Journal of FISH BIOLOGY
Published for the Fisheries Society of the British Isles

Journal of Fish Biology (2009) **75**, 2527–2551
doi:10.1111/j.1095-8649.2009.02444.x, available online at www.interscience.wiley.com

Life-history characteristics of the large Amazonian migratory catfish *Brachyplatystoma rousseauxii* in the Iquitos region, Peru

A. García Vásquez*, J.-C. Alonso†, F. Carvajal*‡§‖, J. Moreau¶,
J. Nuñez§‖, J.-F. Renno*‖, S. Tello*, V. Montreuil*
and F. Duponchelle§‖**

**Instituto de Investigación de la Amazonía Peruana (IIAP), Iquitos-Quistococha, Perú, †Instituto Amazónico de Investigaciones Científicas (SINCHI), av. Vasquez Cobo, Laeticia, Colombia, ‡Unidad de Limnología y Recursos Acuáticos, Universidad Mayor de San Simón, Cochabamba, Bolivia, §Universidad Nacional Federico Villareal / FOPCA, 350 calle Roma, Miraflores, Lima, Perú, ‖Institut de Recherche pour le Développement (IRD)-GAMET, UR175-CAVIAR, F-34000 Montpellier, France and ¶Ecole Nationale Supérieure Agronomique de Toulouse (ENSAT), Avenue de l'Agrobiopôle-BP 32607 Auzeville-Tolosane-F 31326, France*

(Received 16 January 2009, Accepted 18 August 2009)

The main life-history traits of the dorado *Brachyplatystoma rousseauxii*, a large Amazonian catfish undertaking the largest migration known for a freshwater fish species (from the nursery area in the estuary of the Amazon to the breeding zones in the head waters of the western Amazon basin close to the Andes), were determined from a 5 year sampling of >15 000 specimens in the Peruvian Amazon. The breeding season occurred during the falling and low-water periods, which is hypothesized to be an adaptation to maximize the chances of young stages to reach the estuary. The size at first sexual maturity was slightly larger for females than males, *c*. 91 and 83 cm standard length (L_S), respectively. Both males and females reproduce for the first time at >3 years old. The fecundity per spawning event ranged from 481 734 to 1 045 284 oocytes for females weighing 25 and 34 kg, respectively. Seasonal variations of body condition were similar among sexes, but differed between immature specimens that had a higher condition during the low-water period and lower condition during rising waters, and mature individuals that showed the opposite pattern. The growth characteristics were estimated by L_S frequency analysis. For females, the best fitting models gave a mean birth date in August, during the height of the breeding cycle, with the following von Bertalanffy growth function parameters: $L_{S\infty} = 153{\cdot}3$, $K = 0{\cdot}29$ and $t_0 = -0{\cdot}37$ years. For males, the best fitting model gave a mean birth date in July, also during the height of the breeding period, with $L_{S\infty} = 142$, $K = 0{\cdot}30$ and $t_0 = -0{\cdot}36$ years. At a given age, females were systematically larger than males and the size difference increased with age. The largest females sampled (148 cm L_S) was 11 years old and the largest male (134 cm L_S) was 9 years old. The mortality estimates were higher for males total (Z) = 1·34, natural (M) = 0·52 and fishing (F) = 0·82 than for females ($Z = 0{\cdot}98$, $M = 0{\cdot}50$, $F = 0{\cdot}48$). The life-history patterns of *B. rousseauxii* are discussed in light of the available knowledge about this species and the understanding of its complex life cycle.

Key words: breeding season; fecundity; growth; maturity; mortality.

**Author to whom correspondence should be addressed. Tel.: + 33 511 445 6898; fax: +33 511 441 3223; email: fabrice.duponchelle@ird.fr

INTRODUCTION

With recent estimates of 6000–8000 species, the Amazon basin harbours the highest freshwater fish diversity on the planet (Vari & Malabarba, 1998; Reis *et al.*, 2004). One particularity of the Amazonian fish community is the exceptional abundance of large predatory species, among which the most widespread are catfishes of the family Pimelodidae (Barthem & Goulding, 1997). While most other predatory species (mainly characids, gymnotoids and cichlids) are more abundant in tributaries and floodplains than in the main river channels, the >15 species of large pimelodid catfishes (>50 cm total length, L_T; Barthem & Goulding, 1997; Barthem & Fabré, 2004; Buitrago-Suarez & Burr, 2007; Torrico *et al.*, 2009) are primarily found in the main channels, where their only competitors are dolphins (Barthem & Goulding, 1997). Some of these species are also commonly found in the Amazon Estuary. Among these species, the dorado, *Brachyplatystoma rousseauxii* (Castelnau), in a lesser extent *Brachyplatystoma vailanti* (Valenciennes) and perhaps also *Brachyplatystoma platynemum* Boulenger and *Brachyplatystoma filamentosum* (Lichtenstein) are believed to display unusual life cycles involving the largest migrations known for freshwater fishes. Knowledge about their exceptional life cycle was deduced: (1) from the mean lengths in the fisheries catches, which increase across the axis Amazon Estuary, Santarem, Manaus, Téfé, Leticia and Iquitos, (2) almost no individual with developed gonads was ever caught in the central and lower Amazon River and (3) that large mature individuals are almost only found in the western Amazon: from around Tefé–Leticia and upstream (Barthem *et al.*, 1991; Barthem & Petrere, 1995; Barthem & Goulding, 1997; Alonso, 2002; Alonso & Fabré, 2003; Petrere *et al.*, 2004; Alonso & Pirker, 2005). While the adults breed in the head waters in the western part of the Amazon drainage, close to the Andes in Bolivia, Colombia, Ecuador and Peru (Fig. 1), the resulting larvae and juveniles, helped by the currents, descend for several thousand kilometres down to their nursery area in the Amazon Estuary where they spend their first years before migrating up river while acquiring maturity to breed in the head waters (Barthem *et al.*, 1991; Barthem & Petrere, 1995; Barthem & Goulding, 1997, 2007; Alonso, 2002; Alonso & Fabré, 2003; Petrere *et al.*, 2004).

Brachyplatystoma rousseauxii, *B. vallantii* and *B. filamentosum* are among the most important species in the fisheries of the Amazon River basin, but recent evidence points towards decreasing catches and probable overexploitation (Barthem & Petrere, 1995; Alonso, 2002; Petrere *et al.*, 2004; Batista *et al.*, 2005; Garcia *et al.*, 2009). Indeed, 18 600 t of *B. rousseauxii* are caught every year in the main Amazon River channel alone (Parente *et al.*, 2005). The exceptional life cycle of these species and of *B. rousseauxii* in particular, encompassing the entire length of the Amazon River, requires concerted conservation and management measures over the entire distribution area, which includes at least five different countries (Bolivia, Brazil, Colombia, Ecuador and Peru) with contrasting fishing practices and regulations (Barthem & Goulding, 1997; Agudelo *et al.*, 2000; Petrere *et al.*, 2004; Alonso & Pirker, 2005; Fabré *et al.*, 2005; Batista & Gomes, 2006). A recent molecular analysis added to the existing complexity by suggesting that *B. rousseauxii* may be returning to their home tributary to spawn (Batista *et al.*, 2005; Batista & Gomes, 2006), which would imply the existence of several distinct populations along their extensive geographical area, with potential differences in genetic and life-history characteristics.

