Life history trait variations and population dynamics of *Calophysus macropterus* (Siluriformes: Pimelodidae) in two river systems of the Colombian and Peruvian Amazon

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The catfish *Calophysus macropterus* is heavily exploited in the Amazon basin, yet its life history characteristics are poorly documented, hampering proper fisheries management. In order to fill this gap, monthly sampling in the upper Putumayo River and in the Amazonas, lower Marañón and Ucayali (AMU) rivers were carried out over several years (2013–2015 in the AMU, 2013–2017 in the Putumayo) to provide detailed information about its reproduction, growth and mortality patterns (using length frequency data). Reproduction, which occurs during the dry and early flooding season, was only observed in the upper Putumayo River and not in the sampled portion of the AMU system, suggesting that the species reproduces closer to the Andes than other pimelodid catfishes. Size at first sexual maturity did not differ significantly among sex or among river systems, ranging from 25–28 cm SL. In both river systems, females had a faster growth than males and both genders also tended to have a better growth in the AMU than in the upper Putumayo. Mortality and exploitation estimate all indicated overexploitation of the species in both river systems. The implications of these results for fisheries management and conservation are discussed.

Keywords: Amazonas-Marañón-Ucayali, Catfish, Growth, Overfishing, Putumayo.

El bagre *Calophysus macropterus* está fuertemente explotado en la cuenca Amazónica. Sin embargo, su ciclo de vida está poco documentado, lo que dificulta su gestión pesquera. Para llenar este vacío, se realizaron muestreos mensuales en el alto río Putumayo alrededor de Puerto Leguízamo y en el Amazonas y los ríos bajo Marañón y Ucayali (AMU) cerca de Iquitos durante varios años (2013–2015 en AMU, 2013–2017 en Putumayo) para generar información sobre su reproducción, crecimiento y mortalidad. La reproducción, que se produce durante la estación seca y el inicio de la inundación, sólo se observó en el curso superior del río Putumayo y no en la parte muestreada del sistema de la AMU, lo que sugiere que la especie se reproduce más cerca de los Andes que otros pimelodidos. El tamaño de primera madurez sexual no difirió entre sexos o entre sistemas fluviales, oscilando entre 25-28 cm. En ambos sistemas fluviales, las hembras tuvieron un crecimiento más rápido que los machos y ambos géneros también tendieron a tener un mejor crecimiento en el AMU que en el alto Putumayo. Estimaciones de mortalidad y explotación indicaron una sobreexplotación en ambos sistemas. Se discuten las implicaciones de estos resultados para la gestión y conservación de las pesquerías.

Palabras clave: Amazonas-Marañón-Ucayali, Bagre, Crecimiento, Putumayo, Sobrepesca.

INTRODUCTION

The migratory catfish *Calophysus macropterus* (Lichtenstein, 1819) is largely distributed in rivers and floodplains of the Amazon and Orinoco basins (Pérez, Fabré, 2009). Being a single species genus in the family Pimelodidae, it was traditionally not a prime target in Amazonian fisheries (Agudelo *et al.*, 2000; Pérez, Fabré, 2002), except in the Putumayo River in Colombia where it has long been one of the main landed species (Bonilla-Castillo *et al.*, 2011). In the last two decades, however, landings of *C. macropterus* have greatly increased in Colombia and Peru, possibly owing to the decreasing abundance of the main catfish targets such as the large *Brachyplatystoma* Bleeker, 1862 and *Pseudoplatystoma* Bleeker, 1862 species and to the growing demand in Colombian big cities, where it is sold fraudulently as the 'capaz', *Pimelodus grosskopfii* Steindachner, 1879, a highly appreciated and now endangered catfish species from the Magdalena River (García Vasquez *et al.*, 2009, García-Vasquez *et al.*, 2012; Bonilla-Castillo *et al.*, 2011, 2012; Mosquera-Guerra *et al.*, 2015). While its catches barely accounted for 0.3% of total landings in the Loreto region (Peru) in 2000, *C. macropterus* was the 7th most landed species in 2016, accountin`g for ~ 4% of total landings in the Loreto and > 6% in the Ucayali region (García Vasquez *et al.*, unpublished data). In the Putumayo River, Colombia, it already accounted for ~ 21% of total landings in 2000 (Bonilla-Castillo *et al.*, 2012) and in 2016, it accounted for ~ 50% of total landing, together with *Pinirampus pirinampu* (Spix & Agassiz, 1829), another pimelodid species (Bonilla-Castillo, Agudelo, unpublished data).

Although its diet can be classified as opportunistic omnivorous to piscivorous, based on its main food items: fish (dominant item), plant material (including seeds)

and invertebrates (García Vasquez *et al.*, 2017), the species also have a pronounced necrophagous tendency, which explains why it was traditionally rejected in central Amazonia (Pérez, Fabré 2009; Cunha *et al.*, 2015). Additionally, the feeding habits of *C. macropterus* often result in methyl-mercury bioaccumulation largely exceeding the maximum reference value (0.5 mg.kg^{-1}) established by the World Health Organisation (Mosquera-Guerra *et al.*, 2015). As a consequence, its fishing has been banned for 5 years (2016–2020) by normative actions in Brazil (Franco *et al.*, 2016) and indefinitely in Colombia since 2017 (resolution N°1710/2017, AUNAP). In Brazil, using mtDNA sequencing, Cunha *et al.* (2015) evidenced that *C. macropterus* processed as fillet was frequently sold by fish-processing plants and markets under deceptive names, in spite to the rejection of scavenger fishes by Brazilian consumers. Although fishing *C. macropterus* has been officially banned in Brazil, several factors suggest that its fisheries might still be operating: the existence of an established production chain that largely exports to Colombia (Franco *et al.*, 2016) together with a widespread retail market in Brazil (Cunha *et al.*, 2015), the fact that it yields important income with much less effort than other fisheries in the Amazon (Iriarte, Marmontel, 2013) and the lack of enforcement by government agencies (Cunha *et al.*, 2015). Yet, in spite of its recently acquired economic importance and popularity, albeit infamous, in most Amazonian countries, the few studies about the life history characteristics of *C. macropterus* are geographically restricted to Central Amazonia (Pérez, Fabré, 2002, 2009) and a portion of the Colombian Amazon (Agudelo *et al.*, 2000). Apart from some information about its reproduction in the Putumayo River (Camacho *et al.*, 2006), little is known about its life history traits and population dynamics in the Putumayo and in the Peruvian Amazon, where this species strongly contributes to fisheries landings. The present study aimed at characterising important life history traits (reproductive, growth and mortality patterns) for fisheries management and conservation in the main landing site of the Peruvian Amazon, Iquitos, and in Puerto Leguízamo, located in the upper Putumayo River, shared by Colombia and Perú. Indeed, previous studies have shown important differences in the life history traits of different species between the two river systems (Duponchelle *et al.*, 2012, 2015; Bonilla-Castillo *et al.*, 2018).

