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► **To cite this version:**

Fabrice Duponchelle, Marc Pouilly, Christophe Pécheyran, Marilia Hauser, Jean-François Renno, et al.. Trans-Amazonian natal homing in giant catfish. *Journal of Applied Ecology*, 2016, 10.1111/1365-2664.12665 . hal-01308113

HAL Id: hal-01308113

<https://hal.sorbonne-universite.fr/hal-01308113>

Submitted on 27 Apr 2016

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Trans-Amazonian natal homing in giant catfish

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42 **Summary**

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

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

52 3. We sampled adults close to major breeding areas in the Amazon basin (upper Madeira
53 and upper Amazonas) and assessed their lifetime movements by measuring variations in
54 $^{87}\text{Sr}/^{86}\text{Sr}$ along transverse sections of their otoliths (ear stones) using laser ablation
55 multicollector mass spectrometry (LA-MC-ICPMS).

56 4. We demonstrate that larvae migrate downstream from the Andean piedmont to the
57 lower Amazon, where they grow over a protracted period before migrating upstream as
58 adults. Contrary to prevailing inferences, not all fish spend their nursery stages in the Amazon
59 estuary. By contrast, the passage in the lower or central Amazon seems an obligate part of the
60 life cycle. We further evidence that most adults home to their natal geographic area within the
61 Madeira sub-basin. Such long-distance natal homing is exceptional in purely freshwater
62 fishes.

63 5. *Synthesis and applications.* By using otolith microchemistry, we were able to
64 demonstrate a seemingly compulsory basin-wide migratory life cycle of large Amazonian
65 catfishes. This makes them the organisms performing the longest migrations (>8000 km) in
66 fresh waters. This exceptional life history is already jeopardized by two dams recently built in

67 the Madeira River, which block a major migration route and access to a substantial part of
68 their spawning grounds. Major impacts can be anticipated from the current and forthcoming
69 hydroelectric development in the Amazon basin, not only on the populations and fisheries of
70 this apex predator, but also on Amazonian food webs through trophic cascades.

71

72 **Key-words:** *Brachyplatystoma* spp., $^{87}\text{Sr}/^{87}\text{Sr}$ ratios, migration, otoliths, hydroelectric dams,
73 Amazon, anthropogenic activities, freshwater fish

74

75 **Introduction**

76

77 Inland waters and their biodiversity provide a wealth of goods and services, but are
78 increasingly threatened by anthropogenic activities worldwide (Nilsson *et al.* 2005;
79 Hoeinghaus *et al.* 2009; Vörösmarty *et al.* 2010; Winemiller *et al.* 2016). Although relatively
80 preserved until recently in comparison with other large river systems, the Amazon basin,
81 which holds the most diverse freshwater fish fauna on Earth (Pimm *et al.* 2014), is no longer
82 an exception (Castello *et al.* 2013). Fisheries, one of the most important ecosystem services of
83 Amazonian fresh waters, largely rely on migratory Characiformes and Siluriformes (Lucas &
84 Baras 2001; Carolsfeld *et al.* 2003). The utmost importance of migratory animals in
85 ecosystem functioning and resilience has been stressed in recent studies, emphasizing their
86 major roles in coupling resident communities and shaping food web dynamics along their
87 migration routes (Wilcove & Wikelski 2008; Bauer & Hoye 2014). In-depth knowledge of the
88 movement patterns of these migratory species is required to fully appraise their structuring
89 importance and to implement relevant management policies. Such crucial information is
90 lacking for most migratory Amazonian fishes and in particular for some of the most
91 ecologically and economically important species, the *Brachyplatystoma* spp. (Pimelodidae).
92 These large (up to 3 m) catfishes are apex consumers (Barthem & Goulding 1997). They

93 support the largest fisheries of the Amazon basin and are often overexploited (Petrere Jr *et al.*
94 2004 ; García Vasquez *et al.* 2009 ; Agudelo *et al.* 2013). Based on strong circumstantial
95 evidence, these catfishes – at least *B. rousseauxii* (Castelnau 1855) – were hypothesized to
96 undertake the longest migrations ever described in fresh waters, from the spawning areas in
97 the Andean piedmont to the nursery in the Amazon estuary and back (Barthem & Goulding
98 1997): small juveniles are caught in the lower Amazon and in the freshwater part of the
99 estuary, body size in fisheries landings increases with distance from the estuary, while ripe
100 adults and newly hatched larvae are exclusively observed in white water tributaries of the
101 Andean piedmont in Bolivia, Colombia, Ecuador and Peru (Barthem & Goulding 1997;
102 García Vasquez *et al.* 2009 ; Cañas & Pine 2011; Agudelo *et al.* 2013). Recently, using
103 otolith microchemistry Hegg, Giarrizzo & Kennedy (2015) provided evidence that the
104 Amazon estuary might not be the sole nursery area for this species, as was thought originally
105 (Barthem & Goulding 1997). The hypothesis of a single panmictic population of *B.*
106 *rousseauixii* at the scale of the Amazon basin (Batista & Alves-Gomes 2006) was recently
107 refuted by the existence of several reproductive units, with at least one exclusively found in
108 the Madeira sub-basin (Carvajal-Vallejos *et al.* 2014). This genetic structure can be explained
109 either by a resident lifestyle, with individuals spending their entire life in the Madeira or by a
110 natal homing behaviour. Natal homing, the return of migratory individuals to reproduce in the
111 geographic area where they originated is widespread among terrestrial and aquatic animals
112 (Papi 1992). Some of the most fascinating examples of this adaptive strategy are found in
113 diadromous and marine fishes (Lucas & Baras 2001), such as salmon (Scheer 1939), eels
114 (Tesch & White 2008) and tunas (Rooker *et al.* 2008). Evidence of long-range natal homing is
115 scarce, however, for purely freshwater fishes (Lucas & Baras 2001). This behaviour has been
116 hypothesized in *B. rousseauxii* (Batista & Alves-Gomes 2006 ; Carvajal-Vallejos *et al.* 2014)
117 but never demonstrated.

