

Original article

## Population dynamics of *Prochilodus nigricans* (Characiformes: Prochilodontidae) in the Putumayo River

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The black prochilodus (*Prochilodus nigricans*) is one of the most landed scaled fish species of the middle and upper parts of the Putumayo River, in the tri-national area between Colombia, Ecuador and Peru. Despite its importance, biological information about this species is too scant to guide fisheries management in this portion of the Colombian Amazon. In this study, 10884 individuals were sampled in the fish markets of Puerto Leguízamo between 2009 and 2017. This sampling was used to document reproductive patterns, but also growth and mortality parameters from length frequency distributions. The size at which all fish were mature was 22 cm Ls, which should be the established as the minimum size of capture to ensure that all fish have had a chance to reproduce before being caught. Growth and mortality parameters indicated a slower growth in the Putumayo than in other Amazonian rivers and a relatively high exploitation rate.

**Keywords:** Black prochilodus, Colombia, Growth, Mortality, Reproduction.

El bocachico (*Prochilodus nigricans*) es uno de los peces de escama más comercializados en la cuenca media y alta del río Putumayo en la zona tri-nacional entre Colombia, Ecuador y Perú. Sin embargo, a pesar de su importancia, existe muy poca información biológica sobre esta especie que permita guiar el manejo pesquero para este sector de la Amazonia colombiana. Para ello, fueron analizados 10884 ejemplares colectados en puntos de expendio de pescado y zonas de pesca aledaños a la ciudad de Puerto Leguízamo entre los años 2009 a 2017. Se determinaron los parámetros de reproducción, así como de crecimiento y de mortalidad en base a análisis de distribución de frecuencia de tallas. Se recomienda establecer la talla mínima de captura a 22 cm Le, talla a la cual todos los peces son maduros y han tenido la posibilidad de reproducirse por lo menos una vez ante su captura. Los parámetros de crecimiento y mortalidad indicaron un crecimiento más lento en el Putumayo que en otras cuencas de la Amazonia y una tasa de explotación relativamente elevada.

**Palabras clave:** Bocachico, Colombia, Crecimiento, Mortalidad, Reproducción.

### Introduction

In the Colombian Amazon, large catfishes have long been considered the most important commercial species for both the international trade with neighbouring countries and the national market (Agudelo *et al.*, 2000; Agudelo *et al.*, 2006). Historical trends in the fisheries of Puerto Leguízamo city on the Putumayo River indicate that catfish species, such as *Brachyplatystoma platynemum* (baboso) or *Calophysus macropterus* (simí), are indeed the most marketable species (Agudelo *et al.*, 2000; Bonilla-Castillo *et al.*, 2011a, 2011b). Yet, smaller characid species, such as *Prochilodus nigricans* Spix & Agassiz, 1829 (bocachico),

*Brycon cephalus* (sábalo) and *Mylossoma* spp. (garopa), are among the most landed species of the Putumayo River, playing very important roles for artisanal fisheries and food security of local communities (Agudelo *et al.*, 2006; Agudelo, Alonso, 2011). The bocachico, *P. nigricans*, is also among the most landed species in all major amazonian cities (Gonçalves, Batista, 2008; García *et al.*, 2009; Batista, Isaac, 2012; Doria *et al.*, 2012). This detritivorous species performs extensive breeding and feeding migrations in response to seasonal river fluctuations and occupies a wide variety of habitats in the river basins of the Bolivian, Brazilian, Colombian, Ecuadorian and Peruvian Amazon (Carolsfeld *et al.*, 2003; González-Cañón *et al.*, 2011).

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Owing to their abundance, detritivorous habits and migratory behaviour, fishes of the genus *Prochilodus*, including *P. nigricans*, are functionally important components of Amazonian aquatic ecosystems, significantly contributing to energy and carbon flows within the food chains, to production transfer from seasonal floodplains to the river channels or from nutrient-rich to nutrient-poor tributaries, and to ecosystem engineering (Flecker, 1996; Barbarino Duque *et al.*, 1998; Winemiller, Jepsen, 1998; Taylor *et al.*, 2006; Agudelo, 2015). Previous molecular studies focussed on phylogenetic relationships among *Prochilodus* species (Sivasundar *et al.*, 2001) or within the Family Prochilodontidae (Melo *et al.*, 2016). Although Melo *et al.* (2016) reported taxonomic issues within the “*Prochilodus nigricans* group”, there are surprisingly few population genetic studies on *P. nigricans*. The only one carried out so far suggested a homogeneous population along the Amazon main stem (Machado *et al.*, 2017).

The reproductive, growth and mortality patterns of *P. nigricans* have been studied in Bolivia (Loubens, Panfili, 1995), Ecuador (Silva, Stewart, 2006) and Brazil (Ruffino, Isaac, 1995; Catarino *et al.*, 2014; Camargo *et al.*, 2015). Surprisingly, in spite of its commercial importance, very few studies have been carried out on this species in Colombian and Peruvian rivers, apart from preliminary studies on its growth (Montreuil, Tello, 1988) and reproductive biology in Peru (Montreuil *et al.*, 2001; Riofrío, 2002). Information about the population dynamics of this species is lacking to guide fisheries management. This paper aims at filling this gap by providing information about the reproduction, growth and mortality patterns of *P. nigricans* in the Putumayo River, which marks the boundary between the Colombian and Peruvian Amazon.

## Material and Methods

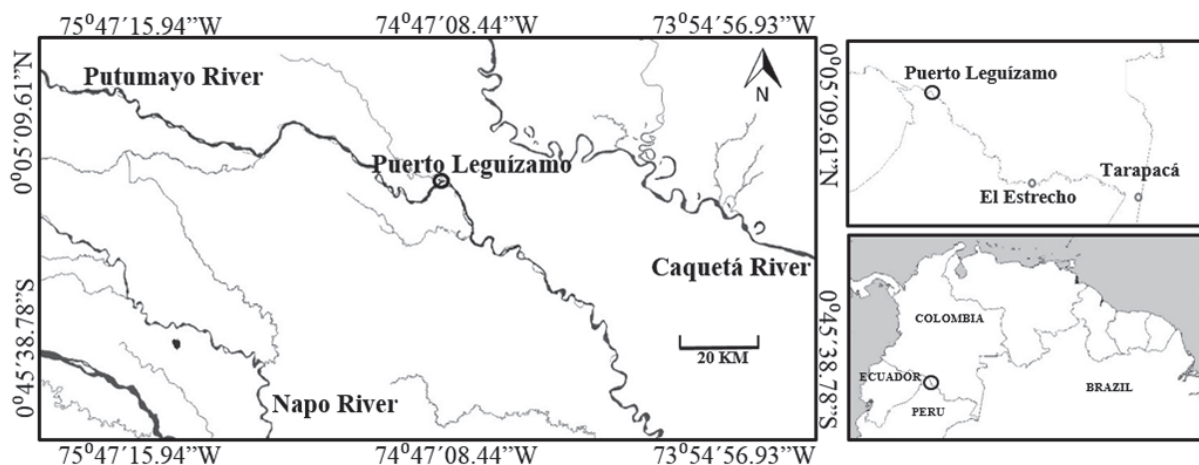
**Sampling area.** With an estimated area of 174.028 km<sup>2</sup>, the Putumayo River basin is one of the main Andean tributaries from the Colombian and Ecuadorian portions of the Amazon

basin (Murcia, 2006). Puerto Leguizamo city (00°11'53.2 S and 74°46'42.7 W) is located on the Colombian side of the upper Putumayo, at 220 m above the sea level (Fig. 1). Its climate is hot and humid with annual mean precipitations of 2600 mm (Bonilla-Castillo *et al.*, 2017). The mean annual conductivity and pH in the upper Putumayo River are 76.87µS/cm and 6.08, respectively (Agudelo *et al.*, 2000).

**Fish sampling.** Fish were sampled between 2009 and 2017 from artisanal fishermen landing their products in the fish market of Puerto Leguizamo. Fishing areas are usually localized within a 140 km radius from Puerto Leguizamo, up to the Ecuadorian border. In several instances, we accompanied fishermen during their fishing trips in order to obtain complete specimens for reproductive analyses. Most fishing boats are made of wood, with a maximum capacity of 500 kg, motorized by external 5 Hp motors (locally known as “peque-peque”) and equipped with isothermal holds of ~ 150 kg capacity.

