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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 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: *Brachyplatystoma* spp., ^{87}Sr/^{87}Sr ratios, migration, otoliths, hydroelectric dams, Amazon, anthropogenic activities, freshwater fish

Introduction

Inland waters and their biodiversity provide a wealth of goods and services, but are increasingly threatened by anthropogenic activities worldwide (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 Jr *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. 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).

Material 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 tri-frontier 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 in 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).

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; Kennedy *et al.* 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) provide heuristic opportunities for identifying fish geographical 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 Villaroel 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 second^{-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 second^{-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 non-linear 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 if they migrated to WAT in the meanwhile (Fig. 2b, 2e). 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, 2h, 2j). 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 2k. Intermediate runs in more radiogenic GST would produce univocal profiles, similar to those illustrated in Fig. 2f or 2l. 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 (Fig. 3a, Fig. 2b). 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, 2e). 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 2f, 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 Madeira at 3.7 ± 1.6 cm SL (mean ± S.D.) 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, 2h and 2j, 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 3d 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 3d 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 (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 cross 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 data base 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 auto-correlated, 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 (Celia-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). Second, *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 ichtyofauna 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 Jr 2014; Winemiller *et al.* 2016), which hosts the world's richest biodiversity.

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Data accessibility

Source data of fish 87Sr/86Sr profiles are available in Supporting Information Table S3.

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Figure Legends

Figure 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 multi-year 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.

Figure 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).

Figure 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 (Fig. 3a) represents the size at first sexual maturity of *B. rousseauxii* in the Madeira basin (Fig. S2).

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.

