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Age validation and contrasted growth performances of *Pseudoplatystoma punctifer* (Siluriformes: Pimelodidae) in two river systems of the Western Amazon

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The doncella *Pseudoplatystoma punctifer* is an economically and ecologically important catfish in the Amazon basin. However, little is known about its age, growth and population dynamics parameters. This study aims to validate the formation of growth marks in vertebrae of individuals collected from two rivers systems of the Peruvian Amazon (Amazon-Marañón-Ucayali and Putumayo) and compare growth parameters using the von Bertalanffy growth function between sexes and systems. A total of 372 individuals from the Amazon-Marañón-Ucayali (AMU) system and 93 from the Putumayo River were analyzed. The formation of one growth ring per year was validated and the individual ages ranged from zero to nine years old. Females grew significantly larger than males in both systems. Both females and males grew significantly better in the AMU system than in the Putumayo River. Maximum observed length and size at maturity in the AMU system were lower than those reported in previous studies in the area, and together with an important proportion of juveniles in the catches, suggest that the species is heavily exploited. Further studies on the reproductive biology and population dynamics of the doncella are needed in order to implement management measures more in line with the current situation.

Keywords: Amazonas-Marañón-Ucayali, Catfish, Fisheries management, Putumayo, Vertebrae.

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La doncella *Pseudoplatystoma punctifer* es un bagre de importancia económica y ecológica en la cuenca Amazonica. Pese a ello, poco se conoce acerca de parámetros de edad, crecimiento y dinámica poblacional. Este estudio tuvo como objetivo validar la formación de marcas de crecimiento en vértebras de individuos colectados en dos sistemas fluviales de la Amazonia Peruana (Amazonas-Marañón-Ucayali y Putumayo) y comparar los parámetros de crecimiento usando la función de von Bertalanffy entre sexos y sistemas. Fueron analizados 372 individuos del sistema Amazonas-Marañón-Ucayali (AMU) y 93 del Putumayo. Se validó la formación de un anillo de crecimiento por año, la edad osciló entre cero y nueve años. Las hembras fueron significativamente más grandes que los machos en ambos sistemas. Para ambos sexos el crecimiento fue significativamente mayor en el sistema AMU que en el Putumayo. Las máximas tallas y edades de primera madurez observadas en el sistema AMU fueron menores a las reportadas en estudios previos en el área, y junto con un considerable porcentaje de juveniles presentes en las capturas, se sugiere que la especie está siendo fuertemente explotada. Son necesarios estudios de biología reproductiva y dinámica poblacional de doncella para implementar medidas de manejo acordes a la situación actual.

Palabras clave: Amazonas-Marañón-Ucayali, Bagre, Manejo de pesquerías, Putumayo, Vértebra.

INTRODUCTION

The Amazon basin is home to the highest diversity of freshwater fish species on earth (Jézéquel *et al*., 2020). The order Siluriformes, fish with plates or bare skin, is one of the most diverse and widely distributed groups in the Amazon basin (Burgess, 1989). It is also one of the most exploited by fishing activity (Garcia *et al*., 2009; Barletta *et al*., 2016; Doria *et al*., 2018; García-Dávila *et al*., 2018). Within the order, the family Pimelodidae hosts many large and commercially important catfishes, such as the species *Pseudoplatystoma punctifer* (Castelnau, 1855), known as "doncella" in Peru and "surubim" in Brazil. The doncella has a wide distribution in the Amazon, being found in countries such as Peru, Colombia, Bolivia, Ecuador and Brazil, although it is rare or absent at the mouth of the Amazon. It inhabits the headwaters of rivers and is also frequent in areas protected by trunks, branches and vegetation of lotic environments (Reid, 1983; Loubens, Panfili, 2000). It has migratory habits and plays an important ecological role as an efficient predator (Barthem, Goulding, 1997, 2007). The species was formerly known as *P. fasciatum* (Linnaeus, 1766) before Buitrago-Suárez, Burr (2007), in a systematic review based on morphological characters, decided that *P. fasciatum* was restricted to the Guyana shield basins and that the species distributed in the rest of the Amazon basin was *P. punctifer*. This segregation, however, was not supported by subsequent molecular analyses, that could not differentiate between *P. fasciatum* and *P. punctifer* (Torrico *et al*., 2009; Carvalho-Costa *et al*., 2011). Furthermore, more recent molecular analyses evidenced the existence of two clearly separated species within what Buitrago-Suárez, Burr (2007) described as *P. punctifer*: a species with the typical black-and-white striping pattern of *P. fasciatum* and another, less common one lacking the black stripes and having a distinct mouth shape that closely resembles what Castelnau had described as *Platystoma punctifer* in 1855 (García-Dávila *et al*., 2013). Although a systematic revision of these species is clearly called for, for the sake of homogeneity, we will keep referring to *Pseudoplatystoma punctifer* in the rest of the text while talking about the typical black-and white-striped species.

Despite the species' wide distribution, economic and ecological importance, little is known about its population dynamics, reproduction or age and growth patterns. As for many others fish of commercial importance, fishing has become one of the main threats to the species (de Jesus, Kohler, 2004; Barletta *et al*., 2016; Castello, Macedo, 2016; Duponchelle *et al*., 2021). Owing to its large size (>1 m) and few intra-muscular spines, this species is one of the main components in the fisheries landings of the Amazon (Barthem, Goulding 1997, 2007; Garcia *et al*., 2009; Barletta *et al*., 2016; Doria *et al*., 2018; García-Dávila *et al*., 2018). Young stages are also marketed for ornamental purposes (Padilla-Pérez *et al*., 2001; García-Dávila *et al*., 2018, 2021). The doncella has been a major component of fisheries landings of the Peruvian Amazon since the early nineties (Garcia *et al*., 2009) and its extraction was 562 tons in 2019, representing 3.2% of the Amazonian fish landings (PRODUCE, 2020).

Age and growth studies are important tools for the interpretation of population dynamics in fish and provide the basis for establishing resource management strategies (Campana, Thorrold, 2001; Hutchinson, TenBrink, 2011). Counting growth marks on calcareous structures, such as otoliths, vertebrae or scales, is a widely used method for age estimation in fish and its effectiveness requires that the results are validated (Campana, 2001). In the Amazon basin, counting growth marks in calcareous structures has been successfully carried out in different species (*e.g*., Loubens, Panfili, 1992, 1997, 2001; Loubens, 2003; Cutrim, Batista, 2005; Silva, Stewart, 2006; Duponchelle *et al*., 2007; Pérez, Fabré, 2009; Duponchelle *et al*., 2012; Hauser *et al*., 2018), including the genus *Pseudoplatystoma* Bleeker, 1862 in the Mamoré River basin in Bolivia, where the formation of a single annual growth mark was validated using vertebrae (Loubens, Panfili, 2000). In the Peruvian Amazon, where the doncella is among the most commercially important species (Garcia *et al*., 2009), information regarding age and growth parameters of this species are lacking. The current fishing regulations impose a minimum size of capture for the entire Peruvian Amazon (Ministerial Resolution N° 147-2001-PE and Supreme Decree N° 015-2009-PRODUCE) without considering that, in widely distributed species such as the doncella, populations of the same species could have different growth rates, hence different size at maturity (Vazzoler, 1982) and might therefore require different management measures. Previous studies have reported a slower growth in populations of *Osteoglossum bicirrhosum* (Cuvier, 1829) (Duponchelle *et al*., 2012) and *Prochilodus nigricans* Spix & Agassiz, 1829 (Bonilla-Castillo *et al*., 2018) in the Putumayo River when compared to populations of the Amazon-Ucayali-Marañón system. The aim of this study was to validate the formation of growth marks in doncella vertebrae from two different river systems (Amazon-Marañón-Ucayali and Putumayo) of the Peruvian Amazon, and investigate the potential existence of age and growth differences between river systems, hypothesising that as for the previously mentioned species, *P. punctifer* would have a slower growth in the Putumayo River.

MATERIAL AND METHODS

Fish sampling and study area. Vertebrae of the typical black-and-white-striped doncella were collected between July 2008 and July 2010 at landing sites in the Amazonas (Caballococha), Ucayali (Jenaro Herrera, Requena and Pucallpa), Marañón (Nauta) and Putumayo rivers (San Antonio del Estrecho) (Fig. 1). The Marañón and Ucayali are white-water rivers born in the Andean Piedmont in Perú and their confluence form the Amazonas River. These rivers carry suspended solids (both organic and inorganic) and rich nutrients from the Andes. Their network is characterized by meanders, oxbows, and streams, many of which flood annually during the rainy season (Hales, Petry, 2008). The Marañón River has a length of 1707 km (ANA, 2011), its average velocity on the lower portion is 1.65 $m.s^{-1}$ with flow ranging between 7000 to 25000 $m^3.s^{-1}$ (IRD *et al*., 2011). The Ucayali River has a length of 2670 km, its average velocity is between 1.5 to 2.5 $m.s^{-1}$ (MTC, 2005) with a flow ranging from 2700 to 20000 $m^3.s^{-1}$ in the lower portion (IRD *et al*., 2011). From the confluence of these two rivers in Peru to the Atlantic Ocean in Brazil, the Amazon River is approximately 3750 km long representing the largest river system on earth (Hales, Petry, 2008) with an average velocity of 1.48 $m.s^{-1}$ and flow between 10000 to 46000 $m^3.s^{-1}$ in the Peruvian portion (IRD *et al*., 2011). In the estuary, the discharge is estimated at 209000 $m^3.s^{-1}$ (Guyot *et al*., 2007). The Putumayo River is one of the two major affluents of Colombia flowing into the Amazon River, with a length of 2000 km, of which ~1500 travels the Colombian, Ecuadorian and Peruvian territories (in high and median altitudes) whereas the last 450 km are in Brazil (González *et al*., 2006). It is also a white-water river and its origin is in the Andes mountains of Colombia. Due to its equatorial latitudinal position, the Putumayo River basin is a region with particularly abundant rainfall throughout the year (Salazar *et al*., 2006). The average velocity of the Putumayo River is between 0.5 to 1.0 $m.s^{-1}$ with a flow ranging from 250 to 7000 $m^3.s^{-1}$ (IDEAM, 2004).

Fish vertebrae were acquired directly from known traders with whom previous agreement was made to ensure the geographic origin of the individuals. The collected individuals were measured at the landing sites to the nearest mm, recording standard length (L_S), total length (L_T), and body mass with a digital handheld scale of 20 kg capacity and 0.01 kg sensitivity. The stage of gonadal maturity was determined by direct observation according to the scale of Núñez, Duponchelle (2009). The first five vertebrae were extracted from each individual and taken to the facilities of the Quistococha Experimental Centre of the Peruvian Amazon Research Institute (IIAP) for processing. In addition, a collection was made in the Ucayali River (Pucallpa) in November 2017 to complete the size range of small individuals and improve data modelling. This material was processed in the Ichthyology Department of Museo de Historia Natural of Universidad Nacional Mayor de San Marcos (MHN-UNMSM). Specimens were deposited at the Ichthyological Collection of MHN-UNMSM under the catalog numbers: MUSM 46080, 50947, 69601–69604.

