Breeding, growth and exploitation of *Brachyplatystoma rousseauxii* Castelnau, 1855 in the Caqueta River, Colombia

Edwin Agudelo Córdoba[1,2], Ángela Viviana Joven León[3], César Augusto Bonilla-Castillo[4], Miguel Petrere Junior[5], Marlón Peláez[6] and Fabrice Duponchelle[2,7]

The main life history traits of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* were determined in the Caqueta River, Colombia. The breeding season occurred during the rising and falling water periods. The size at first sexual maturity was significantly larger for females (88.5 cm Ls) than males (81.7 cm). Both males and females reproduce for the first time between their third and fourth year. The growth characteristics were estimated using length frequency analyses. Females grew systematically larger than males, the difference being about 9% after the first year and increasing to 12% for ten years old individuals. Mortality estimates, calculated from different models, some taking into account the effect of body size, ranged from 0.32 to 0.42 year^{-1} for natural mortality and from 0.72 to 0.82 year^{-1} for fishing mortality, indicating high fishing pressure in the Caqueta River, higher than in the Peruvian Amazon. Resulting exploitation rates (0.63 to 0.72) pointed towards overexploitation of the species in the Caqueta. The situation calls for a concerted management between the countries sharing this resource (Brazil, Colombia, and Peru) and potential solutions are proposed.

Se determinaron las principales características del ciclo biológico de dorado *Brachyplatystoma rousseauxii* en el río Caquetá, Colombia. La época reproductiva ocurre durante la transición del período de aguas altas a aguas en descenso. La talla de primera madurez sexual fue significativamente mayor en hembras (88,5 cm Ls) que en machos (81,7 cm). Tanto hembras como machos se reproducen por primera vez entre su tercer y cuarto año de vida. Los parámetros de crecimiento fueron estimados mediante el análisis de frecuencia de tallas. Las hembras alcanzan un mayor tamaño que los machos, con una diferencia de cerca del 9% en el primer año que luego aumenta hasta un 12% en el décimo año de edad. La estimación de mortalidad, calculada a partir de diferentes modelos, variaron entre 0,32 a 0,42 años^{-1} para la mortalidad natural y 0,72 a 0,82 años^{-1} para la mortalidad por pesca, lo que indica una alta presión de la pesca en el río Caquetá, mucho más elevada que en la Amazonía peruana. Las tasas de explotación resultantes (0,63 a 0,72) para el río Caquetá, señalan una sobre-utilización del recurso. La situación exige una gestión concertada entre los países que comparten y utilizan con elevada frecuencia este recurso amazónico (Brasil, Colombia y Perú), por lo que se proponen posibles estrategias de solución.

Key words: Amazonia, Dorado, Life history, Migratory catfish, Pimelodidae.

[1]Instituto Amazónico de Investigaciones Científicas SINCHI, doctorando en Ciencias Ambientales de la Universidad Autónoma de Barcelona- ICTA. Av. Vásquez Cobo entre Calles 15 y 16. Leticia, Amazonas, Colombia. eagudelo@sinchi.org.co

[2]Laboratoire Mixte International - Evolution et Domestication de l'Ichtyofaune Amazonienne (LMI - EDIA), AQUAREC station, Iquitos-Quistococha, Perú.

[3]Convenio Universidad de la Amazonia – Instituto SINCHI Av. Circunvalación, Barrio el Porvenir. Florencia, Caquetá, Colombia. angelitajoven1@hotmail.com

[4]Instituto Amazónico de Investigaciones Científicas SINCHI. Estación Biológica de Puerto Leguízamo. Carrera 3 No. 2-19. Puerto Leguízamo, Putumayo, Colombia. biocaesar@gmail.com

[5]Centro de Ciências e Tecnologias para a Sustentabilidade (CCTS), Programa de Pós-graduação em Diversidade Biológica e Conservação (PPGDBC), Universidade Federal de São Carlos (UFSCar). Rod. João Leme dos Santos, km 110, 18052-780 Sorocaba, São Paulo, Brazil. UNISANTA, Programa de Pós-Graduação em Sustentabilidade de Ecossistemas Costeiros e Marinhos. Rua Oswaldo Cruz, 277, Boqueirão, 11045-907 Santos, São Paulo, Brazil. mpetrere@rc.unesp.br

[6]Convenio Universidad de la Amazonia, Instituto SINCHI. Av. Circunvalación, Barrio el Porvenir. Florencia, Caquetá, Colombia. mpelaez@uniamazonia.edu.co

[7]Institut de Recherche pour le Développement (IRD) - UMR-ISEM (Institut des Sciences de l'Evolution de Montpellier), Université Montpellier 2, Bâtiment 22, C.C. 065, 34095 Montpellier cedex 5, France. Present address: IRD-Universidad Nacional Federico Villareal / FOPCA, 350 calle Roma, Miraflores, Lima Perú. fabrice.duponchelle@ird.fr

Introduction

The Amazon basin covers a total area of 7,989,004 km², of which Colombia possesses 5.5%, equivalent to 413,000 km² and 36% of its national territory. The Colombian Amazon has extensive forest areas, abundant faunal and hydro-biological resources and the most important are found in the Putumayo, Caquetá and Amazon River basins (Gutierrez *et al.*, 2004). Most indigenous Amazonian people live along the river's banks and fishing activities take an important part of their daily routine. Fishing activities can be classified in three main categories: subsistence, ornamental, and commercial fisheries. This last and most important one is carried out with a major participation of indigenous and non-indigenous fishermen, who develop this activity along with horticulture, hunting and gathering of wild species (Agudelo *et al.*, 2000; Fabré & Barthem, 2005). Consequently, fishing activities hold a particular economic, social and cultural importance for the Amazonian region, but also are the main protein source. Rural Amazonian communities living along the river banks directly depend, at all seasons, upon the aquatic ecosystem resources (Fabré & Alonso, 1998; Agudelo *et al.*, 2000; Agudelo *et al.*, 2006; Barthem & Goulding, 2007; Agudelo *et al.*, 2009).

The large catfishes of the family Pimelodidae are the most important group in the commercial fisheries of the Colombian Amazon, with 13 species among the most commercialized fishes inside the country (Agudelo *et al.*, 2000). These species are also those supporting the major exploitation pressure from commercial fishermen of the Putumayo, Caqueta and Amazon rivers (Fabré & Alonso, 1998; Agudelo *et al.*, 2000; Petrere *et al.*, 2004). Among these species, the dorado, *Brachyplatystoma rousseauxii*, is the most popular in occidental Amazonia and, owing to its large distribution, is exploited in the main channels of the Amazon, Caqueta, Madeira, Purus and Juruá Rivers (Rodríguez, 1991; Barthem & Goulding, 1997), using harpoons, arrows, hook and lines, gill nets, drifting nets, and bottom nets, depending on the local conditions (Arboleda, 1989; Rodríguez, 1991; Muñoz-Sosa, 1993; Agudelo, 1994; Agudelo *et al.*, 2000). *Brachyplatystoma rousseauxii* displays the longest migration known to a freshwater fish species: the adults breed in the head waters of the Andean tributaries in Bolivia, Colombia, Ecuador, Peru and the resulting eggs and larvae are transported downriver to the Amazon estuary in Brazil, where they spend their first years before migrating upriver to complete their cycle (Barthem & Goulding, 1997, 2007; Alonso, 2002; Fabré & Barthem, 2005).

