


## RESEARCH ARTICLE

# Shedding light on the migratory patterns of the Amazonian goliath catfish, *Brachyplatystoma platynemum*, using otolith $^{87}\text{Sr}/^{86}\text{Sr}$ analyses

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## Abstract

1. In the Amazon, migratory catfishes of the genus *Brachyplatystoma* are apex predators that are important for fisheries and conservation. The life cycle of *Brachyplatystoma platynemum* Boulenger, 1898 is poorly known, although it has been hypothesized to be very similar to that of *Brachyplatystoma rousseauxii* Castelnau, 1855, 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. In total, 94 individuals were sampled close to major breeding areas in the Amazon basin (78 fish from the middle and upper Madeira River and 14 fish from the upper Amazon), and their lifetime movements were assessed by measuring variations in  $^{87}\text{Sr}/^{86}\text{Sr}$  along transverse sections of their otoliths (ear stones), using laser ablation multi-collector 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 both migration and access to breeding grounds, ultimately affecting the recruitment and population dynamics of these apex predators.
5. The conservation of *B. platynemum* is crucial for the stability of the Amazonian aquatic food webs. This requires building effective fish passage on the two existing Madeira dams and considering alternative options to the large-scale hydropower development in the Amazon basin.

#### KEYWORDS

catchment, conservation evaluation, fish, fishing, hydroelectric dams, migration, river

## 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 ecosystem dynamics through large-scale flows of energy, nutrients, and processes (Bauer & Hoye, 2014; Flecker, McIntyre, Moore, & Hall, 2010). Understanding the spatial and temporal patterns of fish movements is fundamental for the management and conservation of these important resources (Bauer & Hoye, 2014; Elsdon & Gillanders, 2003; Wilcove & Wikelski, 2008), 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, Reidy, Dynesius, & Revenga, 2005), emphasizes the need for such information, particularly for species such as goliath catfishes in the Amazon basin, which are a key source of protein for millions of people (Barthem & Goulding, 1997, 2007; Batista, Alonso, Ladle, & Fabré, 2018).

The pimelodid genus *Brachyplatystoma* includes the commercially important goliath catfishes. Official statistics from the Brazilian fisheries authorities estimate that three species of this genus (*Brachyplatystoma filamentosum* (Lichtenstein, 1819), *Brachyplatystoma rousseauxii* Castelnau, 1855, and *Brachyplatystoma vaillantii* (Valenciennes, 1840)) alone account for the production of more than 40 000 t year<sup>-1</sup> (MPA, 2013). Until recently, among these goliath catfishes *Brachyplatystoma platynemum* Boulenger, 1898, popularly known as babão in Brazil and as baboso, tabla barba, or mota flemosa in other South American countries, was considered of little commercial interest in the total landings of the Amazon basin (Ochoa et al., 2015). Declines in the catch of the other large *Brachyplatystoma* species, however, have contributed to increased catches of *B. platynemum* in recent years (Petrere, 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 1.0 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 apex predators of the main river channels in the Amazon (Barthem & Goulding, 1997; Petrere et al., 2004). As such, they fulfil particularly important ecological roles for the stability of aquatic food chains. The role of top predators in ecosystem structure, functioning, and resilience is so important that modifying their abundance frequently leads to profound ecosystem alterations through cascading effects (Baum & Worm, 2009; Estes et al., 2011; Myers, Baum, Shepherd, Powers, & Peterson, 2007; Pace, Cole, Carpenter, & Kitchell, 1999). Goliath catfishes are particularly important for conservation strategies, and have therefore been suggested as 'umbrella species' (Agostinho, Thomaz, & Gomes, 2005).

Yet, apart from information on population dynamics (Sant'Anna, Doria, & Freitas, 2014), very little is known about the ecology and migration patterns of *B. platynemum*. It has been hypothesized to perform the same Amazon basin-wide migration as *B. rousseauxii* (Barthem & Goulding, 2007). The life cycle of *B. rousseauxii* involves the largest known migration in fresh waters, with a round trip of more than 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 et al., 2017; Barthem & Goulding, 1997; Duponchelle et al., 2016; Hermann, Stewart, Limburg, & Castello, 2016). However, recent basin-wide analysis of larval sizes and distribution of *Brachyplatystoma* species suggested that the migration pattern of *B. platynemum* would be more restricted than that of *B. rousseauxii* (Barthem et al., 2017). This latter hypothesis is consistent with molecular studies that indicate a stronger geographical 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 unlike *B. rousseauxii* their spawning areas might not be sited exclusively in the far western Amazon, nor their nurseries only in the eastern Amazon. A 4-year monitoring of fish reproductive activity in the Brazilian portion of the Madeira (2009–12) yielded no *B. platynemum* with ripe gonads, indicating that their breeding areas are probably located in the upper Madeira (Cella-Ribeiro, Torrente-Vilara, Lima-Filho, & Doria, 2016), within Bolivia and Peru. The available evidence regarding the