Vertebrae processing and analysis. The processing followed the guidelines of Loubens, Panfili (2000). The vertebrae were boiled in water until most of the adhering soft tissue was released and the remaining tissue was removed with a soft-bristled brush. They were then placed in an oven at 40 °C for approximately 48 hours until they

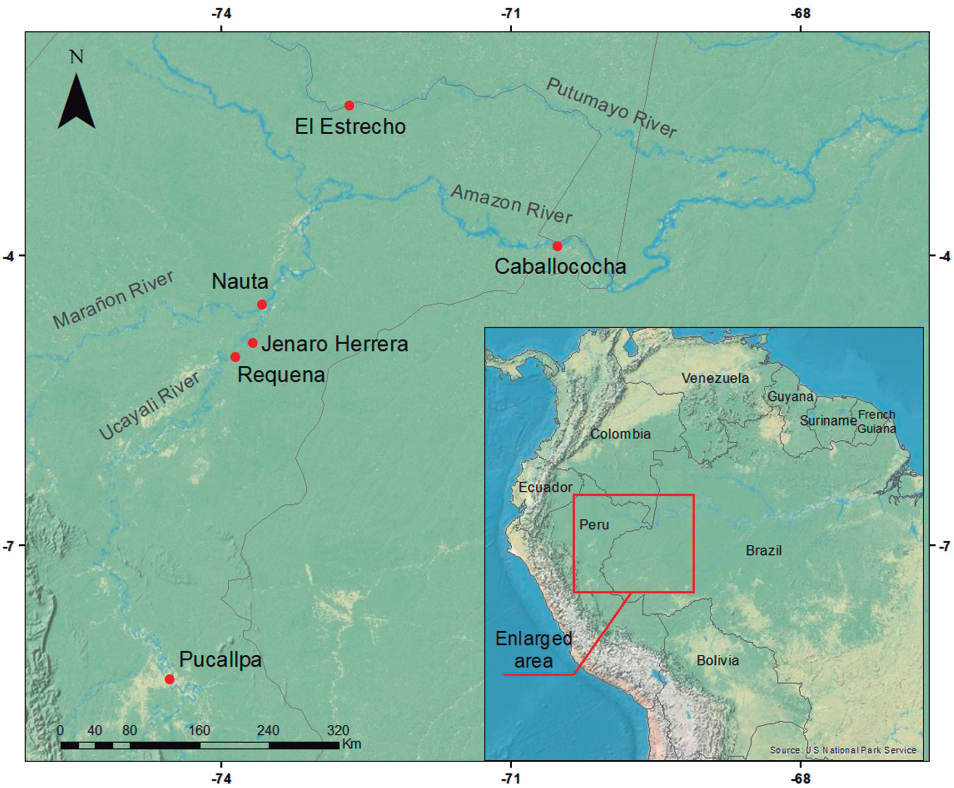

FIGURE 1 | Map of sampling sites of *Pseudoplatystoma punctifer* in the Peruvian Amazon River systems. Sampling sites are symbolized by red dots.

were completely dry to be stored in individual packaging duly labelled. The vertebrae were observed in frontal section and with light reflected on a dark background with a Leica MZ16 stereoscopic microscope with a built-in camera connected to a computer, from which a photographic record was made. Each vertebrae was then cross-sectioned (transversal section) with a slow-speed electric cutter to confirm the readings on the corpus calcareum (Loubens, Panfili, 2000). The images obtained were analysed with the software AxioVision v4.8.

Growth marks were identified by their formation around the centre of the vertebra, under reflected light, following Loubens, Panfili (2000): broad light bands (opaque zones) alternating with thin dark bands (hyaline rings) were observed. The set of a light band and a dark band corresponds to a growth ring, the distance between the light bands becoming shorter as they move away from the centre of the vertebra. Light, broad bands form during the fast growth stages of the fish, while dark, thin bands form during the slow growth stages; when fish are very old, the light and dark bands can become very thin, making it difficult to identify growth rings (Panfili *et al.*, 2002). The identification of the growth marks was carried out independently by two separate observers, at a 90° angle in order to more reliably compare individual results. When the two independent lectures were in disagreement, the vertebrae were re-interpretated by the observers, this time together. When the disagreement remained, the vertebrae were discarded. All the interpretation were finally agreed by the two observers, so, there were no discarded vertebrae. Distance in mm, on a known scale, were taken from the centre of the vertebrae to each hyaline ring and to the edge or the vertebrae.

Given the relative proximity of the areas sampled in the Marañón, Ucayali and Amazon systems (Fig. 1), their similarity in hydrological dynamics, and considering the migratory habits of the species, vertebrae from these rivers were pooled for the analyses in order to obtain a better coverage of length for growth curves and of months for the validation process. We will there after refer to the Amazon, Marañón and Ucayali rivers as AMU system. Vertebrae from the Putumayo River were analysed independently.

Validation of ring formation and hydrological data. The period of growth ring formation was determined by the Relative Marginal Increment (RMI) method:

$$\text{RMI} = [(R_t - R_n) / (R_n - R_{n-1})]x100$$

where R_t is the total radius of the vertebra, R_n is the distance from the core to the last ring (hyaline ring) and R_{n-1} is the distance from the core to the penultimate ring (Haimovici, Reis, 1984; Fabré, Saint-Paul, 1988). The sudden significant decrease in monthly mean RMI values followed by a gradual increase in it was interpreted as the period of hyaline ring formation. The RMI values for each month during the entire collection period were averaged to obtain data for all possible months in both the AMU system and the Putumayo River.

Water levels were obtained from ORE-HYBAM (Observatoire régional, Hydrologie du bassin Amazonien) and SENAMHI (Servicio Nacional de Meteorología e Hidrología, Perú) from the Tamshiyacu station for the AMU system due to its location in an area where the three rivers converge, with hydrological data from years 2008–2010 with daily values average per month. For the Putumayo River, water levels were obtained from IDEAM (Instituto de Hidrología, Meteorología y Estudios Ambientales) with hydrological data from the El Estrecho station with daily values averaged per month from years 2008–2010.

Individual age in months was calculated by taking into account the month of capture, the number of growth rings and the month of birth (Panfili *et al*., 2002). The month of birth was considered to be the month with the highest proportion of breeding females: February in the AMU system (García *et al*., 2001; Deza-Taboada *et al*., 2005) and April in the Putumayo River (Camacho *et al*., 2006). The following formulae were applied:

- for individuals captured before the month of birth: $E = (12 x A) + 12 + C - N$
- for those captured after the month of birth: $E = (12 x A) + C - N$,

where E is the age of each individual in months, A is the number of growth rings, C is the month of capture and N is the month of birth.

Statistical Analyses. The growth parameters were calculated by the Von Bertalanffy Growth Function (VBGF) using a non-linear estimation (quasi-Newton method) according to the following equation:

$$L_t = L_\infty \left(1 - e^{-K(t-t0)}\right)$$

where L_t is the length at age t, L_∞ is the infinite length, K is the growth rate, t is the age of the fish at L_t, t_0 is the theoretical age of the fish at length 0.

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 (Panfili *et al*., 2002).

Length at first maturity (L_{50}, average length at which 50% of individuals are able to breed) was estimated by fitting the percentage of mature individuals, from stage 2 onwards using the maturity scale of Núñez, Duponchelle (2009), at 5 cm L_S intervals to a logistic function, using non-linear regression, weighted by the number of individuals in each length class (Duponchelle, Panfili, 1998):

$$\%MF = 1/\left[1+e^{(-ax(L-L50))}\right]$$

where *%MF* is the percentage of mature individuals per standard length class, L is the central value of each length class, a is a constant and L_{50} is estimated by the model.

For comparison of length at maturity with previous studies in the Peruvian Amazon (in the discussion section), where the L^{50} is given in fork length (L^F), values were converted using the following equation: $L_S = 0.9776{*}L^F - 1.8379$, $R^2 = 0.9984$, $P<0.001$ (Garcia Vasquez *et al*., unpublished data).

The age at first sexual maturity (A_{50}, average age at which 50% of individuals are able to breed) was calculated form the VBGF as follows (Duponchelle *et al*., 2007):

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

where L_{50} is the size at first sexual maturity and L_∞, K, and t_0 are parameters from the VBGF.

Growth curves were compared between sexes and geographical populations using the maximum likelihood test (Tomassone *et al*., 1993) and applying Kimura (1980) sum of squares. For k populations the maximum likelihood test (S_{ML}) was compared with the X^2 test with 3 degrees of freedom (3 parameters):

$$S_{ML} = \Sigma^k{}_i = n_i x[ln(S_C{}^2) - ln(S_K{}^2)]$$

where n is the number of individuals in the k^{th} population, $S_C{}^2$ is the residual variance of the overall model, $S_K{}^2$ is the residual variance of the k populations. The same test was used for comparisons of growth curves among sexes within a geographical population and between geographical population. Statistical modelling and analyses were performed with Statistica 12.5 software (StatSoft Inc.) (Weiß, 2007).

RESULTS

Vertebrae were collected from 465 individuals of *P. punctifer* during the study period (19.5–92.5 cm L_S): 372 from the AMU system and 93 from the Putumayo River (Tab.

TABLE 1 | Standard length and mass ranges, mean ± standard deviation (SD) and number (N) of *Pseudoplatystoma punctifer* females and males analyzed in AMU system and Putumayo River.