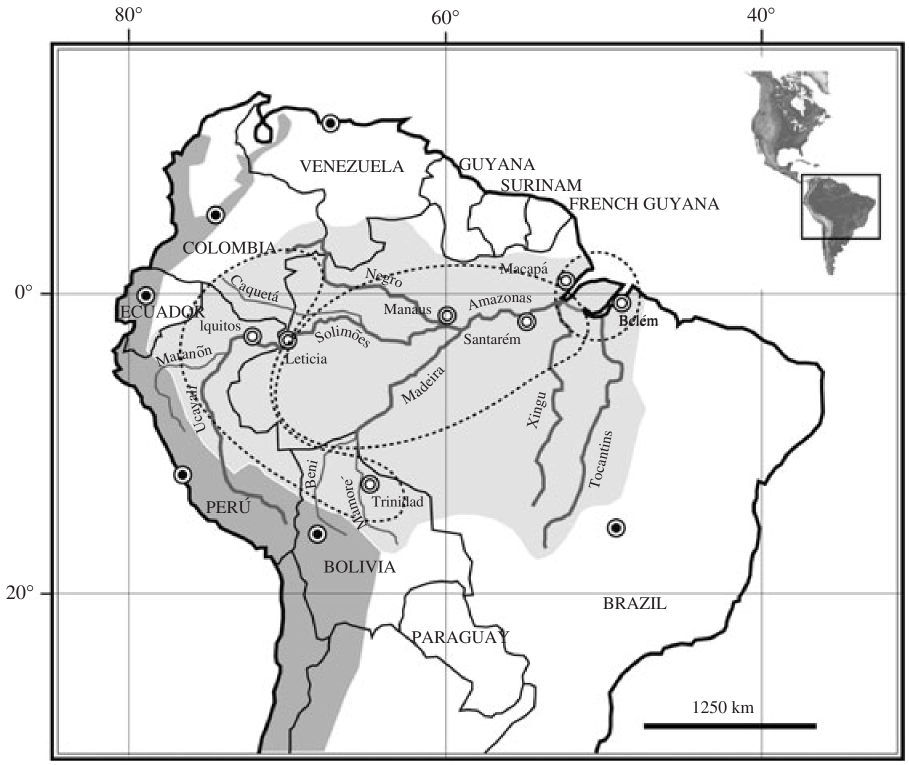


FIG. 1. Schematic map of the Amazon basin (░) illustrating the extent of *Brachyplatystoma rousseauxii* migration from the nursery area in the estuary (1) to the feeding-growing zone in the Central Amazon (2) and to the breeding zones in the head waters (3) close to the Andes (▒) (Barthem & Goulding, 1997, 2007).

Despite their commercial importance, scientific interest and the urgent need for concerted conservation measures, however, information on the genetic structure and life histories of these species, and particularly of *B. rousseauxii*, remains scarce and geographically restricted. Apart from a preliminary work in the Iquitos region (Garcia *et al.*, 1996), or a specific study of age structure and growth of *B. rousseauxii* along the Amazon River channel (Alonso, 2002; Alonso & Fabré, 2003), the available information comes from unpublished theses from the Brazilian (Zuanon, 1990; Rezende, 1999) and Colombian rivers (Castro & Santamaria, 1993; Celis, 1994; Salinas, 1994; Gomez, 1996; Muñoz-Sosa, 1996; Gil, 2008) synthesized in Agudelo *et al.* (2000).

The present study aimed at participating in the conservation and management of *B. rousseauxii* by providing important information about its reproductive and growth patterns in the Peruvian Amazon.

MATERIALS AND METHODS

FISH SAMPLING

This study was carried out between May 1995 and August 1999, with a gap in data collection between April and June 1996. *Brachyplatystoma rousseauxii* were sampled daily (except

Sunday) at the catfish-landing sites of the Iquitos market, Loreto region, Peru. Fish came from the commercial fisheries specialized in large catfishes operating in the lower Ucayali–upper Solimões (called Amazonas in Peru) and Marañon Rivers. Every landed specimen was measured (standard length, L_S), weighed (wet mass, W_t) and whenever possible sexed. Indeed, during the whole sampling period, most specimens arrived eviscerated at the market, which explains that the total number of fish measured always exceeded the summed number of females and males (Table I). For this reason, sex ratios were not calculated. In order to assess potential differences among sexes, only whole fish (excluding specimens landed eviscerated) were taken into account in the L_S and W_t relationships and body condition (K) calculations.

The sampling stopped in August 1999 when nearly every landed specimen was eviscerated.

BIOLOGICAL SAMPLE ANALYSIS

The L_T, fork length (L_F), L_S, head length (L_H) and W_t of each fish were measured to the nearest 1 cm and 250 g, respectively. The L_S and W relationships were calculated only from the whole fish (excluding eviscerated specimens). Gonads were weighed to the nearest 0·1 g and macroscopically checked for maturity stage determination.

The breeding season was estimated from the monthly proportions of female gonadal maturation stages. The maturity scale of gonadal maturation stages used was adapted from Garcia *et al.* (1996) to fit Nuñez & Duponchelle's (2009) scale. For females, the stages of gonadal maturation were: stage 1, immature; stage 2, maturing; stage 3, advanced maturation; stage 4, ripe; stage 5, spent; stage 5–1 describes gonads of resting females. Gonads of 12 females in advanced vitellogenesis (stage 3) were preserved in Gilson's fluid for later determination of fecundity. 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.

TABLE I. Standard length (L_S) and mass (W_t) ranges, means ± S.D. and number of fish sampled each year of females (F), males (M) and total (females, males and unsexed individuals, T). Different superscript lower case letters indicate among years statistical differences of mean L_S or W_t for each sex. P (L_S) and P (W_t) indicate for each year, among sex statistical differences of mean L_S and W, respectively (*, <0·05)

Sex	Year	n	L_S range (cm)	Mean ± S.D. L_S (cm)	P (L_S)	W_t range (kg)	Mean ± S.D. W_t (kg)	P (W_t)
F	95	264	69–143	99 ± 16^{a}	*	4·0–39·0	15·0 ± 8^{a}	*
	96	539	69–141	99 ± 14^{a}	*	4·0–34·0	13·0 ± 6^{a}	*
	97	1426	65–144	94 ± 13^{b}	*	3·5–38·0	12·0 ± 6^{a,b}	*
	98	1693	63–148	91 ± 13^{c}	*	3·3–44·0	11·0 ± 5^{c}	*
	99	749	62–138	93 ± 13^{b,c}	*	3·5–38·0	11·0 ± 5^{b,c}	*
M	95	198	62–116	85 ± 9^{a}		2·5–18·0	8·0 ± 3^{a}	
	96	429	64–116	85 ± 9^{a}		3·0–19·0	8·0 ± 3^{a,b}	
	97	1154	64–126	83 ± 8^{b}		3·0–25·0	8·0 ± 3^{a,b,c}	
	98	1507	61–134	82 ± 9^{c}		2·7–22·0	8·0 ± 3^{a,b,c}	
	99	565	64–115	82 ± 13^{c}		3·0–18·0	8·0 ± 5^{a,c}	
T	95	1832	59–143	93 ± 15^{a}		2·5–39·0	12·0 ± 7^{a}	
	96	1761	64–147	93 ± 14^{a}		3·0–52·0	11·0 ± 5^{a}	
	97	4736	49–145	89 ± 13^{b}		1·5–39·5	10·0 ± 5^{b}	
	98	4835	60–148	87 ± 13^{c}		2·5–44·0	10·0 ± 5^{c}	
	99	1957	62–138	89 ± 13^{b}		2·7–38·0	10·0 ± 5^{b,c}	

Note: As every fish could not always be weighed, minimum W_t at 1 year do not systematically corresponds to the minimum L_S this same year and *vice versa*.

The size at first sexual maturity (L_{S50}) is defined as the L_S 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). The L_{S50} is estimated by fitting (using the Statistica Software; www.statsoft.com) the fraction of mature individuals per 10 mm L_S intervals to a logistic regression function (Duponchelle & Panfili, 1998; Duponchelle *et al.*, 2007): $y = 1(1 + e^{(-\mathrm{a}(L-L_{S50}))})^{-1}$, where y is percentage of mature individuals by 10 mm L_S class, L is central value of each L_S class and a is constant of the model. The percent of mature individuals in each L_S class was weighted by the total number of individuals in the same L_S class.

