

Original article

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

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

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

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

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

Introduction

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

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

This species also performs the most extensive freshwater migration ever described, from the spawning areas in the Andean piedmont of Bolivia, Colombia, Ecuador and Peru, to the nursery areas in the Amazon estuary (Barthem, Goulding, 1997; Duponchelle *et al.*, 2016; Barthem *et al.*, 2017). Barthem, Goulding (1997) first deduced this exceptional life cycle from size frequency and ripe gonad distributions between the estuary and the headwaters of the main Amazon tributaries. Duponchelle

et al. (2016) confirmed this life cycle at the individual level using otolith $^{87}S_r/^{86}S_r$ ratios, and further demonstrated natal homing behaviour. Using data from spawning adults, drifting larvae and juveniles, Barthem *et al.* (2017) recently showed that the life cycle of *B. rousseauxii* involves a round trip migration of over 11,000 km.

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

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

Materials and Methods

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

University of Rond nia, Porto Velho, Brazil (UFRO-I 14016, UFRO-I 15044, UFRO-I 15175).

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

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

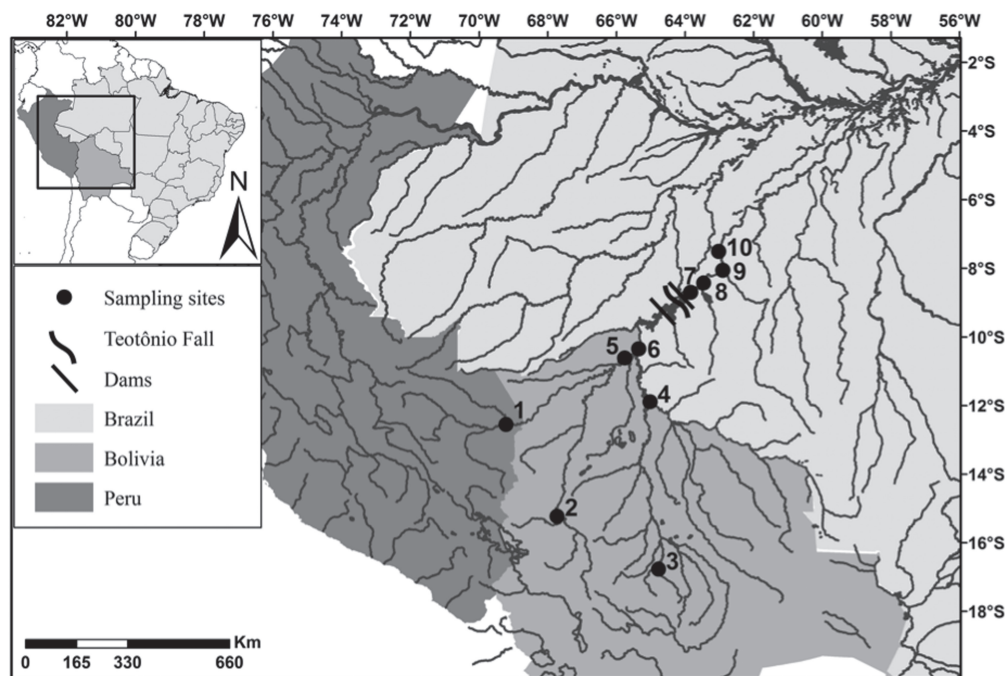


Fig. 1. Map of the sampling sites of *Brachyplatystoma rousseauxii* in the Madeira River basin. 1- Puerto Maldonado, 2- Rurrenabaque, 3- Puerto Villarroel, 4- Surpresa, 5- Cachuella Esperanza, 6- Iata/Vila Murтинho, 7- S o Sebasti o, 8- S o Carlos, 9- Calama and 10- Humait .