River system	Sex	N	Mean length ± SD (cm)	Length range (cm)	Mean mass ± SD (g)	Mass range (g)
AMU	Females	205	51.4 ± 17.5	21.0–92.5	2329 ± 2318	80–12000
	Males	167	45.1 ± 13.4	19.5–83.0	1417 ± 1278	80–7700
Putumayo	Females	49	50.8 ± 12.2	23.5–74.0	1715 ± 1118	120–4990
	Males	44	45.7 ± 8.8	23.5–58.0	1119 ± 532	150–2240

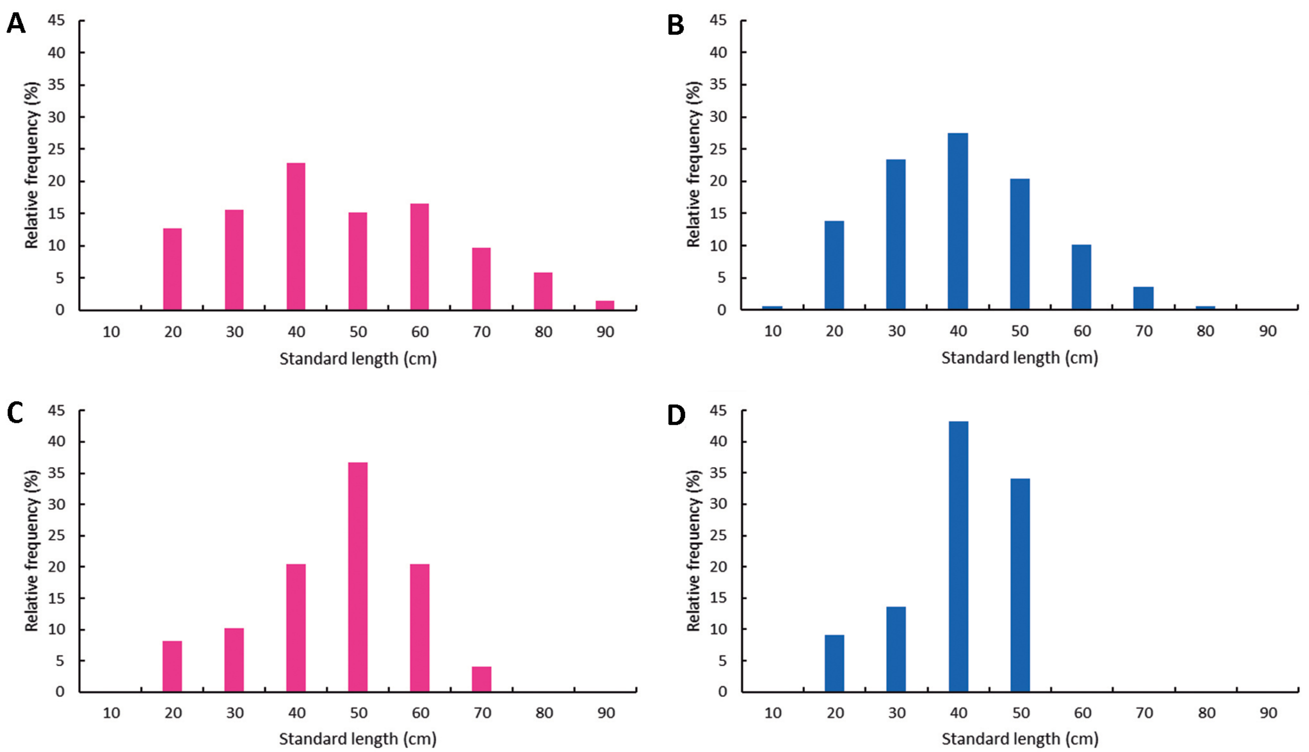

FIGURE 2 | Standard length frequency distributions of *Pseudoplatystoma punctifer* females (left) and males (right) in the **A–B**. AMU system and **C–D**. Putumayo River.

1). In both systems females predominated between 40–60 cm L_S (Figs. 2A, C) and males between 30–50 cm L_S (Figs. 2B, D). All vertebrae were interpreted and included in the analyses for age and growth estimates.

Interpretation of growth rings and validation. Single (a dark band), double (two dark bands close together) and multiple (several dark bands close together) hyaline rings were identified in the vertebrae of *P. punctifer* from the Peruvian Amazon (Figs. 3A–B). Double or multiple rings were occasionally observed only in the first growth marks and occurred before the single rings. In some cases, in the frontal view of the vertebrae, similar but thinner and less intense bands were identified between the hyaline rings, making the identification of growth rings difficult. These marks, however, were differentiated from the hyaline rings in the transversal sections, where the difference in intensity between the two zones was more clearly distinguished; these less intense bands were interpreted as intermediate marks (Figs. 3C–D). Similarly, before the formation of the first ring, very thin and less intense bands were identified very close to the center of the vertebrae and were easily differentiated from the hyaline rings in the transversal section; these bands were interpreted as pre-marks (Figs. 3E–F).

In the AMU system, the first growth ring formed on mean ± SD of 5.34 ± 0.807 mm from the core of the vertebra, the second at 8.75 ± 1.131 mm, the third at 11.55 ± 1.506 mm with a trend of increasing standard deviation as growth rings increased (Fig. 4A).

FIGURE 3 | *Pseudoplatystoma punctifer* vertebrae showing **A–B**. Five growth rings: the first one is multiple, the second one double and the third, fourth and fifth are simple, **C–D**. Two growth rings and **E–F**. One growth ring. Vertebrae center (ctr), hyaline rings (red lines), intermediate mark (i), pre mark (p). Left images: vertebrae frontal view. Right images: vertebrae cross section view with the confirmation of the rings on the corpus calcareum.

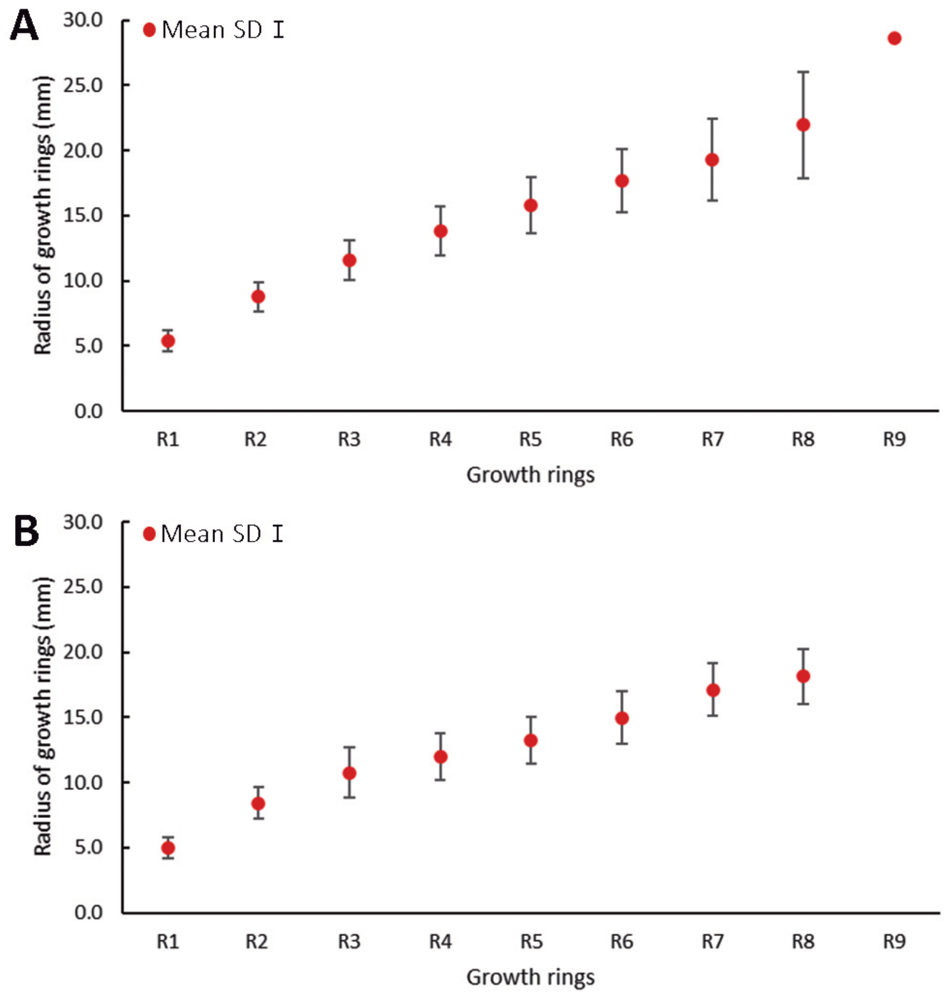

FIGURE 4 | Mean and standard deviation (SD) of each growth ring radius in vertebrae of *Pseudoplatystoma punctifer* from the **A**. AMU system and **B**. Putumayo River.

In the Putumayo River the first growth ring formed at 5.01 ± 0.785 mm, the second at 8.44 ± 1.179 mm, the third at 10.77 ± 1.930 mm with little variation in standard deviation thereafter as growth rings increased (Fig. 4B).

In the AMU system, RMI (carried out on 217 individuals) significantly varied among months (one-way ANOVA, $F_{9,207}$ = 7.45, P<0.001) (details describe in Tab. **S1**) with lowest mean monthly value (17.28 ± 8.31%, mean ± SD) observed in September, after a high value in August (59.70 ± 25.26%), this lower value coinciding with the lowest water level (Fig. 5A). In the Putumayo River, the RMI (carried out on 69 individuals) also significantly varied among months (one-way ANOVA, $F_{6,62}$ = 14.32, P<0.001) (details described in Tab. **S2**) with lowest mean monthly value occurred in November (9.65 ± 3.12%) after a high value in October (41.01 ± 16.58%), also coinciding with a period of low water level (Fig. 5B). In both cases, although samples could not be obtained at some months, the sudden significant drop in monthly mean RMI values (Tabs. **S1** and **S2**) followed by gradually rising values occurred only once over an annual cycle, suggesting the formation of a single hyaline ring (dark band) and thus the formation of one growth ring per year. The broad light bands correspond to fast growth zones related to high metabolic rates and form during the high-water period, while the narrow dark bands correspond to slow growth zones and are related to low metabolic rates that form during the low water period. The formation of the slow-growth (dark) bands occurred in a slightly shorter time than the fast-growth (clear) bands during an annual cycle in both groups (Fig. 5).

Growth and age. In both river systems, individuals below 4 years old and between 20.0 and 60.0 cm L_S predominated, with very few specimens older than 8.0 years and/or larger than 80.0 cm L_S (Fig. 6). The largest and oldest individuals were captured in