Batch fecundity (*i.e.* the number of oocytes laid per spawning event) was estimated for 12 ripe (*i.e.* stage 3) females. The number of oocytes (N_o) was estimated using the gravimetric method described in Tressierra & Culquichicón (1993) from three ovarian fragments for each female: $N_o = \mathrm{W_o W_{gf}^{-1}} n$, where W_o is ovaries mass, W_{gf} is mass of the gonad fragment and n is number of oocytes in the gonad fragment.

Each ovarian fragment was analysed individually, and when there was <5% difference in the three counts, they were pooled to calculate fecundity by reference to the mass of the gonads. When different, the three fragments were discarded and other slightly larger gonad fragments were analysed.

Body condition, mass for a given L_S, was estimated using the L_S and W_t relationship $\log_{10}$ transformed to obtain a linear relationship (Froese, 2006; Hoeinghaus *et al.*, 2006): $\log_{10}(W_t) = a + b(\log_{10} L_S)$. Body condition was compared at two levels: among sexes and among hydrological periods. Hydrological periods were defined following Hoeinghaus *et al.* (2006): falling waters (June to July), low waters (August to October) and rising waters (November to May).

Growth and mortality parameters were calculated using procedures provided in the FiSAT II (FAO–ICLARM Fish Stock Assessment Tools) package (http://www.fao.org/fi/statist/fisoft/fisat/index.htm).

Age and growth characteristics were estimated from the modal progressions of L_S frequency distributions (Ricker, 1975) of *B. rousseauxii* at every month sampled. This method has potential biases in tropical conditions, where lack of seasonality, long spawning periods and non-year events giving rise to variations in growth and survival rates (hence to age and size modes) may lead to erroneously interpret size modes as differing in age by units of year. Indeed, tropical species often have extended breeding seasons during which multiple broods are produced and several cohorts (*i.e.* a group of fishes born at the same time) are likely to be encountered. In these conditions, following year classes is often difficult and hampers precise interpretation of length progression series (Fryer & Iles, 1972; Casselman, 1987; Lowe-McConnell, 1987; King, 1995). When reasonably accurate information on the species biology is available, such as the breeding season and the maximum length, it is still possible to obtain correct estimates of growth using modal length progression analysis. As detailed below, *B. rousseauxii* has a relatively restricted breeding season. Also, as an extensive sampling was done daily over five annual cycles (over 15 000 specimens), it was assumed that the maximum observed L_S was close to the asymptotic length ($L_{S\infty}$) and was used in selecting the best set of parameters.

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 Electronic LEngth Frequency ANalysis, ELEFAN, routine) was retained. This process also diminished the tendency of ELEFAN to underestimate the growth coefficient K and overestimate $L_{S\infty}$ (Moreau *et al.*, 1995).

The growth parameters were calculated by the von Bertalanffy growth function (VBGF) equation fitted by the ELEFAN method (Pauly, 1987) using the FAO–ICLARM Package FiSAT II (Gayanilo & Pauly, 1997; Gayanilo *et al.*, 2005): $L_t = L_\infty(1 - e^{(-K(t-t_0))})$, where L_t is the mean L_S at age t (L_{St}), $L_\infty = L_{S\infty}$, and t_0 the theoretical age at $L_S = 0$. t_0, which is not calculated by the ELEFAN routine, was calculated from the following equation (Pauly, 1979): $\log_{10}(-t_0) = -0{\cdot}392 - 0{\cdot}275 \log_{10} L_\infty - 1{\cdot}038 \log_{10} K$.

Among the several growth models available (*e.g.* VBGF, Richards, Gompertz, logistic, quadratic and exponential; Schnute, 1981), the VBGF model was chosen for comparative purposes as it has been largely used for Neotropical freshwater species, including all the available information about age and growth of *B. rousseauxii*.

Mortality estimates were obtained as described in Moreau *et al.* (1991) and Moreau & Nyakageni (1992). Total mortality (Z) was estimated by using length-converted catch curves (LCC) (Pauly, 1983). This method consists in pooling all the distributions while keeping their relative importance to obtain a single frequency distribution, which decreases part of the sampling biases (Pauly, 1983). Z is then calculated on the descending part of this single global distribution. As Z is determined in a given age or size range, the estimation makes sense only within this range. Natural mortality (M) was evaluated using Pauly's equation (Pauly, 1980) based on $L_{S\infty}$, K and the mean annual environmental temperature of the species concerned, as implemented in the FiSAT II package. The mean annual temperature used for M estimates was 27° C. It was averaged from the mean minimum and maximum temperatures of the Amazon River during the different hydrological periods between 1977 and 1981 (Guerra Flores, 1995). Fishing mortality (F) was calculated as $F = Z - M$. All these methods were provided by the FiSAT II package.

The age at first sexual maturity (A_{50}) was calculated from the VBGF as follows (Duponchelle *et al.*, 2007): $A_{50} = \{-\ln[1 - (L_{s50}\, L_{S\infty}{}^{-1})]K^{-1}\} + t_o$.

The longevity was calculated as the age at 95% of $L_{S\infty}$ from the equation of Taylor (1958):$A_p = t_0 - [\ln(1 - p)K^{-1}]$, where p is a fraction of $L_{S\infty}$ (in this case 0·95).

Longevity (t_{max}) was also calculated from the equation of Froese & Binohlan (2000): $\log_{10} \mathrm{t}_{max} = 0{\cdot}5496 + 0{\cdot}957 \log_{10}(A_{50})$.

ENVIRONMENTAL DATA

Water levels (m above sea level, m a.s.l.) for the Iquitos region were provided by the Servicio de Hidrografía y Navegación de la Amazonia (Ministerio de Defensa, Marina de Guerra del Perú, pers. data).

STATISTICS

Differences of mean L_S or W_t for each sex among years were tested with Kruskal–Wallis ANOVA on ranks, and Dunn's all pair-wise *post hoc* test, using Bonferonni correction to keep the experiment-wide error rate at the desired α (0·05, 0·01 or 0·001).

Among sex differences of mean L_S and W_t for each year were tested with a Mann–Whitney rank-sum test.

ANCOVA was used to test for differences among slope or intercepts (when slopes did not differ) of the $\log_{10}$-transformed L_S and W_t relationships, using $\log_{10} W_t$ as the dependent variable, $\log_{10} L_s$ as the covariate, and hydrological periods or sex as independent variables. When testing for significant main effect of the three hydrological periods, pair-wise comparisons were carried out using the Bonferonni correction to keep the experiment-wide error rate at the desired α (0·05, 0·01 or 0·001).

For each year and sex, logistic regression models provided an estimate ± S.D. of L_{S50}. Values of L_{S50} between sexes or sampling years were compared using t-tests (d.f. calculated from the number of L_S classes), using the Bonferonni correction to keep the experiment-wide error rate at the desired α (0·05, 0·01 or 0·001).

RESULTS

A total of 15 121 *B. rousseauxii* individuals were sampled over 5 years (1995–1999), with the best collections in 1997 and 1998 (Table I). As fish frequently arrived eviscerated at the market, only 25·2% of the individuals could be sexed in 1995, 55% in 1996, 54·5% in 1997, 66·2% in 1998 and 67·1% in 1999.