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

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

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

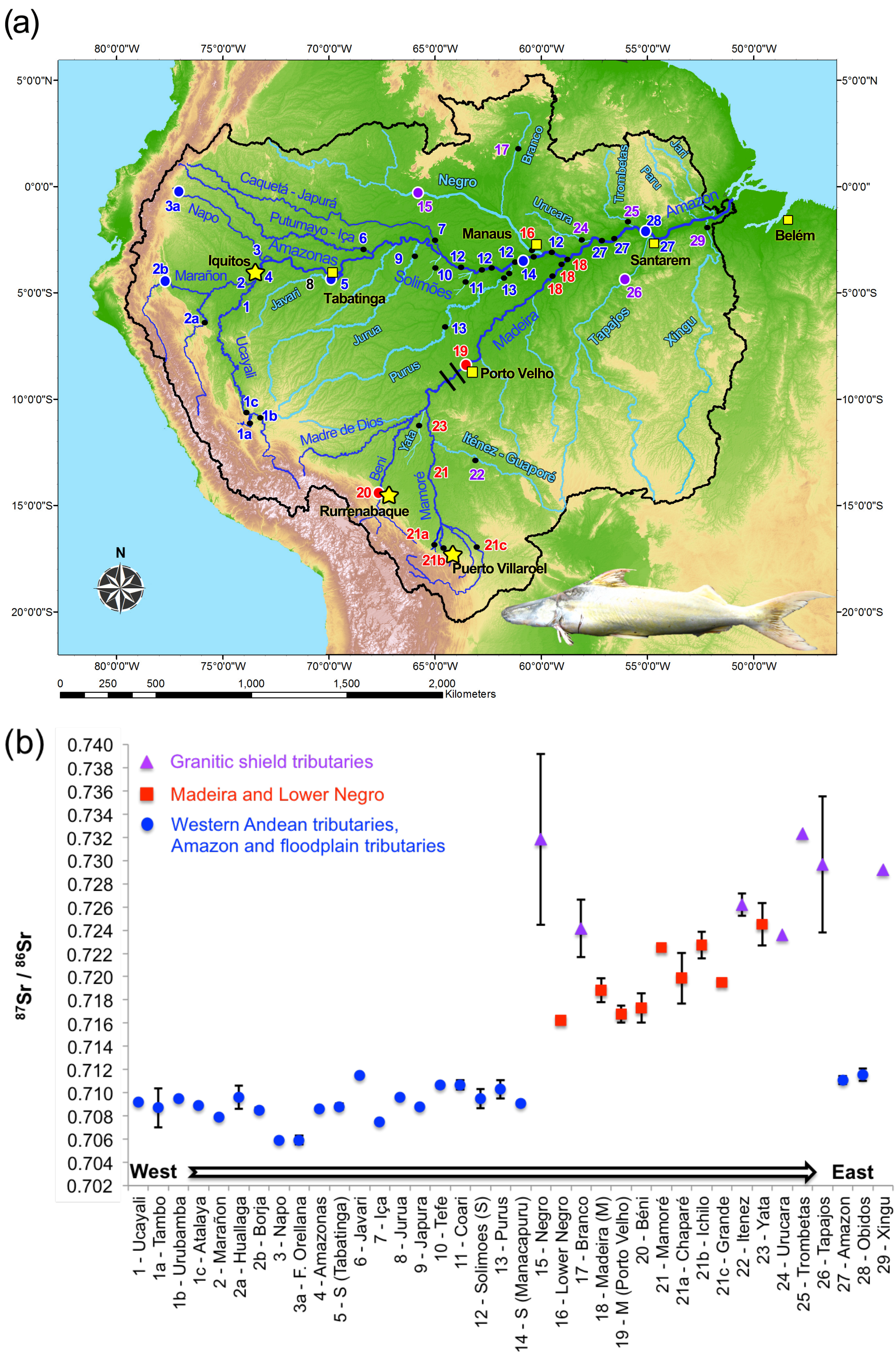

(a)
80°0'0"W
75°0'0"W
70°0'0"W
65°0'0"W
60°0'0"W
55°0'0"W
50°0'0"W
5°0'0"N
0°0'0"
5°0'0"S
10°0'0"S
15°0'0"S
20°0'0"S
Caquetá - Japurá
Napo
Putumayo - Içá
Amazonas
Marañon
Javari
Ucayali
Jurua
Purus
Solimões
Negro
Branco
Urucara
Trombetas
Paru
Jari
Amazon
Madeira
Tapajós
Xingu
Madre de Dios
Beni
Yata
Mamoré
Iténez - Guaporé
Iquitos
Tabatinga
Manaus
Santarem
Belém
Porto Velho
Rurrenabaque
Puerto Villarroel
N
1, 1a, 1b, 1c, 2, 2a, 2b, 3, 3a, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 21a, 21b, 21c, 22, 23, 24, 25, 26, 27, 28, 29
0
250
500
1,000
1,500
2,000
Kilometers
(b)
0.740
0.738
0.736
0.734
0.732
0.730
0.728
0.726
0.724
0.722
0.720
0.718
0.716
0.714
0.712
0.710
0.708
0.706
0.704
0.702
$^{87}Sr/^{86}Sr$
▲ Granitic shield tributaries
■ Madeira and Lower Negro
● Western Andean tributaries, Amazon and floodplain tributaries
West
East
1 - Ucayali
1a - Tambo
1b - Urubamba
1c - Atalaya
2 - Marañon
2a - Huallaga
2b - Borja
3 - Napo
3a - F. Orellana
4 - Amazonas
5 - S (Tabatinga)
6 - Javari
7 - Iça
8 - Jurua
9 - Japura
10 - Tefe
11 - Coari
12 - Solimoes (S)
13 - Purus
14 - S (Manacapuru)
15 - Negro
16 - Lower Negro
17 - Branco
18 - Madeira (M)
19 - M (Porto Velho)
20 - Béni
21 - Mamoré
21a - Chaparé
21b - Ichilo
21c - Grande
22 - Itenez
23 - Yata
24 - Urucara
25 - Trombetas
26 - Tapajos
27 - Amazon
28 - Obidos
29 - Xingu

Fig. 1.

