Original article

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

César A. Bonilla-Castillo[1,2], Edwin Agudelo Córdoba[1,2], Guber Gómez[1,2] and Fabrice Duponchelle[2,3]

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).

[1]Instituto Amazónico de Investigaciones Científicas - SINCHI. Sede Principal: Av. Vásquez Cobo entre Calles 15 y 16, Leticia, Amazonas, Colombia. (CABC) cbonilla@sinchi.org.co, ⓘhttps://orcid.org/0000-0001-9816-529X (corresponding author), (EAC) eagudelo@sinchi.org.co, (GG) ggomez@sinchi.org.co
[2]Laboratoire Mixte International - Evolution et Domestication de l'Ichtyofaune Amazonienne (LMI-EDIA).
[3]Institut de Recherche pour le Développement (IRD), UMR BOREA (MNHN, CNRS-7208, IRD-207, Sorbonne Université, Université Caen Normandie, Université des Antilles), France. fabrice.duponchelle@ird.fr

Owing to their abundance, detrivorous 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 Prochilodondidae (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 km², the Putumayo River basin is one of the main Andean tributaries from the Colombian and Ecuadorian portions of the Amazon basin (Murcia, 2006). Puerto Leguízamo 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 see 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 Leguízamo. Fishing areas are usually localized within a 140 km radius from Puerto Leguízamo, 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.
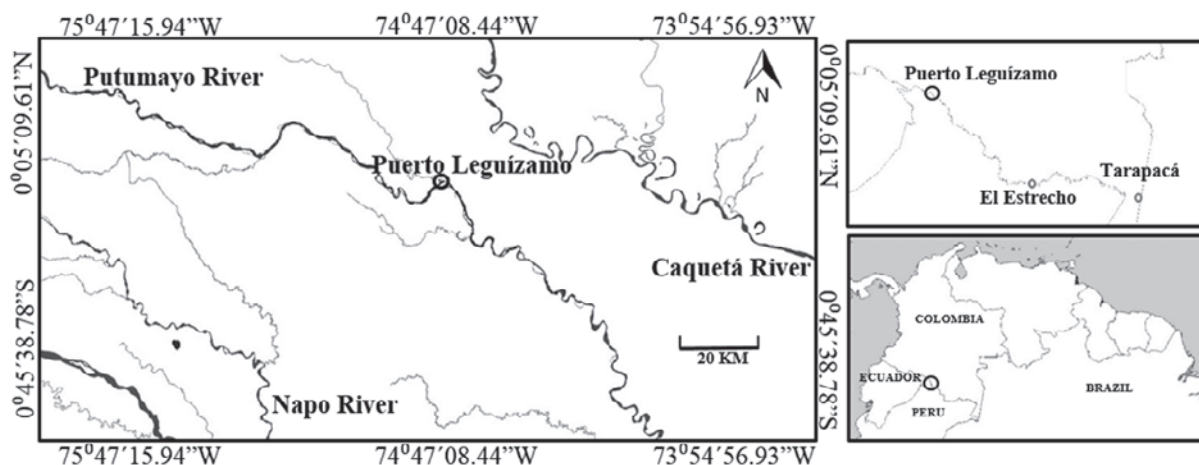

Fig. 1. Geographic location of the study area around Puerto Leguízamo in the Putumayo River, Colombian Amazon.

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 gonado-somatic 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 log10 transformed to obtain a linear relationship (Cone, 1989; Hoeinghaus *et al.*, 2006): log10(Wt) = a + b(log10 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∞ (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_∞ 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):

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

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

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

$$A_p = t_o - [\ln(1-p)K^{-1}]$$

where t_0, and K are the VBGF parameters and p is a fraction of L_∞ (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_∞, 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):

$$-0.006-0.270*Log10(L_\infty)+0.6543*Log(K)+0.4634*Log10(T°),$$

where L_∞ and K are the VBGF parameters and T° 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 $E = F.Z^{-1}$.