MATERIAL AND METHODS

Sampling area. The city of Puerto Leguízamo (00°11'53.2"S 74°46'42.7"W) is located in the upper part of the Putumayo River at a height of 220 m.a.s.l. its climate is hot and humid (Bonilla-Castillo *et al.*, 2018) (Fig. 1). Iquitos (03°44'56.83"S 73°15'13.79"W), on the other hand, is located at ~ 90 m.a.s.l., slightly below where the Marañón and Ucayali, two of the major tributaries of the Amazon basin, meet to form the Amazonas River. We will thereafter refer to the lower Marañón, lower Ucayali and Amazonas around Iquitos as the AMU system. The AMU is mainly constituted of nutrient-rich white waters originating from the Andes (Hanek, 1982). The hydrological conditions in the AMU produce flood pulses that inundate large, highly productive areas responsible for the best fisheries production of the Peruvian Amazon (Tello, Bayley, 2001). The Marañón River has a length of 1,707 km, its average velocity on the lower portion is 1.65 m.s^{-1} with flow ranging between 7,000 to 25,000 m³.s-1 (MINAM, 2011). The

FIGURE 1 | Geographic location of biological monitoring points for *Calophysus macropterus* at Puerto Leguízamo in the Putumayo River (Colombia) and Iquitos (Amazonas, lower Marañón and Ucayali rivers, AMU).

Ucayali River has a length of ,2670 km, its average velocity is between 1.5 to 2.5 m.s⁻¹, with a flow ranging from 2,700 to 20,000 m³.s⁻¹ in the lower portion (MINAM, 2011). The Putumayo is one of the two major affluents of Colombia flowing into the Amazon River. It has a length of 2,000 km, of which 1,500 travels the Colombian territory and 450 km in Brazil (Alonso *et al.*, 2006). The Putumayo River is a white-water system of Andean origin. At the Puerto Leguízamo is has a flow of 268 m³.s⁻¹ average, with a maximum value of 417 m³.s⁻¹ in the month of May. The transparency of the water is approximately 16 cm, the conductivity of the river is 36.96 µS/cm, pH of 6.26 average, dissolved oxygen of 7.85 mg/L and average water temperature of 27.2°C (Núñez-Avellaneda *et al.*, 2006).

Fish sampling. In the Putumayo, fish were sampled monthly between 2013 and 2017 in the main landing sites of the city of Puerto Leguízamo (Colombia), where fishermen exert their activity ~140 km around the city (Fig. 1). In Iquitos (Peru), fish were sampled monthly between 2013 and 2015 in the main landing sites of the city, where fishermen land their products from the Amazonas, the lower Marañón and the lower Ucayali rivers (AMU system).

In both sampling sites, fishermen mainly use two methods for the capture of *C. macropterus*. The first is using bait, usually blood and decomposing meat (mainly beef and pork viscera and grease) that is submerged near the boat along the river preferably during the hours of night and early morning. Once the fish have concentrated around the bait, they are caught by purse seines of 2 inches mesh-size. This method is used during all hydrological periods, although less frequently on nights with full moon. It is

non selective, as all sizes get caught.

The second fishing method uses a nylon line with 30 to 50 hooks size #6, submerged perpendicularly to the main river channel. Hooks are baited with fish parts (see García Vásquez *et al.*, 2017 for further details). This method is more selective as hook size determines bait size and hence the size of fish caught. But as the same size of hooks is used in both the AMU and the Putumayo, selectivity should not impact the size distribution of fish caught in the two sampling areas.

Specimens were compared with reference collections of this species in the Amazon Icthyological Collection of Instituto Amazónico de Investigaciones Científicas Sinchi (*e.g.*, voucher Sinchi: CIACOL:455, Leticia, 04°12'30.5"S 69°56'0.5"W, Amazon River, Amazonas, Colombia) to verify identification.

For each fish, standard length (SL) was recorded to the nearest cm, and when possible total and eviscerated body mass (to the nearest g, Wt and We, respectively). When the fish were not eviscerated, gonads were photographed and macroscopically checked for gender and maturity stage determination, then weighed to the nearest 0.1 g. The gonadal maturation scale used was that of Núñez, Duponchelle (2009). Briefly, males at stage 1 are immature, at stage 2 they are either maturing or resting and at stage 3 they are ripe. Females at stage 1 are also immature; at stage 2 they are maturing; at stage 3 they are in advanced maturation; at stage 4 they are ripe; at stage 5 they have just spawned and at stage 6 they are resting.

Reproductive aspect. The reproduction period was estimated from the monthly proportions of gonadal maturation stages and of the gonado-somatic index (GSI = gonad mass/total body mass *100) in adult females. The average size at first sexual maturity (L_{50}) is defined as the standard length at which 50% of the individuals are at an advanced stage of the first sexual cycle during the breeding season (Sparre, Venema, 1998). Practically, this is the size at which 50% of the fish have reached stage 2 of the maturity scale for females and males (Núñez, Duponchelle, 2009). For each river system and for each gender, the mean S_L at first maturity (L_{50}) was estimated by fitting the fraction of mature individuals per 5 mm S_L intervals to a logistic regression function weighted by the total number of individuals in each size class (Bonilla-Castillo *et al.,* 2018):

$$\%M = 100/1 + e^{(-ax(L-L50)}$$

where %M = percentage of mature individual by size class, L = central value of each size class, and a and L_{50} = constants of the model.

Growth aspect. Age and growth characteristics were calculated from the modal progressions of SL frequency distributions (King, 2007) 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_∞ (Sparre, Venema, 1998). The growth parameters were calculated by the von Bertalanffy Growth Function (VBGF) equation fitted by the ELEFAN method:

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

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 (1980):

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

The estimated L_∞ and K values were used to calculate the growth performance index (phi prime, ǿ) defined by Pauly, Munro (1984) as

ǿ = logK + 2log L_∞.

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

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

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

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

$$Ap = to - [\ln(1-p)K^{-1}]$$

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. 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 (Pauly, 1980) and several empirical models linking M to life history attributes such as age at maturity or growth were proposed for fish (reviews in 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. Several of these relationships were calculated in order to provide a range of natural mortality values and assess their effect on the estimation of fishing mortality and exploitation rate (E). Hence, natural mortality was evaluated using Pauly (1980)'s equation, as implemented in the FiSAT package, for a mean annual temperature of

27°C (Bonilla-Castillo *et al.*, 2018):

$$-0.006-0.270^{\star}\mathrm{Log}_{10}(L_{\infty})+0.6543^{\star}\mathrm{Log}(K)+0.4634^{\star}\mathrm{Log}_{10}(T^{\circ}),$$

where L_{∞} and K are the VBGF parameters and T° the mean annual temperature.

Other empirical methods were used to estimate natural mortality (M), among them: Equation of Gislason *et al.* (2010) with the mathematical expression $0.55 - 1.61\mathrm{Ln}(L) + 1.44\mathrm{Ln}(L_{\infty}) + \mathrm{Ln}(K)$; Rikhter, Efanov (1976): $1.521/(L50)^{0.72} - 0.155$; Charnov *et al.* (2013): $[(L/L_{\infty})^{-1.5})] \times K$; Jensen (1996) using K: $1.6^{\star}K$; Jensen (1996) using A_{50}: $1.65/A_{50}$ (A_{50}: Age at which 50% of the population reaches sexual maturity.