Amazon main stem also indicates that the reproduction of *B. platynemum* occurs in the upper Amazon, in the whitewater 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 present hydroelectric development in the Amazon basin is likely to have several critical impacts on the Amazonian ecosystem and its exceptional biodiversity (Agostinho, Pelicice, & Gomes, 2008; Anderson et al., 2018; Castello et al., 2013; Castello & Macedo, 2016; Finer & Jenkins, 2012; Forsberg et al., 2017; Latrubesse et al., 2017; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016; Winemiller et al., 2016). One of the major threats to fish, and migratory species in particular, undoubtedly lies in the disruption or interruption of connectivity (Agostinho et al., 2008; Anderson et al., 2018; Barthem et al., 2017; Castello et al., 2013; Duponchelle et al., 2016; Pelicice, Pompeu, & Agostinho, 2015). The recent construction of two run-of-the-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 to understand better the spatial and temporal patterns of goliath catfish movements.

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

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The Amazon basin encompasses  $6.3 \times 10^6$  km<sup>2</sup>, of which approximately  $5 \times 10^6$  km<sup>2</sup> is in Brazil 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 an altitude >6000 m a.s.l.), where the source of the Amazon lies in the Peruvian Andes, to the north by the Guyanese shield uplands (>3000 m a.s.l.), to the south by the Brazilian shield uplands (~1200 m a.s.l.), and to the east by the Atlantic Ocean, where waters channelled through ~7000 rivers into the Amazon main stem drain  $\sim 3 \times 10^6$  t of sediment per day (Fioravanti, 2008).

The Madeira River is the largest tributary of the Amazon basin, with a length of approximately 3250 km. It is subdivided into a lower stretch, with 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 greatest of which are the Guaporé (or Itenez in Bolivia), Mamoré, Madre de Dios, and Béni. The vast inundation area of the upper basin includes many floodplain lakes (Crespo & Van Damme, 2011). The abrupt change in elevation 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 3300 km upstream from the confluence of the Madeira and Amazon rivers (near Itacoatiara), with the steepest and most important falls 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, with the most famous being the Jirau and Teotônio falls (Cella-Ribeiro, Torrente-Vilara, Hungria, & Oliveira, 2013). Recently, however, the construction of two large run-of-the-river hydroelectric dams – Jirau with 50 bulb turbines of 75 MW each (3750 MW total) and Santo Antônio with 50 bulb turbines of 71.6 MW each (3568 MW total) – permanently flooded the Jirau and Teotônio falls in 2011 and 2012, respectively (Figure 1).

The Peruvian Amazon represents more than  $300 \times 10^3$  km<sup>2</sup> 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 subdivided into several sub-basins: the Ucayali, Marañón, 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 tributaries of the Marañón (such as the Pastaza) also have their source in Ecuador. The largest sub-basins of the Peruvian Amazon are the Marañón and the Ucayali, where most *B. platynemum* were sampled. With respective lengths of >1600 and >1500 km, the Marañón and the Ucayali both contribute significant flows that originate in the Andes or in the 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.



**FIGURE 1** Map of the reference water  $^{87}\text{Sr}/^{86}\text{Sr}$  values in the Amazon basin (Table S1). Yellow squares refer to some of the cities mentioned in the text, pink squares refer to fish sampling localities, and black dots refer to water sampling stations used in this study, with the following colour codes: blue for the Western Andean tributaries of the Amazon (WATs) (up to the confluence with the Negro River; 0.705–0.710), the Amazon main stem and floodplain tributaries (from the confluence with the Negro River to the Óbidos), and the 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)

## 2.2 | Water sampling and analysis

In order to complete the database of  $^{87}\text{Sr}/^{86}\text{Sr}$  water sources of the Amazon basin, compiled from (i) SO-HYBAm (Observation Service for the geodynamic, hydrological, and biogeochemical control of erosion/alteration and material transport in the Amazon, Orinoco, and Congo basins, [www.ore-hybam.org](http://www.ore-hybam.org)), (ii) Palmer and Edmond (1992), (iii) Gaillardet, Dupre, Allegre, and Négrel (1997), (iv) Pouilly et al. (2014), and (v) Santos et al. (2015) (for details, see Duponchelle et al., 2016), water samples were collected between October 2014 and February 2017 at 34 sites distributed throughout the main

sub-basin of the upper Madeira (Madre de Dios, Mamore, Beni, and Yata) and the upper Amazon basin (Marañón, Ucayali, and Napo) (Figure 1). Detailed  $^{87}\text{Sr}/^{86}\text{Sr}$  values of these sites are given in Table S1.