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 = $0.0199*SL^{3.0453}$, $r^2 = 0.925$, P<0.001 for females; Wt = $0.044*SL^{2.777}$, $r^2 = 0.904$, 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 = $0.020*SL^{2.988}$, $r^2 = 0.925$, P<0.001 for females; We = $0.028*SL^{2.880}$, $r^2 = 0.909$, 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).
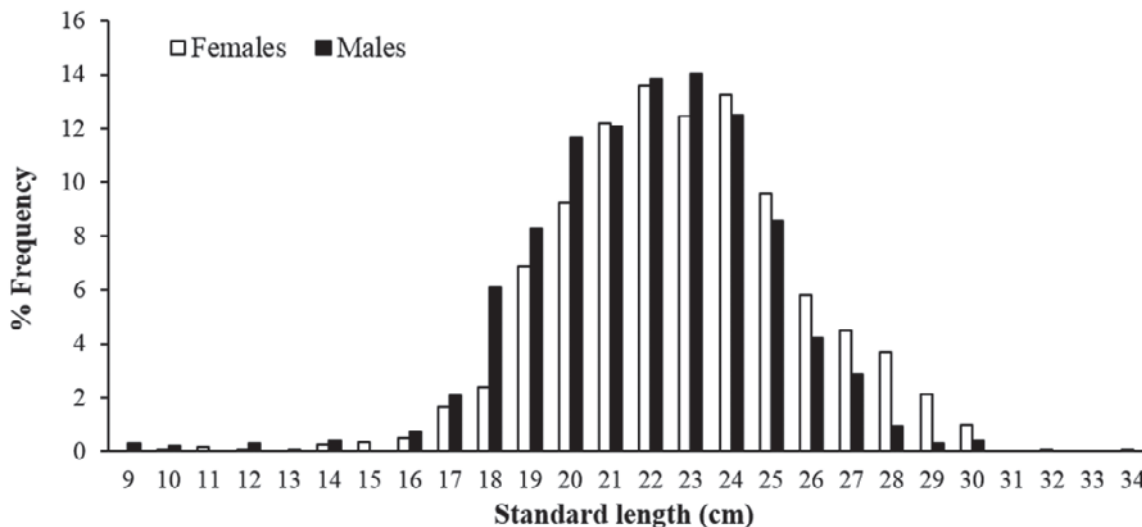

Fig. 2. Size frequency distribution for both *Prochilodus nigricans* females and males in the upper Putumayo River between 2009 and 2017.

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Tab. 1. Mean (± 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 artesanal fisheries in the Putumayo River. N = number of fish analysed.

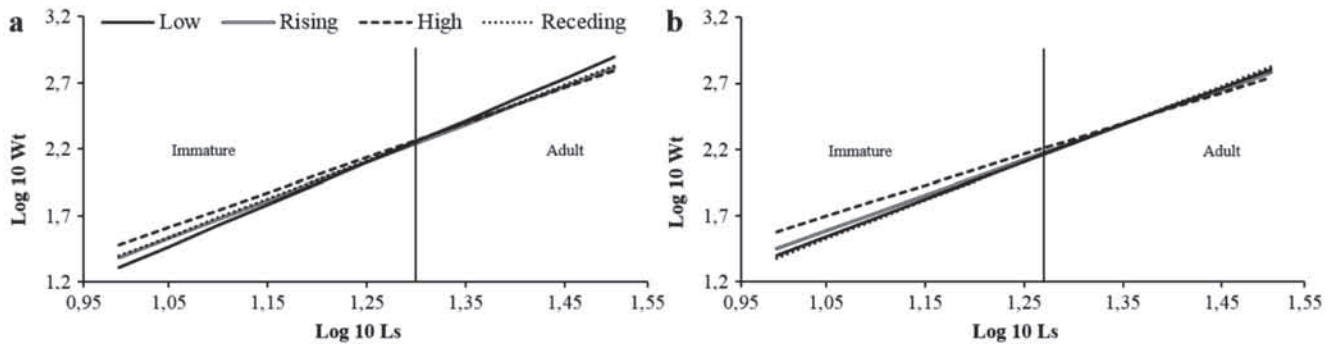| Sex	N	Mean Ls (cm) ± SD	Range (cm)	Mean Wt (g) ± SD	Range (g)	Mean We (g) ± SD	Range (g)
F	1117	22.7 ± 3.0	10.2 - 33.9	286.4 ± 126.6	24 - 1017	243.5 ± 104.6	21 - 817.8
M	949	21.8 ± 2.8	8.8 – 30.3	241.7 ± 92.3	12 – 709.2	210.1 ± 81.9	9 – 628.6
T	10884	23.2 ± 2.9	8.2 - 34				