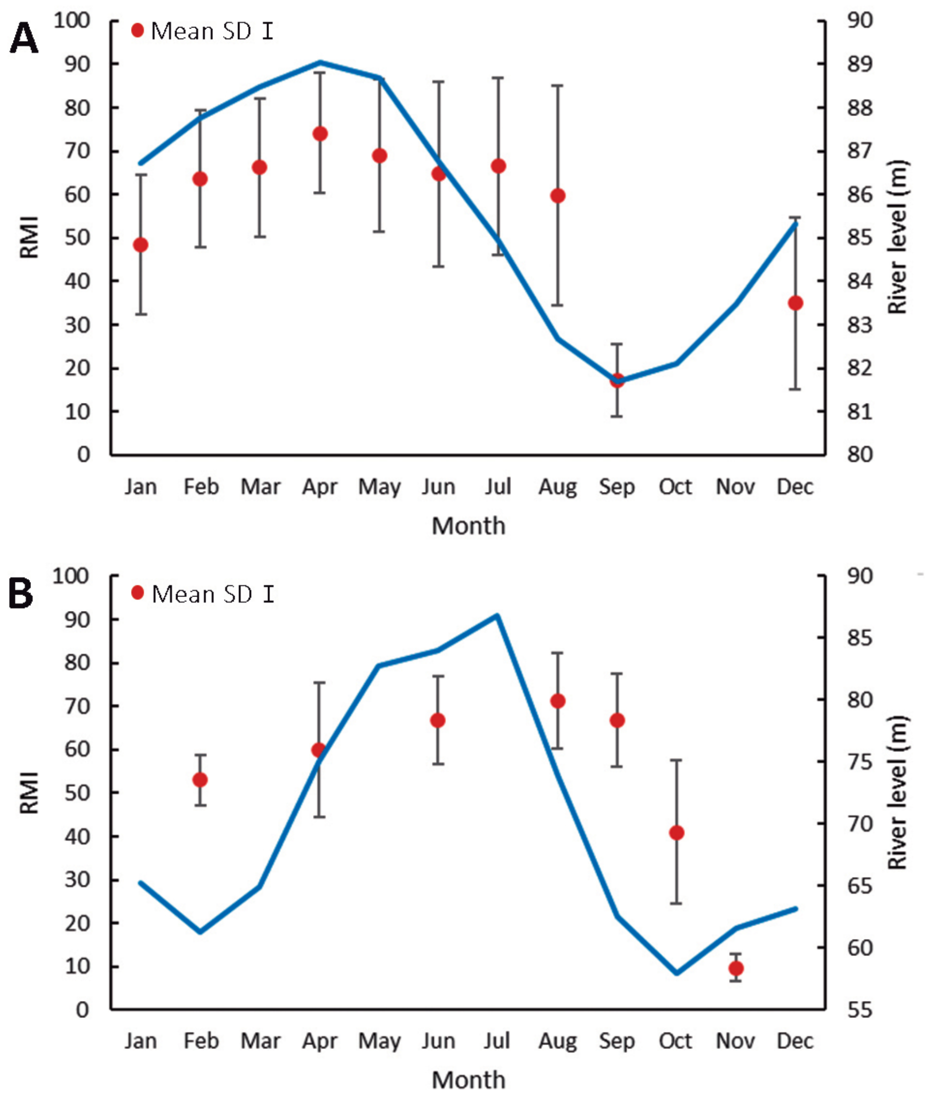

FIGURE 5 | Mean monthly relative marginal increment (RMI ± SD) of *Pseudoplatystoma punctifer* vertebrae in relation to the hydrological cycle in the **A**. AMU system and **B**. Putumayo River. The illustrated hydrological cycles represent the average monthly values from the period 2008–2010.

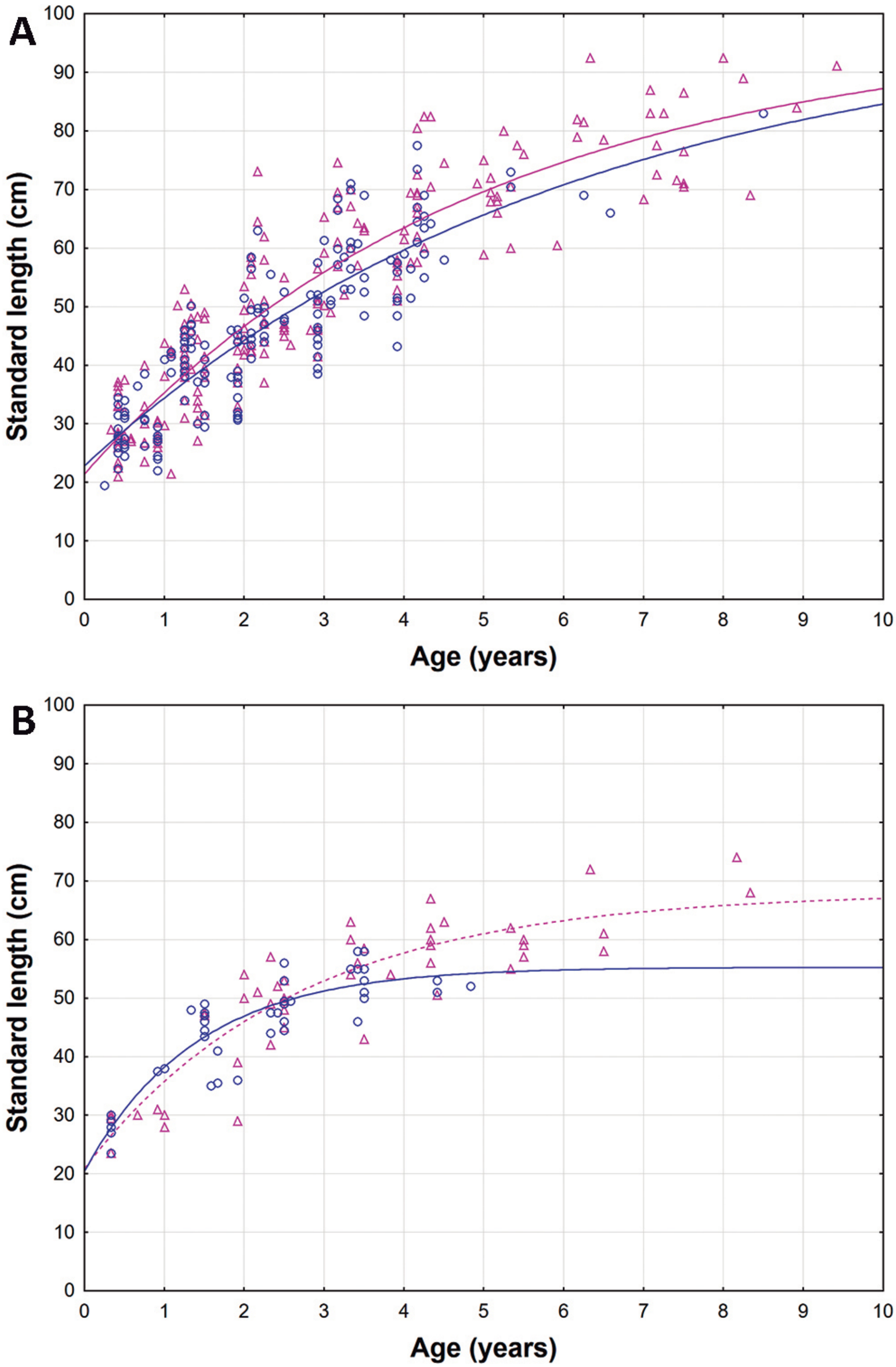

FIGURE 6 | Von Bertalanffy growth curves for *Pseudoplatystoma punctifer* females (pink triangles) and males (blue circles) in the **A**. AMU system and **B**. Putumayo River.

TABLE 2 | Von Bertalanffy growth parameters for *Pseudoplatystoma punctifer* females and males in the AMU system and Putumayo River.

River system	L_∞ (cm)		K		t_0	
	Females	Males	Females	Males	Females	Males
AMU	97.3	99.5	0.20	0.16	-1.23	-1.59
Putumayo	68.1	55.3	0.38	0.71	-0.97	-0.64

the AMU system: the oldest individual was a female of 9.4 years and 91.1 cm L_S; while the largest individuals were two females, both of 92.5 cm L_S and 6.3 and 8.0 years old (Fig. 6A). In the Putumayo River, the largest and oldest individuals were also females of 74.0 and 72.0 cm L_S and 8.2 and 6.3 years old, respectively (Fig. 6B). In contrast with the situation observed in the Putumayo River, the growth curves in the AMU system did not reach the asymptote, despite a larger sample size.

The growth parameters estimated with the von Bertalanffy function are presented in Tab. 2. As observed in Fig. 6, after two or three years old, females had a significantly better growth than males in both the AMU system (S_{ML} = 8.919, P<0.05) and the Putumayo River (S_{ML} = 9.317, P<0.05).

Growth was very similar during the first two to three years in the AMU system and in the Putumayo River for both females and males, then it progressively started to diverge. Overall, fish from the AMU system had largest length–at–age than fish from the Putumayo River, hence a better growth (Fig. 6; Tab. 3). The difference was significant for both females (S_{ML} = 31.773, P<0.0125) and males (S_{ML} = 25.978, P<0.0125): it reached almost 20.0 cm for females and 27.0 cm for males at 9.0 years old (the largest observed age in our sampling, Tab. 3).

TABLE 3 | Standard length-at-age for females and males of *Pseudoplatystoma punctifer* in the AMU system and Putumayo River.

Age (years)	Females length-at-age (cm)		Males length-at-age (cm)	
	AMU	Putumayo	AMU	Putumayo
1	35.3	35.8	34.4	38.2
2	46.6	46.0	44.2	46.9
3	55.9	52.9	52.6	51.2
4	63.5	57.7	59.7	53.3
5	69.6	61.0	65.7	54.3
6	74.7	63.2	70.8	54.8
7	78.8	64.7	75.1	55.0
8	82.2	65.8	78.8	55.2
9	85.0	66.5	81.9	55.2
10	87.2	67.0	84.6	55.3

Sexual maturation. In the AMU system, females were slightly larger (49.5 ± 9.2 cm SD *vs*. 41.0 ± 9.9 cm) and older (2.4 *vs*. 1.7 years old) at sexual maturity than males (Figs. 7 A, B), although differences were not statistically significant (t = 0.63, P = 0.53). The same was observed in the Putumayo River: 42.0 ± 0.2 cm at 1.6 years old for females and 39.0 ± 0.2 cm at 1.1 years old for males (Figs. 7C, D). Owing to the better growth of fishes from the AMU system, both females and males tended to reach maturity at larger sizes in the AMU system than in the Putumayo River, although the differences were not statistically significant (t = 0.82, P = 0.42 and t = 0.20, P = 0.84, for females and males, respectively).