Samples of near-surface water from the middle of the river were collected in acid-washed high-density polyethylene (HDPE) containers for geochemical analysis of dissolved solids. These water samples were filtered through 0.47- $\mu\text{m}$  Millipore DURAPORE® filters and stored in acid-washed HDPE bottles. Samples were acidified with concentrated supra-pure  $\text{HNO}_3$ . The analyses of  $^{87}\text{Sr}/^{86}\text{Sr}$  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 1 mL of 2 N 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 Santos et al., 2015).

## 2.3 | Fish sampling

Eighty-three fish (66–103 cm total length, TL) were sampled between April 2009 and June 2015 in the upper Madeira River at three fish-landing sites along the Brazilian portion (Surpresa, Guajará Mirim, and 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 TL) were sampled in the upper Amazon basin in the Ucayali and Marañon rivers, between September 2014 and July 2015 (Figure 1; Table 1). Each specimen was processed at the ichthyology and fishing laboratory (LIP/UNIR) (Porto Velho, Brazil). The total length (TL) was measured (to the nearest cm) and otoliths (lapilli) were extracted, rinsed in clear water, dried, and stored for later examination.

## 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 dorsoventral slice including the otolith core. The section was then ground and polished using polishing papers (1200 and 2400  $\mu\text{m}$ ) and ultrapure 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 LCABIE-IPREM laboratory (Université de Pau et des Pays de l'Adour, Pau, France) and in the PSO-IFREMER laboratory (Pole Spectrometrie Océan, Brest, France). The 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, an in-lab  $^{87}\text{Sr}/^{86}\text{Sr}$  certified otolith powder pellet (NIES22, certified Reference Material produced by the National Institute for Environmental Studies, Tsukuba, Ibaraki Prefecture, Japan) was analysed to check the reliability of  $^{87}\text{Sr}/^{86}\text{Sr}$  measurements (Allègre et al., 2010; Bareille et al., 2005; Yoshinaga, Nakama, Morita, & Edmonds, 2000). In all cases the  $^{87}\text{Sr}/^{86}\text{Sr}$  values measured by fs-LA-MC-ICP-MS (mean  $\pm$  2 SD; LCABIE-IPREM-Pau =  $0.709214 \pm 0.000786$ ; PSO-IFREMER-Brest =  $0.709137 \pm 0.000145$ ) corresponded to certified values.

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

## 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 (0.714–0.726), 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 (WATs) and Amazon main stem (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 of approximately 0.718–0.720.

### 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 completion of the dams (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 ( $\sim 0.714$ – $0.720$ ).

**TABLE 1** Information about individuals of *Brachyplatystoma platynemum* Boulenger, 1898 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 on the Madeira River

Basin	River	Country	Locality	Date	n	Individual codes	Dams	SL (cm) $\pm$ SD
Middle Madeira	Madeira	Brazil	Porto Velho	Dec 09–May 10	3	BP SS 052, 329, and 399	Before	81 $\pm$ 1.4
Upper Madeira	Mamoré	Bolivia/Brazil	Iata	Apr 10–Nov 11	19	BP IATA 003–533	Before	85 $\pm$ 8
Upper Madeira	Mamoré	Bolivia/Brazil	Surpresa	Sep 12–Oct 12	8	BP SUR 376–456	Before	88 $\pm$ 3
Upper Madeira	Madre de Dios	Peru	Puerto Maldonado	Jun 15	20	BP 202–225	Before	89 $\pm$ 10.4
Middle Madeira	Madeira	Brazil	Porto Velho	Jan 12–Oct 12	13	BP SS 20715–20888	After	80 $\pm$ 8
Upper Madeira	Mamoré	Bolivia/Brazil	Guajará-Mirim	Aug 15–Oct 15	26	BP 1833–1861	After	90 $\pm$ 21
Upper Amazon	Marañon	Peru	Marañon	Sep 14–Apr 15	2	BP 105 and BP 135	After	62.4 $\pm$
Upper Amazon	Ucayali	Peru	Pucallpa	Sep 14–Jul 15	12	BP 001–012	After	74.5 $\pm$ 7.64