Over the study period, L_S and W_t relationships were $W_t = 0{\cdot}000009\ L_s^{3{\cdot}098}$, $r^2 = 0{\cdot}938$, $P < 0{\cdot}001$ ($n = 2244$) for females, $W_t = 0{\cdot}000009\ L_s^{3{\cdot}101}$, $r^2 = 0{\cdot}890$,

$P < 0{\cdot}001$ ($n = 2528$) for males and $W_t = 0{\cdot}000009\ L_s^{3{\cdot}092}$, $R^2 = 0{\cdot}936$, $P < 0{\cdot}001$ ($n = 7381$) for the total number of fish sampled (females, males and unsexed individuals). Every year, females were significantly larger and heavier than males (Table I). Mean L_S (Kruskal–Wallis ANOVA on ranks: d.f. = 4, $P < 0{\cdot}001$ for females and d.f. = 4, $P < 0{\cdot}001$ for males) and W_t (d.f. = 4, $P < 0{\cdot}001$ for females and d.f. = 4, $P < 0{\cdot}001$ for males) also differed significantly among years within each sex, with a tendency to decrease from 1995–1996 towards 1998–1999 for females but not for males (Table I).

Table II gives the relationships between L_T, L_F, L_S and L_H for *B. rousseauxii* in the Peruvian Amazon.

BREEDING SEASON

Over the study period, females with maturing gonads (stage 2) were observed from March and April to December, but were mostly abundant between May and September [Fig. 2(a)]. The breeding season generally started in May and June, *c.* 2 months after the appearance of the first maturing females. The per cent of breeding females peaked between July and September and ended in October and November, although some residual reproductive activity was observed in December 1995 [Fig. 2(b)]. Some variations, however, were observed from 1 year to another. In 1997, the breeding season was shorter than the other years: it started 1 month later and ended 1 month earlier. In 1995, the observed two peaks are probably an artefact of the exceptionally high number of eviscerated fish that arrived at the market from August to October, resulting in very few females with gonads at these months. It is likely that the breeding season in 1995 actually followed the pattern observed during the following years. In 1999, the sampling seems to have stopped in the middle of the breeding period because from August 1999 onwards, nearly every specimen arrived eviscerated at the market.

During the 5 years of study, gonad maturation started during the high-water period and breeding started *c.* 2 months later during the falling waters, peaked during low waters and ended at the beginning of rising waters.

TABLE II. Relationships between total length (L_T), fork length (L_F), standard length (L_S) and head length (L_H)

	n	L_T	L_F	L_S
L_T	10 375		$L_T = 1{\cdot}100\ L_F + 5{\cdot}064$ $r^2 = 0{\cdot}979$	$L_T = 1{\cdot}138\ L_S + 6{\cdot}885$ $r^2 = 0{\cdot}978$
L_F	15 121	$L_F = 0{\cdot}890\ L_T - 2{\cdot}490$ $r^2 = 0{\cdot}979$		$L_F = 1{\cdot}033\ L_S + 1{\cdot}869$ $r^2 = 0{\cdot}997$
L_S	15 121	$L_S = 0{\cdot}859\ L_T - 3{\cdot}916$ $r^2 = 0{\cdot}978$	$L_S = 0{\cdot}965\ L_F - 1{\cdot}504$ $r^2 = 0{\cdot}997$	
L_H	9477	$L_H = 0{\cdot}208\ L_T + 0{\cdot}539$ $r^2 = 0{\cdot}867$	$L_H = 0{\cdot}238\ L_F + 0{\cdot}904$ $r^2 = 0{\cdot}858$	$L_H = 0{\cdot}246\ L_S + 1{\cdot}296$ $r^2 = 0{\cdot}85$

n, number of fish used.

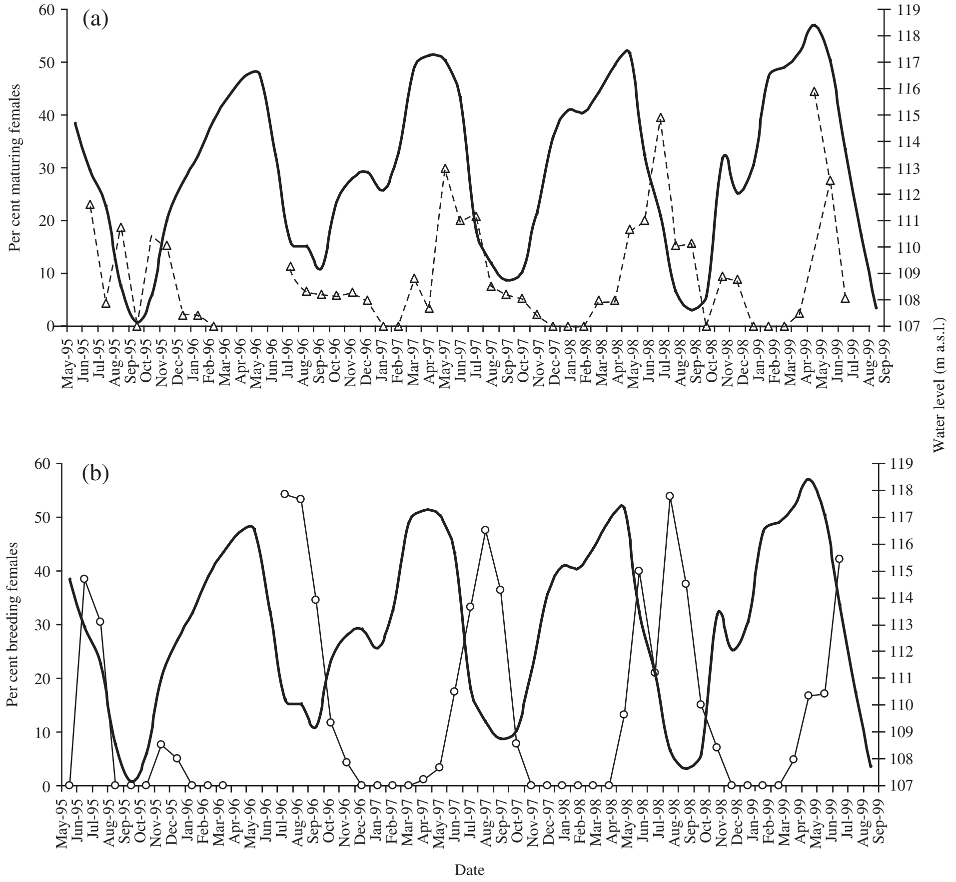


FIG. 2. Monthly percentages of (a) maturing (stage 2; △) and (b) breeding (stages 3 and 4; ○) *Brachyplatystoma rousseauxii* females in the Peruvian Amazon between 1995 and 1999, in relation to the water level (in metres above the sea level, m a.s.l.; —).

CONDITION, GROWTH AND MORTALITY PATTERNS

Females had significantly better condition than males at every hydrological periods (Table III), except during rising waters when condition was similar among sexes (ANCOVA, d.f. = 2, $P < 0{\cdot}001$ for both the falling and low-water periods). Overall, the mean condition of both males and females varied significantly from one hydrological period to the other (Table III). The females <90–100 cm (corresponding to immature females) had a higher condition during the low-water period, intermediate condition during falling waters and lower condition during rising waters, whereas the opposite pattern was observed for mature females >90–100 cm (Fig. 3). A similar trend was observed for males, with a size shift *c*. 80–90 cm, the mean size at which males reached maturity.