For the equations of Gislason *et al.* (2010) and Charnov *et al.* (2013) "L" was established as the average length in immature and for mature individuals.

Fishing mortality (F) was calculated as $F = Z-M$ (Pauly, 1980). The exploitation rate was estimated as $E = F.Z^{-1}$. For comparison purposes, both F and E were calculated for the different estimates of M.

Biometric indicator. The weight-length relationship was estimated by expression $Wt=a^{\star}SL^{b}$, after logarithmic transformation $\log(Wt)=\log(a)+b^{\star}\log(SL)$, Wt the total weight, SL the standard length, "a" the intercept of the curve and "b" the allometry coefficient of the weight-length ratio (Zar, 2010).

Statistical analyses. Differences in mean Ls, Wt and We between sexes were tested with a Mann–Whitney rank-sum test. Parametric tests could be carried out as either normality of distributions or homocedasticity were not met. Differences in size at first sexual maturity were tested using t-test.

RESULTS

A total of 8,064 specimens of *C. macropterus* were analysed from Puerto Leguízamo (upper Putumayo River), 3.2% (254) in 2013 (November and December), 26.9% (2,161) in 2014, 28.9% (2,319) in 2015, 31.1% (2,528) in 2016 and 10% (802) in 2017 (January to June). A total of 1,710 specimens were analysed from Iquitos, 37% (634) in 2013, 40% (688) in 2014 and 23% (388) in 2015. The smallest size class observed in the Putumayo River was 22 cm, whereas individuals of 16 cm were caught in commercial fisheries of the AMU system around Iquitos (Figs. 2A, B). Overall, in both river systems females were significantly larger (Mann–Whitney Rank Sum test: U = 401256, P<0.001 in the Putumayo River; U = 18224, P<0.001 in the AMU rivers) and heavier (U = 466462.5, P<0.001 in the Putumayo River; U = 17729.5, P<0.001 in the AMU) than males in commercial landings (Tab. 1).

Although maximum observed length (Lmax) only varied by 4% and 2% between females and males in the Putumayo and AMU, respectively, maximum observed body mass (Wmax) varied by 14% and 22% in the Putumayo and AMU, respectively. However, when looking at mean observed lengths and masses, differences between males and females varied by 20% in length and 51% in mass for the Putumayo and by

TABLE 1 | Mean length of catch and range of standard length (SL), total weight (Wt), range of weight, length-weight relationship (*a* and *b*), 95% confidence interval (CI), r² determination coefficient of females (F), males (M) and all individuals (sex and unsexed, T) combined of *Calophysus macropterus* specimens analysed from Puerto Leguízamo (upper Putumayo River) and Iquitos (Amazonas, lower Marañón and Ucayali rivers, AMU). N = number of fish analysed.

River	Sex	N	S_L mean (cm)	(S_L cm) range	Wt Mean (g)	Wt Range (g)	*a* ($CI_{95\%}$)	*b* ($CI_{95\%}$)	r²
Upper Putumayo	F	2706	39.0	23.0-47.5	807	128-1453	0.010 (0.009-0.011)	3.08 (3.04-3.12)	0.9014
	M	4115	31.0	22.0-45.8	395	140-1254	0.014 (0.012-0.015)	2.99 (2.95-3.02)	0.8898
	T	8064	34.0	22.0-47.5	550	128-1454	0.011 (0.010-0.011)	3.06 (3.04-3.07)	0.9578
AMU	F	1112	35.0	23.0-46.6	588	61-1312	0.009 (0.008-0.011)	3.08 (3.04-3.12)	0.9656
	M	597	28.4	22.0-45.8	304	74-1020	0.011 (0.009-0.013)	3.04 (2.98-3.09)	0.9510
	T	1710	32.7	16.5-46.6	489	61-1312	0.010 (0.009-0.010)	3.08 (3.07-3.10)	0.9623

19% in length and 48% in mass in the AMU (Figs. 2A, B; Tab. 1).

Over the study period, standard length (SL) – total mass relationships (M_t) were $Wt = 0.0099 \, SL^{3.078}$ ($R^2 = 0.901$, $P<0.001$) and $Wt = 0.0135 \, SL^{2.988}$ ($R^2 = 0.890$, $P<0.001$) in the Putumayo for females and males, respectively and $Wt = 0.0093 \, SL^{3.081}$ ($R^2 = 0.966$, $P<0.001$) and $Wt = 0.0109 \, SL^{3.037}$ ($R^2 = 0.951$, $P<0.001$) in AMU for females and males, respectively.

Reproduction. In the upper Putumayo River, both the gonado–somatic index (GSI) and the monthly proportions of ripe females indicated a breeding period between December and March, corresponding to the low water and early flooding period (Fig. 3A). This pattern was consistent across years. On the other hand, not a single ripe female or even a female with developed gonads was observed in the AMU (Iquitos area) during the two and a half years of study. This is also reflected in the constantly very low GSI values (Fig. 3B).

Age and growth. The S_L frequency histograms and the corresponding VBGF curves for the whole time series are presented for all individuals (sexed and unsexed pooled together). The best fitting models obtained from the ELEFAN routine gave mean birth dates corresponding to the peak of the breeding season in the upper Putumayo River (Fig. 4A). As no single reproductively active individuals could be observed in the AMU around Iquitos during the period of study, the best fitting model giving a mean birth date during the low–water season, beginning of the rising water period (corresponding to the observed breeding period in the upper Putumayo) was selected (Fig. 4B). The corresponding VBGF parameters for males, females, and all individuals (sexed and unsexed) pooled together, are presented in Tab. 2.

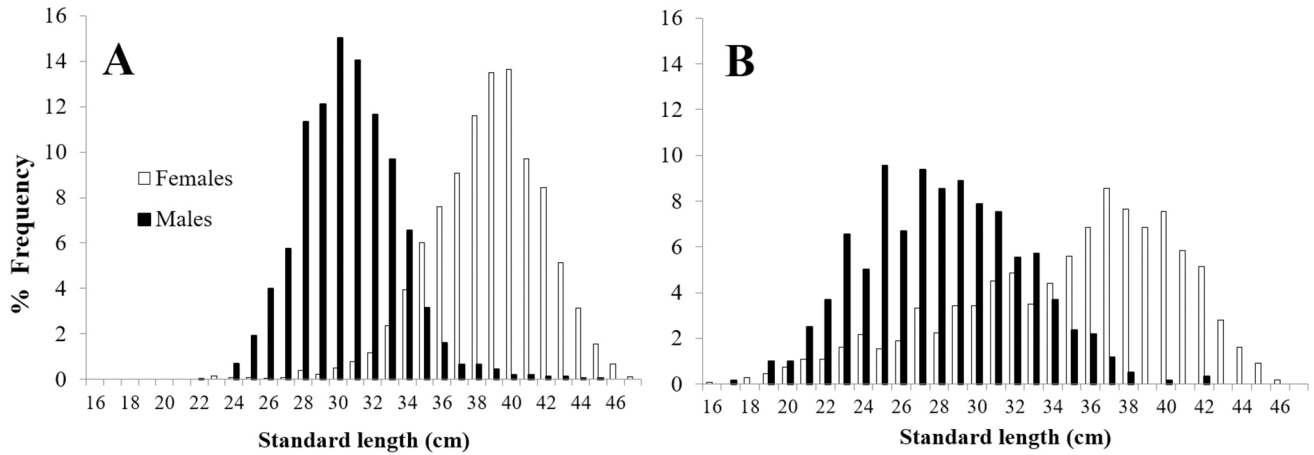In both the upper Putumayo and in the AMU, females tended to have a better