**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 <sup>-1</sup> )	13	16
Auxiliary gas (L min <sup>-1</sup> )	0.8	0.8
Nebulizer gas (L min <sup>-1</sup> )	24	0.6
Additional gas (L min <sup>-1</sup> )	He = 0.5	0.5
Nebulizer	Glass micro-concentric 200 µL min <sup>-1</sup>	PFA 50 µL min <sup>-1</sup>
Spray chamber	Cyclonic	Dual inlet
Acquisition time	5 s	n × 2s
Gas blank	10s	30s
On-peak zero correction	Yes	Yes
Method validation	NIST-987	NIST-987
Mass discrimination correction model	Exponential	Exponential
Interference correction	<sup>87</sup> Rb, <sup>86</sup> Kr	<sup>87</sup> Rb, <sup>86</sup> Kr
LASER		
System	Lambda 3 Nexeya	213LSX CETAC
Source	UV-257 nm	Nd-YAG UV
Spot size (µm)	50–150	50–150
Ablation speed (µm s <sup>-1</sup> )	5	5
Energy (mJ)	10	4
Frequency (Hz)	2000	20
He flow (L min <sup>-1</sup> )	0.35	0.6
Pre-ablation	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 Spectrométrie Océan)

All fish from the Surpresa (Figure 2a) and the Iata communities (Figure 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 the Madre de Dios (Inambari or Tambopata) sub-basins. Four specimens were hatched in water signatures of >0.720 (Figure 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), in the Mamoré, Yata, or Itenez sub-basins, until the moment of capture (Figure 2a, b). Only a few specimens remained in waters with signatures of <0.720 during the major part of their lives (Figure 2b: BP IATA 005, 014, and 475). Instead of migrating to more radiogenic waters like most other fish, one specimen (BP IATA 527) first migrated to less radiogenic waters (down to 0.713, probably in the Madre de Dios sub-basin), before also moving to radiogenic waters (values of up to 0.727) and then coming back to the Mamoré, where it was caught.

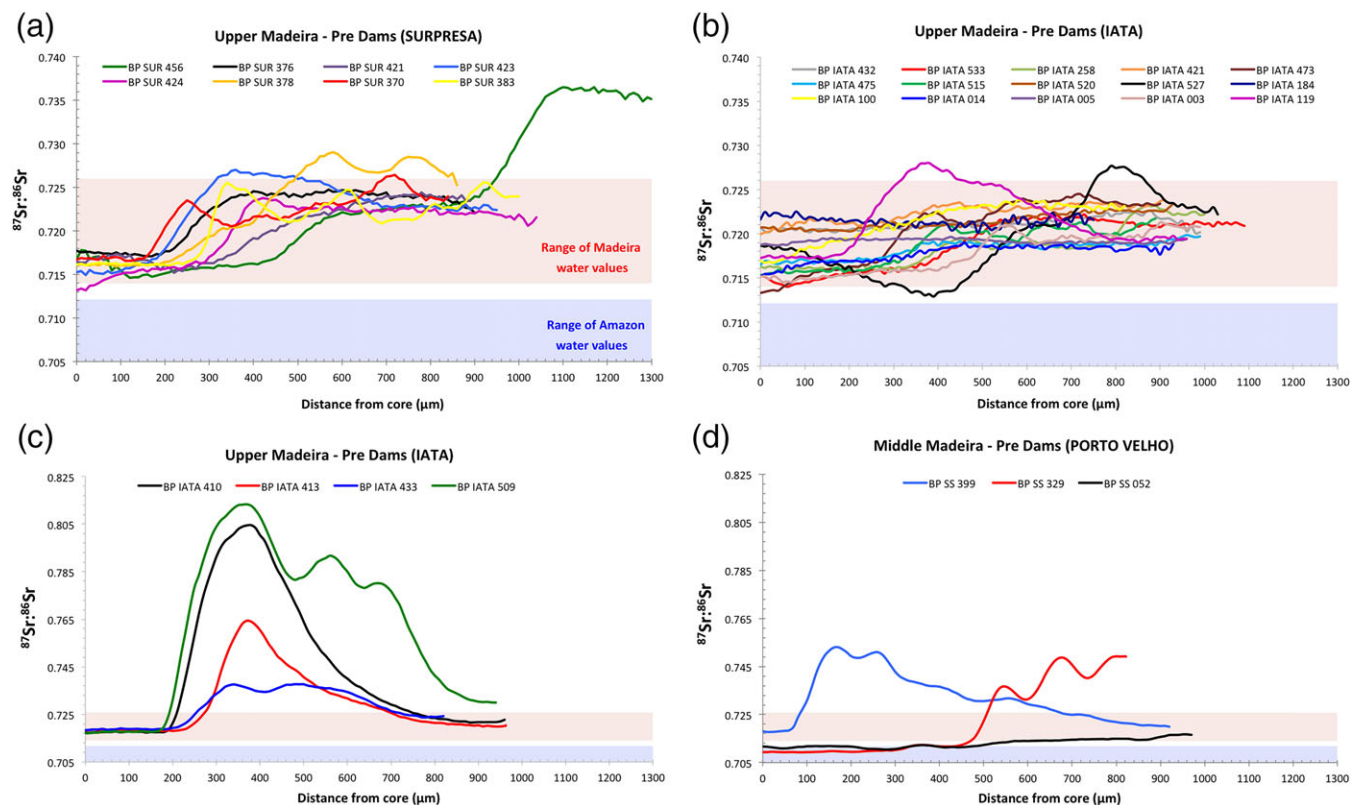
Only two fishes (BP IATA 184 and BP IATA 005) remained in waters with approximately the same isotopic signature from their birth until their capture (Figure 2b). Five specimens (BP IATA 410, 413, 433 and 509) that hatched in the Béni-Madre de Dios system quickly entered water bodies with exceptionally radiogenic waters (up to >0.80 for two of them) (Figure 2c). One of them, BP SUR 456 (Figure 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 (Figure 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 the 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 WATs 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 (Figure 2d). In either case, its final isotopic signature did not correspond to that of the middle Madeira where it was sampled.