The L_S frequency histograms and the corresponding VBGF curves for the whole time series are presented in Fig. 4. For females, the best fitting models gave a mean birth date in August, during the height of the breeding cycle, with the following

TABLE III. Mean mass (W_t) for a given standard length (L_S) of females and males at each hydrological period. Different superscript lower case letters indicate, within each sex, statistically significant differences ($P > 0{\cdot}05$) in mean condition among hydrological periods

		W_t (kg) for a given length L_S (cm)		
Sex	Hydrological periods	70	110	140
Females	Falling^a	4·7	18·3	37·9
	Low^b	5·0	18·3	36·3
	Rising^c	4·5	19·0	41·1
Males	Falling^a	4·6	17·4	
	Low^b	4·8	17·9	
	Rising^c	4·5	19·1	

parameters: $L_{S\infty} = 153{\cdot}3$, $K = 0{\cdot}29$, score $= 0{\cdot}162$ [Fig. 4(a)]. t_0 was calculated as $-0{\cdot}37$ years. For males, the best fitting model gave a mean birth date in July, also during the height of the breeding period, with $L_{S\infty} = 142{\cdot}0$, $K = 0{\cdot}30$ and score $=$ $0{\cdot}158$ [Fig. 4(b)]. t_0 was calculated as $-0{\cdot}36$ years. For the females, males and unsexed individuals combined data, the mean birth date was July and the parameters were: $L_{S\infty} = 155$, $K = 0{\cdot}28$, score $= 0{\cdot}140$, $t_0 = -0{\cdot}380$ years [Fig. 4(c)].

Females had a better growth than males as indicated by the calculated L_S at age (Table IV). At a given age, females were systematically larger than males and the size difference increased with age. Most of this difference, however, was acquired during the first year (*c.* 5%). Only about 2% differences were acquired afterwards, between years 2 and 11. The youngest individual sampled was *c.* 1 year old (49 cm L_S unsexed individual). The youngest female sampled was 1·4 years old (62 cm) and the youngest male was 1·5 years old (61 cm).

The calculated life span for *B. rousseauxii* varied according to the model used. Froese & Binohlan (2000) model resulted in life span estimates of 12·3 and 10·6 years for females and males, respectively, whereas Taylor's (1958) gave lower estimations of 10·7 and 10·4 years for females and males, respectively. Computing age from the VBGF, the largest females sampled (148 cm L_S) was 11 years old and the largest male (134 cm L_S) was 9 years old. Likewise, the smallest female caught (62 cm) was 1·4 years old and the smallest male (61 cm) was 1·5 years old. The smallest unsexed individual captured (49 cm L_S) would have been barely 1 year.

The L_S converted catch curves at a mean temperature of 27° C resulted in higher mortality estimates for males ($Z = 1{\cdot}34$, $M = 0{\cdot}52$ and $F = 0{\cdot}82$) than for females ($Z = 0{\cdot}98$, $M = 0{\cdot}50$, $F = 0{\cdot}48$), owing mainly to the higher fishing mortality for males (Fig. 5). For the global dataset (females, males and unsexed individuals combined), mortality estimates were intermediate between females and males ($Z = 1{\cdot}12$, $M = 0{\cdot}48$ and $F = 0{\cdot}64$) [Fig. 5(c)].

SIZE AND AGE AT FIRST SEXUAL MATURITY

Females had a significantly larger L_{S50} than males in every year (t-test: d.f. $= 24$, 24, 24, 29, 23, $P < 0{\cdot}001$ for 1995, 1996, 1997, 1998 and 1999, respectively) and for the overall 1995–1999 period (t-test, d.f. $= 29$, $P < 0{\cdot}001$) (Fig. 6). The L_{S50} varied from 87·8 (1996) to 95·2 cm (1995) for females and from 80·8 (1999) to

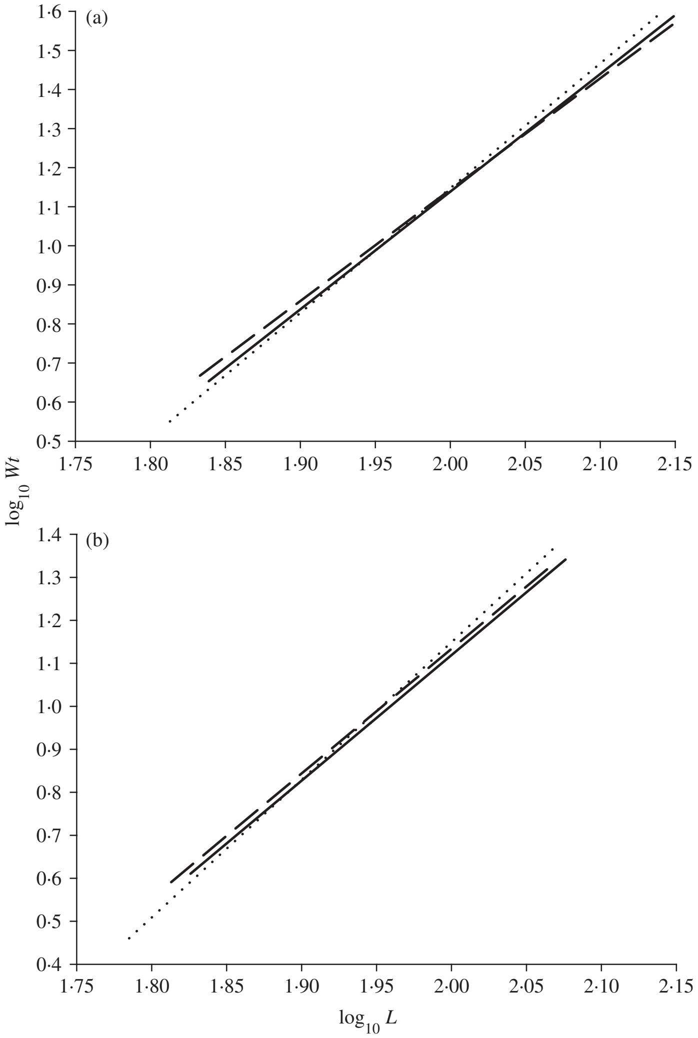


FIG. 3. Changes in the body condition [expressed by the $\log_{10}$-transformed standard length (L_S) and mass (W_t) relationships] of (a) females and (b) males *Brachyplatystoma rousseauxii* during the different hydrological seasons [falling (___), low (_ _ _) and rising (.......)] in the Peruvian Amazon. The curves were fitted by: (a) falling $y = 3{\cdot}011x - 4{\cdot}884$ ($r^2 = 0{\cdot}942$), low $y = 2{\cdot}848x - 4{\cdot}553$ ($r^2 = 0{\cdot}907$) and rising $y = 3{\cdot}192x - 5{\cdot}237$ ($r^2 = 0{\cdot}945$) and (b) falling $y = 2{\cdot}901x - 4{\cdot}627$ ($r^2 = 0{\cdot}885$), low $y = 2{\cdot}901x - 4{\cdot}669$ ($r^2 = 0{\cdot}848$) and rising $y = 3{\cdot}203x - 5{\cdot}257$ ($r^2 = 0{\cdot}905$)

86·6 cm (1995) for males. The smallest mature (stage 2) female observed reached 78 cm and the smallest ripe (stage 3) female 100 cm. The smallest mature male observed reached 70 cm and the smallest ripe male 84 cm (June 1998). Over the study period, most interannual differences of size at maturity were significant for females (except 1996 *v.* 1999) and males (except 1996 *v.* 1998 and 1996 *v.* 1999).

Both males and females reached maturity between 2·5 and 3·0 years old (Fig. 6). In average, males reached maturity slightly earlier than females.