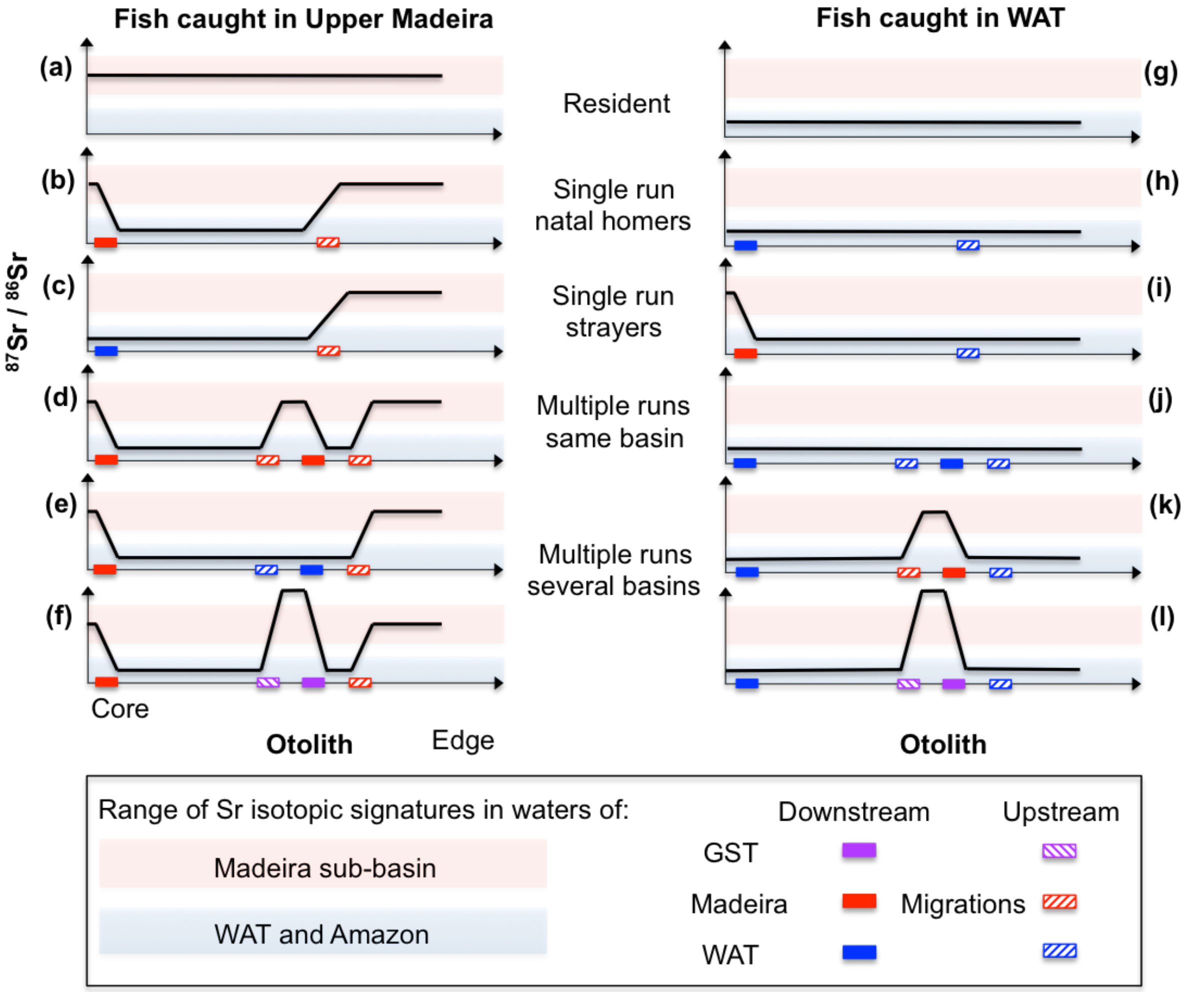