FIGURE 2 | Size frequency distribution of *Calophysus macropterus* females and males caught over the study period in the Putumayo River (**A**) and the Amazonas, lower Marañón and Ucayali rivers (**B**).
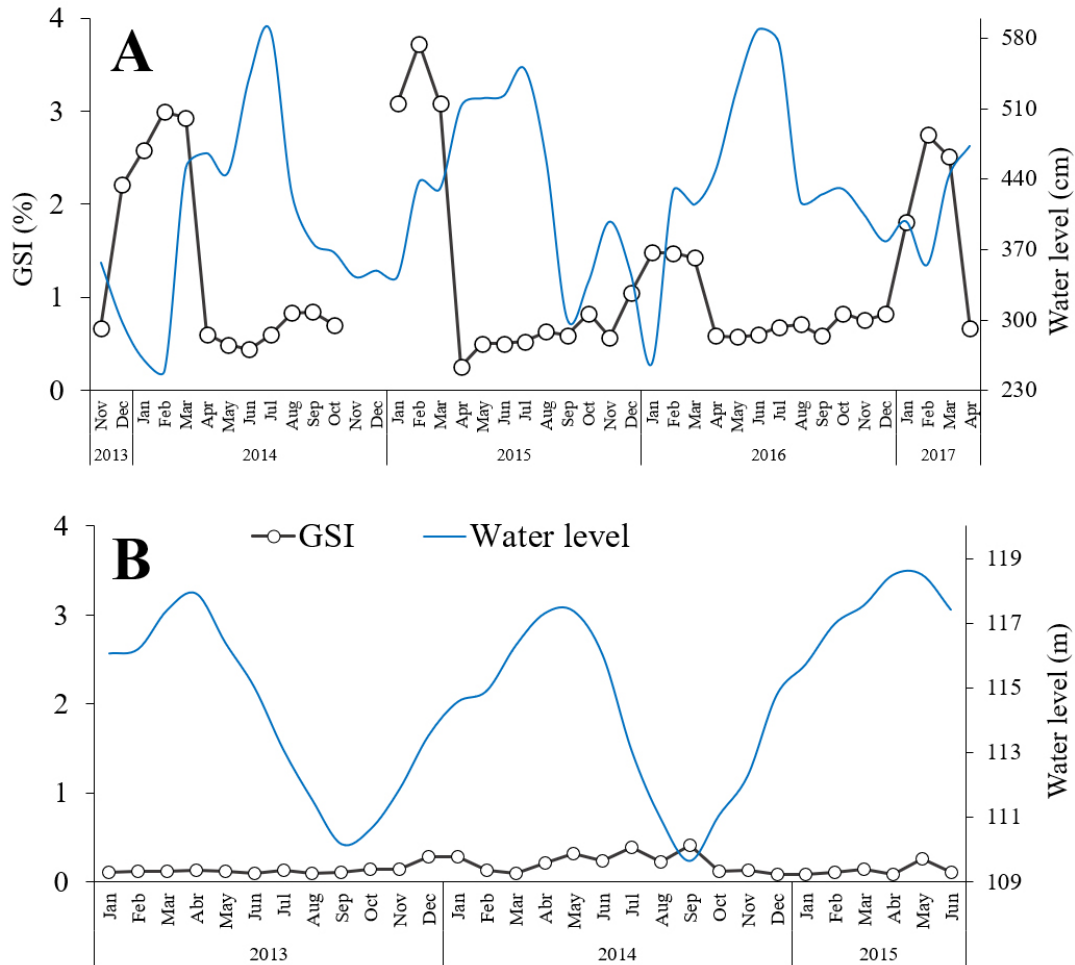

FIGURE 3 | Mean monthly GSI values (circles) of *Calophysus macropterus* females between 2013 and 2017 in relation with the water level (dotted line) in the upper Putumayo River (**A**) and the Amazonas, lower Marañón and Ucayali rivers (**B**).
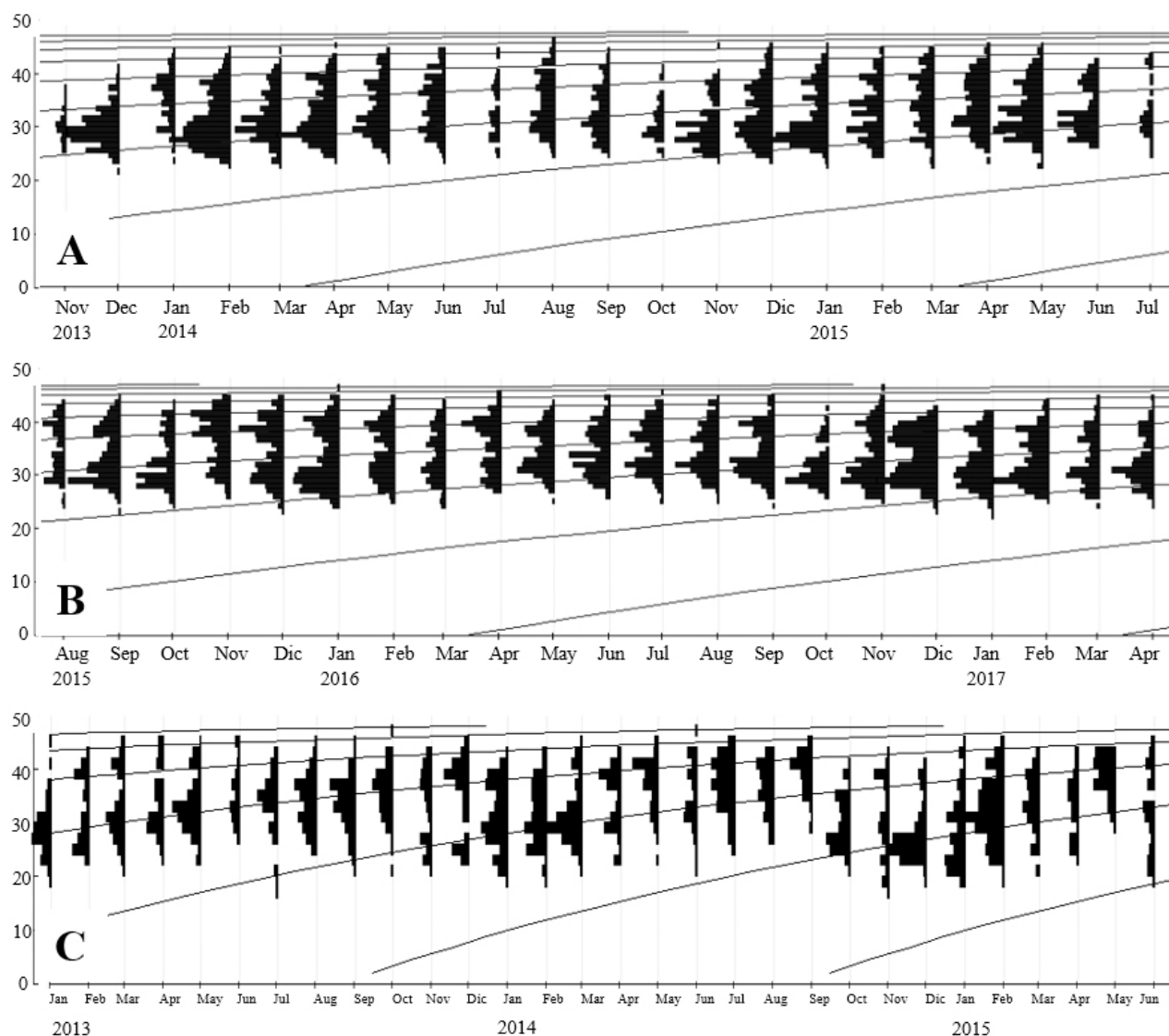
FIGURE 4 | Standard length frequency histograms and the corresponding von Bertalanffy growth function for *Calophysus macropterus* (sexed and unsexed individuals combined) in (**A**, **B**) the upper Putumayo River and in (**C**) the AMU (the Amazonas, lower Marañón and Ucayali rivers).