118 Elucidating the migratory patterns of this large apex predator roaming the rivers of six
119 Amazonian countries with different fisheries policies is paramount for designing adequate
120 conservation and management strategies, especially in view of the current and proposed
121 hydroelectric development throughout the Amazon basin (Finer & Jenkins 2012; Castello *et*
122 *al.* 2013). In particular, two large dams (Santo Antonio and Jirau) have been erected since
123 2011 in the Brazilian part of the Madeira River, near Porto Velho (Fearnside 2014, Fig. 1).
124 The impacts of these and other forthcoming dams on *B. rousseauxii* largely depend on their
125 migration patterns: do these fish actually make basin-wide migrations? Do they make a single
126 or multiple runs? Do they exhibit homing behaviour?

127 Here, in order to address these questions, we sampled adults of *B. rousseauxii* close to
128 some of their main breeding areas in the Upper Amazonas and Upper Madeira (Fig. 1a),
129 before the construction of the Madeira dams. We measured $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in transects along
130 transverse sections of their otoliths and we compared these observed profiles with those
131 expected from different scenarios of space utilization and migration (Fig. 2).

132

133 **Material and methods**

134

135 STUDY AREA

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

141

142 STUDY DESIGN

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

155 Otoliths are made of relatively inert aragonitic calcium carbonate laid down on an
156 organic matrix, and contrary to other hard body parts, they are not subjected to any resorption
157 process. In contrast to the situation of many other chemicals, strontium (Sr) isotopic ratios in
158 otoliths are unaffected by confounding effects of biotic processes (physiological or dietary
159 dynamics) and abiotic factors (such as temperature) (Kennedy *et al.* 1997; Kennedy *et al.*
160 2000; Walther & Limburg 2012). The diversity of bedrocks with contrasting strontium
161 isotopic ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) across the Amazonian Basin, together with the rather limited
162 variability of these ratios across years and seasons (Palmer & Edmond 1992; Gaillardet *et al.*
163 1997; Queiroz *et al.* 2009; Pouilly *et al.* 2014; Santos *et al.* 2015) provide heuristic
164 opportunities for identifying fish geographical origin or reconstructing their migration
165 patterns (Pouilly *et al.* 2014; Garcez *et al.* 2015; Hegg, Giarrizzo & Kennedy 2015), at least at
166 the scale of large sub-basins. A finer discrimination between tributaries is rendered more
167 difficult or impossible by the similarity of their underlying watershed geology.

168 Here we use the classification of Hegg, Giarrizzo & Kennedy (2015), slightly
169 modified in the light of additional data of strontium isotopic ratios in Amazonian waters
170 (Palmer & Edmond 1992). We distinguish three main riverine regions (Fig. 1): (i) the Western
171 Andean tributaries (hereafter, WAT), the Amazon River mainstem and its floodplain
172 tributaries; (ii) the Madeira sub-basin and lower Negro River; and (iii) tributaries draining the
173 Brazilian and Guyanese granitic shields, referred to hereafter as “granitic shield tributaries”
174 (GST). There is some overlap between the Sr isotopic signatures of Madeira waters and those
175 of the lower course of some GST, especially the Tapajos and Lower Negro River (Fig. 1,
176 Table S1). Decades of intensive fisheries and scientific sampling, however, never yielded any
177 ripe adult or larva of *B. rousseauxii* in GST (Barthem & Goulding 1997), in contrast to their
178 routine occurrence in Andean white water tributaries (Barthem & Goulding 1997; García
179 Vasquez *et al.* 2009; Cañas & Pine 2011; Agudelo *et al.* 2013). Therefore, otolith core
180 signatures comprised between 0.715 and 0.726 (range of available $^{87}\text{Sr}/^{86}\text{Sr}$ signatures in the
181 Madeira waters, Fig. 1, Table S1) will be considered as evidence of hatching within the
182 Madeira sub-basin. Likewise, otolith core signatures < 0.712 will be assigned to fish hatched
183 in WAT waters.

184

185 FISH SAMPLING

186 Fish were sampled between 2005 and 2009, before the construction of the Santo Antonio and
187 Jirau hydroelectric dams on the Madeira River. Eighteen fish (95–120 cm standard length,
188 SL) were obtained directly on the fishing grounds of the Bolivian upper Madeira, near Puerto
189 Villaroel on the Mamoré River, and near Rurrenabaque on the Beni River. Nineteen other fish
190 (89–141 cm SL) were purchased in Iquitos market, Peru, which lands fish caught within ~
191 300 km, including the Amazonas, and the lower parts of the Ucayali, Napo and Marañón river
192 systems. For each specimen, SL was measured (nearest cm) and otoliths (lapilli) were

193 extracted, rinsed in clear water, dried and stored for later examination.

194

195 OTOLITH ANALYSIS

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

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

210 Twice a day, we analysed an in-laboratory $^{87}\text{Sr}/^{86}\text{Sr}$ -certified otolith powder pellet (NIES22,
211 certified Reference Material produced by the National Institute for Environmental Studies,
212 Japan) to check the reliability of $^{87}\text{Sr}/^{86}\text{Sr}$ measurements (Martin *et al.* 2013). In all cases fs-
213 LA-MC-ICPMS $^{87}\text{Sr}/^{86}\text{Sr}$ values (mean $\pm 2 \text{ SD} = 0.709289 \pm 0.000379$, $n = 38$) corresponded
214 well with the in-laboratory-certified values (mean $\pm 2 \text{ SD} = 0.709240 \pm 0.000021$, $n = 54$).
215 Further details about analytical processes are given in Appendix S1.

216

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

219 On the basis of environmental signatures, the limit of $^{87}\text{Sr}/^{86}\text{Sr}$ between the Madeira and
220 Amazon waters was set at 0.715 (Fig. 1). We considered that *B. rousseauxii* exited the
221 Madeira when their otolith Sr isotopic ratios were consistently lower than 0.715. Similarly,
222 we assumed that fish had left the Amazon and re-entered the Madeira when their otolith Sr
223 isotopic ratios became anew consistently higher than 0.715. For both events, the distances
224 from the otolith's core were noted (nearest 25 μm). In order to back-calculate the fish SL at
225 these moments, we used a relationship between the otolith dimension along the transverse
226 radius and the fish SL, produced from 351 *B. rousseauxii* caught between 2009 and 2012 by
227 the Laboratory of Ichthyology and Fisheries of the Universidade Federal do Rondônia (UNIR)
228 in the Brazilian stretch of the Madeira River. The relationship is linear in small fish (40–50
229 cm SL) then becomes curvilinear in larger individuals (Fig. S1), as the otoliths of older fish
230 are thicker. Henceforth, two distinct equations were used for fish \leq and $>$ 45 cm SL.