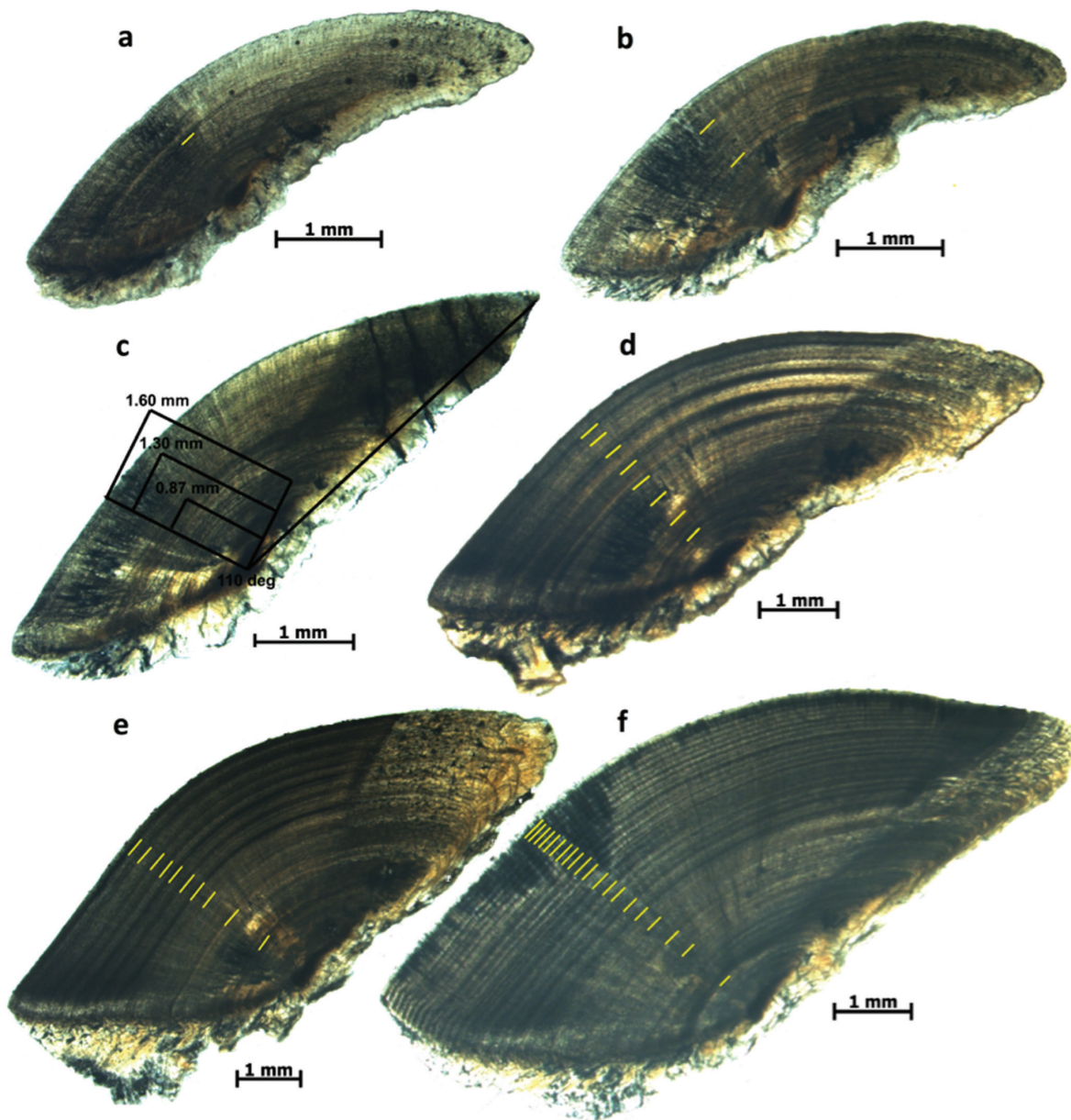


Fig. 2. Transverse thin sections of *Brachyplatystoma rousseauxii*'s otoliths showing: **a.** one ring; **b.** and **c.** two rings; **d.** eight rings; **e.** ten rings; and **f.** twenty rings. The yellow line marks the rings.

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

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

Statistical analysis. Validation of ring formation. The periodicity of translucent ring deposition was determined through the monthly relative marginal increment ratio (RMI):

$$RMI = (R_T - R_N) / (R_N - R_{N1}),$$

where R_T is the total radius of the otolith, R_N is the distance from the core of the otolith to the last ring and R_{N1} is the distance from the core to the penultimate ring (Haimovici, Reis, 1984; Fabr e, Saint-Paul, 1998). RMI mean monthly values were compared using one-way-ANOVA with Tukey's post hoc test. A significant decrease followed by an increase in RMI values was interpreted as the formation of a seasonal translucent ring.