TABLE 2 | Parameters of the von Bertalanffy growth function (L_∞, k, t_0), growth performance index (ϕ) and longevity (t_{max}) of *Calophysus macropterus* in the upper Putumayo River and in the AMU, as modelled in FISAT II using the ELEFAN procedure. Longevity t_{max}^1 and t_{max}^2 were calculated form Taylor (1958) and Froese, Binohlan (2000), respectively.

	Sex	L_∞ (cm)	K (Year⁻¹)	t_0 (Year⁻¹)	ϕ	Score	t_{max}^1 (Year)	t_{max}^2 (Year)
Upper Putumayo	Females	50.4	0.40	-0.357	3.007	0.146	7.1	5.8
	Males	48.4	0.45	-0.319	3.023	0.150	6.3	5.3
	Total	50.1	0.42	-0.340	3.023	0.141	6.8	5.1
AMU	Females	49.9	0.68	- 0.21	3.229	0.394	4.2	3.9
	Males	43.9	0.80	- 0.35	3.188	0.255	3.6	3.2
	Total	50.0	0.6	- 0.29	3.176	0.171	4.7	3.9

growth than males as indicated by the calculated SL-at-age (Tab. 3). Females were systematically larger than males and the size difference tended to increase with age. This among-gender difference, however, tended to be greater in the AMU than in the upper Putumayo. Fish also tended to have a better growth in the AMU than in the upper Putumayo: this difference ranged from > 21% at age one to 2% at age 8 (see # Total, Tab. 3). The youngest individuals sampled were ~ 1 year old (22 cm male) in the upper Putumayo and ~ 4-month-old (16.5 cm female) in the AMU.

The calculated life span for *C. macropterus* varied according to the model used (Tab. 2). Froese, Binohlan's (2000) model resulted in life span estimates of 5.8 and 5.3 years for females and males, respectively, in the upper Putumayo, and of 3.9 and 3.2 years in the AMU. Taylor's model (1958) gave higher estimations of 7.1 and 6.3 years for females and males, respectively in the upper Putumayo, and of 4.2 and 3.6 years in the AMU. Computing age from the VBGF, the largest fish sampled (47.5 cm unsexed individual) was ~ 7 years old in the upper Putumayo and ~ 4 years old (46.6 cm female) in the AMU (Tab. 3).

Growth and mortality patterns. Over the study period, males and females reached maturity at remarkably similar sizes in the upper Putumayo and AMU (Fig. 5): 28.2 cm (±0.15 SD) and 25.6 cm (± 4.45 SD) for females and males, respectively in the upper Putumayo; 27.9 cm (± 8.55 SD) and 24.6 cm (± 8.15 SD) in the AMU. Consequently, there was no significant difference in size at maaturity between the upper Putumayo and AMU for both females (t = 0.090, df = 28, P = 0.993) and males (t = 0.108, df = 26, P = 0.915). Similarly, among-sex differences were not significant either in the upper Putumayo (t = 0.530, df = 26, P = 0.596) or in the AMU (t = 0.279, df = 28, P =

TABLE 3 | Standard length-at-age (cm, calculated from the VBGF) for females (F), males (M) and the combination of sexed and unsexed individuals (Total) of *Calophysus macropterus* in the upper Putumayo River and in the AMU (Amazonas, lower Marañón and Ucayali rivers).. (# F – M): growth difference between females and males. # Total: growth difference between the fish (all individuals combined) from the upper Putumayo and the AMU. A = length-at-age data calculated from the VBGF parameters provided in a previously published study (Pérez, Fabré, 2009).

	Upper Putumayo				AMU					A
Age (t)	F	M	Total	# F-M	F	M	Total	# F-M	# Total	Total
1	21.1	21.7	21.6	- 2.6%	27.9	26.8	26.2	4.0%	21.3%	18.6
2	30.8	31.4	31.3	- 1.9%	38.8	36.2	36.9	7.0%	19.9%	26.8
3	37.2	37.5	37.8	- 0.8%	44.2	40.5	42.8	9.4%	13.2%	32.1
4	41.6	41.5	42.0	0.3%	47.0	42.4	46.1	11.0%	9.8%	35.7
5	44.5	44.0	44.8	1.2%	48.4	43.2	47.8	12.1%	6.7%	38.1
6	46.4	45.6	46.6	1.9%	49.1	43.6	48.8	12.8%	4.7%	39.6
7	47.7	46.6	47.8	2.4%	49.5	43.8	49.3	13.1%	3.1%	40.7
8	48.6	47.3	48.6	2.9%	49.7	43.8	49.6	13.4%	2.1%	41.4

0.782). Given the observed growth differences, however, age at maturity differed more markedly between the upper Putumayo (1.7 years old for females and 1.4 years old for males) and the AMU (1 year old for females and 0.8-year-old for males).

Length converted catch curves resulted in total mortality (Z) estimates of 2.18 year^{-1} for females, 2.48 for males and 2.01 for sexed and unsexed individuals combined in the upper Putumayo (Fig. 6) and of 2.81 for males and 2.67 for sexed and unsexed individuals combined in the AMU (Fig. 7). Natural mortality (M) estimates, using both size-independent (assuming a constant M for all age and size classes) and size-dependant models (taking into account two size classes: mean length of immature fish and mean length of mature fish in the population) are presented in Tab. 4 for both the upper Putumayo and the AMU.