Fig. 3. Changes in the body condition, expressed by the log10-transformed standard length (L_s) 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_s) 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).
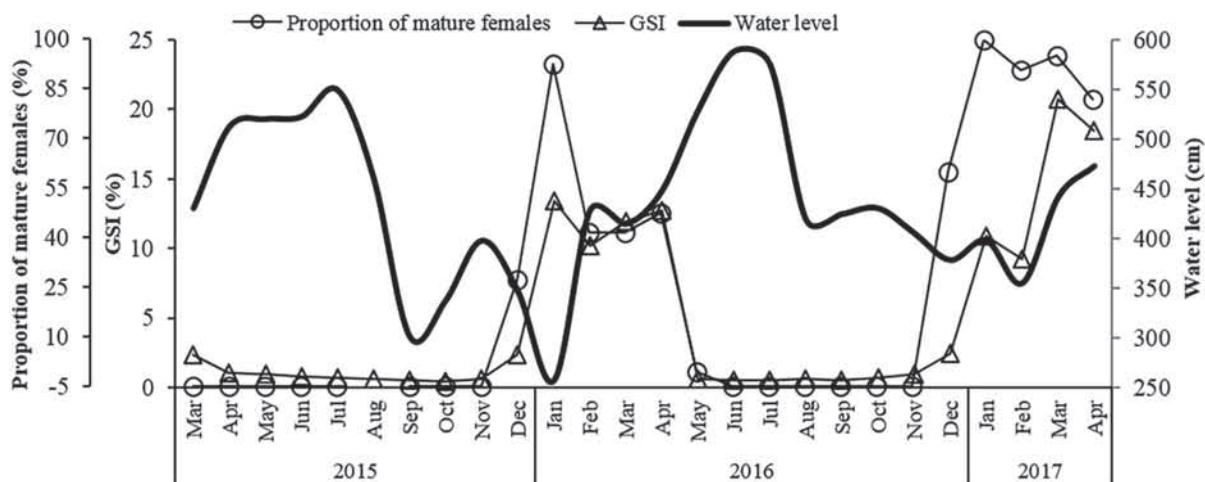
Fig. 4. Mean monthly values of the gonado-somatic index (GSI) and monthly proportions of breeding females for *Prochilodus nigricans* in the Putumayo River in relation to the water level (black smoothed line).
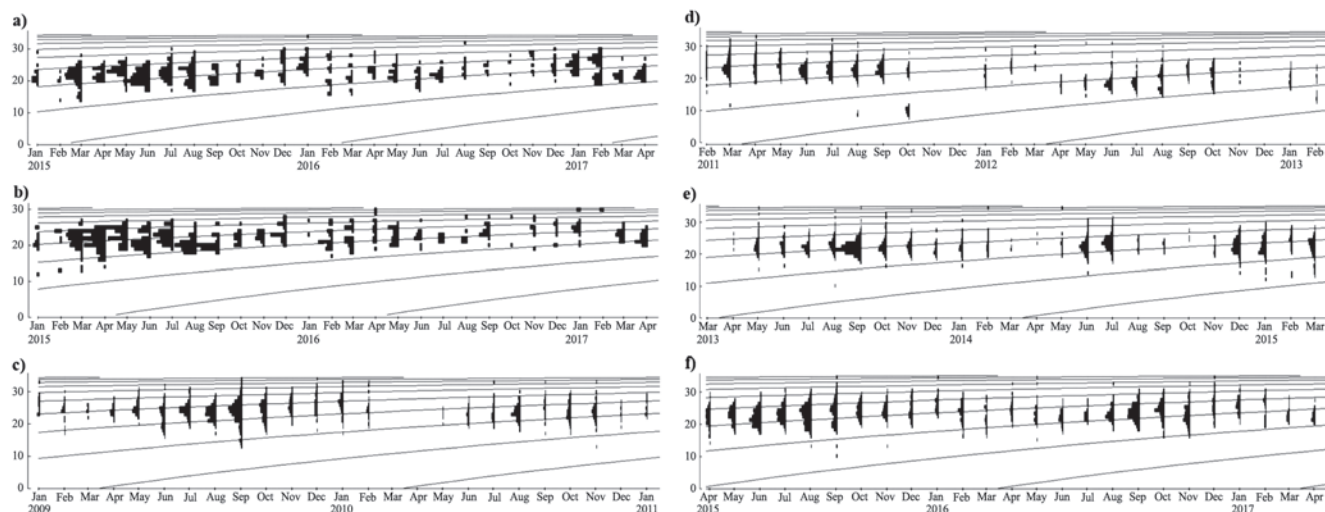

Fig. 5. Standard length frequency histograms and the corresponding von Bertalanffy growth function for females (**a**) and males (**b**) between January 2015 and April 2017 and for all individuals (sexed and unsexed) combined of *Prochilodus nigricans* in the Putumayo River between 2009 and 2017 (**c-f**).