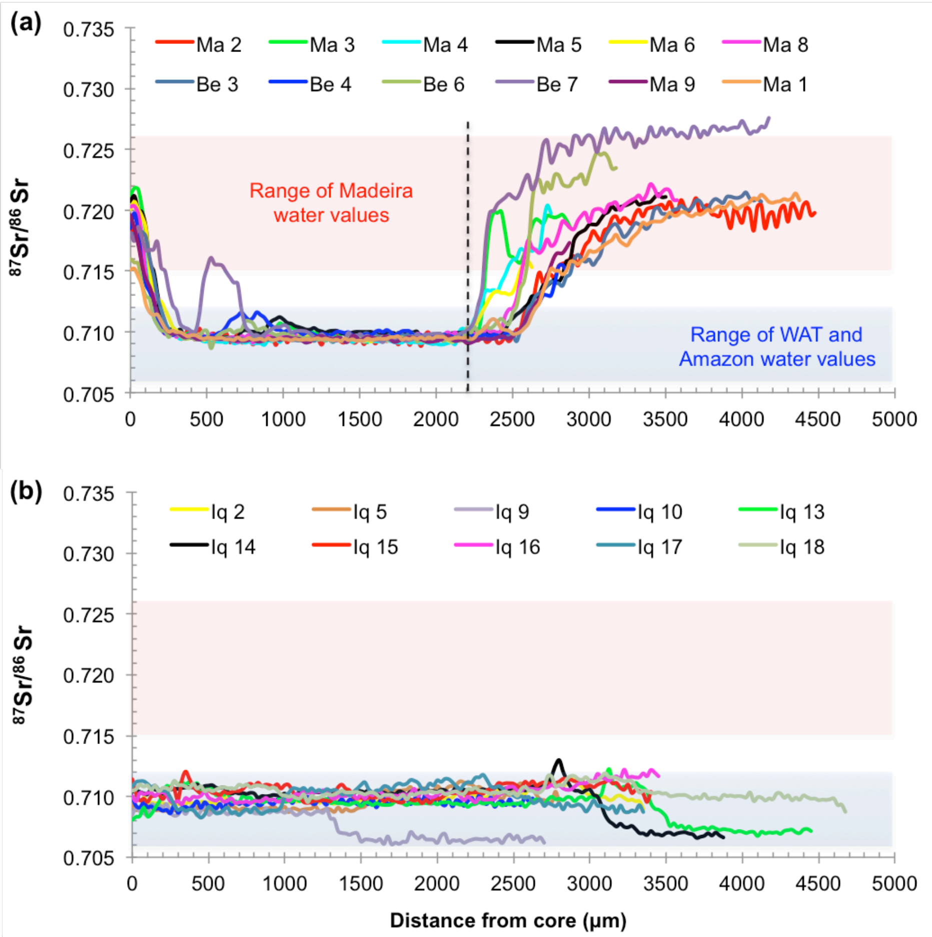