231
232 SIZE OF *B. ROUSSEAUXII* AT FIRST SEXUAL MATURITY

233 The size at first sexual maturity (L_m) is defined as the SL at which 50% of the fish are
234 observed at an advanced maturation stage during the breeding season (Núñez & Duponchelle
235 2009) (i.e. when oocytes are visible to the naked eye, which means vitellogenesis has started).
236 L_m is estimated by fitting the fraction of mature individuals per 5-cm SL intervals to a logistic
237 function (García Vasquez *et al.* 2009; Agudelo *et al.* 2013), where the contribution of each
238 size class to the model is statistically weighted by the total number of individuals in the same
239 size class:

240
$$M = 100(1 + e^{(-a(L_i - L_m))})^{-1}$$

241 where M (%) is the proportion of mature individuals by size class, L_i is the central value of
242 size class i , and a and L_m are the coefficients of the model. Here, the model was adjusted using

243 152 female *B. rousseauxii* (37–125 cm SL) caught in the Brazilian part of the Madeira sub-
244 basin and for which we histologically determined the stage of gonad maturation. The values
245 of coefficients a and L_m in the model (Fig. S2) were fitted using a non-linear regression with
246 the quasi-Newton adjustment and were 0.3402 (± 0.0141 SE) and 73.33 (± 0.14 SE) cm SL,
247 respectively ($P < 0.0001$ in both cases).

248

249 **Results**

250 As for all migratory fishes, several scenarios can be hypothesized for *B. rousseauxii*,
251 including resident behaviour in the hatching tributary or sub-basin, long-range migration from
252 the hatching tributary to the Amazon mainstem followed by homing or straying, and multiple
253 runs between the Amazon mainstem and the same or different sub-basins. The corresponding
254 theoretical $^{87}\text{Sr}/^{86}\text{Sr}$ patterns in the otoliths of fish hatched in the Madeira and WAT are
255 distinct (Fig. 2). Several patterns can be univocal, whereas others may refer to several
256 scenarios. In particular, on the sole basis of Sr isotopic signatures, it is uncertain whether fish
257 ascending the Madeira before their capture did so during their very first upstream run or if
258 they migrated to WAT in the meanwhile (Fig. 2b, 2e). Likewise, it is almost impossible to
259 distinguish between fish spending all their life in WAT and those migrating once or several
260 times between these places and the middle or lower Amazon River (Fig. 2g, 2h, 2j). It is also
261 difficult to discriminate between fish venturing in the Madeira sub-basin and those entering
262 GST, because of the overlap between the Sr isotopic signatures of these rivers (Fig. 1b). This
263 confusion would only arise for intermediate runs, and exclusively in situations where fish in
264 GST would remain in waters with signatures < 0.726 , thereby resulting in otolith profiles
265 resembling those illustrated in Fig. 2d or 2k. Intermediate runs in more radiogenic GST would
266 produce univocal profiles, similar to those illustrated in Fig. 2f or 2l. Regarding the final
267 upstream run, the interpretation is straightforwardly deduced from the capture location.

268

269 INTERPRETATION OF MIGRATION PATTERNS

270 Twelve of the 18 fish sampled in the Madeira sub-basin could be ranked as natal
271 homers (Fig. 3a, Fig. 2b). Their core Sr isotopic signatures (0.716–0.722) were typical of
272 Madeira waters, they moved downstream into waters with Amazon and WAT signatures,
273 grew in these waters, then homed to the Madeira sub-basin, where they remained until their
274 capture. As explained above, it is uncertain whether these fish ventured into WAT before
275 returning to the Madeira (Fig. 2b, 2e). By contrast, it is certain that they did not make any
276 intermediate run in the Madeira or in any GST, as these migratory patterns would have
277 involved a passage in the Amazon on the way back to the Madeira, which would have
278 produced Sr isotopic profiles close to those in Fig. 2d and 2f, respectively. Likewise, there is
279 no ambiguity for the final upstream run, as these fish were captured in the upper Madeira.
280 Based on the relationship between otolith radius and body length in *B. rousseauxii* (Fig. S1),
281 these fish would have exited the Madeira at 3.7 ± 1.6 cm SL (mean \pm S.D.) and returned at
282 86.0 ± 5.7 cm SL, slightly above the mean size at first sexual maturity (73.3 ± 4.7 cm SL; Fig.
283 S2).

284 Ten other fish, all collected in Iquitos, exhibited no single Sr isotopic signal > 0.713 in
285 their otoliths (Fig. 3b). Therefore, it can be assumed that these fish never entered the Madeira
286 or GST, and they remained in the Amazon or WAT for their entire lives. By contrast, it is
287 uncertain whether these profiles correspond to resident or migratory behaviours, with one or
288 several runs between the Amazon and WAT (scenarios in Fig. 2g, 2h and 2j, respectively).
289 Based on existing knowledge, however, it is likely that these fish hatched in WAT, travelled
290 down to the Amazon at a small body size and subsequently returned to WAT. In contrast to
291 the clear-cut situation for fish homing to the Madeira, no information can be obtained here

292 regarding the size of fish during their (presumed) downstream and upstream runs, except that
293 all these fish had passed the size at first sexual maturity when they were captured.

294 Five other fish also hatched in waters with WAT or Amazon signatures and collected
295 later as adults in Iquitos, showed slightly less typical patterns (Fig. 3c). Four of them (Iq3,
296 Iq6, Iq8 and Iq11) repeatedly moved back and forth in waters with Sr isotopic ratios
297 intermediate between those of the Amazon and Madeira. The fifth fish (Iq12) showed a
298 signature profile matching the scenario of multiple runs in several Amazonian sub-basins
299 (Fig. 2l). This fish, which hatched and lived in waters with WAT and Amazon signatures,
300 thereafter migrated in highly radiogenic waters ($^{87}\text{Sr}/^{86}\text{Sr} > 0.730$), which are found
301 exclusively in some GST (probably the Negro or Tapajos rivers, see Fig. 1 and Table S1). It
302 eventually migrated back to the WAT, where it was caught.