Although indigenous fishermen can use bows and harpoons during the high water period, the main fishing gear used year round by artisanal fishermen for *P. nigricans* are monofilament gillnets of 2.5 and 3 inches (~ 60-80 mm) stretched mesh-sizes, between 2 and 3 m height and 30 to 80 m long. Fishermen also use multifilament gillnets from 2.5 to 3.5 inches (up to ~ 90 mm), called “sabaleras”, mainly to catch *Brycon* spp., but in which *P. nigricans* can also be captured. Gillnets are usually set in different types of habitats: at the mouth of tributaries, in lagoons, streams and swamps.

Fishes were measured to the nearest mm (standard length - Ls) and when possible, weighed to the nearest g (total and eviscerated masses, Wt and We, respectively) and sexed (when fish were not landed eviscerated). The gonadal maturity stage was recorded using Nuñez, Duponchelle (2009) maturity scale. Briefly, for females, the stages of gonadal maturation were: stage 1, immature; stage 2, maturing; stage 3, advanced maturation; stage 4, ripe; stage 5, spent and stage 6, resting. For males, stage 1 corresponds to immature fish, stage 2 to maturing or resting individuals and stage 3 to ripe fish.



**Fig. 1.** Geographic location of the study area around Puerto Leguizamo in the Putumayo River, Colombian Amazon.

The number of fish that could be sexed was much higher between 2015 and 2017 and reproductive parameters were estimated only from fish sampled between 2015 and 2017.

The size at first sexual maturity ( $L_{50}$ ) is defined as the standard length at which 50% of the individuals are in maturation stage during the breeding season (*i.e.*, at least stage 2 for females and males).  $L_m$  is estimated by fitting the fraction of mature individuals per 10 mm Ls intervals to a logistic regression function (Barbieri *et al.*, 1994; Duponchelle, Panfili, 1998):

$$\%M = 1 / (1 + e^{-(a(L-L_{50}))})^{-1}$$

where %M = percentage of mature individuals by 10 mm size class, L = central value of each size class, and a and  $L_{50}$  = constants of the model. The % of mature individuals in each size class was weighted by the total number of individuals in the same size class.

The breeding season was determined using only fishes above the mean size at first maturity. It was estimated from the monthly proportions of females' gonadal maturation stages 3 and 4 combined and from the monthly mean gonadosomatic index (GSI) values. GSI was calculated as follows:

$$GSI = (Wg/Wt) \times 100,$$

where Wt = total mass of the individual in g, Wg = gonad mass (g).

Body condition, mass for a given Ls, was estimated using the Ls and Wt relationship  $\log_{10}$  transformed to obtain a linear relationship (Cone, 1989; Hoeninghaus *et al.*, 2006):  $\log_{10}(Wt) = a + b(\log_{10} Ls)$ . Body condition was compared at two levels: among sexes and among hydrological periods. Hydrological periods were defined as: receding waters (August to November), low waters (December to February), rising waters (March to May) and high waters (June-July).

Age and growth characteristics were estimated from the modal progressions of standard length frequency distributions (King, 1995) using the ELEFAN (Electronic Length Frequency Analysis) routine (Pauly, David, 1981) provided in the FiSAT II (FAO-ICLARM Fish Stock Assessment Tools) package (<http://www.fao.org/fi/statist/fisoft/fisat/index.htm>) (Gayanilo *et al.*, 2005). The set of parameters that best corresponded to the breeding patterns observed for the species (*i.e.*, which gave an estimated birth date corresponding to the breeding peak) and that best described the distributions (*i.e.*, which went through the largest number of large modes and yielded the largest Score = "goodness-of-fit" parameter of the ELEFAN routine) was selected (García Vásquez *et al.*, 2009). This process also permitted to diminish the tendency of ELEFAN method to underestimate K and overestimate  $L_{\infty}$  (Moreau *et al.*, 1995). The growth parameters were calculated by the von Bertalanffy Growth Function (VBGF) equation fitted by the ELEFAN method:

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

where  $L_t$  is the mean length at age t,  $L_{\infty}$  is the asymptotic length, K the growth coefficient and  $t_0$  the theoretical age at size 0.

$t_0$  was calculated using the empirical formula proposed by Pauly (1979):

$$\log_{10}(t_0) = -0.392 - 0.275 \log_{10} L_{\infty} - 1.038 \log_{10} K$$

The age at first sexual maturity ( $A_{50}$ ) was calculated from the VBGF as follows (Duponchelle *et al.*, 2007):

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

where  $L_{50}$  is the size at first sexual maturity and  $L_{\infty}$  and K are parameters from the VBGF.

The longevity ( $t_{max}$ ) was calculated as the age at 95% of  $L_{\infty}$  from the equation of Taylor (1958):

$$A_p = t_0 - [\ln(1-p)/K]$$

where  $t_0$  and K are the VBGF parameters and p is a fraction of  $L_{\infty}$  (in this case 0.95). The longevity was also calculated from the equation of Froese, Binohlan (2000):

$$\log_{10} t_{max} = 0.5496 + 0.957 \log_{10} (A_{50})$$

where  $A_{50}$  is the age at first sexual maturity.

Mortality parameters were also estimated using procedures provided in the FISAT II package. Total mortality (Z) was estimated by the method of the length-converted catch curves (LCCC) (Pauly, 1983). Natural mortality (M) is one of the most complicated life history parameters to estimate in natural populations (Vetter, 1988; Brodziak *et al.*, 2011) and several empirical models linking M to life history attributes such as age at maturity or growth were proposed for fish (reviews in Simpfendorfer *et al.*, 2005; Gislason *et al.*, 2010). These empirical relationships assume that M is a species- or stock-specific constant, and users generally apply the estimate to all exploited ages and sizes of the species or stock under study. One of the most commonly used models is Pauly (1980) equation linking M to  $L_{\infty}$ , K and the mean annual environmental temperature (T) for the species concerned. Hence, natural mortality was evaluated using Pauly (1980)'s equation, as implemented in the Fisat package, for a mean annual temperature of 27°C (water temperature varies between 21 and 32°C in the Putumayo river, Núñez-Avellaneda *et al.*, 2006):

$$-0.006 - 0.270 * \log_{10}(L_{\infty}) + 0.6543 * \log_{10}(K) + 0.4634 * \log_{10}(T^{\circ}),$$

where  $L_{\infty}$  and K are the VBGF parameters and  $T^{\circ}$  the mean annual temperature.

In order to verify the accuracy of natural mortality estimate using Pauly's equation and its influence on the

estimation of fishing mortality and exploitation rate (E), however, M was also estimated using Richter and Efanov's formula (Sparre, Venema, 1997), relating mortality to the age at which 50% of the population is mature (estimated by  $A_{50}$ ):

$$1.521/(L_{50})^{0.72} - 0.155,$$

where  $L_{50}$  is the size at first sexual maturity.

Additionally, natural mortality was also estimated using Jensen (1996)'s formulas (Simpfendorfer *et al.*, 2005):

$$M = 1.65/A_{50} \text{ and } M = 1.6 \times K$$

Fishing mortality (F) was calculated as  $F = Z - M$  (Pauly, 1980). The exploitation rate was calculated as  $E = F \cdot Z^{-1}$ .

For comparison purposes, both F and E were calculated for the different estimates of M.

**Statistical analyses.** Differences in mean Ls, Wt and We between sexes were tested with a Mann–Whitney rank-sum test.

Analysis of covariance (ANCOVA) was used to test for differences among slope or intercepts (when slopes did not differ) of the log10-transformed Ls - Wt relationships, using log10Wt as the dependent variable, log10Ls as the covariate, and hydrological periods or sex as independent variables.