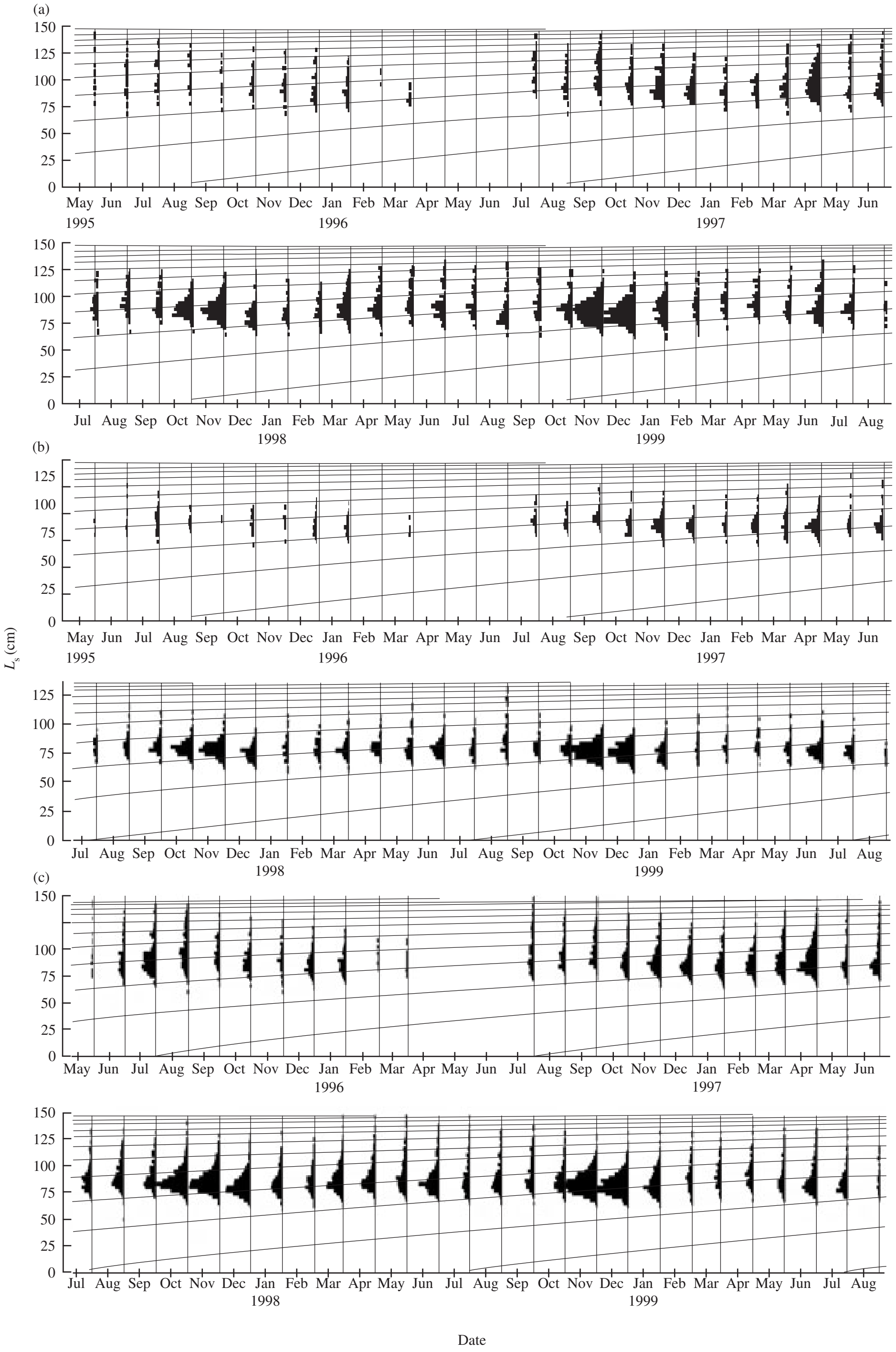


FIG. 4. Standard length (L_S) frequency histograms and the corresponding curves for (a) females, (b) males and (c) females, males and unsexed individuals combined von Bertalanffy growth function of *Brachyplatystoma rousseauxii* in the Peruvian Amazon for the whole time series (1995–1999).

TABLE IV. Standard length (L_S) at age for females, males and total (females, males and unsexed individuals) calculated from the VBGF

Age (years)	L_S at age (cm) Females	Males	Total	F–M
1	50·2	47·6	49·7	2·5 (5·11%)
2	76·1	72·1	76·4	4·0 (5·39%)
3	95·6	90·2	95·8	5·4 (5·81%)
4	110·1	103·6	110·3	6·5 (6·08%)
5	121·0	113·6	121·1	7·4 (6·30%)
6	129·1	120·9	129·2	8·2 (6·56%)
7	135·2	126·4	135·3	8·8 (6·72%)
8	139·8	130·4	139·8	9·3 (6·88%)
9	143·2	133·4	143·2	9·7 (7·01%)
10	145·7	135·7	145·7	10·1 (7·17%)
11	147·6	137·3	147·6	10·3 (7·23%)
12	149·1		149·1	
13	150·1		150·1	

F–M, the growth difference between females and males.

FECUNDITY

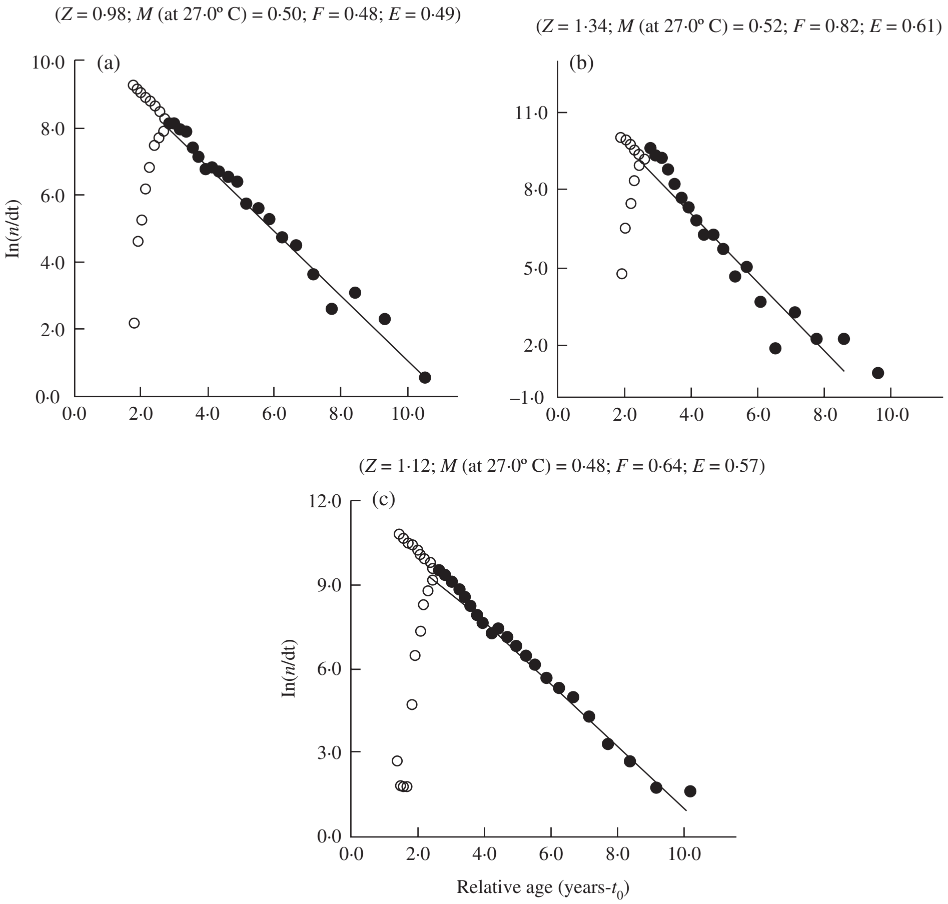
The batch fecundity (F) of *B. rousseauxii* ranged from 481 734 to 1 045 284 oocytes for females weighing 25 and 34 kg, respectively. It increased linearly with the female W_t ($r^2 = 0{\cdot}656$, $P < 0{\cdot}001$; Fig. 7). On the basis of the 12 specimens for which fecundity was estimated, a female produce *c*. 24 302 oocytes kg^{-1} of body mass.