303 For the remaining 10 fish, the edge signatures departed from the core signatures (Fig.
304 3d). For two of the six fish caught in the Upper Madeira (Ma10 and Be8), the core signatures
305 were typical of WAT, matching the straying scenario illustrated in Fig. 2c. The core
306 signatures of the remaining eight fish (0.7125–0.7147) fell in between the ranges of Madeira
307 and WAT.

308

309 **Discussion**

310 The migratory patterns of most fish were relatively univocal and indicated long-range
311 migration and natal homing behaviour (Fig. 3a). By contrast, the isotopic profiles of several
312 fish illustrated in Fig. 3c and 3d were less straightforward and require further discussion. Four
313 fish (Iq3, Iq6, Iq8 and Iq11) apparently moved back and forth in waters with Sr isotopic ratios
314 intermediate between those of the Amazon and Madeira (Fig. 3c). These ratios could
315 correspond to sojourns in non-sampled tributaries or refer to fish movements in confluence
316 areas between waters with highly contrasting signatures (Bouchez *et al.* 2010), as occur in

317 several places in the Amazon River (e.g. confluences with more radiogenic tributaries, such as
318 the Negro, Madeira and Tapajos rivers; Fig. 1). White water tributaries with high sediment
319 loads have a much higher and lasting impact than clear or black water tributaries when mixing
320 with waters of contrasting signatures (Bouchez *et al.* 2010). Hence, it is likely that most
321 profiles depicted in Fig. 3c and 3d correspond to movements within the confluence area of the
322 Amazon and Madeira or similar situations. Eight fish from Fig. 3d had core signatures
323 (0.7125–0.7147) falling in between the ranges of Madeira and WAT. These atypical
324 signatures might correspond to tributaries for which there is currently no information on Sr
325 isotopic ratios, and in this particular case, all eight fish would be strayers. Alternatively, it is
326 possible that these atypical core signatures originated from fish hatched in the Madeira sub-
327 basin, but moving downstream much faster than others, as can typically happen under higher
328 flows. Several authors have indeed demonstrated that *B. rousseauxii* reproduces during
329 contrasting hydrological periods in the main rivers of the Upper Madeira (Cañas & Pine 2011;
330 Cella-Ribeiro *et al.* 2015). On the basis of hydrological data (HYBAm) upon river discharge,
331 flow and width in the Madeira River, it can be reasonably assumed that fish hatching and
332 drifting during high flows could be flushed down into the Amazon at least three times faster
333 than during periods of low flows. While taking into account the methodological limitations
334 pertaining to the depth of laser ablation for otolith screening, such faster movements would
335 inevitably lead to some degree of integration of the Amazon signature into the core
336 signatures, and thus to lower Sr isotopic ratios than expected for fish hatched in Madeira
337 waters. If this hypothesis were valid, then four of the eight fish illustrated in Fig. 3d and that
338 were caught in Iquitos (Iq1, Iq4, Iq7 and Iq19) would be strayers from the Madeira (as
339 illustrated in Fig. 2i) and the remaining four fish caught in the Madeira (Ma7, Be1, Be2 and
340 Be5) would be natal homers.

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

347 There is strong evidence, however, that not all *B. rousseauxii* migrate downstream to
348 the Amazon estuary, as recently suggested by Hegg, Giarrizzo & Kennedy (2015) on the basis
349 of fish caught near Manaus. Indeed, fish hatched in the Madeira or WAT and growing
350 thereafter in the estuary must travel in the meanwhile through the lower Amazon (between the
351 mouth of the Madeira and Santarem, near the estuary), where the contributions of the Madeira
352 River and highly radiogenic GSTs tend to increase significantly the Sr isotopic ratio in the
353 Amazon mainstem to values ranging from 0.7103 to 0.7123 (averaging 0.7115 in Obidos and
354 Santarem, downstream of sampling points 27; Fig. 1, Table S1). Three fish hatched in WAT
355 and later caught in Iquitos (Iq 2, Iq 9 and Iq 10) had no single otolith $^{87}\text{Sr}/^{86}\text{Sr}$ value falling
356 within this range, thereby indicating that these fish never entered the Amazon estuary at any
357 life stage. Two other fish hatched in WAT, one caught in Iquitos (Iq 5) and the other one
358 caught in the Upper Madeira (Ma 10), exhibited such Sr isotopic ratios in their otoliths, but
359 only at relatively large body sizes (50 and 47 cm SL, respectively), thereby indicating that
360 they did not move into the estuary during their early juvenile stages. Our results suggest that
361 the nurseries of these five fish were somewhere upstream of the Obidos-Santarem area. No
362 such evidence of an absence of movement into the estuary can be deduced for fish hatched in
363 the Madeira, as these fish always inevitably cross waters with Sr isotopic ratios between
364 0.7103 and 0.7123 on their way down to the Amazon. Whatever the exact place of the
365 nurseries and their connections with the spawning areas of *B. rousseauxii*, a protracted period

366 in the lower or central Amazon River at the juvenile stage seems an obligate part of the life
367 cycle of *B. rousseauxii*, thereby refuting the hypothesis of an alternative resident lifestyle
368 (Carvajal-Vallejos *et al.* 2014). This certainly applies to fish hatched in the Madeira, for
369 which evidence is provided here, and presumably to those hatched in the WAT.

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

384 The movement patterns highlighted here somehow differ from those recently
385 published for the same species by Hegg, Giarrizzo & Kennedy (2015), who did not evidence
386 fish originating from or moving into the Madeira. These differences presumably owe to at
387 least three factors. Their sampling localities were different, lying in the estuary (Belem) or
388 central Amazon (Manaus), and their fish were caught before their upstream spawning runs.
389 Finally, in contrast to the present study, where fish were collected at all seasons over several
390 years, all fish studied by Hegg, Giarrizzo & Kennedy (2015) were caught within less than a

391 month. The latter context is more likely to generate a sampling bias that could account for the
392 absence of fish hatched in the Madeira in their study. Alternatively it cannot be excluded that
393 fish hatched in the Madeira effectively contribute to the estuarine stock to a lower extent than
394 those hatched in WAT, especially if their main nursery areas were somewhere else. This brief
395 comparison emphasizes the need for further studies to elucidate the migrations of *B.*
396 *rousseauxii* in the Amazonian basin, in particular to understand the contributions of different
397 sub-basins and tributaries to recruitment and fisheries. In the study by Hegg, Giarrizzo &
398 Kennedy (2015) and in the present study, sample size was limited to a few tens of fish, but in
399 both cases the method used generated large numbers of samples over the life of individual
400 fish. These observations may be auto-correlated, but they nevertheless provide unprecedented
401 information on the life of this ecologically and economically important species.