In the Caqueta River, Colombia, fishing is the most important economic activity for rural communities, being either for regional or national consumption (Rodríguez, 1991; Muñoz-Sosa, 1993; Castro & Santamaría, 1993; Agudelo, 1994; Celis, 1994; Gómez, 1996). It targets two species, which made up about 80% of the annual catches: the dorado, *B. rousseauxii* (56.7%) and the lechero, *B. filamentosum* (27.1%; Agudelo, 1994; Celis, 1994). To date, studies have provided some aspects of the biology and commercial importance of the large catfishes in the Caqueta region (Muñoz-Sosa, 1993; Agudelo, 1994; Celis, 1994; Gómez, 1996; Agudelo *et al.*, 2000), but almost nothing is known about their growth and mortality characteristics. This also applies to *B. rousseauxii*, whose catches have been decreasing in the region (Rodríguez, 2010), although very preliminary information about growth and mortality were provided by Muñoz-Sosa (1996). Yet, for such commercially important species, this knowledge is fundamental for the development of proper management strategies (Sparre & Venema, 1995). The present study aims at filling this gap, by providing new information about the reproduction, growth and mortality patterns of *B. rousseauxii* in the Caqueta River.

Material and Methods

Study area. Fish were sampled between 1995 and early 1998 in La Pedrera district and its area of influence, situated north of the Amazonas Department, on the right margin of the Caqueta River in the Colombian Amazon, close to the Brazilian border at about 1°18' S and 69°37' W (Fig. 1). Located about 90 m a.s.l., the mean annual temperature is about 27°C, with minimum values (20°C) in January and June and maximum (35°C) in November (Celis, 1994). Fish were caught by local fishermen in two main zones (Agudelo *et al.*, 2000): between Maria Manteca and Puerto Córdoba, an extension of about 250 km and between Puerto Córdoba and the Brazilian border in Villa Betancourt and Serrinha, an extension of about 50 km. Although the data set is from the period between 1995 and 1998, it is very important because there are no other available data for the Caqueta River. Obtaining such a comprehensive data set (allowing the estimation of the reproductive, growth and mortality parameters) for any river is almost impossible nowadays as fish are almost always eviscerated and beheaded directly on the fishing grounds. Moreover, a scientific sampling for so many specimens would be impractical (*i.e.*, time and costs) and unethical. It must also be emphasized that the results obtained from this relatively old data set will provide a suitable basis for future comparisons on the resource status. Given the life cycle of this particular species, where the smallest fish are in Amazon estuary area, no specimen smaller than 38 cm could be caught during this study.

Data. For this study, data of the Colombian Instituto Amazónico de Investigaciones Científicas SINCHI, used in Agudelo *et al.* (2000), were re-analyzed to take into account methodological flaws pointed out in Garcia *et al.* (2009a) and provide new information regarding reproduction, growth, and mortality parameters. Between September 1995 and December 1997, *B. rousseauxii* were collected during daily sampling in the main landing zones of commercial fishermen in La Pedrera. Every landed specimen was measured and, whenever possible, weighed and sexed (during the whole sampling period, most specimens arrived already eviscerated at the landing zones).

The standard length (Ls), standard corporal length (CLs): from the posterior part of the opercula to the end of the hypural
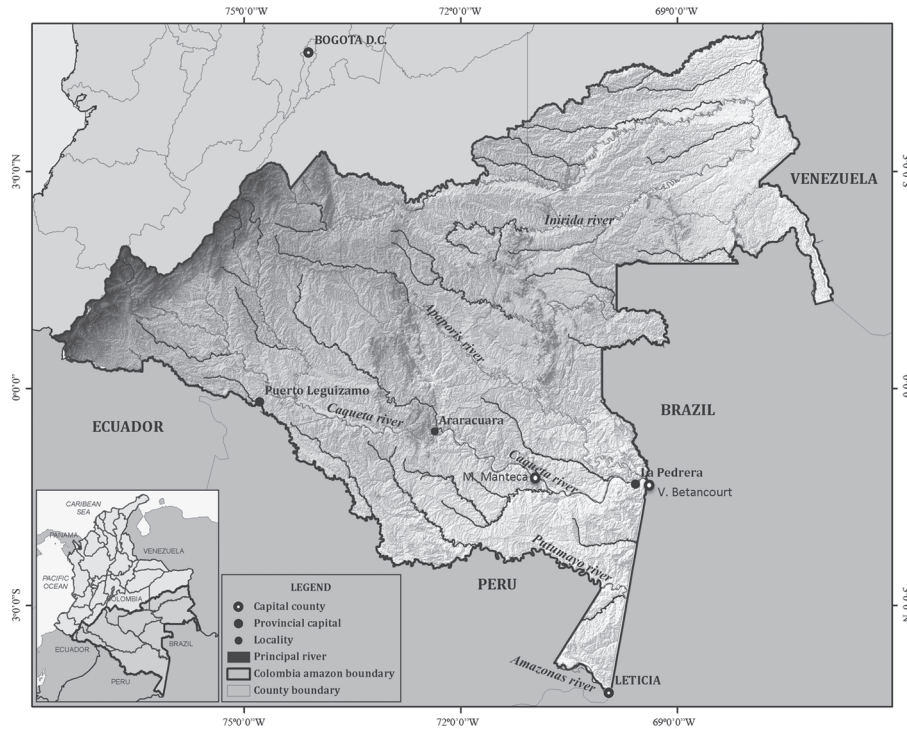
Fig. 1. Map of the Colombian Amazon, its constitutive departments and the principal fishing zones for *Brachyplatystoma rousseauxii* (based on Agudelo *et al.*, 2000; Murcia *et al.*, 2007).

plates) and body mass (W) of each fish were measured to the nearest 1 cm and 50 g, respectively. The standard corporal length was taken to determine the standard length of specimens landed beheaded, using a linear regression between Ls and CLs (CLs = 0.750*Ls – 1.260, r² = 0.952, P < 0.001). Gonads were macroscopically checked for maturity stage determination. The maturity scale of gonadal maturation stages followed Nuñez & Duponchelle (2009). 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 5-1 describes gonads of resting females. For males, stage 1 corresponds to immature fish, stage 2 to maturing or resting individuals and stage 3 to ripe fish. The breeding season was determined using only fishes above the mean size at first maturity. The breeding season was estimated from the monthly proportions of females' gonadal maturation stages 3 and 4 combined.

The size at first sexual maturity (L_m) is defined as the standard length at which 50% of the individuals are at an advanced 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):

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

where %M = percentage of mature individuals by 10 mm size class, L = central value of each size class, and a and L_m =

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.

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 (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 (Garcia *et al.*, 2009a). 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:

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

where L_t is the mean length at age t, L∞ is the asymptotic length, K the growth coefficient and t_o 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_m) was calculated from the VBGF as follows (Duponchelle *et al.*, 2007):

$A_m = \{-\ln[1-(L_m L\infty^{-1})]K^{-1}\} + t_o$

where L_m 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_∞ 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 $L\infty$ (in this case 0.95). The longevity was also calculated from the equation of Froese & Binohlan (2000):

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

where A_m 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 (LCC) (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's (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's equation, as implemented in the Fisat package, for a mean annual temperature of 27°C. In order to verify the accuracy of natural mortality estimate using Pauly's equation and the consequences on the estimation of fishing mortality and exploitation rate, however, M was also estimated using Richter and Efanov's formula (Sparre & Venema, 1995), relating mortality to the age at which 50% of the population is mature (estimated by A_{50}), as implemented in the FiSAT II package. Additionally, natural mortality was also estimated using Jensen (1996)'s formulas (Simpfendorfer *et al.*, 2005): $M = 1.65/A_{50}$ and $M = 1.6 \times K$, K being the VBF growth coefficient.