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

The von Bertalanffy growth function (VBGF) was calculated using a non-linear estimation (quasi-Newton method), which was calculated as equation (2):

$$L_t = L_\infty [1 - e^{-K(t-t_0)}],$$

where L and t are L_S (cm) and age t (years) of the fish respectively, L_∞ is the asymptotic L_S ; K is the growth coefficient representing how fast L_∞ is reached and t_0 is the theoretical age at which $L_S = 0$.

The age at first sexual maturity (A_{50}) was calculated from the VBGF as follows (Duponchelle et al., 2007; Garc a-V squez et al., 2009):

$$A_{50} = \{-\ln[1 - (L_{50}/L_{S\infty})]K^{-1}\} + t_0,$$

where L_{50} is the size at first sexual maturity and L_{∞} and K are parameters from the VBGF. Size at first sexual maturity for the females of this species in the Madeira River was previously estimated at 73 cm L_S from the same data set (Duponchelle et al., 2016).

For comparison purposes, VBGF parameters of *B. rousseauxii* in the Amazon River mainstem (Alonso, 2002), expressed in fork length (L_F), were converted to L_S using the equation provided in Garc a-V squez et al. (2009):

$$L_S = 0.965 L_F - 1.504, r^2 = 0.997, P < 0.001.$$

The growth parameters of the VBGF curves were compared between sexes using the likelihood ratio test (Tomassone et al., 1993) and applying the weighted sum of squares of Kimura (1980). For k populations, the likelihood ratio test S_{ML} was compared with χ^2 using 3 degrees of freedom (3 parameters):

$$S_{ML} = \sum_{i=1}^k n_i * [\ln(S_c^2) - \ln(S_k^2)]$$

where n_i is the number of individuals of the k^{th} population, S_c^2 is the residual variance of the pooled model (for all populations), and S_k^2 is the residual variance of the models of the k populations, with $k = 2$ here.

Results

Over the study period, 562 otoliths of *B. rousseauxii* (11–120 cm L_S) were analysed, of which 65 (11.6 %) were

discarded because they could not be interpreted. Of the 497 fish used, 142 were females (L_S range 67–120 cm, mean \pm SD; 93 ± 9.6 cm), 95 were males (L_S range 49–112 cm, mean \pm SD, 81 ± 12.2 cm), and 260 could not be sexed (L_S range 11–119 cm, mean \pm SD, 79 ± 19.2 cm).

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

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

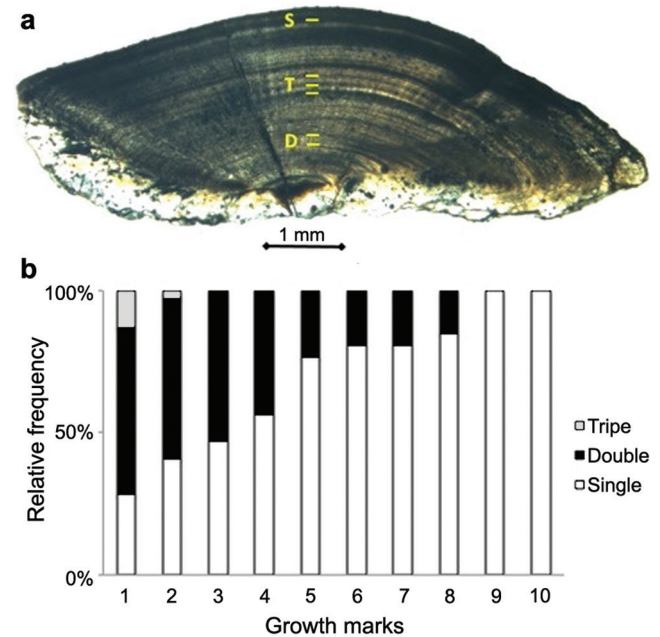


Fig. 3. Mean and standard deviation (SD) of each growth ring radius in otoliths of *Brachyplatystoma rousseauxii* from the Madeira River basin.

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

RMI (carried out on 357 individuals) significantly varied among months (one-way ANOVA, $F_{11, 345} = 2.07$, P

< 0.01), with lowest mean values in April (mean = 71.76 ± SD) and September (mean = 72.10 ± SD) (Fig. 5). This indicates the formation of two opaque rings per year, hence two periods of reduced growth: one during the high-waters in April and the second during the low water period in September.