## Results

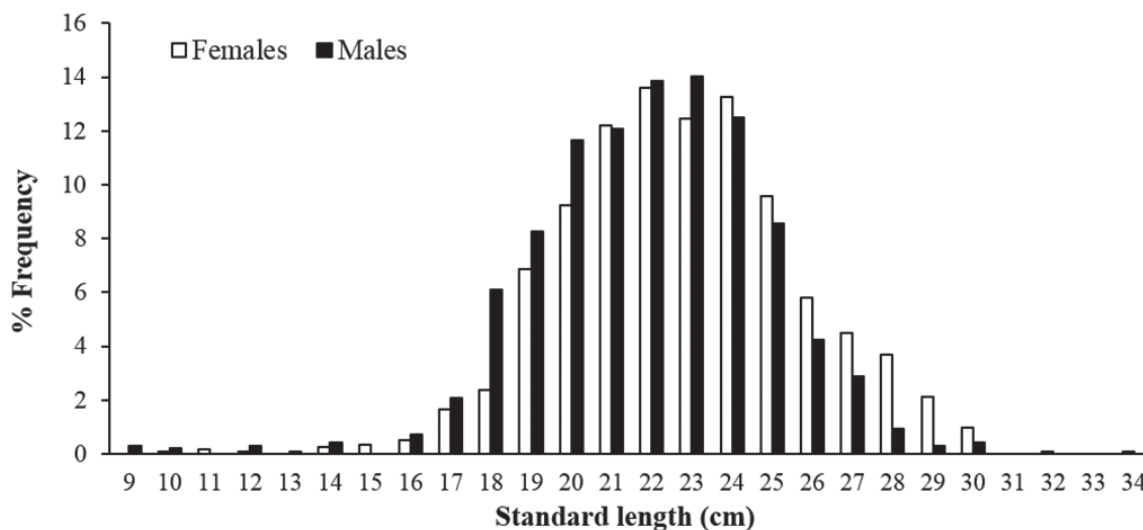
Between 2009 and 2017, a total of 10884 *P. nigricans* were measured. Of these approximately 19% were sexed (1117 females and 949 males, Fig. 2, Tab. 1). Although females had significantly larger length (Mann Whitney Rank Sum test,  $T = 877753$ ,  $P < 0.001$ ), total body mass

( $T = 873011$ ,  $P < 0.001$ ) and eviscerated body mass ( $T = 855149$ ,  $P < 0.001$ ) than males, the most important differences were in body mass: whereas females standard length was 12% larger than males, females maximum body mass was approximately 47% and 30% heavier than that of males, in total and eviscerated mass, respectively (Tab. 1).

For females, the median and mean standard lengths caught were 22.5 and 22.7 cm, respectively, and for males both lengths were 21.8 cm. Relationships between standard length (SL) and total body mass (Wt) were  $Wt = 0.0199 \cdot SL^{3.0453}$ ,  $r^2 = 0.925$ ,  $P < 0.001$  for females;  $Wt = 0.044 \cdot SL^{2.777}$ ,  $r^2 = 0.904$ ,  $P < 0.001$  for males and differed significantly between sexes (ANCOVA,  $F_{1,2065} = 47.365$ ,  $P < 0.001$ ). Relationships between standard length (SL) and eviscerated body mass (We) were  $We = 0.020 \cdot SL^{2.988}$ ,  $r^2 = 0.925$ ,  $P < 0.001$  for females;  $We = 0.028 \cdot SL^{2.880}$ ,  $r^2 = 0.909$ ,  $P < 0.001$  for males and differed significantly between sexes (ANCOVA,  $F_{1,2065} = 7.841$ ,  $P = 0.005$ ).

Condition, expressed as the log-transformed body length *versus* body mass regressions, varied significantly between hydrological seasons for both females (ANCOVA,  $F_{3,861} = 11.071$ ,  $P < 0.001$ ) and males ( $F_{3,869} = 13.931$ ,  $P < 0.001$ ) (Fig. 3). Regression lines intersected at about 1.3 (or 20 cm) for females and at about 1.35 (or 22 cm) for males, indicating a shift in condition according to season between immature and mature fish (the acquisition of sexual maturity is reached around 20 cm, see below). Both immature females and males had the best condition during the high water period and the poorest during receding and low water periods, whereas the opposite pattern was observed for adult females and males (Fig. 3, Tab. 2).

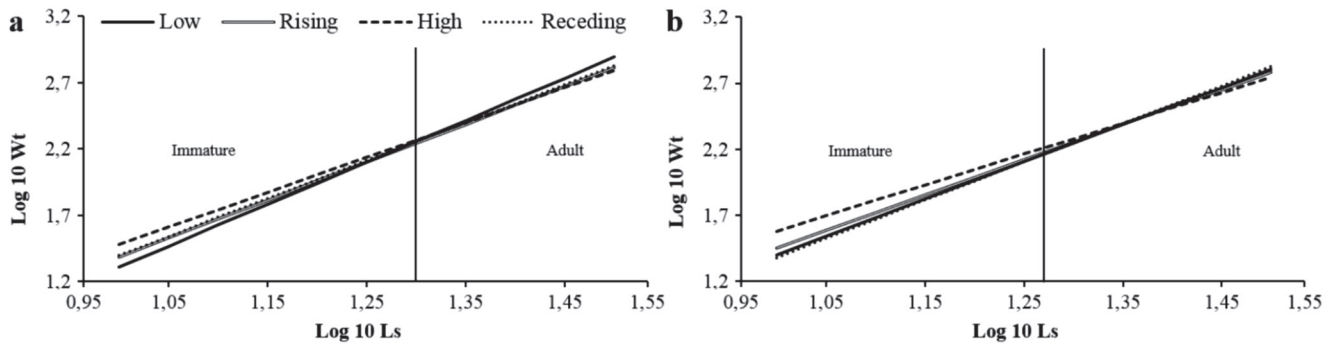
Adult females had better condition than adult males at every hydrological period, whereas juvenile males usually had better condition than juvenile females, except during the receding period (Tab. 2).



**Fig. 2.** Size frequency distribution for both *Prochilodus nigricans* females and males in the upper Putumayo River between 2009 and 2017.

**Tab. 1.** Mean ( $\pm$  standard deviation, SD) and ranges of standard length (Ls) and mass (Wt), for females, males and all individuals (sexed and unsexed) combined of *Prochilodus nigricans* caught by artisanal fisheries in the Putumayo River. N = number of fish analysed.

Sex	N	Mean Ls (cm) $\pm$ SD	Range (cm)	Mean Wt (g) $\pm$ SD	Range (g)	Mean We (g) $\pm$ SD	Range (g)
F	1117	22.7 $\pm$ 3.0	10.2 - 33.9	286.4 $\pm$ 126.6	24 - 1017	243.5 $\pm$ 104.6	21 - 817.8
M	949	21.8 $\pm$ 2.8	8.8 - 30.3	241.7 $\pm$ 92.3	12 - 709.2	210.1 $\pm$ 81.9	9 - 628.6
T	10884	23.2 $\pm$ 2.9	8.2 - 34				



**Fig. 3.** Changes in the body condition, expressed by the log<sub>10</sub>-transformed standard length (L<sub>s</sub>) and total (Wt) mass relationships, of females (a) and males (b) *Prochilodus nigricans* during the different hydrological seasons. Relationships for females:  $y=3.1631x-1.8544$ ,  $r^2=0.9151$  (Low);  $y=2.8597x-1.4749$ ,  $r^2=0.8917$  (Rising);  $y=2.6298x-1.1517$ ,  $r^2=0.8772$  (High);  $y=2.8619x-1.4652$ ,  $r^2=0.9552$  (Receding). Relationships for males:  $y=2.8206x-1.4231$ ,  $r^2=0.871$  (Low);  $y=2.6672x-1.2156$ ,  $r^2=0.8705$  (Rising);  $y=2.3268x-0.7462$ ,  $r^2=0.8687$  (High);  $y=2.8927x-1.5134$ ,  $r^2=0.9569$  (Receding).

**Tab. 2.** Mean total mass (Wt) for a given standard length (L<sub>s</sub>) of females and males of *Prochilodus nigricans* at each hydrological period.