Recent theory and empirical studies on natural mortality indicate that M scales with individual body size (McCoy & Gillooly, 2008; Gislason *et al.*, 2010; Brodziak *et al.*, 2011) and that while the assumption of a constant K may be a valid approximation when only mature individuals are targeted by the fishery, size dependence should be taken into account when immature are caught (Brodziak *et al.*, 2011). Given that important proportion of immature individuals are exploited in the Caqueta River, natural mortality was therefore also estimated, for comparison purposes, separating the immature and mature individuals using:

- Gislason *et al.*'s (2010) equation: $\ln(M) = 0.55 - 1.61 \ln(L) + 1.44 \ln(L\infty) + \ln(K)$,
- and Charnov *et al.*'s (2013) equation: $M = ((L/L\infty)^{-1.5})^*K$,

where $L\infty$ and K are the VBGF parameters and L the body length (cm) for which the M estimate would apply.

Practically, L was fixed as the mean standard lengths of immature (L = 82.5, 75 and 82 cm for females, males, and sexed and unsexed individuals combined) and mature individuals (L = 102, 94 and 100 cm for females, males, and sexed and unsexed individuals combined) in the data set. 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 . Analysis of covariance (ANCOVA) was used to test for differences in the log-transformed length-mass relationships between sexes, using $\log_{10} W$ as the dependent variable, $\log_{10} L_s$ as the covariate, and sex as categorical variable.

Differences of mean standard length or mass for each sex among years were tested with Kruskal-Wallis One Way Analysis of Variance and Dunn's all pairwise post-hoc test, using Bonferonni correction to keep the experiment-wide error rate at the desired á (0.05, 0.01 or 0.001). Differences in mean standard length and mass between sexes for each year were tested with a Mann-Whitney Rank Sum Test.

For each sex, logistic regression models provided an estimate of the $L_m \pm$ standard deviation. Sizes at maturity between sexes were compared using Student t-tests (degrees of freedom calculated from the number of size classes).

Results

A total of 4116 *Brachyplatystoma rousseauxii* were sampled during the study period, of which 70% (1995), 57% (1996), and 96% (1997) could be sexed. Over the study period, length-mass relationships were very similar among females and males: $W = 0.00001*L_s^{3.053}$, $r^2 = 0.912$, P<0.001 (N = 1897) for females, $W = 0.00001 L_s^{3.082}$, $r^2 = 0.914$, P<0.001 (N = 1055) for males and $W = 0.00001 L_s^{3.086}$, $r^2 = 0.953$, P<0.001 (N = 4116) for all fish sampled (sexed and unsexed individuals). Comparison of log-transformed length-body mass linear relationships indicated a significant intercept difference among females and males over the study period (ANCOVA, $F_{2, 2992} = 18.4$, P<0.001). A sexual dimorphism in size was indeed observed, as females grow larger than males (Table 1). Every year during the study period, females were significantly larger (Mann-Whitney Rank Sum Test, T = 24954, P<0.001 for 1995, T = 179580, P<0.001 for 1996 and T = 189889.5, P<0.001 for 1997) and heavier (T = 25015, P<0.001 for 1995, T = 180031, P<0.001 for 1996 and T = 195011, P<0.001 for 1997) than males. The size ranges of sample were 38 - 129 cm for males, 45 - 143 cm for females and 38 - 149 cm when unsexed individuals were included. The largest female was also the heaviest sexed specimen observed, with 44.5 kg. Mean standard length (Kruskal-Wallis ANOVA on ranks: H = 37.9, d.f. = 2, P <0.001) and mass (H = 14.9, d.f. = 2, P <0.001) significantly differed among years for females (Table 1), but not for males (H = 0.03,

Table 1. Standard length (L$_s$, in cm) and mass (W, in kg) means (± SD), ranges and number of fish sampled each year (n) of females (F), males (M) and total (sexed and unsexed individuals, T).

Sex	Year	n	Mean L$_s$ ± SD - (range)	Mean W ± SD - (range)
	1995	324	98.2 ± 10.9 - (45 - 143) [a]	14.7 ± 5.0 - (1.0 - 44.5) [a]
F	1996	766	99.3 ± 9.4 - (60 - 133) [a]	15.3 ± 4.6 - (4.0 - 35.4) [a]
	1997	807	101.6 ± 9.3 - (73 - 136) [b]	15.9 ± 4.8 - (5.0 - 39.0) [b]
	1995	145	91.4 ± 9.7 - (61 - 119) [a]	11.7 ± 3.6 - (3.0 - 23.0) [a]
M	1996	430	91.8 ± 9.2 - (38 - 129) [a]	11.9 ± 3.7 - (1.0 - 32.0) [a]
	1997	480	91.8 ± 7.7 - (66 - 117) [a]	11.5 ± 3.1 - (3.0 - 24.0) [a]
	1995	665	95.2 ± 11.5 - (45 - 130) [a]	13.5 ± 4.8 - (1.0 - 33.0) [a]
T	1996	2112	94.7 ± 12.0 - (38 - 149) [a]	13.3 ± 5.2 - (1.0 - 44) [a]
	1997	1339	97.9 ± 9.9 - (66 - 136) [b]	14.3 ± 4.8 - (3.0 - 39.0) [b]

d.f. = 2, P = 0.987 for LS and H = 2.5, d.f. = 2, P = 0.282 for W). Significant differences among years were also observed when sexed and unsexed individuals were pooled together, both for the mean length (H = 59.3, d.f. = 2, P <0,001) and mass (H = 33.5, d.f. = 2, P <0,001).

Breeding season. The breeding season of *Brachyplatystoma rousseauxii* in the Caqueta River occurs during an extended period of about six months, encompassing the rising and receding water periods (Fig. 2). Some variations were observed among years: it started earlier (March) and finished sooner (September) in 1996 than in 1997 (April-May to September).

Age and growth characteristics. For females, males and the combination of sexed and unsexed individuals, the best fitting models obtained from the ELEFAN routine gave mean birth date corresponding to the peak of the breeding season (June for females and August for males, Fig. 3). The VBGF parameters are presented in Table 2. Females had a better growth than males at every age class (Table 3). The difference between females and males gradually increased from ~9% at one year old to 12% at twelve years old.

The estimated longevity for *B. rousseauxii* varied according to the model used (Table 2) and ranged between 11 and 13 years. Computing age from the VBGF parameters, the
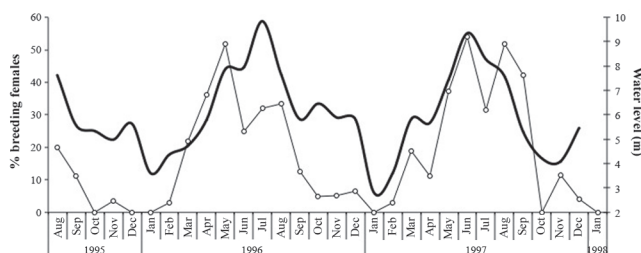

Fig. 2. Monthly percentages of breeding (stages 3 and 4) *Brachyplatystoma rousseauxii* females (white circles) in the Caqueta River, Colombian Amazon, between 1995 and 1997, in relation to the water level (black line).

youngest individuals collected, a male of 38 cm, was 10.9 months old, whereas the smallest female sampled (45 cm) was 12.6 months old. The largest male (129 cm) was 11.7 years old and the largest female (143 cm) was 12.9 years old.

Age and size at first sexual maturity. Over the study period, females reached the first sexual maturity (Fig. 4) at a significantly larger size (88.5 cm ± 0.1) than males (81.7 cm ± 0.01) (t-test, t = 15.1, P<0.001). Both males and females reached maturity between their third and fourth year, at 3.3 and 3.4 years, respectively.