402

403 In synthesis, the present study demonstrates basin-wide migrations of *B. rousseauxii*,
404 with a downstream migration into the Amazon at a small (<3–4 cm SL) body size, a
405 protracted growth period in the lower or central Amazon at the juvenile stage and a return
406 upstream run as adults. On the basis of fish captured in the Madeira, this long-range migratory
407 lifestyle is seemingly compulsory, with no single specimen exhibiting otolith strontium
408 isotopic profiles characteristic of a resident behaviour. These findings have profound
409 consequences for the management of this ecologically and commercially important species.
410 The now demonstrated existence of transboundary movements in *B. rousseauxii* further
411 advocates for the need of an international fisheries management coordination of this resource
412 across the Amazon basin (Fabr e & Barthem 2005). Beyond current issues of overexploitation
413 and complex fisheries management, *B. rousseauxii*, in view of its compulsory basin-wide
414 migrations, might be imperilled to a greater extent than other migratory fishes by disruptions
415 of longitudinal connectivity. Until recently the Amazon basin had been moderately affected

416 by damming (Nilsson *et al.* 2005; Vörösmarty *et al.* 2010), with no single dam below 400 m
417 a.s.l. (Finer & Jenkins 2012) that could have interfered with the migratory life cycle of *B.*
418 *rousseauxii*. Since 2011, two large dams were erected in the lower Madeira River. Their fish
419 passage facilities have been found ineffective for accommodating the upstream runs of large
420 catfishes, including *B. rousseauxii* (Fearnside 2014). As *B. rousseauxii* spawns exclusively in
421 the white water tributaries of the Andean piedmont (WAT and upper Madeira), it can be
422 assumed that the access of *B. rousseauxii* to a substantial part of its possible spawning
423 grounds in the Amazon basin is already strongly compromised. This calls for urgent
424 modifications of the fish passages of both Jirau and Santo Antonio dams in order to restore
425 the connectivity between the upper and lower portions of the Madeira. Our results further
426 urge the need to preserve river connectivity in the still undammed parts of the Amazonian
427 lowlands and midlands, while tens of other dams are already planned in these regions (Finer
428 & Jenkins 2012; Castello *et al.* 2013 ; Fearnside 2014).

429 The impacts of multiple obstacles on the migration routes of *B. rousseauxii* might just
430 be as dramatic as those suffered in temperate regions by anadromous salmonids, which also
431 undertake basin-wide migrations (Lucas & Baras, 2001), or even worse, for two reasons.
432 First, *B. rousseauxii* makes its downstream migrations at a much younger age and smaller
433 body size than salmonids (Celia-Ribeiro *et al.* 2015; present study). Smaller fish have a lower
434 probability to escape predation or adverse physico-chemical conditions in lentic reservoirs
435 upstream of dams, because of their limited swimming capacities, and fish-attracting or
436 deterring devices aiming to facilitate a safe downstream passage are certainly less efficient
437 than for larger fish (Lucas & Baras 2001; Pelicice, Pompeu & Agostinho 2015). Second, *B.*
438 *rousseauxii* is an apex consumer, with key ecological functions (Barthem & Goulding 1997),
439 and its decline could thus have profound top-down effects on the ecosystem through trophic
440 cascades (Estes *et al.* 2011). To our knowledge, it is most infrequent that large piscine

441 predators exhibit long-range migrations in continental ecosystems. As a consequence,
442 damming in the Amazon basin could have more severe impacts on ichthyofauna and food webs
443 than in any other large river system. These issues add to a long list of concerns regarding the
444 sustainability of large-scale hydroelectric development (Nilsson *et al.* 2005; Vörösmarty *et al.*
445 2010; Ansar *et al.* 2014), and may require re-evaluating the actual pros and cons of large
446 hydropower plants in the Amazon basin (Finer & Jenkins 2012; Stickler *et al.* 2013; Kahn,
447 Freitas & Petrere Jr 2014; Winemiller *et al.* 2016), which hosts the world's richest
448 biodiversity.

449 **Acknowledgements**

451 We thank F. Ferraton for technical assistance, W. Santini for iconographical support and M.C.
452 Lucas for commenting on an early version of the manuscript. We also thank an anonymous
453 referee and D. J. Stewart for constructive comments. The study was supported by IRD (PPR
454 AMAZ and LMI EDIA), the World Wildlife Fund (Russell E. Train Education for Nature
455 Program to F.C.-V.) and the French Foundation for Research on Biodiversity (project
456 MARMIPED).

457

458 **Data accessibility**

459 Source data of fish $^{87}\text{Sr}/^{86}\text{Sr}$ profiles are available in Supporting Information Table S3.

460

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589

590 **Figure Legends**

591

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

603

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

613

614 **Figure 3. Laser ablation-MC-ICPMS transects of $^{87}/^{86}\text{Sr}$ along otolith transverse sections**
615 **(from the core to the edge) of *Brachyplatystoma rousseauxii*.** Each curve corresponds to

616 one individual caught either in the upper Madeira (Mamoré, Ma and Beni, Be rivers) or in the
617 upper Amazon (fish landed in Iquitos, Iq; see Fig. 1). Four migratory patterns were identified
618 among transects (a, b, c, d, see text). The dashed line (Fig. 3a) represents the size at first
619 sexual maturity of *B. rousseauxii* in the Madeira basin (Fig. S2).

620

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622

623 **Supporting Information**

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

625

626 **Appendix S1** - Detailed methods.

627

628 **Table S1.** Detailed water $^{87}\text{Sr}/^{86}\text{Sr}$ data.

629

630 **Table S2.** Laser ablation and multicollector settings.