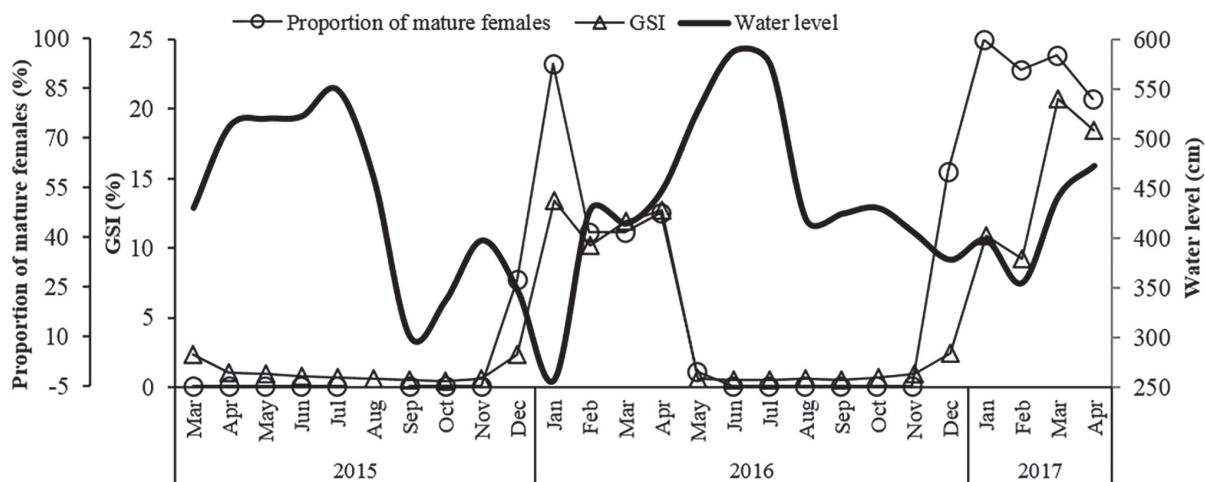
Condition	Sex	Hydrological period	W (gr) per standard length Ls		
			15 cm	25 cm	35 cm
Total mass (Wt)	Females	Low	73.4	369.3	1070.6
		Rising	77.4	333.3	872.5
		High	87.3	334.7	810.8
		Receding	79.6	343.2	899.0
	Males	Low	78.4	331.1	855.3
		Rising	83.4	325.8	799.4
		High	97.8	321.0	702.3
		Receding	77.4	339.2	897.7

**Breeding period.** The gonado-somatic index (GSI) and the proportion of breeding females indicated a reproductive period initiating in December and ending in May, with a peak activity between January and April for 2015-2016 (Fig. 4). The same trend was observed for 2016-2017. The reproductive period started during the dry season and ended during the early rising waters.

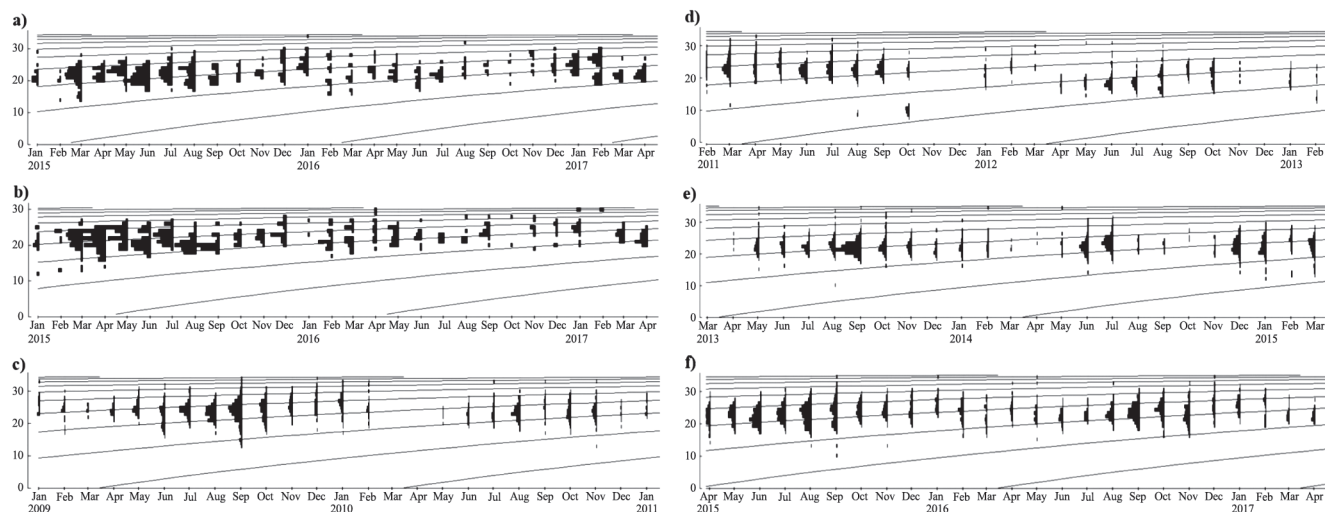
**Age and growth.** Length frequency distributions at each month were obviously limited by the selectivity of the fishing gears used by commercial fisheries, aimed at limiting the number of juvenile fish, which were therefore underrepresented in the samplings excepted at some months during low waters. The best fitting models obtained from length frequency analyses (ELEFAN routine) for the period 2015-2016, indicated a mean birth date coinciding with the height of the breeding season for both females

and males (Figs. 5a-b, respectively). When using the whole sampling period (2009-2017) for all individuals (sexed and unsexed combined), the best fitting model also gave a mean birth period coinciding with the peak breeding activity (Figs. 5c-f).

Parameters of the VBGF were very similar between females and males during the period 2015-2017 (Tab. 3). The parameters for all individuals pooled over the period 2009-2017 were similar to that of females for the period 2015-2016. Estimated longevity for *P. nigricans* in the Putumayo River ranged from 6.2 to 7.7 years, depending on the model (Tab. 3). When computing age from the VBGF, the largest female (33.9 cm) and male (30.3 cm) sampled reached 7.6 and 8.2 years, respectively. Despite the very similar VBGF parameters, females had a slightly faster growth than males: this growth differences ranged from 11.5% at 1 year old to 13% at 4 years old and older (Tab. 4).



**Fig. 4.** Mean monthly values of the gonado-somatic index (GSI) and monthly proportions of breeding females for *Prochilodus nigricans* in the Putumayo River in relation to the water level (black smoothed line).

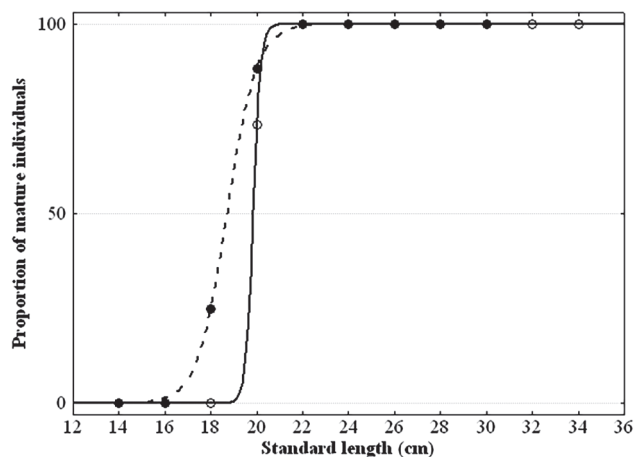


**Fig. 5.** Standard length frequency histograms and the corresponding von Bertalanffy growth function for females (a) and males (b) between January 2015 and April 2017 and for all individuals (sexed and unsexed) combined of *Prochilodus nigricans* in the Putumayo River between 2009 and 2017 (c-f).

**Tab. 3.** Parameters of the von Bertalanffy growth function and longevity ( $t_{max}$ ) of *Prochilodus nigricans* in the Putumayo River, as modelled in FISAT II using the ELEFAN procedure. Longevity  $t_{max}^1$  and  $t_{max}^2$  were calculated from Taylor (1958) and Froese, Binohlan (2000), respectively.

	$L_{\infty}$ (cm)	K (year <sup>-1</sup> )	$T_0$ (year <sup>-1</sup> )	Score	$t_{max}^1$ (year)	$t_{max}^2$ (year)
Females	35.7	0.37	-0.426	0.152	7.7	6.2
Males	31.6	0.37	-0.440	0.237	7.7	6.9
Total	35.7	0.37	-0.425	0.133	7.7	

**Age and size at first sexual maturity.** The size at which 50% of the individuals are mature was reached at 19.8 cm (1.8 years) for females and 18.7 cm (2 years) for males (Fig. 6). The size at which 100% of the individuals were mature was reached at 22 cm for both sexes and at 2.2 and 2.8 years for females and males, respectively. The smallest individuals with mature gonads were a 19 cm SL (1.6 years) female and a 17 cm (1.7 years) male.



**Fig. 6.** Standard length at first sexual maturity for males (black dots) and females (white circles) of *Prochilodus nigricans* in the Putumayo River.

Over the study period the mean size at capture varied between 20.6 and 25.2 cm (mean 23.1 cm  $\pm$  1.4 SD, Tab. 5). Overall, the proportion of fish caught below the size at first sexual maturity was  $12 \pm 13\%$  and ranged between 3 and 46% according to years (Tab. 5). Apart from the particularly high value in 2012 (46%), this proportion remained below 15% during the other years. The mean proportion of fish caught below the size at which 100% of the fish are mature was  $31.5 \pm 17.1\%$  and ranged between 14 and 66% (again in 2012).