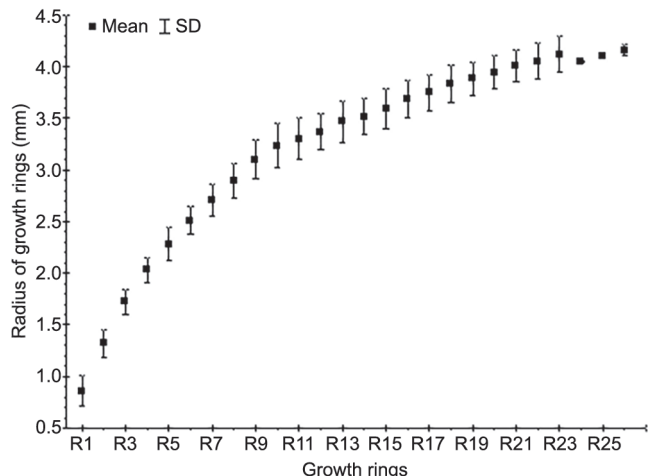


Fig. 4a. Different types of growth rings; and **b.** their relative proportions, in transverse thin sections of *Brachyplatystoma rousseauxii* from the Madeira River basin. *S*-single, *D*-double, *T*-triple rings.

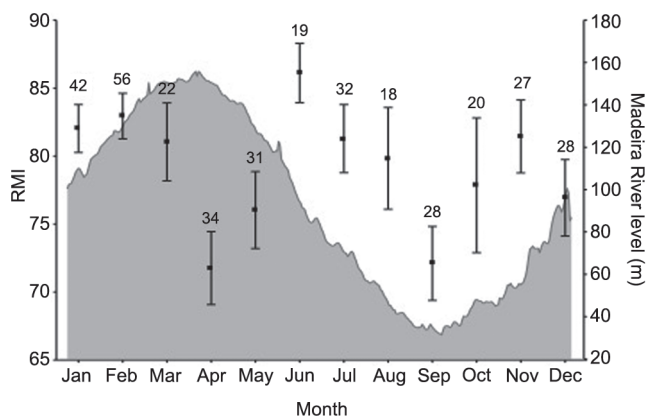


Fig. 5. Mean monthly relative marginal increment (RMI ± S.D.) of 357 *Brachyplatystoma rousseauxii*'s otoliths in relation to the hydrological cycle in the Madeira River basin. The values above bars indicate the number of otoliths analysed each month.