Fish caught in Upper Madeira
Fish caught in WAT
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
$^{87}Sr / ^{86}Sr$
Resident
Single run natal homers
Single run strayers
Multiple runs same basin
Multiple runs several basins
Core
Otolith
Edge
Otolith
Range of Sr isotopic signatures in waters of:
Madeira sub-basin
WAT and Amazon
Downstream
Upstream
GST
Madeira
Migrations
WAT

Fig. 2.


(a)
Ma 2
Ma 3
Ma 4
Ma 5
Ma 6
Ma 8
Be 3
Be 4
Be 6
Be 7
Ma 9
Ma 1
Range of Madeira water values
Range of WAT and Amazon water values
⁸⁷Sr/⁸⁶Sr
0.735
0.730
0.725
0.720
0.715
0.710
0.705
0
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
(b)
Iq 2
Iq 5
Iq 9
Iq 10
Iq 13
Iq 14
Iq 15
Iq 16
Iq 17
Iq 18
⁸⁷Sr/⁸⁶Sr
Distance from core (µm)

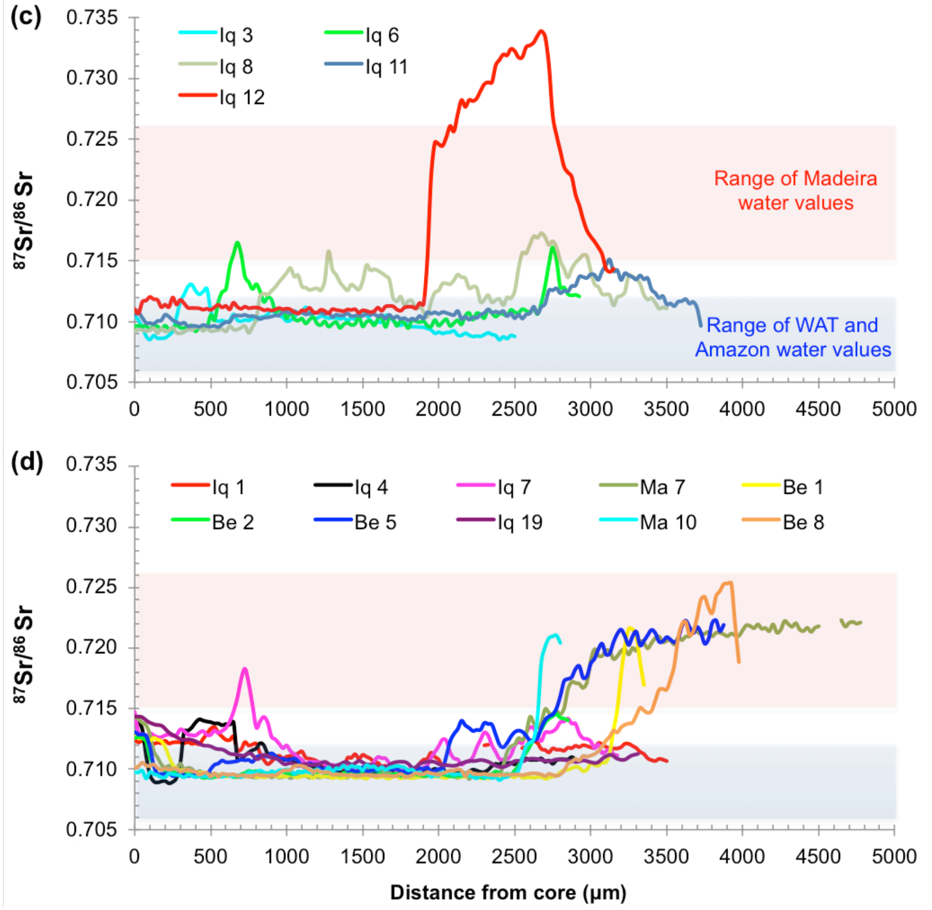

(c)
Iq 3
Iq 6
Iq 8
Iq 11
Iq 12
Range of Madeira water values
Range of WAT and Amazon water values
⁸⁷Sr/⁸⁶Sr
0.735
0.730
0.725
0.720
0.715
0.710
0.705
0
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
(d)
Iq 1
Iq 4
Iq 7
Ma 7
Be 1
Be 2
Be 5
Iq 19
Ma 10
Be 8
⁸⁷Sr/⁸⁶Sr
Distance from core (µm)

Fig. 3

Supporting Information for Duponchelle, F. et al. “Trans-Amazonian natal homing in giant catfish”

Appendix S1: detailed methods

Reconstructing fish migrations using microchemistry of hard body parts. The bones, cartilages, scales and otoliths (ear bones) of a fish grow continuously during its life, forming seasonal growth rings. The screening of these body hard parts for chemical elements or isotopes gives the opportunity to reconstruct habitat conditions during the fish’s life (Campana 1999). As fish grow, natural chemical elements such as strontium, barium, lead or zinc, and their isotopes, readily substitute for calcium in their hard body parts, generally in proportion to their ambient dissolved concentrations or occurrence in food. Their quantitative analysis in fish hard body parts can thus be used as a proxy of the fish’s habitat at a particular age or size. Otoliths are made of relatively inert aragonitic calcium carbonate laid down on an organic matrix. In contrast to other hard body parts, they are not affected by any resorption process and are thus considered as reliable internal data loggers registering ambient environmental conditions (Panfili *et al.* 2002). Trace element concentrations or elemental ratios, which vary widely between marine and fresh waters, have been extensively used for studying the migrations of diadromous fishes (Tsukamoto *et al.* 2008 ; Campana & Thorrold 2001 ; Walther & Limburg 2012). However, their use in purely freshwater fishes has proved more challenging, owing to reduced chemical gradients across a river basin and possible confounding effects of biotic processes (physiological or dietary dynamics) or abiotic factors (temperature) on their incorporation into fish otoliths. By contrast, strontium (Sr) isotopic ratios in otoliths are unaffected by the latter potential biases; they depend almost exclusively on the age and bedrock geological composition of watersheds, and thus, they barely vary across years and represent accurate habitat signatures (Walther & Limburg 2012; Kennedy *et* *al*. 1997 ; Kennedy *et al*. 2000). Recently, 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 have opened new horizons in fish science, as they enable the fine reconstruction of habitat use during part or the entire fish's life (Outridge *et al*. 2002; Barnett-Johnson *et al*. 2005). The utility of Sr isotopic ratios and LA-MC-ICPMS for retracing the movements and habitat use of Amazonian fish has recently been demonstrated (Pouilly *et al*. 2014; Santos *et al*. 2015; Hegg, Giarrizzo & Kennedy 2015).