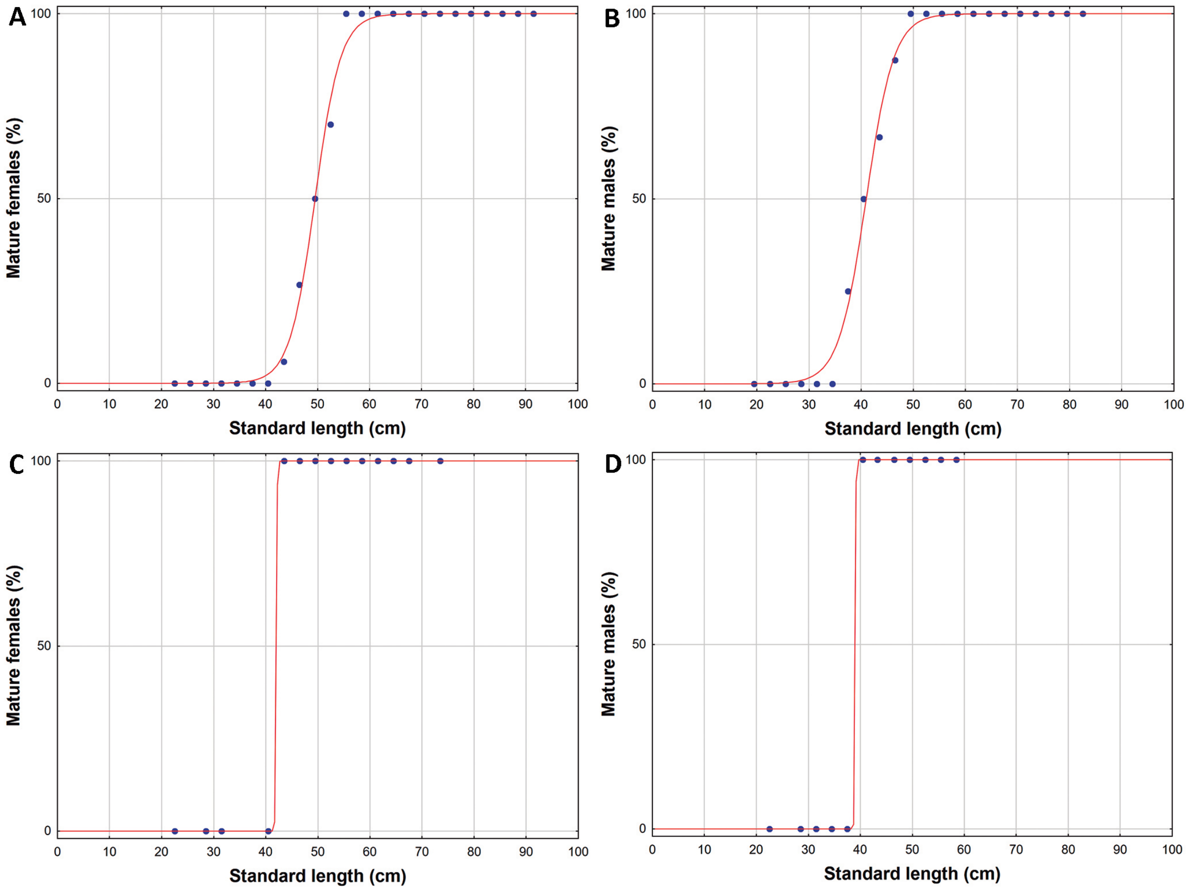

FIGURE 7 | Standard length at first sexual maturity (L_{50}) of *Pseudoplatystoma punctifer* in the **A–B**. AMU system and **C–D**. Putumayo River.

TABLE 4 | Percentage, standard length mean ± standard deviation (SD) and ranges of immature females and males of *Pseudoplatystoma punctifer* in the AMU system and Putumayo River.

River system	Females			Males		
	Percentage	Mean length ± SD (cm)	Length range (cm)	Percentage	Mean length ± SD (cm)	Length range (cm)
AMU	50.5	36.9 ± 8.0	21.0–52.0	40.2	32.6 ± 6.6	19.5–46.0
Putumayo	18.4	30.0 ± 4.0	23.5–39.0	22.7	31.95 ± 5.1	23.5–38.0

The proportion of immature individuals sampled during the study was higher in the AMU system (50.5%) than in the Putumayo River (18.4%) for females, and for males: 40.2% and 22.7% for in the AMU system and Putumayo River, respectively (Tab. 4).

DISCUSSION

The annual formation of growth marks in calcareous structures is composed of fast and slow growth zones, related to high and low metabolic rates (Panfili *et al*., 2002). The timing of mark formation usually depends on food availability, which is closely linked to the hydrological cycle of rivers in the Amazon basin (Junk *et al*., 1989). The seasonality of the water pulse or "flood pulse concept" is the main driver of the performance of organisms and patterns of ecological processes (Junk *et al*., 1989; Junk, Wantzen, 2004). The number of marks and period of formation of the fast and slow growth zones will depend on each species and their ecological patterns. Fish species usually form one yearly growth ring during the low water season in the western and southern parts of the Amazon basin, such as in the order Osteoglossiformes: *Osteoglossum bicirrhosum* in Peru (Duponchelle *et al*., 2012); Characiformes: *Pygocentrus nattereri* Kner, 1858 in Bolivia (Duponchelle *et al*., 2007), *Prochilodus nigricans* in Bolivia (Loubens, Panfili, 1992) and Ecuador (Silva, Stewart, 2006), *Colossoma macropomum* (Cuvier, 1816) (Loubens, Panfili, 1997) and *Piaractus brachypomus* (Cuvier, 1818) (Loubens, Panfili, 2001) in Bolivia; and Perciformes: *Plagioscion squamosissimus* (Heckel, 1840) in Bolivia (Loubens, 2003). On the other hand, many related species tend to form two growth marks per year in the Central Brazilian Amazonia such as the Siluriformes: *Brachyplatystoma rousseauxii* (Castelnau, 1855) (Hauser *et al*., 2018), *Hypophthalmus marginatus* Valenciennes, 1840 (Cutrim, Batista, 2005) and *Calophysus macropterus* (Lichtenstein, 1819) (Pérez, Fabré, 2009); and Osteoglossiformes: *Arapaima* sp. (Arantes *et al*., 2010).

Despite insufficient data at some months in our results, it was possible to determinate that the hyaline rings were formed during the dry season (lower water levels) and early wet season (onset of increased water levels due to increased rainfall intensity) in both, the AMU system and the Putumayo River, indicating the formation of one growth ring per year. These results are consistent with those of Loubens, Panfili (2000) in *P. punctifer* and *P. tigrinum* (Valenciennes, 1840) in the Bolivian Amazon: the zones of slow growth were formed during the dry season and the beginning of the rainy season, coinciding with difficulties in capturing prey and the beginning of the reproductive stage of the species. During the dry season the species would have greater difficulties in capturing prey due to high densities and competition with other predators such as larger catfish and/or dolphins (Barthem, Goulding, 1997; Loubens, Panfili, 2000). Low growth rates in fish due to competition and high densities among predators have been reported in Amazonian catfish (Nuñez *et al*., 2008; Hauser *et al*., 2018) and salmonids (Mazur *et al*., 1993; Taniguchi, Nakano, 2000; Vollestad, 2002; Puffer *et al*., 2017). The reproductive period of a species usually entails great metabolic expenditure for gonadal maturation at the expense of growth rate (Giesel, 1976; Panfili *et al*., 2002). The breeding period of *P. punctifer* starts in November in the AMU system (García *et al*., 2001; Deza-Taboada *et al*., 2005) and in March-April in the Putumayo River (Camacho *et al*., 2006), coinciding with the rising-water period in both systems. In both river systems, growth mark formation may therefore be related to competition – density factors and reproduction. The rapid growth period corresponds to the receding water period, when fish that were sheltered in flooded forests would return to the main river channels and become prey for predators that would strategically wait for capture during this process (Wantzen *et al*., 2002; McKey *et al*., 2016) as described for the doncella by Loubens, Panfili (2000). Using otoliths, a recent study on another species, *P. metaense* Buitrago-Suárez & Burr, 2007 in the Orinoco basin also revealed the formation of a single annual growth mark during the low water period (Pérez, Fabré, 2018). The presence of intermediate and pre-marks, could be attributed to stress conditions that were not necessarily regular during the life history of the individual (Panfili *et al*., 2002), possibly related to feeding competition with other predators.

The observed sexual dimorphism, in which females are larger than males, is common in Amazonian catfish (*e.g*., Alonso, 2002; García Vásquez *et al*., 2009; Córdoba *et al*., 2013; Hauser *et al*., 2018) and has even been reported for the genus *Pseudoplatystoma* in other regions such as in the Bolivian Amazon (Loubens, Panfili, 2000) and in the Orinoco basin (Barbarino, 2005; Pérez, Fabré, 2018). In our results, females were the largest and oldest individuals in both river systems and predominated over males from 60 cm L_S onwards (Fig. 6). Similarly, Loubens, Panfili (2000) in the Mamoré River basin in Bolivia found that the largest individuals of doncella were females, with males rarely exceeding 80 cm L_S while females reached up to 104.5 cm and the oldest individual was a female of 8.7 years. Inturias (2008), also in the Bolivian Amazon, recorded females up to 90.0 cm L_S and 9.9 years of age, while males did not exceed 66.0 cm L_S and 7.8 years. García *et al*. (2001) and Deza-Toboada (2005) also found that females reached larger sizes than males. The maximum sizes of doncella captured in the present study corresponded to two females from the AMU system, both with 92.5 cm L_S. These sizes were below those previously reported in the same region by García *et al*. (2001) and Deza-Taboada *et al*. (2005) with individuals of ~120.0 cm L_S. In the Putumayo River, the largest size was a female of 74 cm L_S, being smaller than that previously reported by Camacho *et al*. (2006) in the same region where individuals exceeding 100.0 cm L_S were sometimes captured.

The reduction in size and longevity in our results, compared to earlier studies, emphasizes the fact that it is becoming less and less feasible to obtain large individuals. As they are highly valued and marketed, they become scarce in the wild due to a strong fishing pressure, as observed in *Cichla temensis* Humbolt, 1821 in the Negro River (Lubich *et al*., 2021). This is reflected in the growth curves where the asymptotic phase of growth is not reached in the AMU system (Fig. 6A). High L_∞ values often occur when there are not enough old, slow-growing individuals in the samples (Pauly, 1979), which was the case in our sampling in spite of a two years sampling effort. In large and commercially valuable species such as the doncella, the decrease of large and long-lived individuals in the wild and, therefore, in landings, is a documented effect of the intensification of fishing exploitation (Castello *et al*., 2013) and of the high selectivity of artisanal and commercial fisheries towards large preferred species, driven by large urban markets (Tregidgo *et al*., 2021). Similar conditions were found in the genus *Pseudoplatystoma* in the lower Paraná River basin (Resende, 2003), in *P. metaense* in the Orinoco River basin (Pérez, Fabré, 2018); in *P. tigrinum* and *P. punctifer* in the central Amazon (Isaac *et al*., 1998; Ruffino, Isaac, 1999); and in *B. rousseauxii* (Córdoba *et al*., 2013) in the Colombian Amazon, where the resource is overexploited. The high fishing pressure supported by doncella in the sampling area is attested by the relatively high proportion of immature individuals in the catches. Although our sampling was not meant to be representative of the landed size distribution, but rather of the entire length distribution available, it nevertheless reflected what the fishers caught, and immature individuals accounted for a large portion of our sampling, particularly is in the AMU system. Capturing fish that have not yet had the opportunity to reproduce, hence to contribute to future generations is an acknowledged source of stock depletion (Myers, Mertz, 1998; Froese, 2004).