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

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

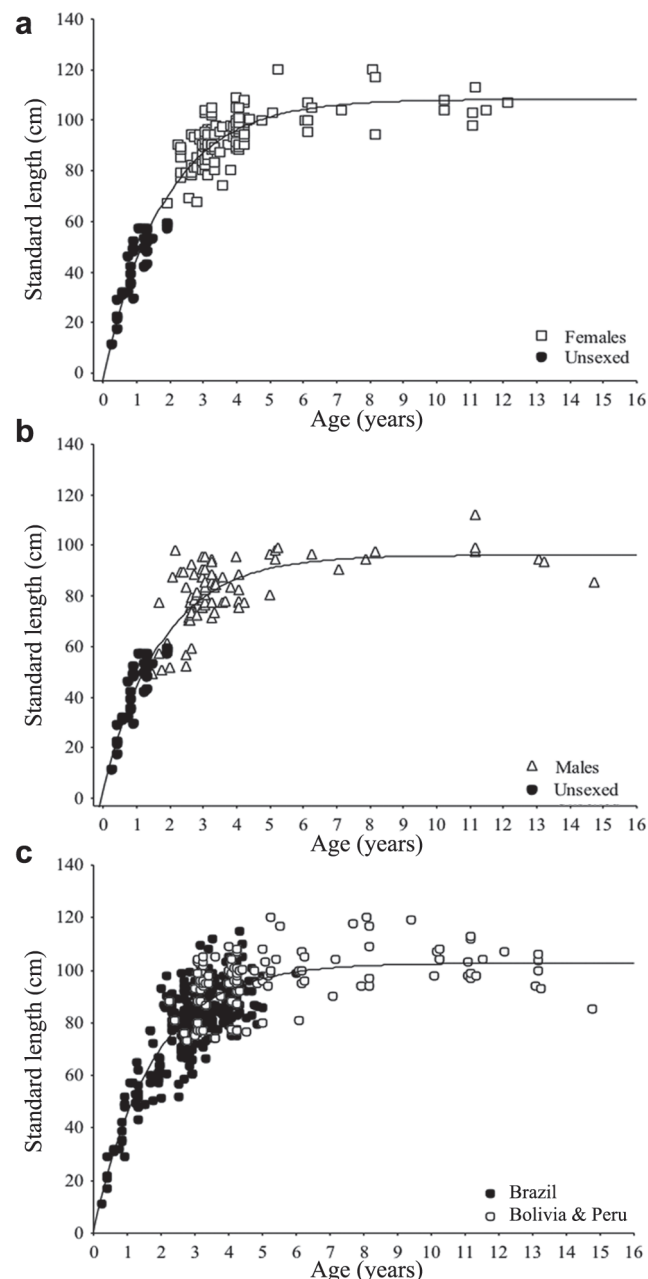


Fig. 6. Length-at-age distribution and von Bertalanffy growth function (solid lines) of *Brachyplatystoma rousseauxii*: **a.** females ($N = 142$); **b.** males ($N = 95$); and **c.** females, males and unsexed individuals pooled ($N = 497$) in the lower / middle (Brazil) and in the upper (Bolivia and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

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

Tab. 1. Standard length-at-age of *Brachyplatystoma rousseauxii* in the Madeira River basin and along the Amazon River mainstem (from the Estuary to Iquitos; Alonso 2002), calculated from the VBGF. Total refers to females + males + unsexed individuals. *Although Alonso (2002) did not observe fish older than 8 years, we know from other studies using length-frequency analyses (Garc a-V squez et al., 2009, C rdoba et al., 2013) that this species grow at least as old as 13 years in the Amazonas, hence we calculated length-at-age up to 15 years old as well, using VBG parameters taken from Alonso.

Age (years)	Length-at-age (cm)					
	Madeira			Amazon †		
	Total	Females	Males	Total	Females	Males
1	45.3	44.8	43.8	52.2	54.7	49.4
2	70.3	71.7	66.6	73.2	76.4	69.0
3	84.4	87.2	79.4	88.8	92.2	83.6
4	92.4	96.1	86.7	100.3	103.6	94.5
5	96.9	101.3	90.8	109.0	112.0	102.7
6	99.5	104.2	93.2	115.4	118.0	108.8
7	100.9	106.0	94.5	120.2	122.4	113.4
8	101.8	106.9	95.2	123.7	125.6	116.8
9	102.2	107.5	95.7	126.3	127.9	119.4
10	102.5	107.9	95.9	128.3	129.5	121.3
11	102.6	108.0	96.0	129.8	130.8	122.7
12	102.7	108.2	96.1	130.8	131.7	123.8
13	102.8	108.2	96.1	131.7	132.0	124.6
14	102.8	108.3	96.2	132.3	132.8	125.2
15	102.8	108.3	96.2	132.7	133.1	125.7