**Mortality and exploitation rate.** The LCCC gave total mortality (Z) estimates of 1.49, 1.56 and 1.58 years<sup>-1</sup> for

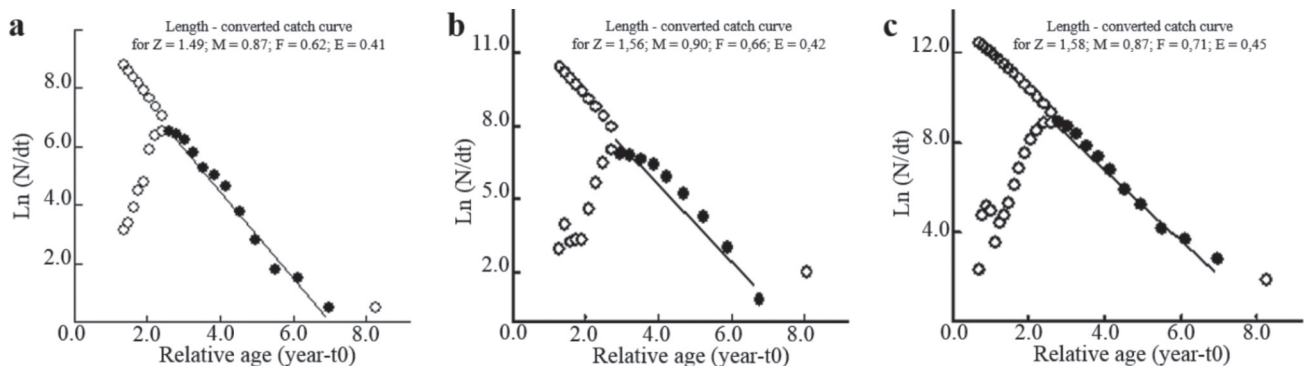
females, males and all individuals (sexed and unsexed) combined, respectively (Fig. 7). The LCCC estimates for natural mortality (M) fell within the upper range of values provided by other methods (Tab. 6) for females, males and all individuals combined. The LCCC estimates for fishing mortality (F) and exploitation rate (E), however, were in the lower range of values obtained from other methods for females, males and all individuals combined. The average exploitation rates calculated from all mortality methods (Tab. 6) were higher than those obtained from LCCC (Fig. 7) and remained below 0.5 only for females (0.45): 0.5 for males and 0.54 for all individuals (sexed and unsexed) combined.

**Tab. 4.** Standard length (Ls)-at-age (cm, calculated from the VBGF) for females (F), males (M) and the combination of sexed and unsexed individuals (Total) of *Prochilodus nigricans* in the Putumayo River. # F - M : growth difference between females and males. Length-at-age data calculated from the VBGF parameters provided in previous published studies (Ruffino, Isaac (1995), Loubens, Panfili (1995), Silva, Stewart (2006), Camargo *et al.* (2015)). For Ruffino, Isaac (1995) and Camargo *et al.* (2015), total lengths were converted to standard lengths using the equation provided in Loubens, Panfili (1995).

Age (t)	F	M	# F-M	Total	Ruffino, Isaac (1995)	Loubens, Panfili (1995)	Silva, Stewart (2006)	Catarino <i>et al.</i> (2014)	Camargo <i>et al.</i> (2015)
1	14.6	13.1	1.6 (11.5%)	14.6	17.1	21.7	18.2	12.3	10.5
2	21.2	18.8	2.4 (12.8%)	21.1	28.8	29.0	23.5	20.2	18.6
3	25.7	22.8	2.9 (12.8%)	25.6	36.3	33.0	27.5	25.4	24.0
4	28.8	25.5	3.3 (13%)	28.8	41.1	35.2	30.6	28.6	27.7
5	30.9	27.4	3.5 (12.8%)	30.9	44.1	36.5	32.9	30.8	30.2
6	32.4	28.7	3.7 (12.9%)	32.4	46.1	37.1	34.6	32.1	31.9
7	33.4	29.6	3.8 (12.9%)	33.4	47.3	37.5	35.9	33.0	33.1
8	34.1	30.2	3.9 (13%)	34.1	48.1	37.7	36.9	33.6	33.8

**Tab. 5.** Annual mean standard length (SL), range, number of *Prochilodus nigricans* individuals smaller than 20 cm (=female's  $L_{50}$ ) and smaller than 22 cm (size at which 100% fish are mature) of all the fish (females, males and unsexed individuals) caught between 2009 and 2017.

	2009	2010	2011	2012	2013	2014	2015	2016	2017
Mean LS	24.3	24.3	23.0	20.6	21.9	22.5	22.7	23.4	25.2
Range LS	13 - 34	13 - 33.5	8.2 - 33	15 - 31	10 - 34	14 - 34	10 - 34	14.7 - 34	19 - 31.4
Fish < 20 cm	116	21	83	301	136	71	331	134	11
Fish < 22 cm	311	122	283	437	623	316	859	451	26
% fish < $L_{50}$	6	3	7	46	10	8	14	9	6
% fish < $L_{100}$	16	16	23	66	47	36	36	29	14
Total (N)	1896	776	1231	659	1320	883	2403	1535	181



**Fig. 7.** Standard length-converted catch curves (SL) and mortality estimates for *Prochilodus nigricans* females (a), males (b) and all individuals (sexed and unsexed) combined (c) calculated from the von Bertalanffy growth function parameters at a mean temperature of 27°C. Z, M and F represent the instantaneous rates of total, natural and fishing mortality, respectively. E is the exploitation rate ( $E = F \cdot Z^{-1}$ ). Black dots = data points in the curve on which the regression was fitted.

**Tab. 6.** Natural mortality (M, year<sup>-1</sup>) calculated using different models and corresponding fishing mortality (F, year<sup>-1</sup>) and exploitation rate (E) for females, males and total (sexed and unsexed individuals combined) of *Prochilodus nigricans* in the Putumayo River. Total mortality (Z) was calculated from length-converted catch curves illustrated in Fig. 7 (Z=1.49 for females, Z=1.56 for males and Z=1.58 for total). Fishing mortality, F=Z-M. E=F/Z.

Group	Formula used for calculating M	M	F	E
Females	Richter, Efanov (Sparre, Venema, 1995)	0.86	0.63	0.42
	Pauly (1980)	0.87	0.62	0.41
	Jensen (1996) using K	0.59	0.56	0.60
	Jensen (1996) using A <sub>50</sub>	0.94	0.55	0.37
Males	Richter, Efanov (Sparre, Venema, 1995)	0.78	0.78	0.50
	Pauly (1980)	0.90	0.66	0.42
	Jensen (1996) using K	0.59	0.97	0.62
	Jensen (1996) using A <sub>50</sub>	0.83	0.73	0.47
Total	Pauly (1980)	0.87	0.71	0.45
	Jensen (1996) using K	0.59	0.99	0.63

### Discussion

During the period from 2009 to 2017 and out of the > 10000 specimens measured, the maximum observed length for *P. nigricans* in the upper Putumayo was 34 cm SL for a total body mass of 1.02 kg. This is considerably smaller than the 40.5 cm SL and 1.24 kg reported in the Aguarico River (300 m.a.s.l) in the Ecuadorian Amazon (Silva, Stewart, 2017), the 43 cm SL and 2.6 kg observed in the Caquetá River (~ 120 m.a.s.l) in Colombia (Bonilla-Castillo *et al.*, unpublished data) or the 45 cm and 2.65 kg observed in the middle Mamoré River (~160 m.a.s.l) in the Bolivian Amazon (Loubens, Panfili, 1995), but comparable to the 33 cm SL and 0.9 kg reported in Manacapuru Lake (~30 m.a.s.l, downstream of the Solimões River) in Brazil (Catarino *et al.*, 2014) and 37 cm TL and 650 g in the Ucayali River (~ 150 m.a.s.l, Riofrío, 2002). A potential explanation for the smallest maximum sizes observed in the Putumayo could lie in the size selectivity of the fishing gears used in Puerto Leguizamo. However, when using bows and harpoons fishermen tend to select the largest fish, which are more easily seen and caught and the mesh sizes used (between 2.5 to 3.5") by fishermen in Puerto Leguizamo were the same as those used in most studies cited above, which reported larger specimens. Moreover, in a study carried out between 2001 and 2005, using the same fishing gears in Puerto Leguizamo, El Estrecho and Tarapacá, which covers most of the Colombian portion of the Putumayo River (see Fig. 1), Camacho *et al.* (2006) obtained larger specimens (N = 2320, range 14-42 cm SL, mean = 26.6 ± 3.8 cm, and over 10% of the fish were above 30 cm). Although these authors did not observe relationship between fish length and location along the river for *P. nigricans*, they commented that for others species (*Brycon* spp., *Calophysus macropterus*), the largest specimens were observed in the upper portion of the Putumayo, in Puerto Leguizamo, where the present study was also carried out. Size-selectivity therefore is unlikely to explain the observed size differences between the upper