Our results indicate important growth differences in doncella between the AMU system and Putumayo River. In addition, differences in size at sexual maturity, although not significant in the present study, were observed, suggesting the existence of different populations in the areas evaluated. These differences in doncella life history traits between watersheds could be due to both genetic and environmental factors (Giesel, 1976; Caswell, 1983; Partridge, Harvey, 1988; Stearns, 1992). Previous studies have shown that distances of ~200 km between geographical populations of *P. punctifer* in Central Amazonia could results in significantly different genetic populations using microsatellite markers (Telles *et al*., 2014). Pereira *et al*. (2009) have also demonstrated the existence of six genetically distinct groups of *P. corruscans* (Spix & Agassiz, 1829) in the Paraná-Paraguay system. The geographic distance between the sampling sites in the AMU system and Putumayo River were much larger than 200 km following the course of the river (Fig. 1) and a genetic differentiation resulting in a better growth in the AMU system can therefore not be excluded. Other studies, however, have reported a lower growth in fish species of the Putumayo River, when compared with the AMU system like in *O. biccirhosum* (Duponchelle *et al*., 2012) and in *P. nigricans* (Bonilla-Castillo *et al*., 2018). The fact that fish of different species tend to have a slower growth in the Putumayo River suggests that stochastic genetic variation (drift, mutations, etc.), which is supposed to be random (Hartl, Clarck, 2007), cannot account alone for the observed patterns and that less favourable environmental conditions in the Putumayo River, compared to other river basins, are a likely complementary explanation. Of course, life-history traits adjustment to local environmental condition could be achieve through phenotypic variation and/or genetic adaptation, *i.e*., progressive selection for genomes better adapted to the local environmental conditions (Partridge, Harvey, 1988; Stearns, 1992; Hartl, Clarck, 2007), but sorting out their relative importance is beyond the scope of this study.

The Putumayo River with its poorly fertile soils with low nutrients contents resulting in low pH, conductivity and chlorophyll-a values characteristics of oligotrophic waters, has previously been considered as less productive than other Amazonian rivers (González *et al*., 2006; Salazar *et al*., 2006). Additionally, chemical contamination resulting from the culture of coca, deforestation, illegal mining (Sierra *et al*., 2017) or high mercury levels in fish (Nuñez-Avellaneda *et al*., 2006) have been reported in the Putumayo, but there is no data yet to support the hypothesis that such contamination would be higher than in the AMU system. As previously pointed out by Bonilla-Castillo *et al*. (2018) a higher fishery exploitation in the Putumayo River than in the AMU system could also account for slower growth in fish populations of the Putumayo River, where the more heavily exploited populations tend to have smaller maximum sizes and slower growth. The available evidence, such as a higher proportion of immature individuals in the catches of the AMU system does not lend support to this hypothesis, nor does the fact that human population density is much higher around Iquitos, which should entail a higher fishing pressure. Nevertheless, further studies would need to be carried out to test these two alternatives and not mutually exclusive hypotheses. Yet, whatever the reasons underlying the observed differences in growth patterns, these have important implication for fisheries management.

In order to maintain the sustainability of a fishery resource, catches should consist of 100% mature individuals and 100% individuals at an optimum size that exceeds the size at first sexual maturity (Froese, 2004). In our results, the existence of immature individuals as part of the catch indicates that juveniles that have not had the opportunity to reproduce at least once in their lives are being harvested, putting the stability of the resource at risk (Myers, Mertz, 1998; Froese, 2004). Several studies have also shown that in large, long-lived fish species, large old female ("megaspawners") provide a better quality of progeny and disproportionately contribute to future generations (Berkeley *et al*., 2004; Froese, 2004; Birkeland, Dayton, 2005; Venturelli *et al*., 2009; Arnold *et al*., 2018), so their permanence in the wild should be taken into account in management measures to ensure the stability and prevalence of the resource.

In the AMU system, very few individuals exceeded 80 cm L_S, not reaching the lengths at first maturity determined by García *et al*. (2001) more than a decade earlier: 90 cm L_F (~86 cm L_S following equation: $L_S = 0.9776{*}L_F - 1{,}8379$, $R^2 = 0.9984$, $P<0.001$, Garcia Vasquez *et al*., unpublished data) for females and 82.5 cm L_F (~79 cm L_S) for males, and set at 86 cm L_F (~82 cm L_S) as minimum catch size in the fishing regulation of the Peruvian Amazon (Ministerial Resolution N° 147–2001–PE and Supreme Decree N° 015–2009–PRODUCE). Although the present study did not aim at precisely determining size at maturity, the results nevertheless suggest a strong decrease in the mean size at maturity of the doncella in the AMU system, from 86 cm L_S in 1996–1997 (García *et al*., 2001) to ~50 cm L_S in 2008–2010 (present study). The reduction in age and size at sexual maturity in a population is an indicator of a higher adult to juvenile mortality ratio (Reznick *et al*., 1990; Stearns, 1992), and is a sign of heavy exploitation of the resource. This and the observed decrease in maximum observed lengths suggest of a strong fishing pressure on the doncella, at least in the AMU system. These results warrant further studies to precisely estimate the state of exploitation of this important resource in the Peruvian Amazon.

The existence of differences in the growth of doncella between river systems should be taken into account for the implementation of management measures, as well as the updating of minimum catch sizes based on the size at sexual maturity. Although part of the sampling occurred in Pucallpa, most samples of the AMU system where from the Loreto region around Iquitos. Further sampling and increased sample numbers in the upper portions of the Ucayali and Marañón systems could reveal growth and other life history traits variations within what we considered here as AMU system. The doncella, despite its ecological and economical importance remains understudied in the Peruvian Amazon. Our results provide evidence of strong fishing pressure on both adults and juveniles and of populations structuring. Further studies investigating the population structure (genetic and life history trait variations) of this important resource in the Peruvian Amazon are needed to provide a sound basis for the development of appropriate fisheries management and conservation measures to ensure the sustainability of the resource.

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REFERENCES

- **Alonso JC.** Padrão espaço-temporal da estrutura populacional e estado atual da exploração pesqueira da dourada *Brachyplatystoma flavicans*, Castelnau, 1855 (Siluriformes: Pimelodidae), no sistema estuário-Amazonas-Solimões. [PhD Thesis]. Manaus, AM: Instituto Nacional de Pesquisas da Amazônia; 2002. https://bdtd.inpa.gov.br/handle/tede/2952
- **Arantes CC, Castello L, Stewart DJ, Cetra M, Queiroz HL.** Population density, growth and reproduction of arapaima in an Amazonian river-floodplain. Ecol Freshw Fish. 2010; 19(3):455–65. https://doi.org/10.1111/j.1600-0633.2010.00431.x
- **Arnold LM, Smith WD, Spencer PD, Evans AN, Heppell SA, Heppell SS.** The role of maternal age and context-dependent maternal effects in the offspring provisioning of a long-lived marine teleost. R. R. Soc. open sci. 2018; 5:(170966). 170966. https://doi.org/10.1098/rsos.170966
- **Autoridad Nacional del Agua (ANA).** Codificación y clasificación de cursos de agua superficiales del Perú [Internet]. Lima; 2011. https://repositorio.ana.gob.pe/handle/20.500.12543/596
- **Barbarino A.** Aspectos biológicos y pesqueros de los bagres rayados *Pseudoplatystoma fasciatum* (Linnaeus 1766) y *P. tigrinum* (Valenciennes 1840) (Siluriformes: Pimelodidae) en la parte baja de los ríos Apure y Arauca, Venezuela. Mem Fund La Salle Cienc Nat. 2005; 163:71–91. http://flasa.msinfo.info/portal/bases/biblo/texto/memoria/men_2005_65_163_71-91.pdf
- **Barletta M, Cussac VE, Agostinho AA, Baigún C, Okada EK, Catella AC *et al*.** Fisheries ecology in South American river basins. In: Craig JF, editor. Freshwater fisheries ecology. John Wiley & Sons; 2016. p.311–48. https://doi.org/10.1002/9781118394380.ch27
- **Barthem R, Goulding M.** Un ecosistema inesperado: la Amazonía revelada por la pesca. Lima: Asociación para la Conservación de la Cuenca Amazónica; 2007.
- **Barthem R, Goulding M.** The catfish connection: ecology, migration, and conservation of Amazon predators. New York: Columbia University Press; 1997.
- **Berkeley SA, Chapman C, Sogard SM.** Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology. 2004; 85(5):1258–64. https://doi.org/10.1890/03-0706

- **Birkeland C, Dayton PK.** The importance in fishery management of leaving the big ones. Trends Ecol Evol. 2005; 20(7):356–58. https://doi.org/10.1016/j.tree.2005.03.015
- **Bonilla-Castillo CA, Córdoba EA, Gómez G, Duponchelle F.** Population dynamics of *Prochilodus nigricans* (Characiformes: Prochilodontidae) in the Putumayo River. Neotrop Ichthyol. 2018; 16(2):1–12. https://doi.org/10.1590/1982-0224-20170139
- **Buitrago-Suárez UA, Burr BM.** Taxonomy of the catfish genus *Pseudoplatystoma* Bleeker (Siluriformes: Pimelodidae) with recognition of eight species. Zootaxa. 2007; 1512(1):1–38. https://doi.org/10.11646/zootaxa.1512.1.1
- **Burgess WE.** An atlas of freshwater and marine catfishes. A preliminary survey of the Siluriformes. New Jersey: TFH Publication, Neptune City; 1989.
- **Camacho K, Alonso JC, Cipamocha C, Agudelo E, Sánchez CL, Freitas A *et al.*** Estructura de tamaños y aspectos reproductivos del recurso pesquero aprovechado en la frontera Colombo-Peruana del río Putumayo. In: Agudelo E, Alonso JC, Moya LA, editors. Perspectivas para el ordenamiento de la pesca y la Acuicultura en el área de integración fronteriza Colombo-Peruana del río Putumayo. Bogotá (DC): Instituto Amazónico de Investigaciones Científicas SINCHI & Instituto Nacional de Desarrollo INADE; 2006. p.47–58.
- **Campana SE.** Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J Fish Biol. 2001; 59(2):197–242. https://doi.org/10.1006/jfbi.2001.1668
- **Campana SE, Thorrold SR.** Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Can J Fish Aquat Sci. 2001; 58(1):30–38. https://doi.org/10.1139/f00-177
- **Carvalho-Costa LF, Piorski NM, Willis SC, Galetti PM, Ortí G.** Molecular systematics of the neotropical shovelnose catfish genus *Pseudoplatystoma* Bleeker 1862 based on nuclear and mtDNA markers. Mol Phylogenet Evol. 2011; 59(1):177–94. https://doi.org/10.1016/j.ympev.2011.02.005
- **Castello L, Macedo MN.** Large-scale degradation of Amazonian freshwater ecosystems. Glob Change Biol. 2016; 22(3):990–1007. https://doi.org/10.1111/gcb.13173
- **Castello L, Mcgrath DG, Hess LL, Coe MT, Lefebvre PA, Petry P *et al*.** The vulnerability of Amazon freshwater ecosystems. Conserv Lett. 2013; 6(4):217–29. https://doi.org/10.1111/conl.12008
- **Caswell H.** Phenotypic plasticity in life-history traits: demographic effects and evolutionary consequences. Am Zool. 1983; 23(1):35–46. https://www.jstor.org/stable/3882552
- **Córdoba EA, León ÁVJ, Bonilla-Castillo CA, Junior MP, Peláez M, Duponchelle F.** Breeding, growth and exploitation of *Brachyplatystoma rousseauxii* Castelnau, 1855 in the Caqueta River, Colombia. Neotrop Ichthyol. 2013; 11(3):637–47. https://doi.org/10.1590/S1679-62252013000300017
- **Cutrim L, Batista VS.** Determinação de idade e crescimento do mapará (*Hypophthalmus marginatus*) na Amazônia Central. Acta Amaz. 2005; 35(1):85–92. https://doi.org/10.1590/S0044-59672005000100013
- **Deza-Taboada SA, Bazán-Albites RS, Culquichicón-M ZG.** Bioecología y pesquería de *Pseudoplatystoma fasciatum* (Linnaeus, 1766; Pisces), Doncella, en la región Ucayali. Folia Amazónica. 2005; 14(2):5–18. https://doi.org/10.24841/fa.v14i2.143
- **Doria CRC, Duponchelle F, Lima MAL, Garcia A, Carvajal-Vallejos FM, Méndez CC *et al*.** Review of fisheries resource use and status in the Madeira River Basin (Brazil, Bolivia, and Peru) before hydroelectric dam completion. Rev Fish Sci Aquac. 2018; 26(4):494–514. https://doi.org/10.1080/23308249.2018.1463511
- **Duponchelle F, Isaac VJ, Doria C, Van Damme PA, Herrera-R GA, Anderson EP *et al*.** Conservation of migratory fishes in the Amazon basin. Aquat Conserv. 2021; 31(5):1087–105. https://doi.org/10.1002/aqc.3550
- **Duponchelle F, Lino F, Hubert N, Panfili J, Renno JF, Baras E *et al*.** Environment-related life-history trait variations of the red-bellied piranha *Pygocentrus nattereri* in two river basins of the Bolivian Amazon. J Fish Biol. 2007; 71(4):1113–34. https://doi.org/10.1111/j.1095-8649.2007.01583.x