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

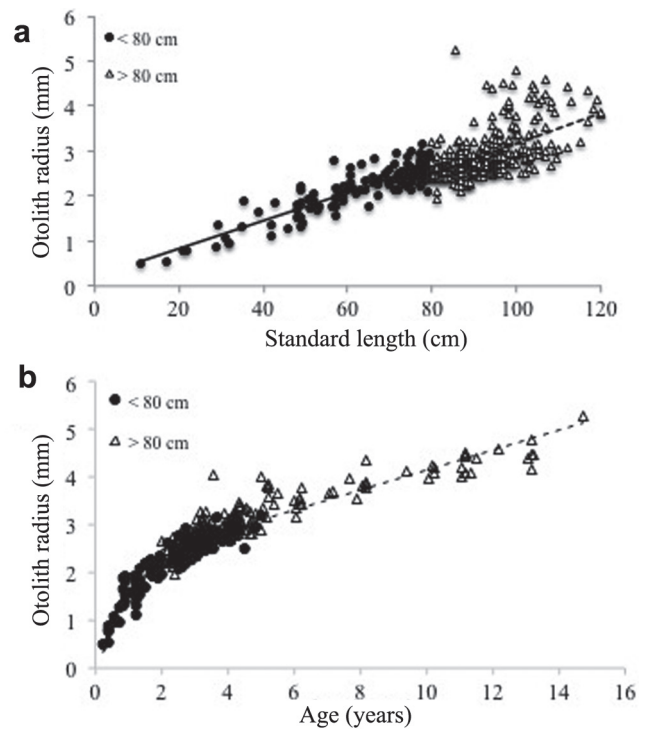


Fig. 7.a. Relationship between fish standard length and otolith radius for *Brachyplatystoma rousseauxii* below 80 cm (black circles, black line: $y = 0.031x + 0.209$, $r^2 = 0.805$, $P < 0.001$) and above 80 cm (white triangles, broken line: $y = 0.034x - 0.223$, $r^2 = 0.328$, $P < 0.001$); and **b.**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

Discussion

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

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

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

The number of growth rings formed during a complete annual cycle in the otoliths and other body hard parts (mainly scales and vertebrae) of Amazonian fishes is particularly interesting. All fish studied in western Amazonia, close to the Andes, display a single growth ring per year during the low water period, whether they belong to the Characiformes, *Prochilodus nigricans* Spix & Agassiz, 1829 in Bolivia (Loubens, Panfili, 1992) and Ecuador (Silva, Stewart, 2006), *Colossoma macropomum* (Cuvier, 1816), *Piaractus brachipomus* (Cuvier, 1818), and *Pygocentrus nattereri* Kner, 1858 in Bolivia (Loubens, Panfili 1997, 2001; Duponchelle *et al.*, 2007, respectively), the Siluriformes, *Pseudoplatystoma fasciatum* (Linnaeus, 1766) and *Pseudoplatystoma tigrinum* (Valenciennes, 1840) in Bolivia (Loubens, Panfili, 2000), the Perciformes, *Plagioscion squamosissimus* (Heckel, 1840) in Bolivia (Loubens, 2003) or the Osteoglossiformes, *Osteoglossum bicirrhosum* (Cuvier, 1829) in Peru (Duponchelle *et al.*, 2012).

On the other hand, fish of these same orders, and sometimes the same species, tend to present two growth rings per annual cycle in central Amazonia, Brazil: in Characiformes, *P. nigricans* (Oliveira, 1996), *C. macropomum* (Villacorta-Correa, 1997), *Semaprochilodus insignis* (Jardine, 1841)

(Viera, 1999); in Siluriformes: *Calophysus macropterus* (Lichtenstein, 1819) (Pérez, Fabr , 2009), *Hypophthalmus marginatus* Valenciennes, 1840 (Cutrim, Batista, 2005); and in Osteoglossiformes: *Arapaima* sp. (Arantes *et al.*, 2010). One of these biannuals usually forms during the low water season as well, similar to the only annual ring formed in western Amazonian fishes, and the other ring forms during the flood. The interpretation of these two periods of reduced growth varies according to studies or species: it could be associated with food limitations during the low water period and with reproductive activities during the flood, according to P rez, Fabr  (2009) and Arantes *et al.* (2010), or to reproductive migrations during the low waters and food limitations during the flood according to Cutrim, Batista (2005). Notable exceptions in central Amazonia are *Schizodon fasciatus* Spix & Agassiz, 1829, which forms a single ring per year during the flood (Fabr , Saint Paul, 1998) and *Cichla temensis* Humboldt, 1821, which forms a single ring during the receding water period (Campos *et al.*, 2015).

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

The reason why a second annual ring forms during the low water season in *B. rousseauxii* could also relate to food limitation, although not for the same causes. During the low water season, the concentration in the main river channels of fish upon which *B. rousseauxii* preys is supposed to be maximum and should therefore provide optimum growth conditions. This is also the period of the hydrological cycle, however, when all the other large predatory species, including all large catfishes (*Brachyplatystoma* spp., *Pseudoplatystoma* spp. and *Zungaro zungaro* (Humboldt, 1821)) (Doria, Lima, 2015) and river dolphins (Silva *et al.*, 2008; Crema *et al.*, 2014) are concentrated in the river channels and compete over the same resources. Although *B. rousseauxii* is an apex predator, this competitive situation could result in an unfavourable ratio of energy expenditure over food availability and hence, in a reduced growth rate. Similar patterns of reduced growth rate in fishes under increased densities and related competition has been widely reported in the literature, for Chinook Salmon (Mazur *et al.*, 1993), Brown Trout (V llestad *et al.*, 2002) and other salmonids (Taniguchi, Nakano, 2000; Puffer *et al.*, 2015).