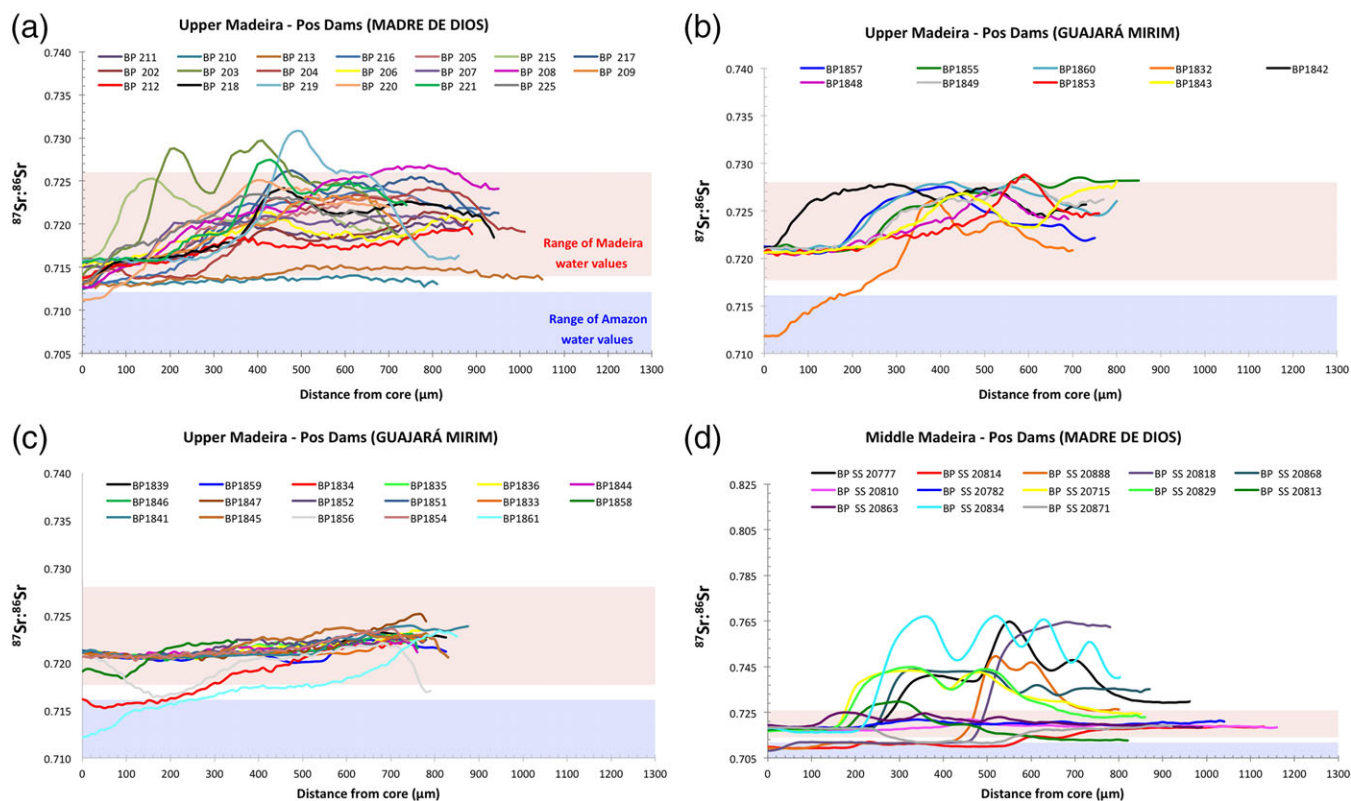
### 3.3 | Fish sampled following dam construction in the Madeira