DISCUSSION

The largest size observed in the Iquitos region of the >15 000 specimens sampled during this study, 148 cm L_S (175 cm L_T), was smaller than the maximum size of 192 cm L_t reported for this species by Barthem & Goulding (1997) or than that reported by Muñoz-Sosa (1996) in the Caqueta River, Colombia, 167 cm L_S. It was similar, however, to that reported for the Iquitos region by Tello *et al*. (1995) or by Torres (1974) 20 years earlier. The smallest sizes observed during the present study were close to the mean sizes reported for the middle Amazon region by Zuanon (1990) and Rezende (1999): 62·7 and 66·5 cm, respectively. A sexual dimorphism favouring females has been reported for *B. rousseauxii* in Colombia (Muñoz-Sosa, 1996; Agudelo *et al*., 2000) and for other members of the family Pimelodidae, *Pseudoplatystoma* spp. (Muñoz & Van Damme, 1998; Loubens & Panfili, 2000). This was also observed in the Peruvian Amazon, where *B. rousseauxii* females were consistently larger and heavier than males.

BREEDING SEASON

Over the study period, the breeding season of *B. rousseauxii* started during the falling-water period, peaked during low waters and ended at the beginning of rising



($Z = 0{\cdot}98$; M (at 27·0º C) $= 0{\cdot}50$; $F = 0{\cdot}48$; $E = 0{\cdot}49$)

($Z = 1{\cdot}34$; M (at 27·0º C) $= 0{\cdot}52$; $F = 0{\cdot}82$; $E = 0{\cdot}61$)

($Z = 1{\cdot}12$; M (at 27·0º C) $= 0{\cdot}48$; $F = 0{\cdot}64$; $E = 0{\cdot}57$)

Fig. 5. Standard length (L_S) converted catch curve and mortality estimates for (a) females, (b) males and (c) females, males 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 ($E = FZ^{-1}$). ●, data points on the curve on which the regression was fitted.

waters. Based on the analysis of reproductive patterns in South American fishes, Winemiller (1989) has defined three general reproductive strategies: namely, the opportunistic, periodic and equilibrium strategies. These were subsequently tested on North American fishes and reformulated into endpoints of a tri-dimensional continuum resulting from species adaptive responses to environmental seasonality and predictability (Winemiller & Rose, 1992). *Brachyplatystoma rousseauxii* typically falls within the periodic strategy, characterized by large size, long generation time, long life span, the production of large numbers of small eggs and a breeding cycle synchronized with the hydrological periodicity. The remarkable synchrony of *B. rousseauxii*'s reproduction with the hydrological cycle was then to be expected. In seasonal tropical fresh waters, however, reproductive timing of periodic species is restricted to a short period of a few months of high waters (Tedesco & Hugueny,

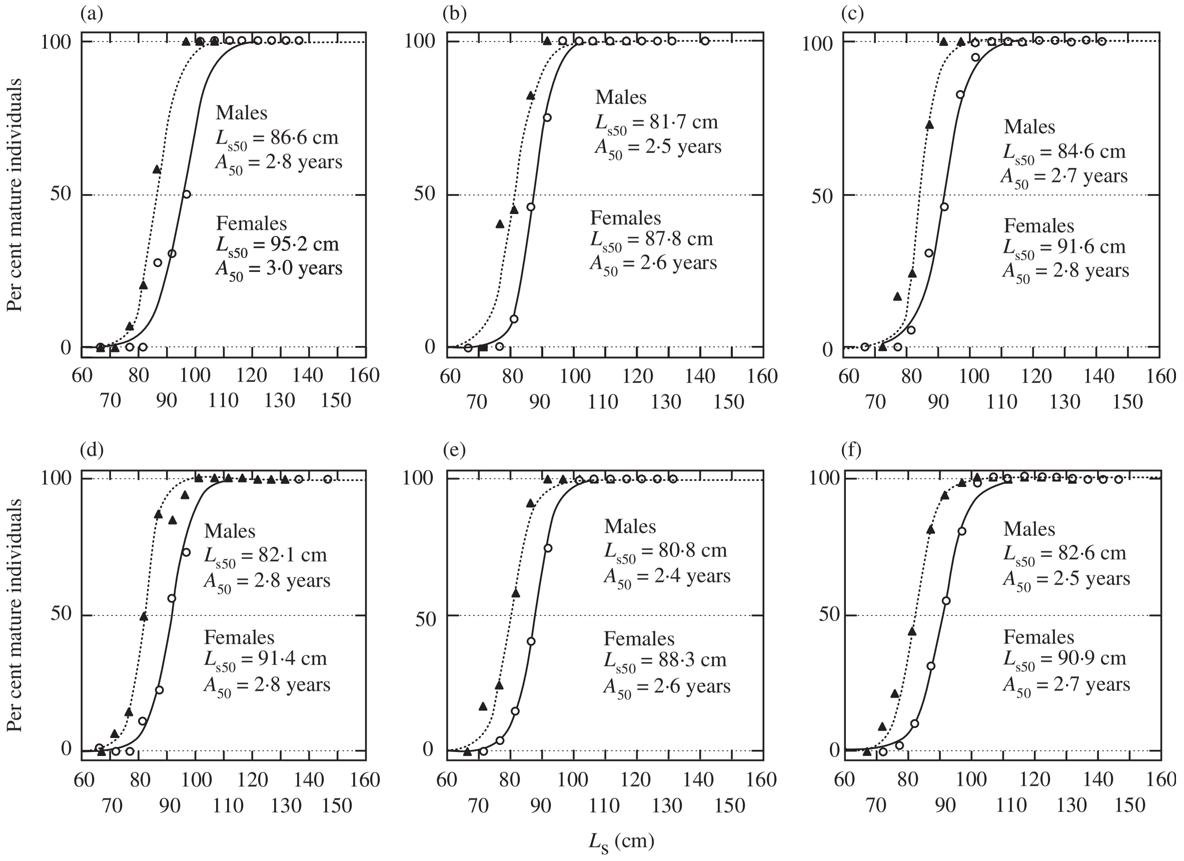


FIG. 6. Standard length (L_S) and L_S and age at first sexual maturity (L_{S50} and A_{50}) of males (▲) and females (○) *Brachyplatystoma rousseauxii* in (a) 1995, (b) 1996, (c) 1997, (d) 1998, (e) 1999 and (f) overall (1995–1999), in the Peruvian Amazon.

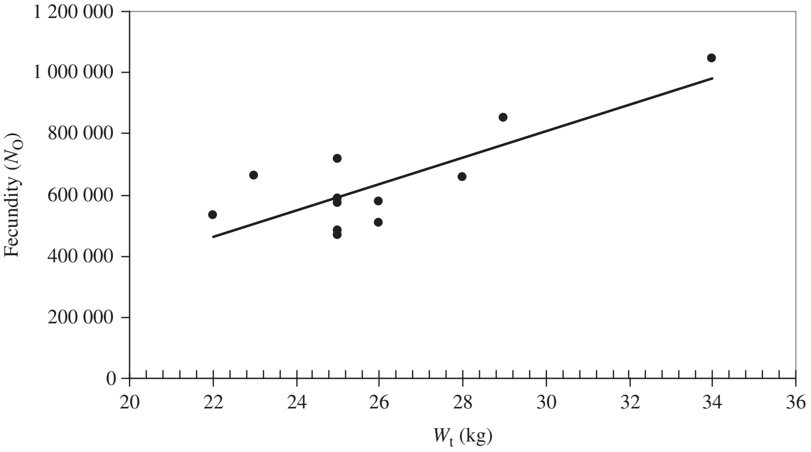


FIG. 7. Linear regression between batch fecundity (N_O) and female body mass (W_t) of *Brachyplatystoma rousseauxii* in the Peruvian Amazon. The curve was fitted by: $y = 43\ 496x - 495\ 597$.