Growth. Despite the fact that more than half the fish could not be sexed, the growth dimorphism in favour of females,

already reported in the Amazon River mainstem (Alonso, 2002; Garc a-V squez *et al.*, 2009; C rdoba *et al.*, 2013) was also observed in the Madeira basin. Females did grow faster than males. Fish from the Madeira, however, had an overall slower growth than fish from the Amazon River mainstem (Tab. 1). The difference ranged, on average, from about 10 cm at one year old to 25 cm at 15 years old for females, from over 5 cm at one year old to ~ 30 cm at 15 years old for males, and from 7 cm at one year old to nearly 30 cm at 15 years old for females, males and unsexed individuals together. This important difference also translates in the maximum observed lengths between the two systems: *B. rousseauxii* of 150 cm L_s are, or at least were, regularly observed in the upper Amazon (Garc a-V squez *et al.*, 2009; C rdoba *et al.*, 2013), whereas they barely reach 130 cm L_s in the upper Madeira (Van Damme *et al.*, 2011; Carvajal-Vallejos *et al.*, 2014). Out of the ~ 500 individuals analysed for the present study none was larger than 120 cm L_s . This growth difference is further emphasized by the differences in level of exploitation between the two systems. Indeed, fisheries usually harvest the largest specimens and often induce a decrease in the maximum size of exploited populations (Rochet, Trenckel, 2003). Fishery exploitation is close to over-exploitation in both the Peruvian (Garc a-V squez *et al.*, 2009) and Colombian (C rdoba *et al.*, 2013) waters, whereas it started later and remains relatively weak in the Bolivian Amazon (Goulding, 1979; Van Damme *et al.*, 2011). Yet, in spite of a lower exploitation pressure, the maximum sizes are smaller in the upper Madeira.

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

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

Another explanation could lie in a poorer nutritious value of the prey fishes consumed in the Madeira vs. the Amazon systems. Whereas *B. rousseauxii* predominantly feeds upon detritivorous-herbivorous (*Brycon* spp., *Mylossoma* spp.) and omnivorous (*Triporthes* spp.) migratory Characiformes

in the Amazon River mainstem (Barthem, Goulding, 1997; Garc a-V squez *et al.*, 2009), its main prey fishes in the Madeira River are the carnivorous *Pimelodina flavipinnis* Steindachner, 1876 and *Hypophthalmus marginatus* (Cella-Ribeiro *et al.*, 2016). These last two species are invertivorous (Santos *et al.*, 2006) and planktivorous (Carvalho, 1980; Cutrim, Batista, 2005; Cella-Ribeiro *et al.*, 2016), respectively. At each transfer from one level of the food web to the upper level, a large part of the energy is lost in heat (Odum, 1988), which should reduce the energy content of species higher in the food web. Vismara *et al.* (2004) indeed observed a decreased caloric content from herbivorous to carnivorous fish species in the upper Paran  river floodplain. Hence, foraging on carnivorous species in the Madeira River instead of on detritivorous-herbivorous species in the Amazon River mainstem might partly account for the slower growth of *B. rousseauxii* in the Madeira.

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

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

In addition to growth differences found in the two systems, one of the most interesting results of this study was the clear age segregation between the lower and upper Madeira. Apart from one specimen, all fish caught in the Brazilian portion of the Madeira were less than 5 years old, including the larger ones, whereas most large individuals caught in Bolivia and Peru were between 5 and 15 years old. This clearly confirms that after their upstream reproductive runs in the upper Mamor , B ni and Madre de Dios Rivers,

B. rousseauxii specimens do not go back down to central Amazonia, which had already been suggested by recent otolith microchemistry analyses (Duponchelle *et al.*, 2016). Furthermore, this result also indicates that once they enter the Madeira, or home back to the Madeira, they do not just stay in the Madeira basin, they remain within the upper portion of the basin, within Bolivia and Peru.

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

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

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