Mortality and Exploitation. Length converted catch curves resulted in total mortality (Z) values of 1.12 year^{-1} for females, 1.09 for males and 1.14 for sexed and unsexed individuals combined (Fig. 5). 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 Table 4. Natural mortality values 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. Size-independent models tended to give M values close to the values observed for immature fish and superior to those obtained for mature fish using the size-dependent model of Gislason *et al.* (2010). On the contrary, size-independent models tended to give M values close to those observed for mature fish and inferior to those obtained for mature fish using the size-dependent model of Charnov *et al.* (2013). All these natural mortality estimates resulted in relatively high values of fishing mortality (F, 0.63 to 0.79 for females and 0.59 to 0.76 for males) and exploitation rate (E, 0.56 to 0.71 for females and 0.54 to 0.70 for males), excluding immature individuals. The highest estimates of both F and E were obtained when considering only mature individuals. Nevertheless, it must be pointed out that even immature individuals had relatively high F and E values. When sexed and unsexed individuals were combined, taking into account the whole database, fishing mortality estimates when even higher and exploitation rates were well above 0.5, even for immature individuals.

Discussion

The maximum observed length in the Caqueta River was 149 cm, similar to those reported by Agudelo *et al.* (2000) for the Guaviare, Caqueta, Putumayo, and Amazon rivers in Colombia, and about 5 cm smaller than the length observed in the Iquitos region, Peru (Garcia *et al.*, 2009a). It was, however, much shorter than the 167 cm reported in the same river during the period 1992-1993 (Muñoz-Sosa, 1996), indicating that larger fishes were caught a few years earlier in the Caqueta river, as was also the case in the Amazon basin (161 cm, Barthem & Goulding, 1997). The fact that from over 4,000 fish sampled here, the largest specimen caught was nearly 20 cm
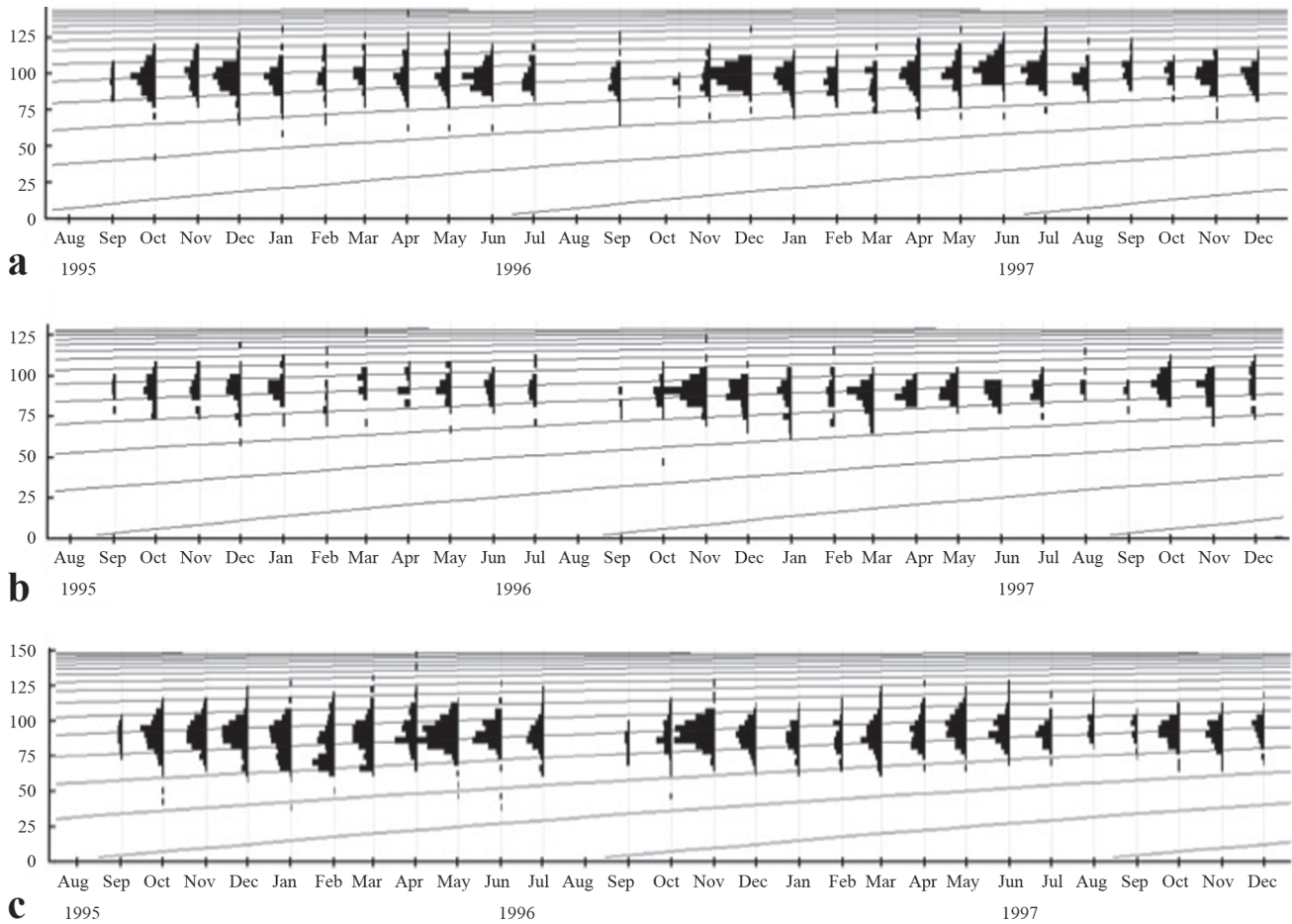
Fig. 3. Standard length (L$_S$) frequency histograms and the corresponding von Bertalanffy growth function for **a)** females, **b)** males and **c)** females, males and unsexed individuals combined of *Brachyplatystoma rousseauxii* in the Caqueta River during the period 1995-1997.

smaller than fish measured earlier in the same river, suggests a decreased maximum size of the species in the Caqueta. In the present study, the observed differences in mean length and body mass among sexes, confirmed the reported size dimorphism in the species in Colombia (Arboleda, 1989; Agudelo *et al.*, 2000), Brazil (Alonso, 2002), and Peru (García *et al.*, 2009a).

The timing of the breeding season relative to the hydrological cycle was very different in the Caqueta than in the Iquitos region. It started during the rising waters and stopped at the end of the descending waters, whereas it started during the descending waters and ended during the early rising waters in the Peruvian Amazon (Garcia *et al.*, 2009a). Breeding during the descending waters and dry period had been hypothesized to be an adaptation of the species to avoid the loss of eggs and larvae in the flood plain, hence ensuring that most descendants would reach the Amazon estuary (Garcia *et al.*, 2009a). This strategy, however, does apparently not apply to the Caqueta River, suggesting a more complex picture.

The growth dimorphism previously reported for the species (Alonso, 2002; Garcia *et al.*, 2009a) was also observed in the Caqueta, with females growing larger and faster than males. Models that do not explicitly account for the effects of fishing and size selectivity usually tend to underestimate L∞ and overestimate K (Taylor *et al.*, 2005), which in turn can

Table 2. Longevity (t$_{max}$) and parameters of the von Bertalanffy growth function of *Brachyplatystoma rousseauxii* in the Caqueta River, Colombia, 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∞ (cm)	K (year^{-1})	t$_0$ (year)	Score	t$_{max}$^{1} (year)	t$_{max}$^{2} (year)
Females	149.1	0.24	-0.45	0.133	12.0	11.1
Males	132.3	0.25	-0.45	0.131	11.5	11.4
Total	153.3	0.22	-0.49	0.131	13.1	11.4

Table 3. Standard length (LS)-at-age (calculated from the VBGF) for females, males and the combination of sexed and unsexed individuals (Total) of *Brachyplatystoma rousseauxii* in the Caqueta River. # F - M : growth difference between females and males (% difference).