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 completion of the dams, ever entered the Amazon (Figure 3). Of all the fish caught in the Madre de Dios sub-basin (Figure 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 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 and BP 213) stayed close to their hatching locality (probably the Inambari or Tambopata rivers) for most of their lives (Figure 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 (Figure 3b, c) hatched in the Mamoré (hatching signature >0.720), apart from two specimens (BP 1832, Figure 3b; BP 1861, Figure 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 completion of the dams, with inter-sub-basin migrations between



**FIGURE 2** Laser ablation MC-ICPMS transects of  $^{87}\text{Sr}/^{86}\text{Sr}$  along otolith transverse sections (from the core to the edge) of *Brachyplatystoma platynemum* Boulenger, 1898. Each curve corresponds to one individual caught either in the upper (a, b, c) or middle (d) Madeira River, before the construction of the Madeira dams



**FIGURE 3** Laser ablation MC-ICPMS transects of  $^{87}\text{Sr}/^{86}\text{Sr}$  along otolith transverse sections (from the core to the edge) of *Brachyplatystoma platynemum* Boulenger, 1898. Each curve corresponds to one individual caught either in the upper (a, b, c) or middle (d) Madeira River, after the construction of the Madeira dams

the hatching rivers and more radiogenic waters within the Mamoré, Yata, or Itenez-Guaporé sub-basins. Two specimens (BP 1834 and BP 1858) probably hatched in the Beni or the Inambari-Tambopata (Madre de Dios sub-basin), and progressively travelled to the Mamoré, where they were caught (Figure 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 WATs 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 the Madre de Dios sub-basins. As these fish were caught between 2 and 10 months after the completion of the Santo Antônio dam, they might have migrated downstream before the completion of the dam, or alternatively have survived the reservoir and the turbines. As already observed for specimens sampled in the Madeira before dam 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, and 20829) before they were caught below Porto Velho, whereas others remained for most of their lives in waters with signatures typical of the Madeira.

### 3.4 | Fish sampled in the upper Amazon

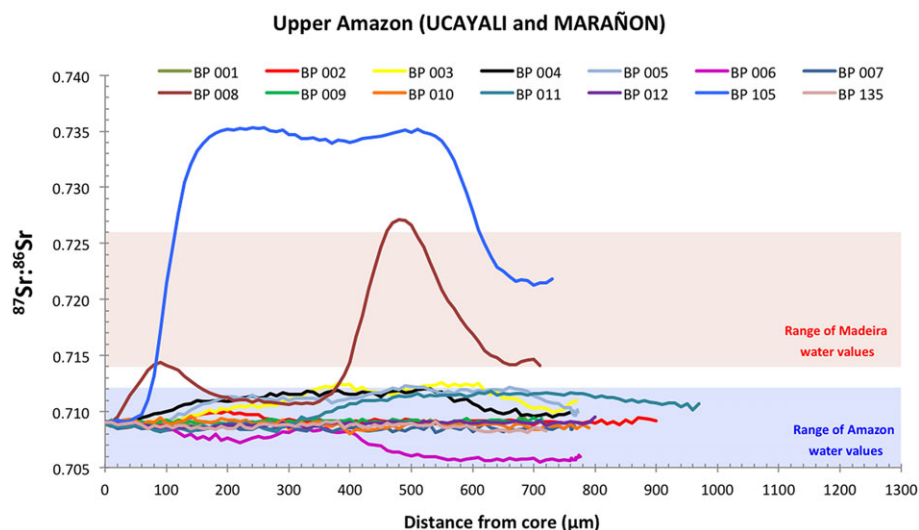
All 14 specimens sampled in the upper Amazon River (12 from the Ucayali and two from the Marañon rivers) hatched in water with signatures of this region (~ 0.709) (Figure 4). Most specimens had flat profiles, seemingly remaining in the same waters, or at least in the main channel of the Amazon and western Andean tributaries, which do not present such contrasts as the Madeira basin, during all of their lives (BP 001, 002, 007, 009, 010, 012, and 135). Two individuals (BP 008 and BP 105) migrated to very radiogenic waters with signatures of >0.725. Some other fish (BP 003, 004, 005, and 011) moved to waters with signatures of up to 0.712–0.713, supposedly in the lower Amazon (or the Madre de Dios in the upper Madeira basin, but the 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, BP 006, spent a considerable part of its life in the Napo River, the only known source of water signatures between 0.705 and 0.706.