- **Duponchelle F, Panfili J.** Variations in age and size of maturity *Oreochromis niloticus*, populations from man-made lakes of Code d´Ivoire. Environ Biol Fish. 1998; 52:453–65. https://doi.org/10.1023/A:1007453731509
- **Duponchelle F, Ruiz Arce A, Waty A, Panfili J, Renno JF, Farfan F *et al*.** Contrasted hydrological systems of the Peruvian Amazon induce differences in growth patterns of the silver arowana, *Osteoglossum bicirrhosum*. Aquat Living Resour. 2012; 25(1):55–66. https://doi.org/10.1051/alr/2012005
- **Fabré NN, Saint-Paul U.** Annulus formation on scales and seasonal growth of the Central Amazonian anostomid *Schizodon fasciatus*. J Fish Biology. 1988; 53(1):1–11. https://doi.org/10.1111/j.1095-8649.1998.tb00103.x
- **Froese R.** Keep it simple: Three indicators to deal with overfishing. Fish Fish. 2004; 5(1):86–91. https://doi.org/10.1111/j.1467-2979.2004.00144.x
- **Garcia A, Tello S, Vargas G, Duponchelle F.** Patterns of commercial fish landings in the Loreto region (Peruvian Amazon) between 1984 and 2006. Fish Physiol Biochem. 2009; 35(1):53–67. https://doi.org/10.1007/s10695-008-9212-7
- **García A, Montreuil V, Rodríguez R.** Talla de primera maduración y época de desova de la “doncella”, *Pseudoplatystoma fasciatum* (Linnaeus) y el “tigre zúngaro”, *Pseudoplatystoma tigrinum* (Valenciennes), en la Amazonía peruana. Bol Mus Para Emilio Goeldi Ser Zool. 2001; 17(1):3–13.
- **García Vásquez A, Alonso JC, Carvajal F, Moreau J, Nuñez J, Renno JF *et al*.** Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. J Fish Biol. 2009; 75(10):2527–51. https://doi.org/10.1111/j.1095-8649.2009.02444.x
- **García-Dávila C, Duponchelle F, Castro-Ruiz D, Villacorta J, Quérouil S, Chota-Macuyama W *et al*.** Molecular identification of a cryptic species in the Amazonian predatory catfish genus *Pseudoplatystoma* (Bleeker, 1962) from Peru. Genetica. 2013; 141(7–9):347–58. https://doi.org/10.1007/s10709-013-9734-5
- **García-Dávila C, Estivals G, Mejia J, Flores M, Angulo G, Sánchez H *et al*.** Peces ornamentales de la Amazonía Peruana. Instituto de Investigaciones de la Amazonía Peruana (IIAP). Iquitos; 2021. https://hdl.handle.net/20.500.12921/596
- **García-Dávila C, Sánchez Riveiro H, FLores Silva MA, Mejía de Loayza JE, Angulo Chávez CAC, Castro Ruiz D *et al*.** Peces de consumo de la Amazonía Peruana. Instituto de Investigaciones de la Amazonía Peruana (IIAP) [Internet]. Iquitos; 2018. https://investigacion.minam.gob.pe/observatorio/sites/default/files/garcia_libro_2018.pdf
- **Giesel JT.** Reproductive strategies as adaptations to life in temporally heterogeneous environments. Annu Rev Ecol Syst. 1976; 7:57–79. https://doi.org/10.1146/annurev.es.07.110176.000421
- **González JCA, Nuñez-Avellaneda M, Córdoba EA, López LFR, Páez CLS.** Ecosistemas acuáticos de la amazonía colombiana: avances y perspectivas. Colomb. Amazónica. 2006; Número Especial:163–80. https://www.sinchi.org.co/files/publicaciones/revista/pdf/0/10%20ecosistemas%20acuticos%20de%20la%20amazonia%20colombiana%20avances%20y%20perspectivas.pdf
- **Guyot JL, Jouanneau JM, Soares L, Boaventura GR, Maillet N, Lagane C.** Clay mineral composition of river sediments in the Amazon Basin. Catena. 2007; 71(2):340–56. https://doi.org/10.1016/j.catena.2007.02.002
- **Haimovici M, Reis EG.** Determinação de idade e crescimento da castanha *Umbrina canosai*, (Pisces, Sciaeinidae) do Sul do Brasil. Atlântica. 1984; 7:25–46.
- **Hales J, Petry P.** Amazon Lowlands [Internet]. Freshwater Ecoregions of the World; 2008. https://www.feow.org/ecoregions/details/316
- **Hartl DL, Clarck AG.** Principles of population genetics. Sunderland, Massachusetts: Sinauer Associates, Inc. Publishers; 2007.
- **Hauser M, Doria CRC, Melo LRC, Santos AR, Ayala DM, Nogueira LD *et al*.** Age and growth of the amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Madeira River basin before the construction of dams. Neotrop Ichthyol. 2018; 16(1):1–14. https://doi.org/10.1590/1982-0224-20170130

- **Hutchinson CE, TenBrink TT.** Age determination of the Yellow Irish Lord: management implications as a result of new estimates of maximum age. N Am J Fish Manage. 2011; 31(6):1116–22. https://doi.org/10.1080/02755947.2011.646453
- **Institut de Recherche pour le Développement (IRD), Hidrologia da Bacia Amazonica (HIBAM), Servicio Nacional de Meteorología e Hidrología (Senamhi).** Evaluación hidrológica de las cuencas amazónicas peruanas [Internet]. Lima: Ministerio del Ambiente; 2011. https://centroderecursos.cultura.pe/es/registrobibliografico/evaluaci%C3%B3n-hidrol%C3%B3gica-de-las-cuencas-amaz%C3%B3nicas-peruanas
- **Instituto de Hidrología y Meteorología y Estudios Ambientales (IDEAM).** Informe anual sobre el estado actual del medio ambiente y los recursos naturales renovables en Colombia [Internet]. Bogotá; 2004. http://documentacion.ideam.gov.co/openbiblio/bvirtual/018781/018781.htm
- **Inturias AD.** Edad, crecimiento y reproducción de *Pseudoplatystoma fasciatum* y *Pseudoplatustoma tigrinum* en la Amazonía Boliviana. [Master Thesis]. La Paz: Universidad Mayor de San Andrés; 2008.
- **Isaac V, Ruffino M, McGrath D.** In search of a new approach to fisheries management in the middle amazon region. Low Wake Fi.1998; 889–902. https://doi.org/10.4027/fsam.1998.49
- **De Jesus MJ, Kohler CC.** The commercial fishery of the Peruvian Amazon. Fisheries. 2004; 29(4):10–16. https://doi.org/10.1577/1548-8446(2004)29[10:TCFOTP]2.0.CO;2
- **Jézéquel C, Tedesco PA, Darwall W, Dias MS, Frederico RG, Hidalgo M *et al*.** Freshwater fish diversity hotspots for conservation. Conserv Biol. 2020; 34(4):956–65. https://doi.org/10.1111/cobi.13466
- **Junk WJ, Bayley PB, Sparks RE.** The flood pulse concept in river-floodplain-systems. In: Dodge DP, editor. Proceedings of International Large River Symposium. Can Spec Publ Fish Aquzt Sci. 106; 1989. p.110–27.
- **Junk WJ, Wantzen KM.** The Flood Pulse Concept: New aspects, approaches and applications-An Update. In: Welcomme RL, Petr T, editors. Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries. Bangkok: Food and Agriculture Organization and the Mekong River Commission, FAO Regional Office for Asia and the Pacific; 2004. p.117–49. http://hdl.handle.net/11858/00-001M-0000-000F-DB40-5
- **Kimura DK.** Likelihood methods for the von Bertalanffy growth curve. Fish B-NOAA. 1980; 77(4):765–76.
- **Loubens G.** Biologie de *Plagioscion squamosissimus* (Teleostei: Sciaenidae) dans le bassin du Mamoré (Amazonie bolivienne). Ichthyol Explor Freshw. 2003; 14(4):335–52. https://www.pfeil-verlag.de/wp-content/uploads/2015/05/ief14_4_07.pdf
- **Loubens G, Panfili J.** Biologie de *Colossoma macropomun* (Teleostei: Serrasalmidae) dans le bassin du Mamoré (Amazonie bolivienne). Ichthyol Explor Freshw. 1997; 8(1):1–22. https://horizon.documentation.ird.fr/exl-doc/pleins_textes/pleins_textes_6/b_fdi_47-48/010010615.pdf
- **Loubens G, Panfili J.** Biologie de *Piaractus brachypomus* (Teleostei: Serrasalmidae) dans le bassin du Mamoré (Amazonie bolivienne). Ichthyol Explor Freshw. 2001; 12(1):51–64. https://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers20-05/010027698.pdf
- **Loubens G, Panfili J.** Biologie de *Pseudoplatystoma fasciatum* et *P. tigrinum* (Teleostei: Pimelodidae) dans le bassin du Mamoré (Amazonie bolivienne). Ichthyol Explor Freshw. 2000; 11(1):13–34. https://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers20-05/010027696.pdf
- **Loubens G, Panfili J.** Estimation de l'âge individuel de *Prochilodus nigricans* (Teleostei: Prochilodidae) dans le Béni (Bolivie): protocole d'étude et application. Aquat Living Resour.1992; 5(1):41–56. https://www.cambridge.org/core/journals/aquatic-living-resources/article/abs/estimation-de-lage-individuel-de-prochilodus-nigricans-teleostei-prochilodidae-dans-le-beni-bolivie-protocole-detude-et-application/CFC2EA4AB22E752F71BF8DB64EF64055