	Length-at-age (cm)			
Age (years)	Females	Males	Total	# F - M
1	43.8	40.2	42.8	3.6 (8.9 %)
2	66.3	60.6	64.7	5.7 (9.4 %)
3	84.0	76.5	82.2	7.5 (9.8 %)
4	97.9	88.8	96.2	9.0 (10.1 %)
5	108.8	98.4	107.5	10.4 (10.6 %)
6	117.4	105.9	116.5	11.5 (10.9 %)
7	124.2	111.8	123.8	12.4 (11.1 %)
8	129.5	116.3	129.6	13.2 (11.3 %)
9	133.7	119.8	134.3	13.8 (11.5 %)
10	137.0	122.6	138.0	14.4 (11.7 %)
11	139.5	124.7	141.1	14.8 (11.9 %)
12	141.6	126.4	143.5	15.2 (12.0 %)
13	143.2	-	145.4	- (12.0 %)

lead to biased mortality estimates derived from the VBG function. Although fishing and size selectivity effects were not specifically taken into account, the estimate of asymptotic length observed in the present study was about 5 cm larger than the largest fish sampled over 3 years and more than 4000 specimens, suggesting that $L\infty$, hence K estimates were not too biased. Published growth and mortality parameters for *B. rousseauxii* in the Amazon basin were recently reviewed and discussed (Garcia *et al.*, 2009a), including the most recent and geographically extensive data obtained using otolith analyses (Alonso, 2002). Consequently, the results of the present study will mainly be compared with Garcia *et al.* (2009a) study, which occurred during the almost exact same period
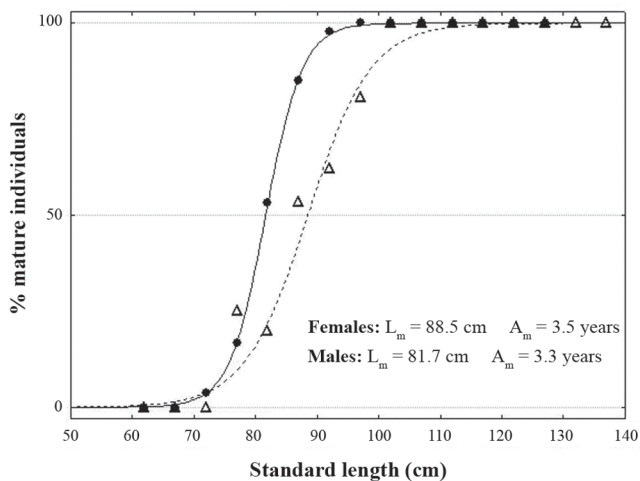

Fig. 4. Standard length at first sexual maturity of *Brachyplatystoma rousseauxii* males (black dots) and females (white triangles) in the Caqueta River, Colombia.
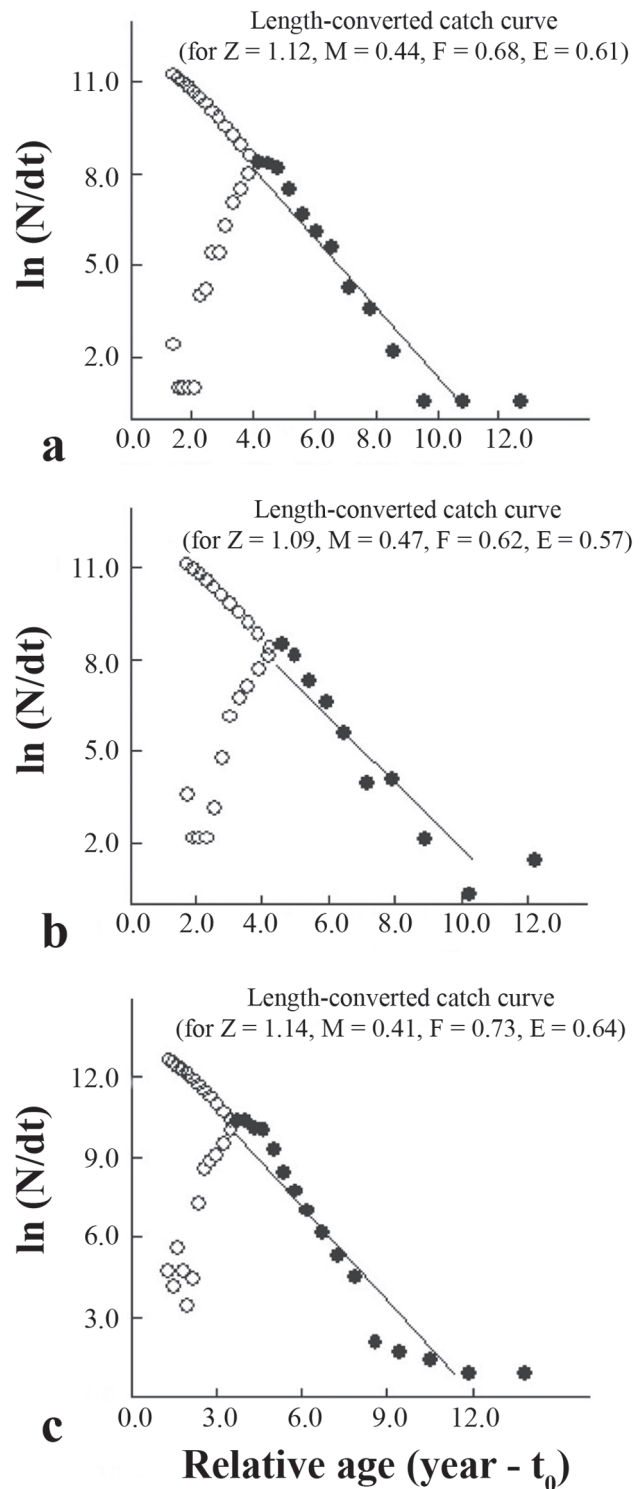

Fig. 5. Standard length (Ls) converted catch curve and mortality estimates for (a) females, (b) males and (c) sexed and unsexed individuals combined, calculated from the parameters of the von Bertalanffy growth function at a mean temperature of 27°C. Z, instantaneous rate of total mortality; M, instantaneous rate of natural mortality; F, instantaneous rate of fishing mortality; E, exploitation rate ($E = F.Z^{-1}$). Black dots = data points in the curve in which the regression was fitted.

Table 4. Mortality estimates (year^{-1}) and exploitation rate (E) for females, males and total (sexed and unsexed individuals combined). Natural mortality (M) was calculated from size-independant (Pauly, 1980; Richter & Evanov, 1997; Jensen, 1996) and size-dependant (Gislason *et al.*, 2010; Charnov *et al.*, 2013) models. Z was calculated from length-converted catch curves illustrated in Fig. 5 (Z=1.12 for females, Z=1.09 for males and Z=1.14 for total). Fishing mortality, F=Z-M. E=F/Z.