Putumayo and other geographic areas. Differential space occupation between size classes could potentially explain the observed size differences in a highly migratory species such as *P. nigricans*, with the larger adults occupying the lower portion of the basin. As attested by the reproductive results, however, the upper Putumayo around Puerto Leguizamo is a breeding area for *P. nigricans*, which implies the presence of large adults, at least on a seasonal basis and it is unlikely that large adults would have escaped the commercial fisheries of Puerto Leguizamo during the 8 years of samplings. Others potential explanations could be the existence of genetically distinct populations, of phenotypic differences in response to contrasted environmental conditions (as reported in the red piranha *P. nattereri*, Duponchelle *et al.*, 2007), or of differential exploitation rates, where the more heavily exploited populations tend to have smaller maximum sizes and sizes at maturity. So far, in spite of its ecological and economical importance, only one study has been carried out on the population genetics of *P. nigricans* in the Amazon basin, using the mitochondrial control region (D-Loop) marker (Machado *et al.*, 2017). This study suggested a homogeneous population along the Amazon main stem (Santarém to Tabatinga), which would likely extend to the Peruvian Amazon. Although we cannot preclude the existence of distinct populations with different life history traits in the Putumayo River (present study) and the Aguarico (Silva, Stewart, 2017) or the Caquetá rivers, differences in environmental conditions or in exploitation regime may be more likely explanations to the observed size differences. Catarino *et al.* (2014) reported that Manacapuru Lake was heavily exploited.

Seasonal variations of body condition were similar among sexes in *P. nigricans*. They differed, however, between immature, which had a better condition during the high waters and a poorer condition during the low and receding waters, and mature individuals, which had the opposite pattern. The better body condition of immature fish during the high waters probably results from increased resource availability in the inundated floodplain



(Goulding, 1980; Lowe-McConnell, 1964, 1987). On the other hand, once the waters recedes from the floodplain, juveniles have to go back to the river channel and initiate their upstream migration, which takes place in the low water season and is likely to negatively affect their body condition. The shift in body condition between immature and adults is also likely to reflect differences in energy allocation, where part of the ingested energy has to be allocated to gonadal products in adults, instead of only growth and maintenance in immature fishes (Wootton, 1998). Adult females and males had indeed the poorest conditions during the rising and high water periods, hence during and just after the reproductive season, when huge amounts of energy were invested in gonadal products (up to 20% body mass, see GSI in Fig. 3). Similar results were obtained in the Aguarico (Silva, Stewart, 2017).

**Breeding season.** In the Putumayo as in the Mamore (Loubens, Panfili, 1995), the Aguarico (Silva, Stewart, 2017), the middle Amazon (Mota, Ruffino, 1997), the Ucayali (Riofrío, 2002) and the Amazonas (Montreuil *et al.*, 2001) rivers, the breeding season of *P. nigricans* coincides with the rising waters, ending before the end of the flood. This reproductive pattern is very common in characid species of the Amazon basin (Goulding, 1980; Tello *et al.*, 1992; Vazzoler, Menezes, 1992; Ruffino, Isaac, 1995; Duponchelle *et al.*, 2007; Garcia-Vásquez *et al.*, 2015). It is regarded as an adaptation to the predictable flood pulse regime, allowing both adults and juveniles to benefit from the abundant food resources and shelters of the newly inundated floodplains (Lowe-McConnell, 1964, 1987; Goulding, 1980).

**Age and size at maturity.** The observed size at maturity ( $L_{50}$ ) of *P. nigricans* in the Putumayo River was slightly smaller than that reported for the Peruvian (24.3 cm fork length, or ~ 21.9 cm SL, using the regression parameters provided in Loubens, Panfili, 1995; Montreuil *et al.*, 2001) and Colombian portions of the Amazon (23.5 cm SL, Ruiz, 1994), both calculated more than 20 years ago, or for the Ucayali (26 cm total length or ~ 21 cm SL, Riofrío, 2002). It was, however, much smaller than the 27 cm SL observed in the Bolivian Amazon (Loubens, Panfili, 1995), although age at maturity was reached at about 2 years in both studies, indicating a slower growth in the Putumayo River. In Manacapuru lake the size at maturity was reached at 18 cm SL at about 1.7 years (Campos *et al.*, 2009), also suggesting a slower growth than in the Bolivian Amazon. The smallest size at maturity observed in the Putumayo River, compared to previous studies in the Amazon basin could result from a heavy exploitation of adults in the Putumayo. Life history theory (Stearns, 1992) and empirical studies (Reznick *et al.*, 1990) have shown that populations in which adults suffer relatively higher mortality rates than juveniles are expected to present younger age and smaller size at maturity. Yet, as explained

earlier, fishing gears used to catch this species are similar in most sectors of the Amazon basin and although size-selective mortality differences can be expected between localities and countries, it is unlikely that this explanation, alone, account for the observed  $L_{50}$  difference with the Bolivian Amazon for example, where fishing pressure was very light and also concentrated on large adults (Loubens, Panfili, 1995). Another potential explanation could be the existence of particular environmental conditions in the Putumayo River.

Over the study period, the proportion of fish caught below the size at first sexual maturity ( $L_{50}$ ) was 12% and that caught below the size at which 100% ( $L_{100}$ ) of the fish are mature was ~ 32%. In order to ensure a healthy population, one of the basic principles of fisheries management is to let the possibility to every fish to reproduce at least once in its life before being caught (Myers, Mertz, 1998; Froese, 2004). This implies that the minimum size at capture should be fixed at the  $L_{100}$  (22 cm) instead of the  $L_{50}$  as is customary in Amazonian fisheries. Here, about a third of exploited fish were below 22 cm SL, suggesting that mesh size of fishing gears should be adapted to catch larger fish.

**Age, growth and mortality.** The length frequency analyses per gender using data from ~ 2 years, and that of all fish combined (sexed and unsexed) over a period of > 7 years gave very comparable results, providing a measure of reliability in the estimates. As already observed for the maximum observed length and mass, both  $L_{\infty}$  and  $K$  were in the lower range of values reported for the species in previous studies in the Amazon basin:  $L_{\infty}$  = 34.6-68 cm and  $K$  = 0.28-0.59 (Loubens, Panfili, 1995; Ruffino, Isaac, 1995; Silva, Stewart, 2006; Catarino *et al.*, 2014; Camargo *et al.*, 2015). Comparison of length-at-age with these previous studies (Tab. 5) indicated that fish from the Putumayo had among the slowest growth recorded in the Amazon basin, very similar to that of black water population from the Xingu River (Camargo *et al.*, 2015) and of the over-exploited population of Manacapuru Lake in Brazil (Catarino *et al.*, 2014). *Prochilodus nigricans* is among the most exploited species in the Putumayo fisheries (Agudelo *et al.*, 2006). Although the exploitation rate calculated using the LCCC were below 0.5, the limit above which a stock, or population, is considered overexploited (Rochet, Trenkel, 2003), the mean exploitation rates calculated from other methods did suggest overexploitation in the Putumayo. Overfishing can therefore not be ruled out. Additionally, the explanation for the low maximum sizes, low  $L_{50}$  and slow growth observed in the Putumayo, compared to other populations from the Amazon basin, can also be explained by unfavourable environmental conditions. Although there are no available data to compare trophic conditions in the Putumayo River to other localities in the Amazon basin, negative impacts of anthropic activities could result in unfavourable environmental conditions in the Putumayo: oil leaks in the upper portion of the river, chemical

pollutions resulting from illicit coca culture, increased suspended solids resulting from deforestation and illicit mining (Sierra *et al.*, 2017), or mercury rates in fishes (Nuñez-Avellaneda *et al.*, 2014). Low maximum sizes and slow growth have already been reported in the Putumayo for the silver Arowana, *Osteoglossum bicirrhosum* (Duponchelle *et al.*, 2012) and fish generally tend to be smaller in the Putumayo than in the Caquetá (Bonilla C., pers. obs.).

In absence of comparative environmental data, the potential influence of overexploitation and less favourable trophic conditions in the Putumayo River compared to the Amazonas, Caquetá or Mamore rivers, in the observed size,  $L_{50}$  and growth differences, is difficult to assess and further investigations will be needed to sort out the relative contributions of both factors.

