4a,c and d,f). Contrary to the natal homers, they had a larger Se band around the core, intermediate Se bands, and low Sr:Ca with little variation throughout the otolith (Figure 4b,c and e,f).

3.3 | Fish from the upper Amazon

Despite relatively flat $^{87}\text{Sr}:^{86}\text{Sr}$ profiles (Figure 5), two of the fish caught in the upper Amazon, BR 130 and BR 004, had similar Sr:Ca and Se:Ca patterns to those of the two homers from the upper Madeira (Figure 3). The same pattern of increasing/ decreasing Sr concentration was also observed, albeit weaker than observed 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,

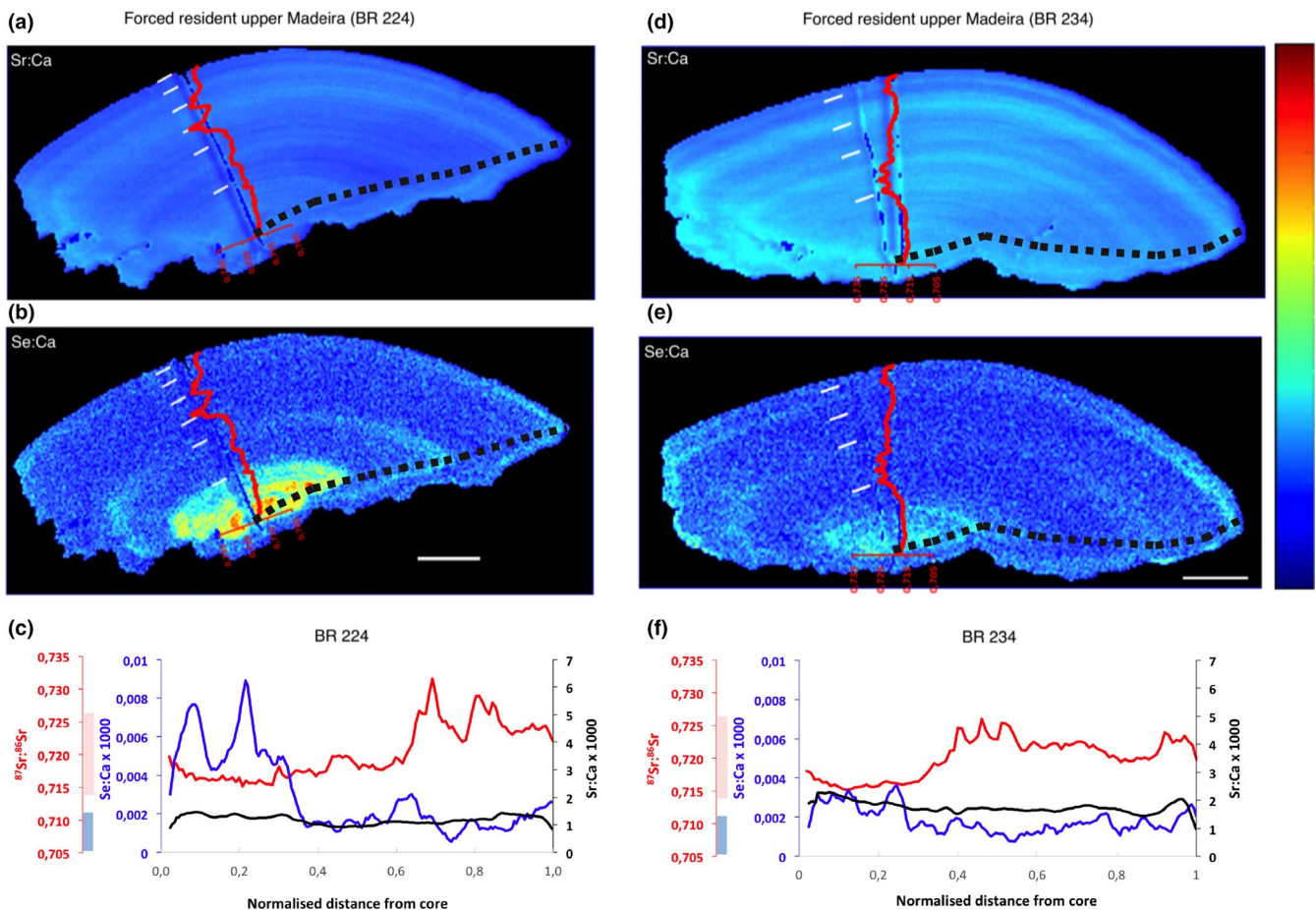


FIGURE 4 Otoliths and corresponding chemical profiles of two *Brachyplatystoma rousseauxii* individuals (BR 224 and BR 234) performing forced-resident behaviour (hatched and caught after the construction of dams) in the upper Madeira (upstream of the dams). (a, d) Sr:Ca maps. (b, e) Se:Ca maps. On each otolith map, the vertical black band in the centre of the otolith corresponds to the raster from which the $^{87}\text{Sr}:^{86}\text{Sr}$ profile (red) was extracted. 