631

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

634

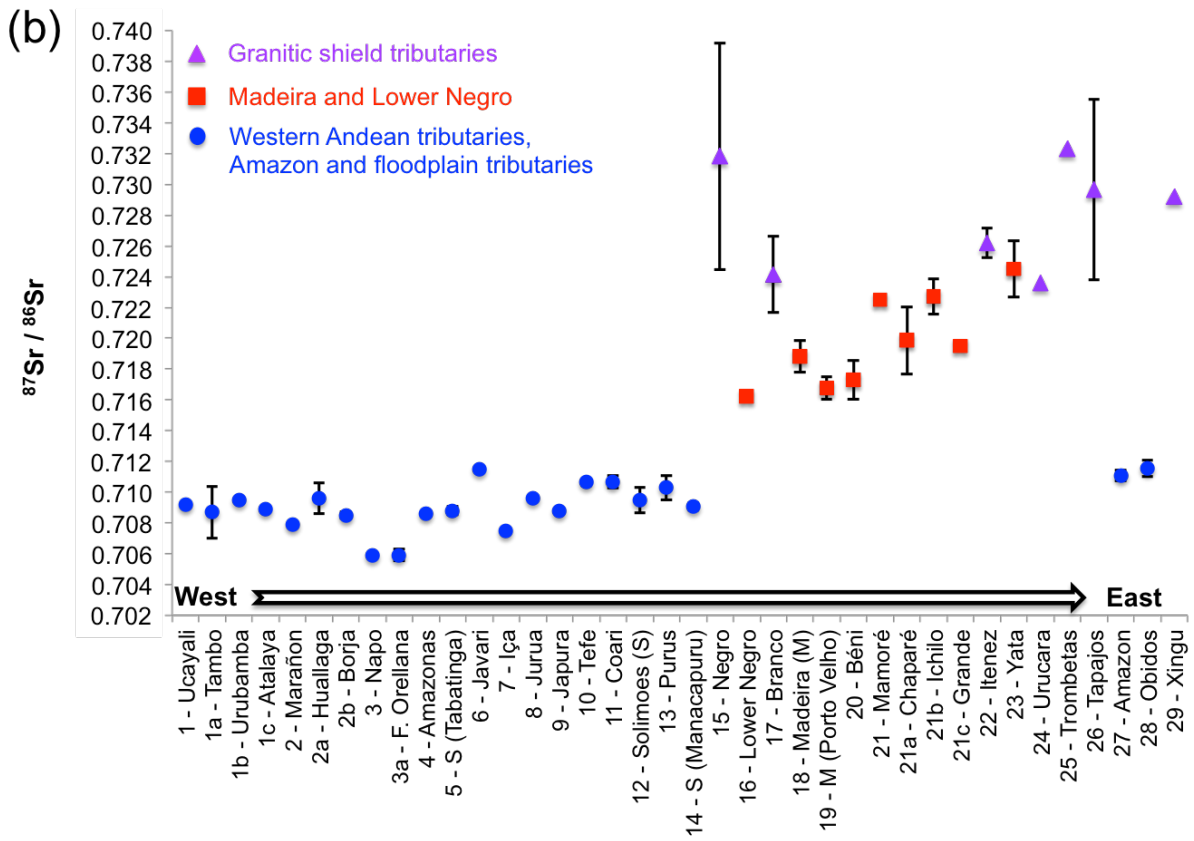
635 **Figure S2.** Percentage of mature individuals as a function of standard body length in female
636 *B. rousseauxii* from the Madeira River basin.