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### References

- Agudelo E, Salinas Y, Sánchez CL, Muñoz-Sosa DL, Alonso JC, Arteaga ME, Rodríguez OJ, Anzola NR, Acosta LE, Núñez M, Valdés H. Bagres de la amazonia colombiana: un recurso sin fronteras. Bogota (DC): Instituto Amazónico de Investigaciones Científicas SINCHI. Programa de Ecosistemas Acuáticos; 2000.
- Agudelo E, Sánchez CL, Acosta LE, Mazon A, Alonso JC, Moya LA, Mori LA. La pesca y la acuicultura 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.59-77.
- Agudelo E, Alonso JC. Contexto de la pesca transfronteriza de los bagres en la región Sur-oriental de la Amazonía colombiana. In: Núñez J, Chu-Koo F, Porto JR, García-Dávila CR, editors. Biología de las Poblaciones de Peces Amazónicos y Piscicultura. Manaus, Brasil. Comunicaciones del Segundo Coloquio Internacional de la Red de Investigación sobre la Ictiofauna Amazónica (RIIA); 2011. p.101-115.
- Agudelo E. Bases científicas para contribuir a la gestión de la pesquería comercial de bagres (familia: Pimelodidae) en la Amazonía colombiana y sus zonas de frontera. [PhD Thesis]. Barcelona: Universidad Autónoma de Barcelona; 2015.
- Barbarino Duque A, Taphorn DC, Winemiller KO. Ecology of the coporo, *Prochilodus mariae* (Characiformes, Prochilodontidae), and status of annual migrations in western Venezuela. Environ Biol Fish. 1998; 53(1):33-46.
- Barbieri LR, Chittenden ME, Jr., Lowerre-Barbieri SK. Maturity, spawning, and ovarian cycle of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. Fish Bull. 1994; 92(4):671-85.
- Batista VS, Isaac VJ, organizers. Peixes e pesca no Solimões Amazonas: uma avaliação integrada. Brasília (DF): Ministério do Meio Ambiente; 2012.
- Bonilla-Castillo CA, Agudelo E, Acosta-Santos A, Ajiaco-Martínez RE, Ramírez-Gil H. Siluriformes: Familia Pimelodidae - *Brachyplatystoma platyneum* Boulenger, 1898. In: Lasso CA, Agudelo E, Jiménez-Segura LF, Ramírez-Gil H, Morales-Betancourt MA, Ajiaco-Martínez RE, Gutierrez FP, Usma JS, Muñoz Torres SE, Sanabria Ochoa AI, editors. Catálogo de los recursos pesqueros continentales de Colombia. Bogotá (DC): Instituto de Investigación de los Recursos Biológicos Alexander von Humboldt; 2011a. p.404-408.
- Bonilla-Castillo CA, Agudelo E, Acosta-Santos A, Gómez G, Ajiaco-Martínez RE, Ramírez-Gil H. Siluriformes: Familia Pimelodidae - *Calophysus macropterus* (Lichtenstein, 1819). In: Lasso CA, Agudelo E, Jiménez-Segura LF, Ramírez-Gil H, Morales-Betancourt MA, Ajiaco-Martínez RE, Gutierrez FP, Usma JS, Muñoz Torres SE, Sanabria Ochoa AI, editors. Catálogo de los recursos pesqueros continentales de Colombia. Bogotá (DC): Instituto de Investigación de los Recursos Biológicos Alexander von Humboldt; 2011b. p.432-435.
- Bonilla-Castillo C, Peña FA, Bonilla-Velazquez C, Velazquez-Figueroa I. La corocora (*Eudocimus ruber*) en la llanura amazónica entre los ríos Caquetá y Putumayo. Ornitología Colombiana. 2017; 16:eNB01-1[4p.].
- Brodziak J, Ianneli J, Lorenzen K, Methot RD, Jr., editors. Estimating natural mortality in stock assessment applications. Seattle (WA): Alaska Fisheries Science Center; 2011. (NOAA Technical Memorandum; NMFS-F/SPO-119).
- Camacho K, Alonso JC, Cipamocha C, Agudelo E, Sánchez CL, Freitas A, Gaya R, Moya LA. 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.
- Camargo M, Giarrizzo T, Isaac VJ. Population and biological parameters of selected fish species from the middle Xingu river, Amazon basin. Braz J Biol. 2015; 75(3,Suppl.1):S112-S124.
- Campos CP, Prestes L, Soares MG, Freitas CEC. Parâmetros populacionais da curimatã (*Prochilodus nigricans*) do lago Grande de Manacapuru (Amazonas-Brasil). [Internet]. Manaus, AM: Registros da 61ª Reunião Anual da SBPC – Amazônia, Ciência e Cultura [update 2009; cited 2017 Oct 10]. Available from: <http://www.sbpnet.org.br/livro/61ra/resumos/resumos/6487.htm>

- Carolsfeld J, Harvey B, Ross C, Baer A, editors. Migratory fishes of South America: biology, fisheries and conservation status. Ottawa: International Development Research Centre & World Bank; 2003.
- Catarino MF, Campos CP, Garcez R, Freitas CEC. Population dynamics of *Prochilodus nigricans* caught in Manacapuru Lake (Amazon basin, Brazil). Bol Inst Pesca. 2014; 40(4):589-95.
- Cone RS. The need to reconsider the use of condition indices in fishery science. Trans Am Fish Soc. 1989; 118(5):510-14.
- Doria CRC, Ruffino ML, Hijazi NC, Cruz RL. A pesca comercial na bacia do rio Madeira no estado de Rondônia, Amazônia brasileira. Acta Amaz. 2012; 42(1):29-40.
- Duponchelle F, Panfili J. Variations in age and size at maturity of female Nile tilapia, *Oreochromis niloticus*, populations from man-made lakes of Côte d'Ivoire. Environ Biol Fish. 1998; 52(4):453-65.
- Duponchelle F, Lino F, Hubert N, Panfili J, Renno JF, Baras E, Torrico JP, Dugue R, Nuñez J. 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.
- Duponchelle F, Ruíz Arce A, Waty A, Panfili J, Renno JF, Farfán F, García-Vásquez A, Chu Koo F, García Dávila C, Vargas G, Ortiz A, Pinedo R, Nuñez J. 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.
- Flecker AS. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology. 1996; 77(6):1845-54.
- Froese R, Binohlan C. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. J Fish Biol. 2000; 56(4):758-73.
- Froese R. Keep it simple: three indicators to deal with overfishing. Fish Fish. 2004; 5(1):86-91.
- García 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.
- García Vásquez A, Alonso JC, Carvajal F, Moreau J, Nuñez J, Renno JF, Tello S, Montreuil V, Duponchelle F. Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. J Fish Biol. 2009; 75(10):2527-51.
- García-Vásquez A, Vargas G, Sánchez H, Tello S, Duponchelle F. Periodic life history strategy of *Psectrogaster rutiloides*, Kner 1858, in the Iquitos region, Peruvian Amazon. J Appl Ichthyol. 2015; 31(S4):31-39.
- Gayanilo FC, Jr., Sparre P, Pauly D. FAO-ICLARM Stock assessment tools II (FISAT II): revised version, user's guide. Rome: Food and Agriculture Organization of the United Nations; 2005. (Computerized Information Series, Fisheries ; No. 8).
- Gislason H, Daan N, Rice JC, Pope JG. Size, growth, temperature and the natural mortality of marine fish. Fish Fish. 2010; 11(2):149-58.
- Gonçalves C, Batista VS. Avaliação do desembarque pesqueiro efetuado em Manacapuru, Amazonas, Brasil. Acta Amaz. 2008; 38(1):135-44.
- González-Cañón G, Gálvis-Galindo I, Nieto-Torres S, Agudelo E, Valderrama M. Characiformes: Familia Prochilodontidae - *Prochilodus nigricans* (Agassiz, 1829) Capítulo 7. In: Lasso CA, Agudelo E, Jiménez-Segura LF, Ramírez-Gil H, Morales-Betancourt MA, Ajiaco-Martínez RE, Gutierrez FP, Usma JS, Muñoz Torres SE, Sanabria Ochoa AI, editors. Catálogo de los recursos pesqueros continentales de Colombia. Bogotá (DC): Instituto de Investigación de los Recursos Biológicos Alexander von Humboldt ; 2011. p.317-320.
- Goulding M. The fishes and the forest: explorations in Amazonian natural history. Berkeley (CA): University of California Press; 1980.
- Hoeinghaus DJ, Winemiller KO, Layman CA, Arrington DA, Jepsen DB. Effects of seasonality and migratory prey on body condition of Cichla species in a tropical floodplain river. Ecol Freshwat Fish. 2006; 15(4):398-407.
- Jensen AL. Beverton and holt life history invariants result from optimal trade-off of reproduction and survival. Can J Fish Aquat Sci. 1996; 53(4):820-22.
- King M. Fisheries biology, assesment and management. Oxford, England: Fishing New Books; 1995.
- Loubens G, Panfili J. Biologie de *Prochilodus nigricans* (Teleostei: Prochilodontidae) dans le bassin du Mamoré (Amazonie bolivienne). Ichthyol Explor Freshw. 1995; 6(1):17-32.
- Lowe-McConnell RH. The fishes of the Rupununi savanna district of British Guiana, South America : Part 1 - Ecological groupings of fish species and effects of the seasonal cycle on the fish. Zool J Linn Soc. 1964; 45(304):103-44.
- Lowe-McConnell RH. Ecological studies in tropical fish communities. Cambridge: Cambridge University Press; 1987.
- Machado VN, Willis SC, Teixeira AS, Hrbek T, Farias IP. Population genetic structure of the Amazonian black flannelmouth characin (Characiformes, Prochilodontidae: *Prochilodus nigricans* Spix & Agassiz, 1829): contemporary and historical gene flow of a migratory and abundant fishery species. Environ Biol Fish. 2017; 100(1):1-16.
- Melo BF, Sidlauskas BL, Hoekzema K, Frable BW, Vari RP, Oliveira C. Molecular phylogenetics of the Neotropical fish family Prochilodontidae (Teleostei: Characiformes). Mol Phylogenet Evol. 2016; 102(2016):189-201.
- Montreuil V, Tello JS. Determinación de edad en 'boquichico' (*Prochilodus nigricans* Agassiz, Teleostei: Characoidei) mediante lectura de esclerites en escamas. Folia Amazónica. 1988; 1(1-2):27-47.
- Montreuil V, García A, Rodríguez R. Biología reproductiva del «Boquichico», *Prochilodus nigricans* (Agassiz, 1829), en la Amazonía Peruana. Folia Amazónica. 2001; 12(1-2):5-13.
- Moreau J, Palomares MLD, Torres FSB, Jr., Pauly D. Atlas démographique des populations de poissons d'eau douce d'Afrique. Paris: Agence de Coopération Culturelle et Technique; 1995. (ICLARM Technical Papers ; No. 45).
- Mota SQ, Ruffino ML. Biología e pesca do curimatá (*Prochilodus nigricans* Agassiz, 1829) (Prochilodontidae) no médio Amazonas. Rev UNIMAR. 1997; 19(2):493-508.