Natural mortality estimates calculated from Pauly's (1980) equation, as implemented in FiSAT II, were within the range of values obtained from the other size-independent models for females and males in both the upper Putumayo and the AMU. In the upper Putumayo, size-independent models (Richter and Efanov and Jensen) tended to give M estimates close to those observed for immature fish and superior to those obtained for mature fish using the size-dependent models (Gislason *et al.*, 2010; Charnov *et al.*, 2013). All these natural mortality estimates resulted in high estimates of fishing mortality (F, 1.19 to 1.64 for females and 1.26 to 1.76 for males) and exploitation rate (E, 0.55 to 0.75 for females and 0.51 to 0.71 for males), excluding immature individuals. Immature individuals also had relatively high F and E values.

In the AMU, size-independent models (Richter and Efanov and Jensen) tended to give M estimates intermediate between those observed for immature and mature fish using the size-dependent models (Gislason *et al.*, 2010; Charnov *et al.*, 2013). Excluding immature individuals, all these natural mortality estimates resulted in higher estimates of fishing mortality (F, 1.64 to 2.31) and lower exploitation rate (E, 0.55 to 0.75) than in the Putumayo for females but lower estimates of fishing mortality (F, 0.37 to 1.53) and lower exploitation rate (E, 0.13 to 0.54) for males.
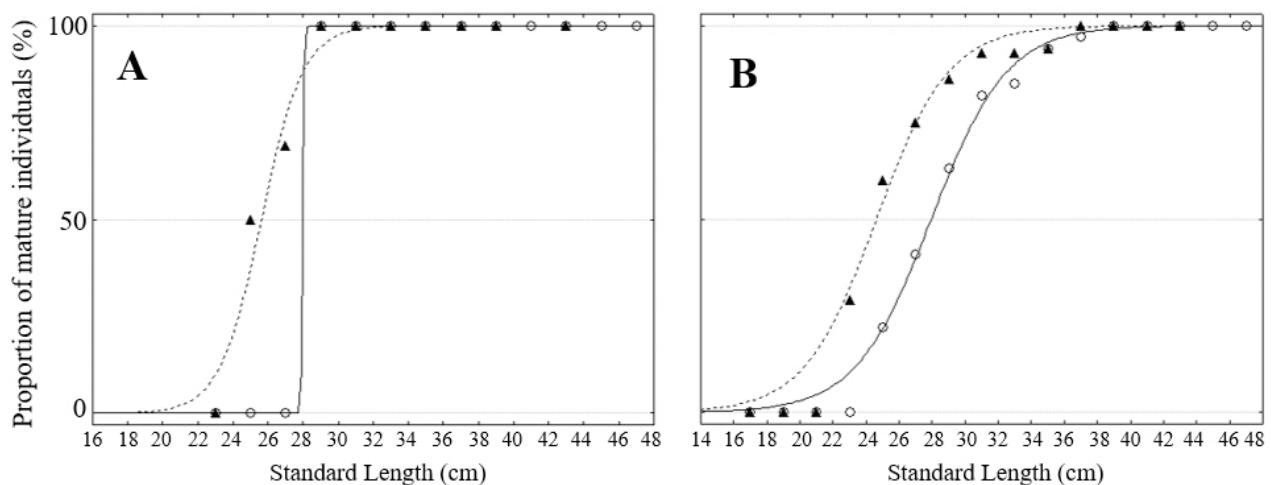

FIGURE 5 | Standard length at first sexual maturity for males (black triangles) and females (white circles) of *Calophysus macropterus* (**A**) in the upper Putumayo River and (**B**) in AMU (the Amazonas, lower Marañón and Ucayali rivers).
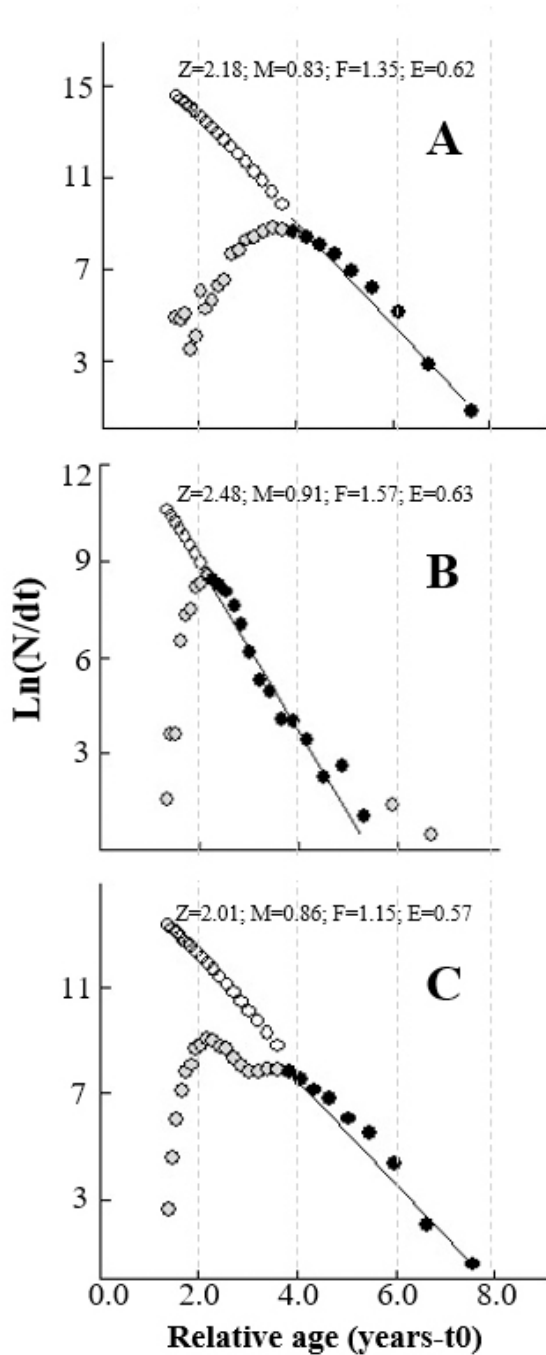
FIGURE 6 | Standard length-converted catch curves (SL) and mortality estimates for *Calophysus macropterus* (**A**) females, (**B**) males and all individuals (sexed and unsexed) combined (**C**) in the upper Putumayo River, calculated from the VBGF parameters at a mean temperature of 27°C. Z, M and 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.