637

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

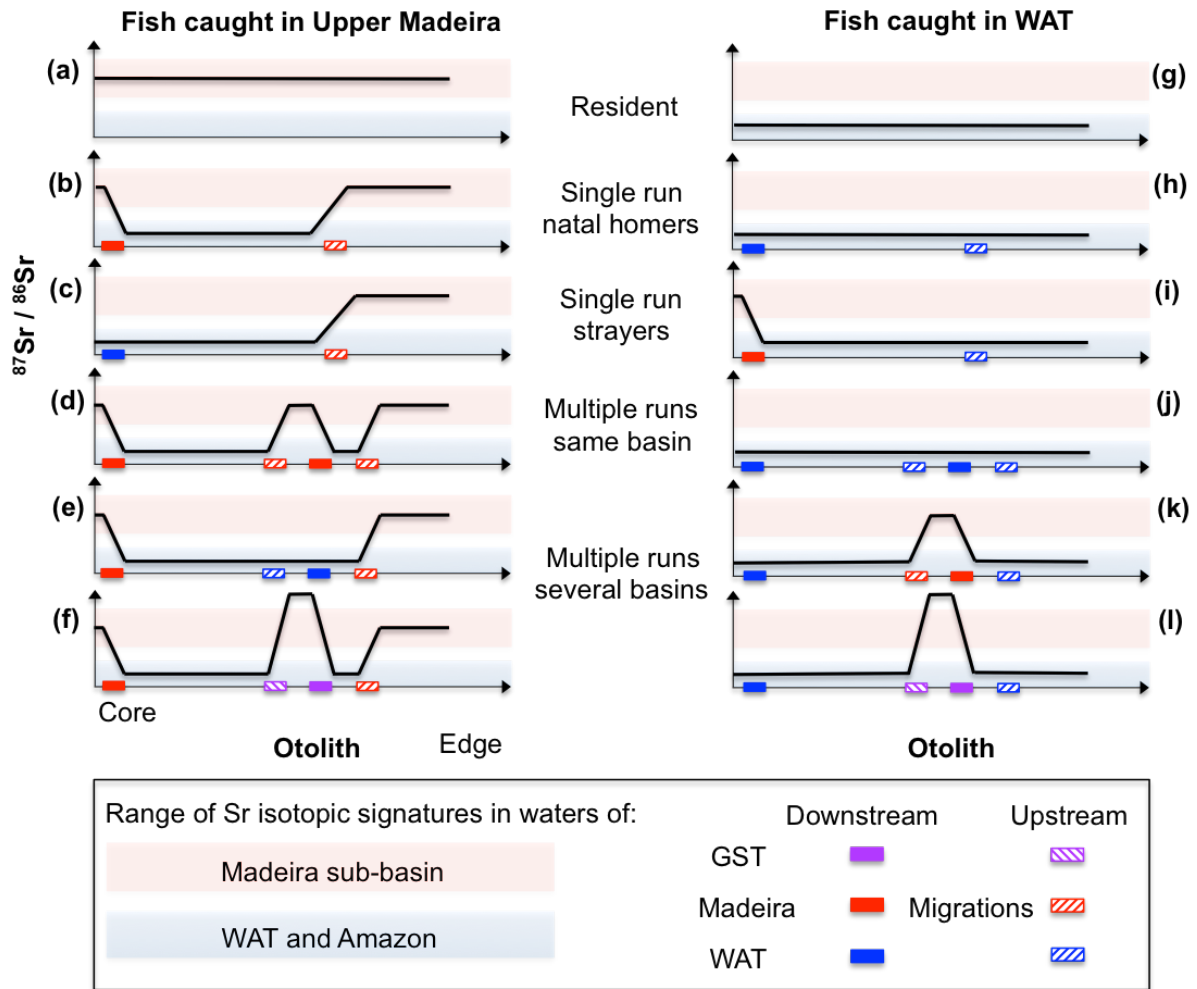


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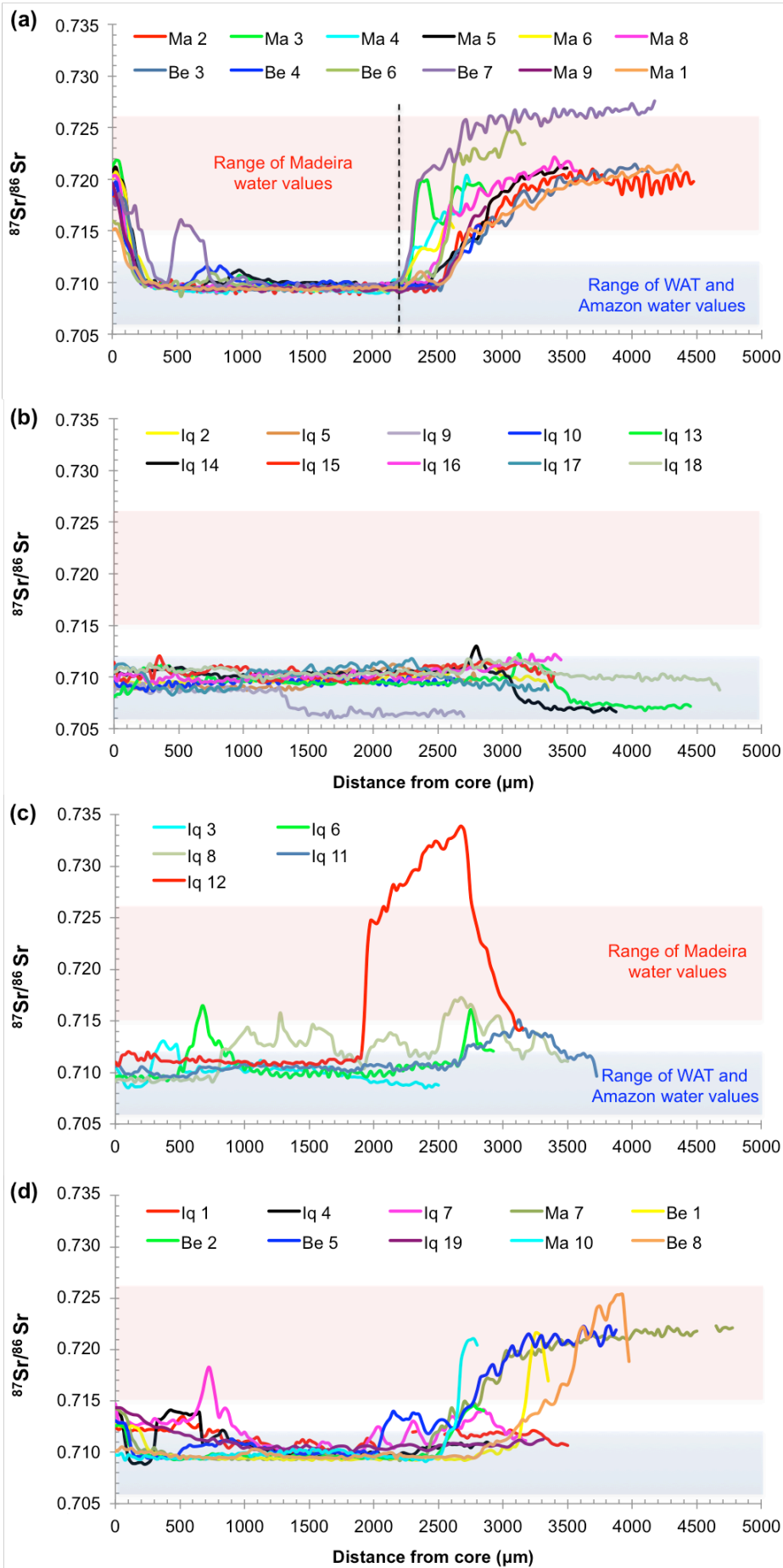
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Fig. 1.



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Fig. 2.



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15 Fig. 3
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1 **Supporting Information for Duponchelle, F. et al. “Trans-**
2 **Amazonian natal homing in giant catfish”**

3
4 **Appendix S1: detailed methods**

5 **Reconstructing fish migrations using microchemistry of hard body parts.** The bones,
6 cartilages, scales and otoliths (ear bones) of a fish grow continuously during its life, forming
7 seasonal growth rings. The screening of these body hard parts for chemical elements or
8 isotopes gives the opportunity to reconstruct habitat conditions during the fish’s life
9 (Campana 1999). As fish grow, natural chemical elements such as strontium, barium, lead or
10 zinc, and their isotopes, readily substitute for calcium in their hard body parts, generally in
11 proportion to their ambient dissolved concentrations or occurrence in food. Their quantitative
12 analysis in fish hard body parts can thus be used as a proxy of the fish’s habitat at a particular
13 age or size. Otoliths are made of relatively inert aragonitic calcium carbonate laid down on an
14 organic matrix. In contrast to other hard body parts, they are not affected by any resorption
15 process and are thus considered as reliable internal data loggers registering ambient
16 environmental conditions (Panfili *et al.* 2002). Trace element concentrations or elemental
17 ratios, which vary widely between marine and fresh waters, have been extensively used for
18 studying the migrations of diadromous fishes (Tsukamoto *et al.* 2008 ; Campana & Thorrold
19 2001 ; Walther & Limburg 2012). However, their use in purely freshwater fishes has proved
20 more challenging, owing to reduced chemical gradients across a river basin and possible
21 confounding effects of biotic processes (physiological or dietary dynamics) or abiotic factors
22 (temperature) on their incorporation into fish otoliths. By contrast, strontium (Sr) isotopic
23 ratios in otoliths are unaffected by the latter potential biases; they depend almost exclusively
24 on the age and bedrock geological composition of watersheds, and thus, they barely vary
25 across years and represent accurate habitat signatures (Walther & Limburg 2012; Kennedy *et*