- Murcia UG. Zonificación ambiental de la cuenca del río Putumayo. Bogota (DC): Instituto Amazónico de Investigaciones Científicas SINCHI & Instituto Nacional de Desarrollo INADE; 2006.
- Myers RA, Mertz G. The limits of exploitation: a precautionary approach. *Ecol Appl*. 1998; 8(Sp1):S165-S169.
- 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.
- Núñez-Avellaneda M, Marín ZY, Alonso JC, Ríos E, Andrade-Sossa C, Freitas A, Gaya R. 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-Avellaneda M, Agudelo E, Gil-Manrique BD. Un análisis descriptivo de la presencia de mercurio en agua, sedimento y peces de interés socio-económico en la Amazonía colombiana. *Revista Colombia Amazónica*. 2014; 7(2014):149-59.
- Pauly D. Theory and management of tropical multispecies stocks: a review, with emphasis on the Southeast Asian demersal fisheries. Manila, Philippines: International Center of Living Aquatic Resources Management; 1979. (ICLARM Studies and Reviews ; No. 1).
- Pauly D. On the interrelationship between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *ICES J Mar Sci*. 1980; 39(2):175-92.
- Pauly D, David N. ELEFAN I, a basic program for the objective extraction of growth parameters from length-frequency data. *Ber Deut Wiss Komm*. 1981; 28(4):205-11.
- Pauly D. Length converted catch curves: a powerful tool for fisheries research in the tropics (Part I). *Fishbyte*. 1983; 1(2):9-13.
- Reznick DA, Bryga H, Endler JA. Experimentally induced life history evolution in a natural population. *Nature* 1990; 346(6282):357-59.
- Riofrío JC. Aspectos biométricos y reproductivos de Boquichico *Prochilodus nigricans* Agassiz, 1829 (Pisces: Prochilodontidae) en Ucayali, Perú. *Rev Peru Biol*. 2002; 9(2):111-15.
- Rochet MJ, Trenkel VM. Which community indicators can measure the impact of fishing?: a review and proposals. *Can. J Fish Aquat Sci*. 2003; 60(1):86-99.
- Ruffino ML, Isaac VJ. Life cycle and biological parameters of several Brazilian Amazon fish species. *Naga, the ICLARM Quarterly*. 1995; 18(4):41-45.
- Ruiz OL. Some aspects of the biology of five fish species *Prochilodus nigricans* (Agassiz, 1829), *Mylossoma duriventre* (Cuvier, 1818), *Brycon melanopterus* (Cope, 1871) *Schizodon fasciatus* (Agassiz, 1829), *Pterygoplichthys punctatus* (Günther, 1864) and basic characterization of the fishing market of Leticia. [Undergraduate Thesis] Bogotá (DC): Departament of Biology. National University of Colombia; 1994.
- Sierra CA, Mahecha M, Poveda G, Álvarez-Dávila E, Gutierrez-Velez VH, Reu B, Feilhauer H, Anáya J, Armenteras D, Benavides AM, Buendía C, Duque A, Estupiñan-Suarez LM, González C, Gonzalez-Caro S, Jimenez R, Kraemer G, Londoño MC, Orrego SA, Posada JM, Ruiz-Carrascal D, Skowronek S. Monitoring ecological change during rapid socio-economic and political transitions: Colombian ecosystems in the post-conflict era. *Environ Sci Policy*. 2017; 76(2017):40-49.
- 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.
- Silva EA, Stewart DJ. Reproduction, feeding and migration patterns of *Prochilodus nigricans* (Characiformes: Prochilodontidae) in northeastern Ecuador. *Neotrop Ichthyol*. 2017; 15(3): e160171[13p.].
- Simpfendorfer CA, Bonfil R, Latour RJ. Mortality estimation. In: Musick JA, Bonfil R, editors. *Management techniques for elasmobranch fisheries*. Rome: Food and Agriculture Organization of the United Nations; 2005. (FAO Fisheries Technical Paper; No. 474). p.127-143.
- Sivasundar A, Bermingham E, Orti G. Population structure and biogeography of migratory freshwater fishes (*Prochilodus*: Characiformes) in major South American rivers. *Mol Ecol*. 2001; 10(2):407-17.
- Sparre P, Venema SC. Introducción a la evaluación de recursos pesqueros tropicales: Parte 1 - Manual. Roma: Organización de las Naciones Unidas para la Agricultura y la Alimentación; 1997. (FAO Documento Tecnico de Pesca; No. 306, Rev. 2).
- Stearns SC. The evolution of life histories. New York: Oxford University Press; 1992.
- Taylor CC. Cod growth and temperature. *ICES J Mar Sci*. 1958; 23(3):366-70.
- Taylor BW, Flecker AS, Hall Jr. RO. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science*. 2006; 313(5788):833-36.
- Tello JS, Montreuil VH, Maco JT, Ismiño RA, Sanchez H. Bioecología de peces de importancia económica de la parte inferior de los ríos Ucayali y Marañón. *Folia Amazónica*. 1992; 4(2):87-106.
- Vazzoler AEAM, Menezes NA. Síntese de conhecimentos sobre o comportamento reproductivo dos Characiformes da América do Sul (Teleostei, Ostariophysi). *Rev Brasl Biol*. 1992; 52(4):627-40.
- Vetter EF. Estimation of natural mortality in fish stocks: a review. *Fish Bull*. 1988; 86(1):25-43.
- Winemiller KO, Jepsen DB. Effects of seasonality and fish movement on tropical river food webs. *J Fish Biol*. 1998; 538(SA):267-96.
- Wootton RJ. The ecology of teleost fishes. 2nd. ed. Netherlands: Kluwer Academic Publisher; 1998.



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