## 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 first information on the migratory behaviour of *B. platynemum* at an individual level. Contrary to what was first hypothesized (Barthem & Goulding, 2007), these results demonstrate that the migration patterns of *B. platynemum* clearly differ from those of *B. rousseauxii* (Duponchelle et al., 2016), in that they are not so extensive and do not involve compulsory passage through the lower Amazon estuary area, nor natal homing behaviour. The results emphasize the importance of carrying out species-specific studies on these large migratory species and demonstrate that generalizations drawn from better studied species may prove to be oversimplified and erroneous when 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, in contrast 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 main stem and another in the Madeira River (Ochoa et al., 2015). They are also consistent with the lack of a 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 observed between the Madeira and the Amazon, the strong genetic structure described between these two basins (Ochoa



**FIGURE 4** Laser ablation MC-ICPMS transects of  $^{87}\text{Sr}/^{86}\text{Sr}$  along otolith transverse sections (from the core to the edge) of *Brachyplatystoma platynemum* Boulenger, 1898. Each curve corresponds to one individual caught in the upper Amazon River



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 the fish caught before and after completion of the run-of-the-river dams were observed in the upper Madeira River. Five out of the 27 (18.5%) specimens caught in the upper Madeira before dam completion exhibited surprisingly high otolith  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios ( $>0.735$ , with two otoliths demonstrating signatures  $>0.800$ ), whereas this was not observed in any of the 46 fish caught after dam completion. On the other hand, for fish caught in the middle Madeira (below the dams), such high isotopic values were observed in similar proportions before (two out of three fish, 66.7%) and after (eight out of 13 fish, 61.5%) completion of the dam. A few of these specimens had a final signature higher than that of the locality in which they were caught, suggesting that the sources of highly radiogenic signatures could be very close to the fishing grounds. It is possible that, unlike *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 rivers to which they are connected (Pouilly et al., 2014). This hypothesis may apply to the fish that exhibited signatures of 0.005 to 0.010 above their site of capture, hence up to 0.735 (Pouilly et al., 2014). It cannot explain otolith Sr isotopic values above 0.750 or as high as 0.813, however (Figure 2c). Although  $^{87}\text{Sr}/^{86}\text{Sr}$  water values as high as 0.920 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* Humboldt, 1821 caught in the Negro River system (Garcez et al., 2015; Sousa et al., 2016). The Orinoco and Negro rivers both drain the same granitic shield, and it is likely that the Negro sub-basin could also hold  $^{87}\text{Sr}/^{86}\text{Sr}$  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 were completed exhibited these exceptionally high isotopic values, and that such values were only observed in fish caught in the lower Madeira, below the dams (Figure 3d), tends to support this hypothesis. It fails, however, to explain why some of these fish, after migrating up the Madeira for ~1000 km (to Porto Velho, Figure 2d, 3d) or more to the upper Madeira fishing grounds of the Mamoré (Figure 2c), had not yet acquired the isotopic signature of the waters in which they were caught. Alternatively, many of the tributaries where *Brachyplatystoma* could potentially venture within the Madeira basin have not been sampled, and the possibility that as yet unknown sources of highly radiogenic waters might exist in the tributaries draining the Brazilian granitic shield cannot be ruled out, e.g. the Itenez-Guapore River (Hegg et al., 2015; Santos et al., 2015) or the Yata River. These hypotheses are not mutually exclusive.