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. (c, f) Sr:Ca (black line) and Se:Ca (blue line) profiles extracted from a core to lateral edge transect (dashed black lines on otolith maps) and $^{87}\text{Sr}:^{86}\text{Sr}$ profiles (red). The light blue and light pink rectangles on the red Y-axis correspond to the range of $^{87}\text{Sr}:^{86}\text{Sr}$ values in waters of the Amazon (0.705–0.712) and Madeira (0.714–0.726), respectively

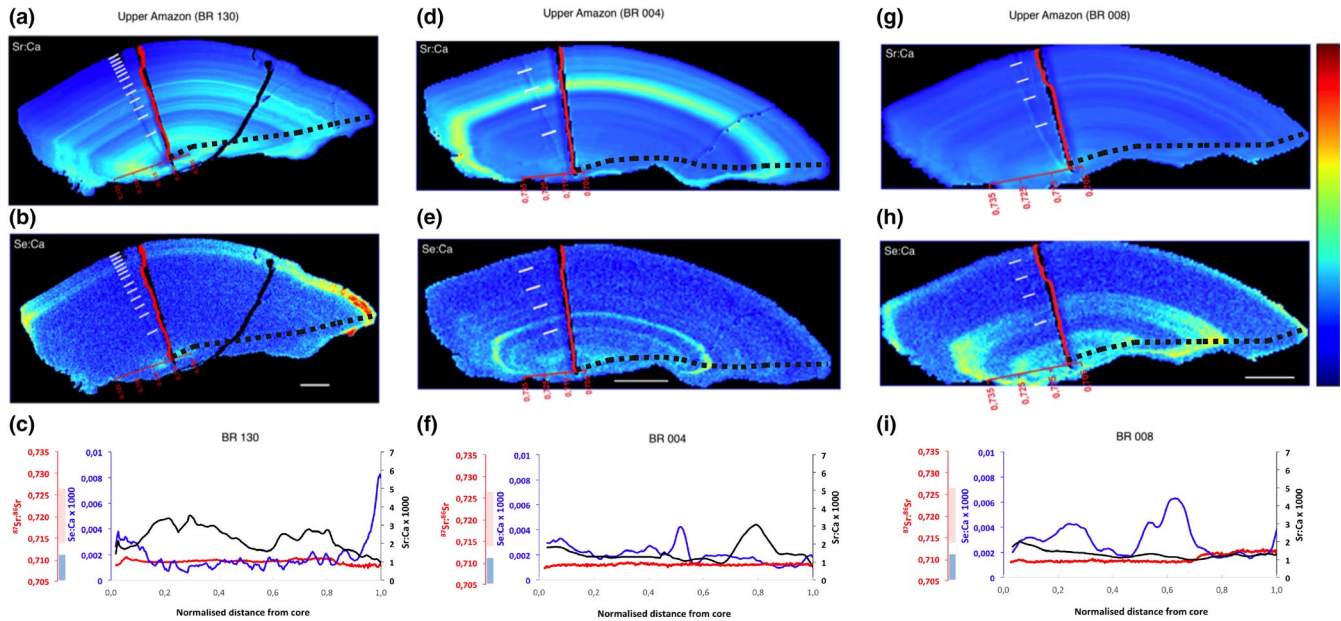


FIGURE 5 Otoliths and corresponding chemical profiles of three *Brachyplatystoma rousseauxii* individuals (BR 130, BR 004 and BR 008) performing alleged natal homing in the upper Amazon River based on $^{87}\text{Sr}:$ ^{86}Sr profiles. (a, d, g) Sr:Ca maps. (b, e, h) Se:Ca maps. On each otolith map, the vertical black band in the centre of the otolith corresponds to the raster from which the $^{87}\text{Sr}:$ ^{86}Sr profile (red) was extracted. 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. (c, f, i) Sr:Ca (black line) and Se:Ca (blue line) profiles extracted from a core to lateral edge transect (dashed black lines on otolith maps) and $^{87}\text{Sr}:$ ^{86}Sr profiles (red). The light blue and light pink rectangles on the red Y-axis correspond to the range of $^{87}\text{Sr}:$ ^{86}Sr values in waters of the Amazon (0.705–0.712) and Madeira (0.714–0.726), respectively