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

	L_∞ (cm)	K (year^{-1})	T_0 (year^{-1})	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.
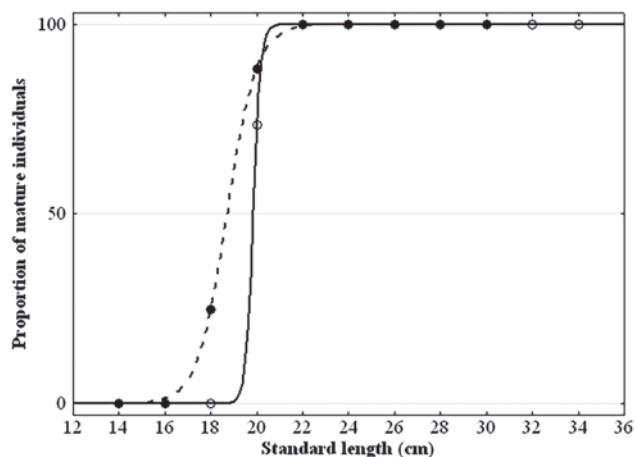

Fig. 6. Standard length at first sexual maturity for males (black dots) and females (white circles) of *Prochilodus nigricans* in the Putumayo River.

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Over the study period the mean size at capture varied between 20.6 and 25.2 cm (mean 23.1 cm ± 1.4 SD, Tab. 5). Overall, the proportion of fish caught below the size at first sexual maturity was 12 ± 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 ± 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^{-1} 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 *et al*. (2014)	Camargo *et al*. (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.

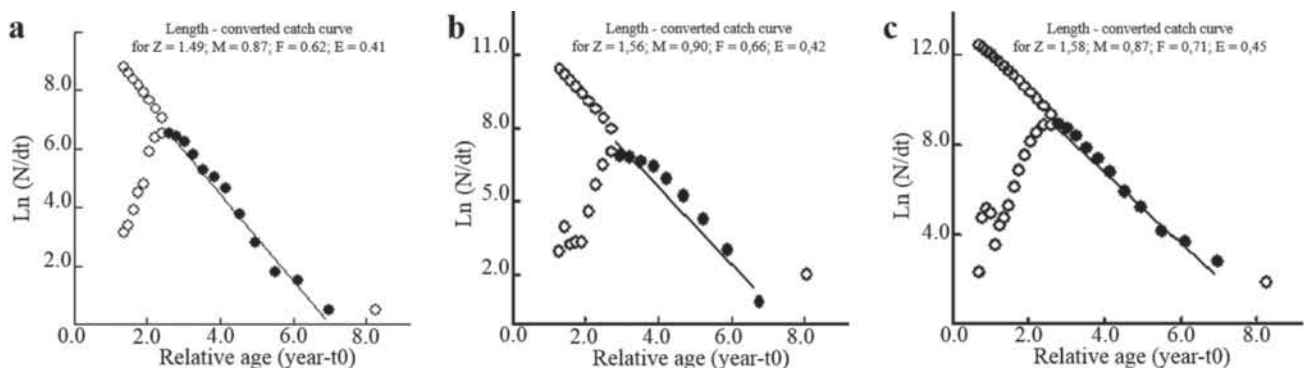|	2009	2010	2011	2012	2013	2014	2015	2016	2017
Mean LS	24.3	24.3	23.0	20.6	21.9	22.5	22.7	23.4	25.2
Range LS	13 - 34	13 - 33.5	8.2 - 33	15 - 31	10 - 34	14 - 34	10 - 34	14.7 - 34	19 - 31.4
Fish < 20 cm	116	21	83	301	136	71	331	134	11
Fish < 22 cm	311	122	283	437	623	316	859	451	26
% fish < L$_{50}$	6	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.Z^{-1}). Black dots = data points in the curve on which the regression was fitted.

Tab. 6. Natural mortality (M, year^{-1}) calculated using different models and corresponding fishing mortality (F, year^{-1}) 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$_{50}$	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$_{50}$	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 Leguízamo. 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 Leguízamo 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 Leguízamo, 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 Leguízamo 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 Leguízamo 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. natterreri*, 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, Ruíz, 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 results 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∞ and K were in the lower range of values reported for the species in previous studies in the Amazon basin: L∞ = 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 results 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*., 20l4). 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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