	Formula used for calculating M	M	F	E
Females	Pauly (1980)	0.44	0.68	0.61
	Richter & Evanov (1977)	0.47	0.65	0.58
	Jensen (1996) using A_{50}	0.49	0.63	0.56
	Jensen (1996) using K	0.38	0.74	0.66
	Gislason *et al.* (2010) immature	0.46	0.66	0.59
	Gislason *et al.* (2010) mature	0.33	0.79	0.71
	Charnov *et al.* (2013) immature	0.58	0.54	0.48
	Charnov *et al.* (2013) mature	0.42	0.70	0.63
Males	Pauly (1980)	0.47	0.62	0.57
	Richter & Evanov (1977)	0.48	0.61	0.56
	Jensen (1996) using A_{50}	0.50	0.59	0.54
	Jensen (1996) using K	0.40	0.69	0.63
	Gislason *et al.* (2010) immature	0.47	0.62	0.57
	Gislason *et al.* (2010) mature	0.33	0.76	0.70
	Charnov *et al.* (2013) immature	0.59	0.5	0.46
	Charnov *et al.* (2013) mature	0.42	0.67	0.62
Total	Pauly (1980)	0.41	0.73	0.64
	Jensen (1996) using K	0.35	0.79	0.69
	Gislason *et al.* (2010) immature	0.44	0.70	0.61
	Gislason *et al.* (2010) mature	0.32	0.82	0.72
	Charnov *et al.* (2013) immature	0.56	0.58	0.51
	Charnov *et al.* (2013) mature	0.42	0.72	0.63

(1995-1999). The growth patterns were markedly different between the Caqueta and the Peruvian Amazon, where *B. rousseauxii* had a rapid growth in the first three years, reaching about 50 cm at the end of the first year (Garcia *et al.*, 2009a). Both L∞ and K were within the range of those previously reported for the species (see Garcia *et al.*, 2009a for review). These parameters, however, were lower in the Caqueta than in the Peruvian Amazon when all specimens (sexed and unsexed) were taken into account (153.3 cm and 0.22 year^{-1} *versus* 155 cm and 0.29 year^{-1}, respectively), and especially the growth coefficient (K). Direct comparisons between the von Bertalanffy growth function parameters may lead to erroneous conclusions, particularly when considered separately (see Zivkov *et al.*, 1999). In the present case, however, these comparisons are supported by important length-at-age differences: during their first eight years, *B. rousseauxii* in the Peruvian Amazon were between 11 cm and up to 17 cm larger than those from the Caqueta, the difference decreasing progressively later on.

The mean sizes at first sexual maturity were relatively similar in the Caqueta and in the Peruvian Amazon (Garcia *et al.*, 2009a), differing only by 2 cm for females and 1 cm for males for the same period. The mean age at maturity, however, differed more markedly, maturity being reached approximately one year later in the Caqueta (3.3 and 3.4 years for females and males, respectively) than in the Peruvian Amazon (2.7 and 2.5 years, respectively; Garcia *et al.*, 2009a). This maturation delay is mainly explained by the slower growth rate in the Caqueta.

As previously discussed, potential bias on the estimation of growth parameters was probably small. Consequently, potential resulting bias in the estimation of derived natural mortality estimates was reduced. Nevertheless, to minimize the well-known risk of obtaining erroneous estimations of natural mortality (Gislason *et al.*, 2010; Brodziak *et al.*, 2011) and consequently of fishing mortality and exploitation rate, different models were used (some taking into account the effects of body size) in addition to Pauly's (1980) popular equation. As for most previously published instantaneous mortality rates for the species (see Garcia *et al.*, 2009a for review), the natural mortality (M) estimates calculated in the Caqueta River were below 0.5 year^{-1} and ranged from 0.32 to 0.42 for the whole data set (sexed and unsexed individuals combined), excluding estimation for immature fish, which yielded higher values. In every case, fishing mortality (F) was much higher than natural mortality in the Caqueta (0.72 to 0.82 year^{-1}), which was also observed in the Peruvian Amazon (0.64 year^{-1}; Garcia *et al.*, 2009a) and along the estuary-Iquitos axis (0.99 year^{-1}; Alonso, 2002). The higher values observed in the Caqueta compared to the Peruvian Amazon suggest a higher fishing pressure in the Caqueta, corroborating previous reports on the high fishing pressure supported by this species in the Caqueta River (Rodríguez, 1991; Agudelo, 1994; Celis, 1994; Muñoz-Sosa, 1996; Agudelo *et al.*, 2000; Petrere, 2001; Fabré & Barthem, 2005). The estimated exploitation rates (E), were well above (0.63 to 0.72) the upper limit reference point (0.5) above which the population is considered over-exploited (Rochet &

Trenkel, 2003, Trenkel & Rochet, 2003). Additionally, it should be pointed out that these results are based on data from almost 15 years ago. Since then, the situation has likely worsened, considering that *B. rousseauxii* is still a favored target (Petrere *et al.*, 2004; Agudelo, 2007; Agudelo *et al.*, 2009; Rodríguez, 2010) and that its proportion in the catches of the Colombian Amazon have significantly decreased in the last twenty years (Fig. 6). Taken together, decreased maximum sizes, high fishing mortality and exploitation rate and decreased catches probably indicate recruitment over-fishing of the species in the Caqueta River.

Brachyplatystoma rousseauxii is a large, highly fecund, relatively long-lived migratory species that typically falls within the "periodic strategists" category defined by Winemiller & Rose (1992). Species displaying such suites of life history traits have long been considered, erroneously (see Sadovy 2001), very resilient to fishery exploitation, although they conform poorly to fisheries management models (Winemiller 2005). Among the many evidences against such belief, reviewed in Sadovy (2001), the dire state of the most important commercial marine fish stocks, generally conformed of periodic species, is a particularly strong one (Sadovy, 2001; Winemiller, 2005). In fact, large species, such as *B. rousseauxii*, have longer generation times and greater vulnerability to exploitation because of their lower potential rates of population increase (Winemiller & Rose, 1992; Jennings *et al.*, 1998; Winemiller, 2005). Additionally, despite their higher compensatory potential, large periodic species performing large migrations are further vulnerable to habitat degradation and dam construction (Winemiller, 2005), a particularly important threat for *B. rousseauxii*.

This situation therefore calls for adaptive management strategies, as a collapse of *B. rousseauxii*'s fisheries would lead to important socio-economical problems in the region. Fishing is the first most important economic activity of rural communities in the Caqueta (Rodríguez, 1991; Muñoz-Sosa, 1993; Castro & Santamaría, 1993; Agudelo, 1994; Celis, 1994; Gómez, 1996) and *B. rousseauxii* is the target species (Agudelo, 1994; Celis, 1994). But *B. rousseauxii* and the other large pimelodid catfishes are also responsible for more than 80% of the fish-related commercial shipments between the Colombian Amazon and the interior of the country (Agudelo, 2007; Agudelo *et al.*, 2009). Given its extensive migratory behavior along the entire Amazon basin, however, efforts at managing this species would make sense only at a regional scale. A good starting point would be the tri-frontier zone between Brazil, Colombia, and Peru including the Putumayo, Caqueta and Amazon rivers, in association with Ecuador, where common fishing rules, mesh size, no-fishing periods and fishing gear recommendations could be implemented. Such concerted management strategy between countries could increase reproductive success by allowing fish to migrate upriver using temporal suspensions of specialized fishing fleets. Limiting the capture of large breeding individuals might also help them to grow older and

larger (mega-spawners), ultimately improving the resilience of the species to exploitation (Froese, 2004). Environmental and fishing authorities, together with fishermen's unions and associations in each country should promote a regional management strategy instead of using one-sided and un-coordinated minimum size and fishing gear regulations for this species and other large catfishes. Indeed, a recent study of fisheries patterns in the Colombian Amazon concluded that, to date, fisheries regulation had not succeeded in avoiding yield decrease of some formerly important species, which were progressively replaced by other species, evidencing a selective collapse of catches (Agudelo, 2007). Similar conclusions were made for the Peruvian Amazon, where catches of all the largest species, including *B. rousseauxii* and *B. filamentosum*, had strongly decreased to be progressively replaced by species with faster turnover, feeding lower in the food web and of lower commercial value (Garcia *et al.*, 2009b). In order to avoid a collapse of the fishery and to promote the sustainable use of *B. rousseauxii* in the region, Colombia and the neighboring countries should urgently establish a multilateral process of participative coordination for the large catfish fisheries in the tri-frontier region (Petrere *et al.*, 2004; Fabré & Barthem, 2005; Agudelo, 2007; Agudelo *et al.*, 2009).