whereas Se:Ca followed an inverse trend (Figure 5a–c). Sr:Ca progressively decreased and reached the lowest values when Se:Ca started to peak again in the last 2 years of life (Figure 5a–c). BR 004, a younger fish (Table 1, Figure 5d), had a slightly different pattern as Sr:Ca remained low until after age 1 year, peaked for a few months and started decreasing again to reach the lowest value close to the otolith edge (Figure 5d,f). By contrast, Se:Ca remained high for over half a year from hatching before strongly decreasing until it started to increase again at the otolith edge (Figure 5e,f).

BR 008, the youngest of the three fish caught in the upper Amazon, presented a completely different pattern (Figure 5g–i), which resembled that of the resident from the upper Madeira (Figure 4), with low Sr:Ca and relatively high Se:Ca throughout the otolith, apart from a decrease in Se:Ca for about 1 year.

4 | DISCUSSION

Our results show that the seemingly dominant natal homing behaviour observed for *B. rousseauxii* in the upper Madeira (Duponchelle et al., 2016) also exists in the upper Amazon. As hypothesised, although the $^{87}\text{Sr}:$ ^{86}Sr profiles of two 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 that both were natal homers from the upper Amazon. They hatched in the upper Amazon and then travelled down to the lower Amazon

estuary reach before returning to the upper Amazon where they were caught. Similar to the natal homers from the upper Madeira, BR 130 also returned at age about 3 years to the upper Amazon, when Se and Sr concentrations increased and decreased, respectively. In contrast, specimen BR 004 delayed its downstream migration to the lower Amazon until it was aged c. 1.5 years and returned to the upper Amazon only about 6 months later. The third fish sampled in the upper Amazon (BR 008), however, did not display such patterns. Instead, it presented Se:Ca and Sr:Ca patterns similar to those of the forced resident from the upper Madeira River (BR 224 and BR 234): with low Sr:Ca throughout the otolith and alternating bands of Se:Ca (with globally relatively high Se:Ca) throughout the otolith, indicating that it had remained in the upper Amazon all its life and was therefore a natural resident.

Our results also emphasise the utility of combining MC-ICPMS and SXFM (Limburg et al., 2007; Hermann et al., 2016) to unravel the migratory patterns of Amazonian fish species. Our results also 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 a barrier to downriver migration.

Apart from extreme cases, not all individuals in a migratory population actually migrate, a phenomenon known as partial migration (Chapman, Brönmark, Nilsson, & Hansson 2011; Chapman et al., 2012). Whether a fish migrates is determined by complex interactions among its genotype, individual condition and environment (Sloat et al., 2014; Kendal et al., 2015), which maximise individual

fitness (Arai, Yang, & Miyazaki 2006). Although resident behaviour was not observed among the 18 *B. rousseauxii* from the upper Madeira analysed in Duponchelle et al. (2016), it is likely that a larger sample size would have revealed this behaviour in some individuals 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 maximises their chances to reach the estuarine nursery area thousands of km downstream (García-Vasquez et al., 2009). By contrast, breeding during the high-water periods would increase this risk and lost juveniles that survive on the floodplain may become residents, as hypothesised by García-Vasquez et al. (2009). Using otolith $^{87}\text{Sr}:$ ^{86}Sr analyses, Hegg, Giarrizzo and Kennedy (2015) also observed one *B. rousseauxii* individual (BR25) with a behaviour similar to what we refer to as resident here: it almost never entered waters with signatures typical of the Amazon mainstem and probably remained most of its life in the Madeira and lower Negro, before being caught in Manaus. This observation prompted the suggestion that not all fish used the estuary as a nursery and that under certain circumstances a rearing phase outside the estuary might improve fitness (Hegg, Giarrizzo and Kennedy, 2015).