FIGURE 7 | Standard length-converted catch curves (SL) and mortality estimates for *Calophysus macropterus* (**A**) females, (**B**) males and all individuals (sexed and unsexed) combined (**C**) in the Amazonas, lower Marañón and lower Ucayali rivers, calculated from the VBGF 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.
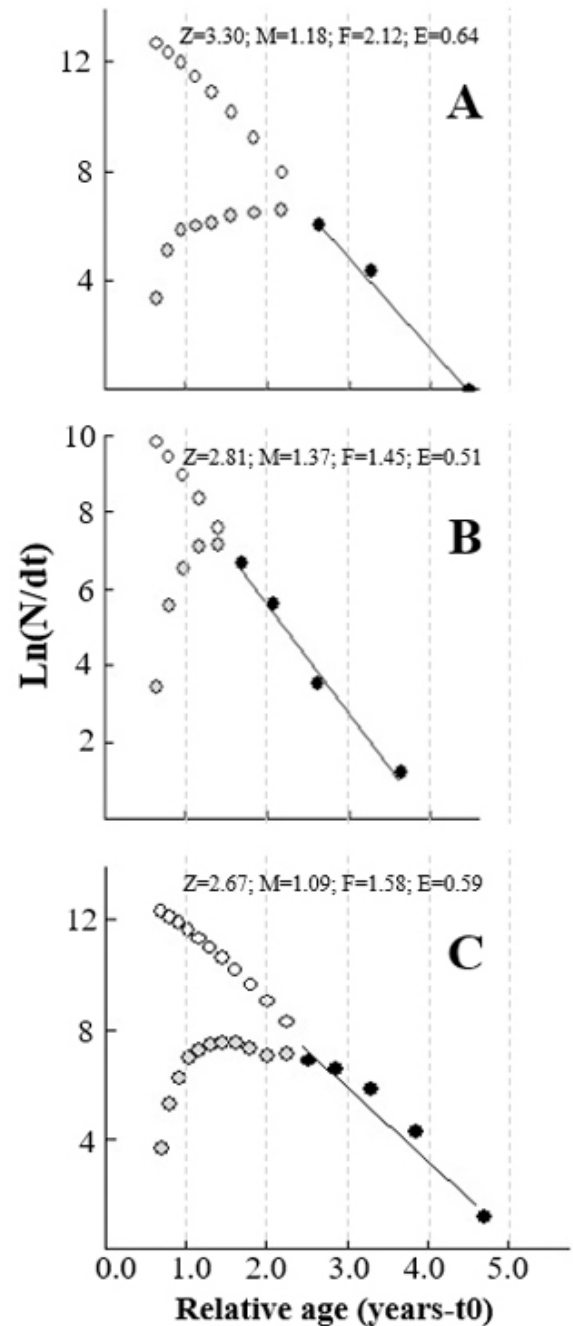
TABLE 4 | Natural mortality (M, year-1) calculated using different models and corresponding fishing mortality (F, year^{-1}) and exploitation rate (E) for females, males and total (sexed and unsexed individuals combined) of *Calophysus macropterus* in the Putumayo and AMU rivers. Total mortality (Z) was calculated from length-converted catch curves illustrated in Figs. 6 and 7. Fishing mortality, F=Z-M. E=F/Z.

		Putumayo			AMU		
	Formulae used for estimating M	M	F	E	M	F	E
Females	Pauly (1980)	0.83	1.35	0.62	1.18	2.12	0.64
	Richter, Efanov (1976)	0.90	1.28	0.59	1.37	1.93	0.58
	Jensen (1996). Using K	0.64	1.54	0.71	1.09	2.21	0.67
	Jensen (1996). Using A_{50}	0.99	1.19	0.55	1.66	1.64	0.50
	Gislason *et al.* (2010). Immature	1.06	1.12	0.51	1.92	1.38	0.42
	Gislason *et al.* (2010). Mature	0.54	1.64	0.75	0.99	2.31	0.70
	Charnov *et al.* (2013). Immature	1.10	1.08	0.49	1.99	1.31	0.40
	Charnov *et al.* (2013). Mature	0.59	1.59	0.73	1.07	2.23	0.68
Males	Pauly (1980)	0.91	1.57	0.63	1.37	1.45	0.51
	Richter, Efanov (1976)	1.07	1.41	0.57	1.86	0.95	0.34
	Jensen (1996). Using K	0.72	1.76	0.71	1.28	1.53	0.54
	Jensen (1996). Using A_{50}	1.22	1.26	0.51	2.44	0.37	0.13
	Gislason *et al.* (2010). Immature	1.07	1.41	0.57	2.11	0.70	0.25
	Gislason *et al.* (2010). Mature	0.82	1.66	0.67	1.35	1.46	0.52
	Charnov *et al.* (2013). Immature	1.12	1.36	0.55	2.15	0.66	0.23
	Charnov *et al.* (2013). Mature	0.87	1.61	0.65	1.42	1.39	0.5
Total	Pauly (1980)	0.86	1.15	0.57	1.09	1.58	0.59
	Jensen (1996). Using K	0.67	1.34	0.67	0.96	1.71	0.64
	Gislason *et al.* (2010). Immature	1.06	0.95	0.47	1.70	0.97	0.36
	Gislason *et al.* (2010). Mature	0.65	1.36	0.67	0.87	1.80	0.67
	Charnov *et al.* (2013). Immature	1.11	0.90	0.45	1.76	0.91	0.34
	Charnov *et al.* (2013). Mature	0.71	1.30	0.65	0.95	1.72	0.65

DISCUSSION

Reproduction. Published information about the reproductive biology of *C. macropterus* in the Amazon basin is scant and circumstantial. In the Caquetá River around La Pedrera, in Colombia, Agudelo *et al.* (2000) mentioned the presence of mature individuals in July, during the early decreasing water period, without showing data. Pérez, Fabré (2002, 2009) did not get any ripe female during their sampling in Central Amazonia (around Manaus) and most individuals were either immature or resting. They suggested, from the slightly higher gonado-somatic index values during the early rising waters, that reproduction probably occurred during that period. The same situation was observed in the present study around Iquitos, where no single ripe female or female with gonads in advanced maturation process was observed during the two and half year's sampling in the AMU, where the breeding cycles of many species (García-Vasquez *et al.*, 2015; Duponchelle *et al.*, 2015), including pimelodid catfishes (García Vasquez *et al.*, 2009) were successfully studied. This situation was also observed in Bolivia around Trinidad, where the breeding cycles of many species (Loubens, 2003), including pimelodid catfishes (Loubens, Panfili, 2000) were successfully studied. The only location in the Amazon basin so far where ripe individuals were officially reported is in the upper Putumayo around Puerto Leguízamo (Camacho *et al.*, 2006, present study). The present study clearly demonstrates, during over three consecutive hydrological cycles, that the breeding season of *C. macropterus* occurs during the low water and early rising water periods. This is consistent with previous studies on fish larvae, collected using plankton nets and specifically identified by barcoding/metabarcoding (COI gene), which found *C. macropterus* larvae in the lower Marañón and lower Ucayali during the low water and early rising water periods (García-Dávila *et al.*, 2015; Mariac *et al.*, 2021). But larvae can travel long distances downstream.

The available evidence strongly suggests that environmental requirements for the reproduction of *C. macropterus* are met higher in the hydrographical networks, closer to the Andes. Although the elevation of the Putumayo in Puerto Leguízamo is only slightly higher than that of the Ucayali in Pucallpa (~177 m *vs*. ~154 m, respectively), it is much closer to the Andean piedmont and the slope is much steeper upstream than in the Ucayali around Pucallpa. Similar topographical situations are found in 1) Puerto Maldonado in the upper Madre de Dios (Peru), where fishermen report the occurrence of ripe females between August and October (Duponchelle F., 2021, pers. comm.), corresponding to the low water, early rising water period (Cañas, Pine, 2011); 2) Puerto Villaroel in the upper Mamoré River (Bolívia), where ripe individuals are also observed (Duponchelle F., 2021, pers. comm.). Ripe individuals were also observed in the Portugues, Guanare, Bocono, Masparro rivers (tributaries of the Apure River) in the Andean foothills of Venezuela (300–150 m.a.s.l), during the period of rising waters (April to June; Bonilla Castillo C., 2021, pers. comm.).