The observed differences in the timing of reproduction, age at maturity and growth of *B. rousseauxii* between the Peruvian Amazon and the Caqueta suggest the existence of distinct populations adapted to particular environmental conditions within the Amazon basin. Although genetic studies did not clearly support population structure (Batista & Gomes, 2006; Batista, 2010), recent genetic analyses in the Upper Madera (Bolivian Amazon) and Western Amazon (Iquitos) provided strong evidence for the existence of a complex population structure of *B. rousseauxii* in the Amazon basin (Carvajal-Vallejos, 2013). This emphasizes our lack of knowledge about this economically and ecologically important migratory species and its close relatives of the genus *Brachyplatystoma*, and the need for recent and more comprehensive information on their life histories and genetic structure at the Amazonian scale. Studies on their life histories, however, are becoming ever more difficult owing to their decreasing abundance (Petrere *et al.*, 2004; Garcia *et al.*, 2009b) and the fact that they arrive almost always eviscerated and beheaded at the markets. Yet, simple monitoring of their growth and mortality patterns, which are essential for management strategies, are still possible to implement, providing good length-frequency data are collected. In addition to the management recommendations expressed above, we stress the importance, for national fishery organizations, of collecting good length-frequency data for large catfishes, in order to keep monitoring the dynamic changes of their populations. Recently published evidence (Petrere *et al.*, 2004; Garcia *et al.*, 2009a) and this study, all based on data collected more than ten years ago, demonstrate the urgent need for recent information on these exceptional resources.

Acknowledgments

Literature Cited

Agudelo, E. 1994. Composición y esfuerzo de las capturas comerciales en el bajo río Caquetá, Sector La pedrera (Amazonia colombiana). Unpublished Dissertation, Universidad del Valle, Cali, Colombia, 131p.

Agudelo, E. 2007. La actividad pesquera en la zona suroriental de la Amazonia colombiana: una descripción de la captura y comercialización de los bagres transfronterizos. Unpublished Dissertation, Universidad Autónoma de Barcelona, Barcelona, España, 100p.

Agudelo, E., J. C. Alonso & C. L. Sánchez. 2009. La utilización de los recursos icticos en la Amazonia sur de Colombia: una estrategia de vida, de ocupación y renta. Pp. 237-247. In: Bernal, H., C. Sierra & M. Angulo (Eds.). Amazonía y Agua: Desarrollo sostenible en el siglo XXI, UNESCO. Servicio Editorial de la Unesco Etxea, Bilbao, España.

Agudelo, E., Y. Salinas, C. L. Sanchez, D. L. Munoz-Sosa, J. C. Alonso, M. E. Arteaga, O. J. Rodriguez, N. R. Anzola, L. E. Acosta, M. Nunez & H. Valdes. 2000. Bagres de la Amazonia Colombiana: un Recurso sin Fronteras. SINCHI. Programa de Ecosistema Acuaticos. Editorial Scipto Ltda., Santa Fé de Bogota D.C., Colombia.

Agudelo, E., C. L. Sánchez, L. E. Acosta, A. Mazorra, J. C. Alonso, L. A. Moya & L. A. Mori. 2006. La pesca y la acuicultura en la frontera colombo - peruana del río putumayo. Pp. 79-98. In: Agudelo, E., J. C. Alonso & Moya, L. A. (Eds.). Perspectivas para el ordenamiento de la pesca y la acuicultura en el área de integración fronteriza colombo-peruana del río Putumayo. Instituto Amazónico de Investigaciones Científicas SINCHI y Instituto Nacional de Desarrollo INADE Bogotá, Colombia.

Alonso, J. C. 2002. Padrão espaço-temporal da estrutura populacional e estado actual da exploração pesqueira da dourada *Brachyplatystoma flavicans*, Castelnau, 1855 (Siluriformes: Pimelodidae), no sistema estuário-Amazonas-Solimões. Unpublished Ph.D. Dissertation, Universidad Federal do Amazonas-INPA, Manaus, 217p.

Arboleda, A. Y. 1989. Biologia pesquera de los grandes bagres del rio Caquetá. Boletín Ecotrópica (Univ. Jorge Tadeo Lozano, Bogotá), 20: 3-54.

Barbieri, L. R., J. M. E. Chittenden & S. K. Lowerre-Barbieri. 1994. Maturity, spawning, and ovarian cycle of Atlantic croaker, *Micropogonias undulatus*, in the Chesapeake Bay and adjacent coastal waters. Fishery Bulletin, 92: 671-685.

Barthem, R. & M. Goulding. 1997. The catfish connection. Ecology, migration and conservation of Amazon predators. Columbia University Press, New York.

Barthem, R. & M. Goulding. 2007. Un ecosistema inesperado: la Amazonía revelada por la pesca. Museu Paraense Emilio Goeldi, Amazon Conservation Association (ACA), Lima, Peru.

Batista, J. 2010. Caracterização genética da dourada - *Brachyplatystoma rousseauxii*, Castelnau, 1855 (Siluriformes: Pimelodidae) na Amazônia por meio de marcadores moleculares mitocondriais e microssatélites: subsídios para conservação e manejo. Unpublished Ph.D. Dissertation, Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus, Brazil, 148p.

Batista, J. S. & J. A. Gomes. 2006. Phylogeography of *Brachyplatystoma rousseauxii* (Siluriformes - Pimelodidae) in the Amazon Basin offers preliminary evidence for the first case of "homing" for an Amazonian migratory catfish. Genetics and Molecular Research, 5: 723-740.

Brodziak, J., J. Ianelli, K. Lorenzen & R. D. J. Methot, 2011. Estimating natural mortality in stock assessment applications. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-F/SPO-119.

Castro, D. M. & C. A. Santamaria. 1993. Informe Sobre el Estado del Stock Pesquero de los Grandes Bagres Comercializados en el Sector de Araracuara Durante el Ano de 1991. Corporacion Colombiana para la Amazonia, Mimeo, Santafe de Bogota, Colombia.

Carvajal-Vallejos, F. M. 2013. Phylogenetic position and genetic variability of *Brachyplatystoma rousseauxii* in the Upper Madera and Western Amazon. Unpublished Ph.D. Dissertation, Université Montpellier 2, Montpellier, France.

Celis, J. A. 1994. Aspectos sobre la biologia pesquera del dorado (*Brachyplatystoma flavicans*, Castelnau, 1855). Pisces: Pimelodidae en el bajo Caqueta, Amazonia colombiana. Unpublished Dissertation, Universidad del Valle, Cali.

Charnov, E. L., H. Gislason, & J. G. Pope, 2013. Evolutionary assembly rules for fish life histories. Fish and Fisheries, 14: 213-224.

Duponchelle, F., F. Lino, N. Hubert, J. Panfili, J.-F. Renno, E. Baras, J. P. Torrico, R. Dugué & J. Nuñez. 2007 Environment-related life history trait variations of the red-bellied piranha, *Pygocentrus nattereri*, in two river basins of the Bolivian Amazon. Journal of Fish Biology, 71: 1113-1134.