Recent evidence regarding the migration patterns of *B. rousseauxii* (Hegg, Giarrizzo and Kennedy, 2015; Duponchelle et al., 2016; Hermann et al., 2016; this study) clearly indicate that its exceptional life history, involving the largest known migration in freshwaters (>11,000 km, Barthem et al. 2017), is more diverse than previously thought. It will be critical to further characterise the extent of this diversity, which suggests a certain amount of plasticity and adaptability, in order to better anticipate the potential consequences of current and future perturbations, particularly overfishing and hydropower development.

The existence of variable life histories may indeed increase resilience of species, allowing them to withstand environmental changes (Hegg, Giarrizzo and Kennedy, 2015; Waldman, Wilson, Mather, & Snyder 2016). The literature on anadromous fishes, and salmonids in particular, have shown that diversity in life-history strategies and the existence of various source populations provide further protection against decline or extinction in the face of environmental disturbance (Hilborn, Quin, Schindler and Rogers, 2003; Copeland and Venditti, 2009; Beechie, Buhle, Ruckelshaus, Fullerton and Holsinger, 2006, see also Hegg, Giarrizzo and Kennedy, 2015 for further discussion). Data on population genetics (Carvajal-Vallejos et al., 2014), life-history traits (García-Vásquez et al., 2009; Hauser et al., 2018), and otolith microchemistry (Duponchelle et al., 2016; Hauser, 2018; current study) suggest the existence two main source populations of *B. rousseauxii* in the Amazon basin: one in the upper Amazon and the other in the other in the upper Madeira. This situation may help provide resilient fisheries over time, provided no

further barriers, such as hydroelectric impoundments, are built on the migration routes of these goliath catfish.

Individuals may also become residents when downstream migration is disrupted by some barrier, as in the case of the two hydroelectric dams built 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) had remained within the upper Madeira all their lives, as demonstrated by both their $^{87}\text{Sr}:$ ^{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 further investigated in future studies based on a larger number of fish samples. It can nevertheless be hypothesised to be a consequence of the hydroelectric dams and perhaps it now has become the more frequent pattern. This hypothesis, amenable to testing with the techniques 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 to be ineffective for accommodating the upstream run of returning pre-adult goliath catfishes, including *B. rousseauxii* (Fearnside, 2014). Currently in the upper Madeira, the probability of observing *B. rousseauxii* that have travelled down to the lower Amazon and back, except for old individuals hatched and returned before the dams, is therefore almost nil.

It will also be important to assess whether the disruption of the seemingly compulsory nursery period in 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 hypothesised 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 and can be due to increased competition, lower productivity, or both (Waples, Zabel, Scheuerell, & Sanderson 2008; Kendal et al., 2015). As smaller individuals have lower fecundity, reduced growth may reduce recruitment (and fitness) of the population, with direct effects on fisheries production. It can therefore be hypothesised that forced residents in the upper Madeira will have slower growth, smaller sizes at age, and reduced fecundity. Taken to the extreme, ineffective fish passage may not only lead to significant changes or losses of certain population components, but will also lull society into the false belief that fishways and hydropower produce *win-win* situations when, in fact, the fish populations suffer (Brown et al., 2013).

The demonstration of a natal homing behaviour 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* in the face of hydropower dams and climate changes. Truncation of habitat available to *B. rousseauxii*

will be very likely to have strong, adverse impacts on the population structure (in terms of growth potential) and abundance due to reduced fecundity, let alone increased vulnerability to local fishers and predators. Given the affirmation of long-distance migration and natal homing, continued dam construction in the Amazon basin will undoubtedly further fragment populations of giant catfishes, with unknown consequences for population health and ecosystem structure and function.

This study, combining the results of LA-MC-ICPMS profiles and SXFM mappings, provides a significant advance in our 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 scenarios in the Amazon and Orinoco basins.

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AUTHOR CONTRIBUTIONS

M.H., F.D., G.T.V., J.F.R., M.P., and C.R.C.D. conceived the ideas; M.H., F.D., T.W.H., K.E.L., and D.J.S. designed methodology; M.H., F.D., A.G.V., C.G.D., and A.M. collected the data; M.H., F.D., T.W.H., K.E.L., C.P., and E.P. performed microchemistry analyses and data workup; M.H. and F.D. wrote the manuscript with co-authors' help. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Source data for the Sr:Ca, Se:Ca, and ^{87}Sr : ^{86}Sr profiles are available in Table S1.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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