As the species is distributed in the whole Amazon basin, the available evidence indicating that it breeds only in the Andean foothills above ~150 m.a.s.l. suggest that its life cycle involves extensive migrations between the breeding areas and the distributing areas as far as Central or Lower Amazonia. Migrations at such a large scale are only known within another Pimelodid catfish genus, *Brachyplatystoma* spp. (Barthem *et al.*, 1997, 2017; see Duponchelle *et al.*, 2021 for review). This hypothesis, amenable to testing

using natural tags such as otolith microchemistry (see review in Hermann *et al.*, 2021), illustrate the large knowledge gaps remaining in the ecology of Amazonian species, including economically important fisheries resources such as *Colossoma macropomum* (Cuvier, 1816).

Despite the important sexual dimorphism in both mean Lmax and Wmax in the Putumayo and in the AMU, L_{50} were remarkably similar among genders. Size at first sexual maturity did not differ either between the Putumayo and the AMU although age at first sexual maturity did differ, owing mainly to the observed growth differences among river systems.

Growth and mortality patterns. The important size dimorphism observed between females and males is a common feature in pimelodid catfishes (Agudelo *et al.*, 2000; Loubens, Panfili, 2000; García Vasquez *et al.*, 2009) and characids (Duponchelle *et al.*, 2007), and was also reported for *C. macropterus* in Bolivia (Loubens, Aquim, 1986). Yet, Loubens, Aquim (1986) observed that sexual dimorphism was particularly pronounced in this species, reaching 20% in maximum observed length (Lmax) and 50% in maximum observed body mass (Wmax), which is consistent with our own observations. Lmax in this study (47.5 and 46.6 cm in the Putumayo and AMU, respectively) were smaller than those reported almost 20 years ago by Agudelo *et al.* (2000) in the same rivers (52 cm in the Putumayo, 52 cm in the Amazonas close to Leticia, Colombia). Agudelo *et al.* (2012) also reported this Lmax reduction of *C. macropterus* in the Putumayo River and suggested it was likely due to the increased exploitation.

In both the upper Putumayo and the AMU, *C. macropterus* presents a fast growth during the first two years, as was also reported in Central Amazonia (Pérez, Fabré, 2009). In the two river systems, females had a faster growth than males and the difference increased with age, which was not observed in Pérez and Fabré (2009), where both sexes had similar growths. Growth dimorphism was reported in other species of the family Pimelodidae such as *Brachyplatystoma rousseauxii* (Castelnau, 1855) (García Vásquez *et al.*, 2009) or *Pseudoplatystoma tigrinum* (Valenciennes, 1840) and *P. fasciatum* (Linnaeus, 1766) (Loubens, Panfili, 2000). The among-sex difference, however, was much greater in the AMU than in the upper Putumayo. Fish also had a better growth in the AMU than in the upper Putumayo although this difference decreased with age from > 21% at age one to 2% at age 8. The growth rate observed in the present study were both better than that observed in Central Amazonia (Pérez, Fabré, 2009). The growth rate observed in the present study, however, remains low compared to growth rates obtained in captivity, where well fed and cared for specimens can reach in four to five months the length observed at one year old in the Putumayo and AMU, respectively (Kossowski, 1998). The length calculated for one-year-old fish by Pérez, Fabré (2009; Tab. 3 present study) was reached after only two months in captivity (Kossowski, 1998).

In both river systems, females tended to grow larger and faster than males, and the growth difference between females and males tended to be more important in the AMU than in the Putumayo. While we cannot rule out the possibility that the AMU would be a feeding site, while the Putumayo works as a spawning ground, the observed differences could also result from better trophic conditions in the AMU than in the Putumayo. When trophic conditions are less favourable, females cannot find enough energy to express their better growth potential to the maximum, which has already been observed

for the red piranha, *Pygocentrus nattereri* Kner, 1858 (Duponchelle *et al.*, 2007). Although there is no data providing direct evidence of less favorable conditions in the Putumayo, this hypothesis finds support in the fact that and fish generally tend to be smaller in the Putumayo than in the Caquetá (ABC, pers. obs.) and that slower growth were already reported for other species in this river: *Prochilodus nigricans* Spix, Agassiz, 1829 (Bonilla-Castillo *et al.*, 2018), *Osteoglossum bicirrhosum* (Cuvier, 1829) (Duponchelle *et al.*, 2015), *Pseudoplatystoma punctifer* (Castelnau, 1855) (Armas *et al.*, *in press*).

As previously emphasized (Bonilla-Castillo *et al.*, 2018), however, inter-basin differences in fishery exploitation could also account for slower growth in fish populations of the Putumayo River, where the more heavily exploited populations tend to have smaller maximum sizes and slower growth. This phenomenon is known as tropicalization of stocks (Stergiou, 2002). As natural mortality (M) is one of the most complicated life history parameters to estimate in natural fish populations (Pauly, 1980), estimations from several different methods were calculated in order to provide a measure of reliability. Natural mortality estimates calculated from Pauly's (1980) equation, as implemented in FiSAT II, were within the range of values obtained from the other size-independent models for females and males in both the upper Putumayo and the AMU. Whatever the method used for calculation, fishing mortality and exploitation rates were high for both the Putumayo and the AMU, indicating overexploitation of *C. macropterus* in both river systems. Fishery exploitation can therefore not be ruled out in the explanation of the observed slower growth in the Putumayo, although further studies will be needed to sort out its importance relative to the hypothesis of poorer trophic conditions in the Putumayo.

Calophysus macropterus has become quite infamous in most Amazonian countries in recent years because of the conservation and health issues associated with its exploitation and consumption. Yet, strong evidence suggests that in absence of proper enforcement, which is most challenging in the Amazon basin, its exploitation and fraudulent commercialization (*i.e.*, Cunha *et al.*, 2015) will likely continue, further endangering the natural populations of aquatic mammals and reptiles. Given its excellent potential for aquaculture (see Kossowski, 1998 for further details) and its relatively low trophic level (Agudelo, 2015), a complementary way of lowering its impact on natural populations of river dolphins, manatees and caimans, while providing healthy animal protein for the growing human populations, would be to encourage the development of its aquaculture in Amazonian countries, using local products as alternative to fish meal and oil. This solution would also allow relieving some of the harvesting pressure on natural populations of *C. macropterus*.

Life history traits of *Calophysus macropterus* varied importantly between the Putumayo and the AMU systems. Reproduction was only observed in the upper Putumayo, suggesting the species needs specific environmental conditions found close to the Andean piedmont and not available in our AMU sampling locations. Females tended to have a better growth than males in both river systems and fish of the AMU tended to grow faster in the AMU than in the Putumayo. The mortality data indicate overexploitation of the species in both river systems.

ACKNOWLEDGMENTS

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