Duponchelle, F. & J. Panfili. 1998. Variations in age and size at maturity of female Nile tilapia, *Oreochromis niloticus*, populations from man-made lakes of Côte d'Ivoire. Environmental Biology of Fishes, 52: 453-465.

Fabré, N. N. & J. C. Alonso. 1998. Recursos ícticos no Alto Amazonas: sua importancia nas populaçoes ribeirinhas. Boletin del Museo Para. Emilio Goeldi, séria Zoologia, 1: 19-55.

Fabré, N. N. & R. Barthem. 2005. O manejo da pesca dos grandes bagres migradores: Piramutaba e Dourada no eixo Solimões-Amazonas. Pp. 114. In: N. N. Fabré & R. Barthem (Eds.). Coleção Documentos Técnicos: Estudos Estrategicos, Ibama, Provarzea, Manaus.

Froese, R. 2004. Keep it simple: three indicators to deal with overfishing. Fish and Fisheries, 5: 86-91.

Froese, R. & C. Binohlan. 2000. 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. Journal of Fish Biology, 56: 758-773.

García, A., J. C. Alonso, F. Carvajal, J. Moreau, J. Nuñez, J.-F. Renno, S. Tello, V. Montreuil & F. Duponchelle. 2009a. Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru. Journal of Fish Biology, 75: 2527-2551.

García, A., S. Tello, G. Vargas & F. Duponchelle. 2009b. Patterns of commercial fish landings in the Loreto region (Peruvian Amazon) between 1984 and 2006. Fish Physiology and Biochemistry, 35: 53-67.

Gayanilo, F. C., P. Sparre & D. Pauly. 2005. FAO-ICLARM Stock Assessment Tool II (FISAT II). Revised version. User's guide. FAO, Rome.

Gislason, H., N. Daan, J. C. Rice & J. G. Pope, 2010. Size, growth, temperature and the natural mortality of marine fish. Fish and Fisheries, 11: 149-158.

Gomez, J. 1996. Contribución al conocimiento de la biología reproductiva y hábitos alimenticios de los bagres plateado (*Brachyplatystoma flavicans*), Castelnau, 1885 y lechero (*Brachyplatystoma filamentosum*), Lichtenstein, 1819 (Pisces:Pimelodidae), en la parte media del rió Caqueta, sector Araracuara. Unpublished Dissertation, Universidad de Bogota Jorge Tadeo Lozano, Santafé de Bogota, Colombia, 102p.

Gutiérrez, F., L. E. Acosta & C. A. Salazar. 2004. Perfiles urbanos en la Amazonia colombiana: un enfoque para el desarrollo sostenible. Editora Guadalupe, Bogotá, 256p.

Jennings, S., J. D. Reynolds & S. C. Mills, 1998. Life history correlates of responses to fisheries exploitation. Proceedings of the Royal Society of London, Series B, 265: 335-339.

Jensen, A. L. 1996. Beverton and holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences, 53: 820-822.

King, M. 1995. Fisheries Biology, Assesment and Management. Fishing New Books, Oxford, England, 341p.

McCoy, M. W. & J. F. Gillooly. 2008. Predicting natural mortality rates of plants and animals. Ecology Letters, 11: 710-716.

Moreau, J., M. L. D. Palomares, F. S. B. Torres Jr. & D. Pauly. 1995. Atlas démographique des populations de poissons d'eau douce d'Afrique. Pp. 140 ICLARM Technical Papers 45, ICLARM.

Muñoz-Sosa, D. 1993. Evaluación de la actividad pesquera del bajo Caquetá entre Araracuara, y la Pedrera, Amazonas-Colombia. Pp. 102. In: F. P. Rastrojo (Ed.), Santa Fe de Bogotá, Colombia.

Muñoz-Sosa, D. L. 1996. Age structure and exploitation of giant catfish populations (*Brachyplatystoma* spp.) in the Lower Caqueta River, Colombia. Unpublished Dissertation, State University of New York, Syracuse, NY, 100p.

Núñez, J. & F. Duponchelle. 2009. Towards a universal scale to assess sexual maturation and related life history traits in oviparous teleost fishes. Fish Physiology and Biochemistry, 35: 167-180.

Pauly, D. 1979. Theory and management of tropical multiespecies stocks. Pp. 35 ICLARM Studies and Reviews 1, ICLARM, Manila, Philippines.

Pauly, D. 1980. On the interrelationship between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. Journal du Conseil International pour l'Exploration de la Mer, 39: 175-192.

Pauly, D. 1983. Length converted catch curves: a powerful tool for fisheries research in the tropics (Part I). Fishbyte, 1: 9-13.

Pauly, D. & N. David. 1981. ELEFAN I, a basic program for the objective extraction of growth parameters from length-frequency data. Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung, 28: 205-211.

Petrere Jr., M. 2001. Desarrollo sostenible del área amazónica fronteriza Bolivia, Brasil y Colombia. Documento técnico, Organización de Estados Americanos, SUDAM.

Petrere Jr., M., R. B. Barthem, E. A. Cordoba & B. C. Gomez. 2004. Review of the large catfish fisheries in the upper Amazon and the stock depletion of piraiba (*Brachyplatystoma filamentosum* Lichtenstein). Reviews in Fish Biology and Fisheries, 14: 403-414.

Rochet, M.-J. & V. M. Trenkel. 2003. Which community indicators can measure the impact of fishing? A review and proposals Canadian Journal of Fisheries and Aquatic Sciences, 60: 86-99.

Rodríguez, C. A. 1991. Bagres, malleros y cuerderos en el bajo río Caquetá (Amazonia Colombiana). Comercial fisheries in the lower Caquetá River. Programa Tropendos Colombia, Sante Fé de Bogota, DC.

Rodríguez, C. A. 2010. Pesca de consumo. Serie: Monitoreos comunitarios para el manejo de los recursos naturales en la Amazonia colombiana. Fundación Tropenbos Colombia, Vol. 3.

Sadovy, Y. 2001. The threat of fishing to highly fecund fishes. Journal of Fish Biology, 59: 90-108.

Simpfendorfer, C. A., R. Bonfil & R. J. Latour. 2005. Mortality estimation. In: Musick, J. A. & R. Bonfil (Eds). Management techniques for elasmobranch fisheries. FAO Fisheries Technical Paper 474. FAO, Rome.

Sparre, P. & S. C. Venema. 1995. Introducción a la evaluación de recursos pesqueros tropicales. Parte 1. FAO Manual. Documento Técnico de Pesca No. 306, FAO, Roma.

Taylor, C. C. 1958. Cod growth and temperature. Journal du Conseil International pour l'Exploration de la Mer, 23: 366-370.

Taylor, N. G., C. J. Walters & S. J. D. Martell. 2005. A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. Canadian Journal of Fisheries and Aquatic Sciences, 62: 215-223.

Trenkel, V. M. & M.-J. Rochet. 2003. Performance of indicators derived from abundance estimates for detecting the impact of fishing on a fish community Canadian Journal of Fisheries and Aquatic Sciences, 60: 67-85.

Vetter, E. F. 1988. Estimation of natural mortality in fish stocks: a review. Fishery Bulletin 86:25-43.

Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. Canadian Journal of Fisheries and Aquatic Sciences, 62: 872-885.

Winemiller, K. O. & K. A. Rose, 1992. Patterns of life history diversification in north American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49: 2196-2218.

Zivkov, M. T., T. A. Trichkova & G. N. Raikova-Petrova. 1999. Biological reasons for the unsuitability of growth parameters and indices for comparing fish growth. Environmental Biology of Fishes, 54: 67-76.