*Brachyplatystoma platynemum* is relatively abundant throughout the year in the catches made at 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* spp. (Cañas & Pine, 2011), including *B. platynemum* (Barthem et al., 2017). Yet, surprisingly, except for three fish (BP 220, 1832, and 1861) that may have hatched in this river, no other fish captured in the upper Madeira, before or after dam 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). With regards to 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 long enough to register the Madre de Dios signature. It is also surprising that none of the fish caught near 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 more than 600 km up the Madre de Dios without one of them registering its signature, an alternative explanation is that all of these fish would have remained all their lives within the Madre de Dios sub-basin, in the Tampopata or Inambari, or in the yet un-sampled tributaries, with isotopic signatures between 0.718 and 0.725. As already suggested, they could also spend a significant period of time in adjacent oxbow lakes or lagunas with higher Sr isotopic signatures than the river to which they are connected (Pouilly et al., 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, with some involving longer migrations, than fish hatched in the Madeira, which usually stayed within the Madeira. Indeed, some fish that hatched in the upper Amazon migrated a long way downstream, and either entered the Madeira, where they were caught (Figure 3d, BP SS 20814, 20818, and 20888), or entered highly radiogenic tributaries in the lower Amazon (Figure 4, BP 105 and BP 008). As observed for some specimens caught in the upper Madeira, BP 105 and BP 008 retained the signature of the granitic tributaries into which they migrated at the moment of their capture in the Upper Amazon (in the Marañon and Ucayali, respectively). One explanation might be rapid upstream migrations to the areas of capture, but it seems unlikely that fish could travel more than 2000 km from the closest known highly radiogenic tributary (the Negro River) without registering the Amazon main-stem 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 for a considerable part of its life in waters characteristic of the Napo River (0.705–0.706), including at the moment of its capture, indicating that it probably travelled very recently into the Ucayali, where it was caught. Other fish also migrated downstream into waters with signatures of up to 0.712–0.713, supposedly in the lower Amazon, as such values have only been observed below Santarém-Óbidos, or at the confluence between the Amazon main stem and the 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 swim a long way

(~2000 km) through the more radiogenic Madeira waters, which would show on their isotopic profiles. Some other fish had almost completely flat profiles, suggesting that they stayed within the upper Amazon.

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

These 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 (as an important apex predator) and economically important goliath catfish. Although the two run-of-the-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* (Duponchelle et al., 2016; Hauser, 2018), they could nevertheless prevent, or disrupt, former migrations of *B. platynemum* from the upper Madeira River towards 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 a 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 (Baum & Worm, 2009; Estes et al., 2011; Myers et al., 2007; Pace et al., 1999). Until recently, the fish pass at the Santo Antônio dam was found to be 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 also requires preserving breeding and feeding habitats as well as the migratory corridors that connect these distant habitats (McIntyre et al., 2016). In the Amazon basin, the situation is further complicated by the sheer size of the basin, mainly shared by five countries (Bolivia, Brazil, Colombia, Ecuador, and Peru), with differing environmental, exploitation, and conservation policies (Castello et al., 2013; Castello & Macedo, 2016). Nevertheless, a first step in the conservation of goliath catfishes would be to make modifications to the fish transposition system at the Santo Antônio dam to ensure the effective passage of these species. A second step would be for an effective pass to be built at the upstream dam (Jirau), which is at present not planned

(Cella-Ribeiro et al., 2017). Such measures are likely to be beneficial to the conservation of goliath catfishes, as well as to 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 would be far more complicated if the other hydroelectric impoundments planned in the Amazon basin were to be carried out (Anderson et al., 2018; Castello et al., 2013; Castello & Macedo, 2016; Finer & Jenkins, 2012; Forsberg et al., 2017; Latrubesse et al., 2017; Lees et al., 2016; Winemiller et al., 2016). Many of these projects involve lowland dams that will further alter the connectivity and disrupt goliath catfish migrations. Even more projects are planned in the Andean piedmont, where these species reproduce (Barthem et al., 2017; Barthem & Goulding, 1997; Cañas & Pine, 2011; Córdoba et al., 2000; Córdoba et al., 2013; García-Vasquez et al., 2009); these dams will disrupt 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 affecting 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 this remains to be demonstrated), provided that effective fish passage is ensured; however, the multiplicity of complete barriers or strong filters to both passive and active movements imposed by hydroelectric impoundments between their nursery and breeding grounds will probably 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 recognition by river managers that hydrological connectivity should be a priority in the Amazon basin (but see Castello et al., 2013; Castello & Macedo, 2016). This in turn probably requires reconsidering the real advantages and disadvantages of large-scale hydropower development in the Amazon basin, which hosts the richest biodiversity in the world, and for which cheaper, greener, and more effective solutions exist (Kahn, Freitas, & Petreire, 2014; Stickler et al., 2013).

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## CONFLICT OF INTERESTS

The authors declare that they have no conflicts of interest regarding the publication of this article.

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## SUPPORTING INFORMATION

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