Sr isotopic analyses in fish otoliths. Analyses of Sr isotopes in fish otoliths were carried out in the Laboratoire de Chimie Analytique Bio-inorganique et Environnement (LCABIE) of the Institut Pluridisciplinaire de Recherche sur l'Environnement et les Matériaux (IPREM) at the Université de Pau et des Pays de l'Adour, France. All measurements were carried out on a Nu Plasma HR-MC-ICPMS (Nu instruments, Wrexham, UK) coupled to an Alfamet femtosecond (fs) laser ablation system (Nexeya SA, Canejan, France). This laser is fitted with a diode-pumped Yb:KGW crystal laser source (HP1, Amplitude Systèmes, Pessac, France) delivering 360-fs pulses at 1030 nm. The laser source operates within a wide range of repetition rates (1-100,000 Hz) and low energy (from <25 µJ pulse^{-1} at 100,000 Hz to <1,000 µJ pulse^{-1} below 1,000 Hz), which represents a new approach in analytical applications where high energy and low repetition rate are commonly used. The laser beam is focused with a 25-mm lens providing a 15-µm diameter spot size, and it can be rapidly moved (up to 0.5 m/s) with high repositioning precision owing to 2D galvanometric scanning module fitted to the optical line. The optical field covered by the laser beam is 25 mm^2. Further details of a similar laser ablation system (operating in the IR region) are described elsewhere (Claverie *et al.* 2009; Tabouret *et al*. 2010). Here the laser was operated at 500 Hz with a pulse energy of 8 µJ to limit the in-depth ablation while the scanner was doing a permanent 200-µm wide back and forth movement at a speed of 1 mm/s then resulting in an apparent 15 x 200 µm laser ablation sample, the long axis of which was parallel to the otolith's growth marks (which are considered as pseudo linear at this scale). This "sharp blade" virtual shaping allows improving MC-ICPMS signal intensity while keeping high spatial resolution. Combined to this back and forth movement, the sample was continuously moved from the core to the edge of the otolith (i.e. perpendicular to the growth marks) at a speed of 5 $\mu m.s^{-1}$. In order to prevent blast effect on the nucleus, the ablation was started 200 µm before the core. The ablation depth never exceeded 30 µm.

The LA-MC-ICPMS coupling was carried out using a 2-m long antistatic tube of 6 mm external diameter and 4 mm internal diameter (Legris SA, Rennes, France) into the ICP torch, using helium as carrier gas. A two-inlet torch was used to mix the laser-generated aerosol together with a liquid aerosol (2% HNO_3 solution in ultra pure water [18.2 MOhm] nebulised by means of a pneumatic 200 $\mu L.min^{-1}$ self-aspirating micro-concentric nebuliser combined with a mini-cyclonic Cinnabar spray chamber) before introduction into the plasma (Barats *et al.* 2007). This dual-flow introduction system enables easy optimization of the MC-ICPMS by nebulising a suitable solution for tuning. Measuring conditions were adjusted for maximum sensitivity, stability, and plasma robustness (see Table S2). The contribution of ^{87}Rb to ^{87}Sr intensity was deduced from the ^{85}Rb signal (Barnett-Johnson *et al.* 2010). The ^{83}Kr intensity was monitored to control any potential interference of ^{84}Kr and ^{86}Kr on ^{84}Sr and ^{88}Sr, respectively. The $^{86}Sr/^{88}Sr$ invariant ratio was used to correct the $^{87}Sr/^{86}Sr$ ratio from instrumental mass bias using an exponential law (Walther *et al.* 2008). At the beginning and the end of each half-day session, an in-lab $^{87}Sr/^{86}Sr$ certified otolith powder pellet (NIES22, certified Reference Material produced by the National Institute for Environmental Studies, Japan) was analysed 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) were in very good agreement with the in-lab certified values (mean ± 2 SD = 0.709240 ± 0.000021, *n* = 54).

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