26 *al.* 1997 ; Kennedy *et al.* 2000). Recently, methodologies using laser ablation (LA) combined
27 with multicollector (MC) and inductively coupled plasma mass spectrometry (ICPMS) for the
28 measurement of Sr isotopes and their ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) along otolith transects have opened new
29 horizons in fish science, as they enable the fine reconstruction of habitat use during part or the
30 entire fish's life (Outridge *et al.* 2002; Barnett-Johnson *et al.* 2005). The utility of Sr isotopic
31 ratios and LA-MC-ICPMS for retracing the movements and habitat use of Amazonian fish
32 has recently been demonstrated (Pouilly *et al.* 2014; Santos *et al.* 2015; Hegg, Giarrizzo &
33 Kennedy 2015).

34

35 **Sr isotopic analyses in fish otoliths.** Analyses of Sr isotopes in fish otoliths were carried out
36 in the Laboratoire de Chimie Analytique Bio-inorganique et Environnement (LCABIE) of the
37 Institut Pluridisciplinaire de Recherche sur l'Environnement et les Matériaux (IPREM) at the
38 Université de Pau et des Pays de l'Adour, France. All measurements were carried out on a Nu
39 Plasma HR-MC-ICPMS (Nu instruments, Wrexham, UK) coupled to an Alfamet femtosecond
40 (fs) laser ablation system (Nexeya SA, Canejan, France). This laser is fitted with a diode-
41 pumped Yb:KGW crystal laser source (HP1, Amplitude Systèmes, Pessac, France) delivering
42 360-fs pulses at 1030 nm. The laser source operates within a wide range of repetition rates (1-
43 100,000 Hz) and low energy (from $<25 \mu\text{J pulse}^{-1}$ at 100,000 Hz to $<1,000 \mu\text{J pulse}^{-1}$ below
44 1,000 Hz), which represents a new approach in analytical applications where high energy and
45 low repetition rate are commonly used. The laser beam is focused with a 25-mm lens
46 providing a 15- μm diameter spot size, and it can be rapidly moved (up to 0.5 m/s) with high
47 repositioning precision owing to 2D galvanometric scanning module fitted to the optical line.
48 The optical field covered by the laser beam is 25 mm². Further details of a similar laser
49 ablation system (operating in the IR region) are described elsewhere (Claverie *et al.* 2009;
50 Tabouret *et al.* 2010). Here the laser was operated at 500 Hz with a pulse energy of 8 μJ to

51 limit the in-depth ablation while the scanner was doing a permanent 200- μm wide back and
52 forth movement at a speed of 1 mm/s then resulting in an apparent 15 x 200 μm laser ablation
53 sample, the long axis of which was parallel to the otolith's growth marks (which are
54 considered as pseudo linear at this scale). This "sharp blade" virtual shaping allows
55 improving MC-ICPMS signal intensity while keeping high spatial resolution. Combined to
56 this back and forth movement, the sample was continuously moved from the core to the edge
57 of the otolith (i.e. perpendicular to the growth marks) at a speed of 5 $\mu\text{m}\cdot\text{s}^{-1}$. In order to
58 prevent blast effect on the nucleus, the ablation was started 200 μm before the core. The
59 ablation depth never exceeded 30 μm .

60 The LA-MC-ICPMS coupling was carried out using a 2-m long antistatic tube of 6 mm
61 external diameter and 4 mm internal diameter (Legris SA, Rennes, France) into the ICP torch,
62 using helium as carrier gas. A two-inlet torch was used to mix the laser-generated aerosol
63 together with a liquid aerosol (2% HNO_3 solution in ultra pure water [18.2 M Ωm] nebulised
64 by means of a pneumatic 200 $\mu\text{L}\cdot\text{min}^{-1}$ self-aspirating micro-concentric nebuliser combined
65 with a mini-cyclonic Cinnabar spray chamber) before introduction into the plasma (Barats *et*
66 *al.* 2007). This dual-flow introduction system enables easy optimization of the MC-ICPMS by
67 nebulising a suitable solution for tuning. Measuring conditions were adjusted for maximum
68 sensitivity, stability, and plasma robustness (see Table S2). The contribution of ^{87}Rb to ^{87}Sr
69 intensity was deduced from the ^{85}Rb signal (Barnett-Johnson *et al.* 2010). The ^{83}Kr intensity
70 was monitored to control any potential interference of ^{84}Kr and ^{86}Kr on ^{84}Sr and ^{88}Sr ,
71 respectively. The $^{86}\text{Sr}/^{88}\text{Sr}$ invariant ratio was used to correct the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio from
72 instrumental mass bias using an exponential law (Walther *et al.* 2008). At the beginning and
73 the end of each half-day session, an in-lab $^{87}\text{Sr}/^{86}\text{Sr}$ certified otolith powder pellet (NIES22,
74 certified Reference Material produced by the National Institute for Environmental Studies,
75 Japan) was analysed to check the reliability of $^{87}\text{Sr}/^{86}\text{Sr}$ measurements (Martin *et al.* 2013). In

76 all cases fs-LA-MC-ICPMS $^{87}\text{Sr}/^{86}\text{Sr}$ values (mean \pm 2 SD = 0.709289 ± 0.000379 , $n = 38$)
77 were in very good agreement with the in-lab certified values (mean \pm 2 SD = $0.709240 \pm$
78 0.000021 , $n = 54$).

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