- **Lubich C, Campos C, Freitas C, Siqueira-Souza.** Effects of fishing oh the population of Speckled Pavon *Cichla temensis* in the Middle Negro River (Amazon State, Brazil): A decrease in the size of the trophy fish? Trans Am Fish Soc. 2021; 150(6):667–78. https://doi.org/10.1002/tafs.10329
- **Mazur CF, Tillapaugh D, Brett JR, Iwama GK.** The effect of feeding level and rearing density on growth, feed conversion and survival in chinook salmon (*Oncorhynchus tshawytscha*) reared in salt water. Aquaculture. 1993; 117(1–2):129–40. https://doi.org/10.1016/0044-8486(93)90129-M
- **McKey DB, Durécu M, Pouilly M, Béarez P, Ovando A, Kalebe M *et al*.** Present-day African analogue of a pre-European Amazonian floodplain fishery shows convergence in cultural niche construction. Proc Natl Acad Sci USA. 2016; 113(52):14938–43. https://doi.org/10.1073/pnas.1613169114
- **Ministerio de la Producción (PRODUCE).** Anuario estadístico pesquero y acuícola 2019. Oficina General de Evaluación de Impacto y Estudios Económicos, Oficina de Estudios Económicos [Internet]. Lima; 2020. https://ogeiee.produce.gob.pe/index.php/en/shortcode/oee-documentos-publicaciones/publicaciones-anuales/item/949-anuario-estadistico-pesquero-y-acuicola-2019
- **Ministerio de Transportes y Comunicaciones (MTC).** Estudio de la navegabilidad del Río Ucayali en el tramo comprendido entre Pucallpa y la confluencia con el Río Marañón. Dirección General de Transporte Acuático [Internet]. Lima; 2005. https://portal.mtc.gob.pe/transportes/acuatico/documentos/estudios/Estudio%20de%20la%20Hidr%C3%A1ulica%20Fluvial%20del%20r%C3%ADo%20Ucayali%20-%20Informe%20Final.pdf
- **Myers RA, Mertz G.** The limits of exploitation: A precautionary approach. Ecol Appl. 1998; 8(1 Supl.):165–69. https://doi.org/10.2307/2641375
- **Nuñez J, Dugué R, Corcuy Arana N, Duponchelle F, Renno JF, Raynaud T *et al*.** Induced breeding and larval rearing of Surubí, *Pseudoplatystoma fasciatum* (Linnaeus, 1766), from the Bolivian Amazon. Aquac Res. 2008; 39(7):764–76. https://doi.org/10.1111/j.1365-2109.2008.01928.x
- **Nuñez-Avellaneda M, Marín Z, Alonso JC, Ríos E, Andrade-Sossa C, Freitas A *et al*.** Los ambientes de pesca en la frontera colombo-peruana del río Putumayo. In: Agudelo E, Alonso JC, Moya LA, editors. Perspectivas para el ordenamiento de la pesca y la Acuicultura en el área de integración fronteriza Colombo-Peruana del río Putumayo. Bogotá (DC): Instituto Amazónico de Investigaciones Científicas SINCHI & Instituto Nacional de Desarrollo INADE; 2006. p.31–45.
- **Núñez J, Duponchelle F.** Towards a universal scale to assess sexual maturation and related life history traits in oviparous teleost fishes. Fish Physiol Biochem. 2009; 35(1):167–80. https://doi.org/10.1007/s10695-008-9241-2
- **Padilla-Pérez PP, Alcántara-Bocanegra F, Ismiño-Orbe R.** Reproducción inducida de *Pseudoplatystoma fasciatum* y desarrollo embionario - larval. Folia Amazónica. 2001; 12(1–2):141–54. https://doi.org/10.24841/fa.v12i1-2.130
- **Panfili J, Pontual H, Troadec H, Wright PJ, editors.** Manual of fish sclerochronology. Brest, France: Ifremer-IRD; 2002.
- **Partridge L, Harvey PH.** The ecological context of life history evolution. Science. 1988; 241(4872):1449–55. https://doi.org/10.1126/science.241.4872.1449
- **Pauly D.** Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy´s growth formula. Kiel: Berichte Aus Dem Institut für Meereskunde an der Christian-Albrechts-Universität Kiel, Nr. 063; 1979. https://doi.org/10.3289/ifm_ber_63
- **Pereira LHG, Foresti F, Oliveira C.** Genetic structure of the migratory catfish *Pseudoplatystoma corruscans* (Siluriformes : Pimelodidae) suggests homing behaviour. Ecol Freshw Fish. 2009; 18(2):215–25. https://doi.org/10.1111/j.1600-0633.2008.00338.x
- **Pérez A, Fabré NN.** Life-history characteristics of *Pseudoplatystoma metaense* (Teleostei: Siluriformes: Pimelodidae) from the northwestern Orinoco River Basin. Neotrop Ichthyol. 2018; 16(1):1–10. https://doi.org/10.1590/1982-0224-20160140

- **Pérez A, Fabré NN.** Seasonal growth and life history of the catfish *Calophysus macropterus* (Lichtenstein, 1819) (Siluriformes: Pimelodidae) from the Amazon floodplain. J Appl Ichthyol. 2009; 25(3):343–49. https://doi.org/10.1111/j.1439-0426.2008.01104.x
- **Puffer M, Berg OK, Huusko A, Vehanen T, Einum S.** Effects of intra- and interspecific competition and hydropeaking on growth of juvenile Atlantic salmon (*Salmo salar*). Ecol Freshw Fish. 2017; 26(1):99–107. https://doi.org/10.1111/eff.12258
- **Reid S.** La biología de los bagres rayados *Pseudoplatystoma fasciatum* y *P. tigrinum* en la cuenca del río Apuré, Venezuela. Revista UNELLEZ de Ciencia y Tecnología. 1983; 1:13–41.
- **Resende EK.** Migratory fishes of the Paraguay-Paraná Basin. In: Carolsfeld J, Harvey B, Ross C, Baer A, editors. Migratory Fishes of South America: biology, fisheries and conservation status. Otawa: International Development Research Centre & World Bank; 2003. p.103–55.
- **Reznick DA, Bryga H, Endler JA.** Experimentally induced life-history evolution in a natural population. Nature. 1990; 346:357–59. https://doi.org/10.1038/346357a0
- **Ruffino ML, Isaac VJ.** Dinâmica populacional surubim-tigre, *Pseudoplatystoma tigrinum* (Valenciennes, 1840) no médio Amazonas (Siluriformes, Pimelodidae). Acta Amazon. 1999; 29(3):463–76. https://doi.org/10.1590/1809-43921999293476
- **Salazar CA, Acosta LE, Agudelo E, Mazorra A, Alonso JC, Núñez-Avellaneda M *et al*.** El área de integración fronteriza Colombo-Peruana del río Putumayo. In: Agudelo E, Alonso JC, Moya LA, editors. Perspectivas para el ordenamiento de la pesca y la Acuicultura en el área de integración fronteriza Colombo-Peruana del río Putumayo. Bogotá (DC): Instituto Amazónico de Investigaciones Científicas SINCHI & Instituto Nacional de Desarrollo INADE; 2006. p.13–30.
- **Sierra CA, Mahecha M, Poveda G, Álvarez-Dávila E, Gutierrez-Velez VH, Reu B *et al*.** Monitoring ecological change during rapid socio-economic and political transitions: Colombian ecosystems in the post-conflict era. Environ Sci Policy. 2017; 76(October):40–49. https://doi.org/10.1016/j.envsci.2017.06.011
- **Silva EA, Stewart DJ.** Age structure, growth and survival rates of the commercial fish *Prochilodus nigricans* (bocachico) in North-eastern Ecuador. Environ Biol Fish. 2006; 77(1):63–77. https://doi.org/10.1007/s10641-006-9055-y
- **Stearns SC.** The evolution of life histories. New York: Oxford University Press; 1992.
- **Taniguchi Y, Nakano S.** Condition-specific competition: implications for the altitudinal distribution of stream fishes. Ecology. 2000; 81(7):2027–39. https://doi.org/10.2307/177290
- **Telles MPC, Collevatti RG, Braga RS, Guedes LBS, Castro TG, Costa MC *et al*.** Geographical genetics of *Pseudoplatystoma punctifer* (Castelnau, 1855) (Siluriformes, Pimelodidae) in the Amazon Basin. Genet Mol Res. 2014; 13(2):3656–66. https://doi.org/10.4238/2014.May.9.8
- **Tomassone R, Dervin C, Masson JP.** Biométrie Modélisation de Phénomènes biologiques. Paris: Masson; 1993.
- **Torrico JP, Hubert N, Desmarais E, Duponchelle F, Nuñez Rodriguez J, Montoya-Burgos J *et al*.** Molecular phylogeny of the genus *Pseudoplatystoma* (Bleeker, 1862): Biogeographic and evolutionary implications. Mol Phylogenet Evol. 2009; 51(3):588–94. https://doi.org/10.1016/j.ympev.2008.11.019
- **Tregidgo D, Parry L, Barlow J, Pompeu PS.** Urban market amplifies strong species selectivity in Amazonian artisanal fisheries. Neotrop Ichthyol. 2021; 19(3):e210097. https://doi.org/10.1590/1982-0224-2021-0097
- **Vazzoler AEAM.** Manual de métodos para estudos biológicos de populações de peixes. Reprodução y crescimento. São Paulo: CNPq; 1982.
- **Venturelli PA, Shuter BJ, Murphy CA.** Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. Proc R Soc B. 2009; 276(1658):919–24. https://doi.org/10.1098/rspb.2008.1507

- **Vollestad LA.** Growth-rate variation in brown trout in small neighbouring streams: evidence for density-dependence? J Fish Biol. 2002; 61(6):1513–27. https://doi.org/10.1006/jfbi.2002.2170
- **Wantzen KM, Arruda Machado F, Voss M, Boriss H, Junk WJ.** Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. Aquat Sci. 2002; 64(3):239–51. https://doi.org/10.1007/PL00013196
- **Weiß CH.** StatSoft, INC., Tulsa, OK.: STATISTICA, Version 8. Adv Stat Anal. 2007; 91:339–41. https://doi.org/10.1007/s10182-007-0038-x

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