2006), whereas *B. rousseauxii* reproduces later, during the falling and dry season. This particular reproductive timing, already suggested by a preliminary study in Iquitos (Garcia *et al*., 1996), contrasts not only with that of most tropical 'periodic' species (Tedesco & Hugueny, 2006; Tedesco *et al*., 2008), but also with that of most other Amazonian species, whose breeding cycle generally coincide with the flooding and high-water period (Goulding, 1980; Lowe-McConnell, 1987; Vazzoler & Menezes, 1992; Ruffino & Isaac, 1995; Barthem & Fabré, 2004), including most other Amazonian migratory periodic species and most catfishes of the family Pimelodidae (Muñoz & Van Damme, 1998; Agudelo *et al*., 2000; Loubens & Panfili, 2000; Garcia *et al*., 2001). Breeding during the rising or high-water period, when newly inundated areas provide abundant food and shelter for both parents and juveniles, has been interpreted as an adaptive mechanism ensuring maximum juvenile growth and survival (Goulding, 1980; Lowe-McConnell, 1987). This departure from the expected trend for a migratory Amazonian species was also observed for other members of the *Brachyplatystoma* genus: *B. filamentosum*, *B. vailantii*, *Brachyplatystoma juruense* (Boulenger) and *B. platynemum* in the Colombian rivers (Agudelo *et al*., 2000). The results of *Agudelo et al*. (2000) were more equivocal for *B. rousseauxii*: it reproduces during the falling-water period in the Guaviare River and in the upper Caqueta River, although they also observed a first peak of activity during the rising waters. On the other hand, this species apparently reproduces during the rising-water period in the lower Caqueta River, although a second peak of activity was observed during the falling period (Agudelo *et al*., 2000). Surprisingly, the authors considered that *B. rousseauxii* was overall reproducing during the high-water period (Agudelo *et al*., 2000). Some flaws in their methodology, however, are very likely to explain the observed differences with the present results. A precise determination of the breeding season consists of an analysis of the relative cumulated percentage of ripe females (at the end of the vitellogenic cycle) in the adult population (fishes in which the size is equal or above the average size at first maturity) at monthly intervals (Nuñez & Duponchelle, 2009). Agudelo *et al*. (2000), however, included maturing females (in early vitellogenesis) in their graphical representations of reproductively active females. Therefore, a large proportion of the females included in the first reproductive peaks observed during the rising and high-water periods were probably maturing and not yet reproductively active females. A re-analysis of their database would probably result in a breeding season coinciding with the falling-water period for *B. rousseauxii* in the Colombian Amazon, as observed in the present study and as they observed for the other *Brachyplatystoma* species. A previous study reported the highest gonado-somatic index values between July and September in the lower Caqueta River for the same species (Celis, 1994), which corresponds to the falling-water period in Agudelo *et al.*'s (2000) figures. Although his study focused primarily on growth patterns, Muñoz-Sosa (1996) also reported a breeding period between October and January for this species in the lower Caqueta River, Colombia, corresponding to the falling and low-water season. A recent study in the Colombian sector of the Amazon in Leticia (*c.* 500 km below Iquitos) also indicates a breeding season during falling and low waters (Gil, 2008).

It appears that catfishes of the pimelodid genus *Brachyplatystoma* do not follow the most general pattern of breeding during the rising or high-water period adopted by most migratory and non-migratory Amazonian species, including several pimelodid catfishes. But why? Some *Brachyplatystoma* species, and particularly *B. rousseauxii*, are believed to complete their life cycle by migrating from their nursery area in the Amazon Estuary to their spawning sites close to the Andes in the Bolivian, Colombian, Ecuadorian and Peruvian Amazon head waters (Barthem *et al.*, 1991; Barthem & Petrere, 1995; Barthem & Goulding, 1997, 2007; Alonso, 2002; Alonso & Fabré, 2003; Petrere *et al.*, 2004). For these species, which live and supposedly reproduce in the main course of the rivers (Barthem & Goulding, 1997; Goulding *et al.*, 2003), breeding during the falling-water period probably limits the risk of the eggs and larvae being swept out in the adjacent flooded areas (Varzea) thus maximizing their chances to reach the nursery area of the estuary thousands of km downriver. Moreover, when returning into the main river bed, the waters of the Varzea, which are enriched in nutrients, phytoplankton, zooplankton and in larvae and early stages of most other fish species, are likely to provide abundant food resources to the *Brachyplastystoma* young stages during their descent to the estuary.

CONDITION, GROWTH AND MORTALITY

Seasonal variations of body condition were similar among sexes in *B. rousseauxii*, but differed between immature and mature individuals. Immature individuals had a higher condition during the low-water period, intermediate condition during falling waters and lower condition during rising waters, whereas the opposite pattern was observed for mature individuals. In the absence of information on potential behavioural or ecological differences between immature and mature individuals for this species, it might be assumed that the observed body condition differences mainly reflect differences in energy allocation. Immature fishes will mainly allocate their ingested energy to growth and maintenance whereas part of this energy has to be allocated to gonadal products in adults (Stearns, 1992; Wootton, 1998). Mature individuals had low condition during the falling and low-water period, when they breed and the lowest during the low waters, after they had reproduced, which is consistent with the expected cost of gamete production. They had the better condition during

TABLE V. Summary of the growth and mortality parameters for *Brachyplatystoma rousseauxii* in the literature. For comparison purposes, the lengths [total (L_T), fork (L_F) and standard (L_S)] were calculated from the equations in Table III

Region	Method	Sex	L_∞ (L_T, L_F, L_S)	K	t_0	M	Z	Reference
Lower Amazon	LFA	T	161*–141–134	0·22		0·40	0·87	Ruffino & Isaac (1995)
Lower Caqueta, Colombia	Ot.	T	207–184–176*	0·08	–1·12	0·54	0·78	Muñoz-Sosa (1996)
Axis Estuary-Amazon-Solimões	LFA	T	192*–168–161	0·21	0·00			Barthem & Goulding (1997)
Axis Estuary-Amazon-Solimões	Ot.	T	159–140*–134	0·30	–0·67	0·32	1·31	Alonso (2002)
Axis Estuary-Amazon-Solimões	Ot.	F	159–140*–134	0·32	–0·64	0·30		Alonso (2002)
Axis Estuary-Amazon-Solimões	Ot.	M	151–133*–127	0·29	–0·70	0·27		Alonso (2002)
Upper Amazon, Iquitos	LFA	T	183–162–155*	0·29	–0·38	0·48	1·12	Present study
Upper Amazon, Iquitos	LFA	F	181–160–153*	0·29	–0·37	0·50	0·98	Present study
Upper Amazon, Iquitos	LFA	M	168–149–142*	0·30	–0·36	0·52	1·34	Present study

*Original length (cm) measured by the authors.

LFA, length frequency analysis; Ot., otoliths; F, females; M, males; T, total (females and males grouped); L_∞, K and t_0, parameters of the von Bertalanffy growth function; M, Z; the instantaneous rates of natural and total mortality.

the rising-water period, when they are known to feed heavily on the characid species starting their annual upstream migrations ('piracema'; Barthem & Goulding, 1997). Most of the immature size classes analysed in this study (*c.* 50–90 cm), however, were large enough to prey on the migrating characids (Barthem & Goulding, 1997), and most probably did, but they have the lowest conditions during the rising waters. It might be that during falling and low-water periods, immature *B. rousseauxii* also largely benefit from the large amounts of recently hatched and adult fishes returning from the floodplain to the main river bed, whereas adult specimens engaged in reproduction do not. There might also have differences in immature and mature *B. rousseauxii* feeding grounds among seasons, but this remains highly speculative as no such information exists. Although the fish analysed were all caught around Iquitos, some of them might have recently migrated, which could have influenced their condition: Alonso (2002) showed that during rising waters, fishes of similar sizes had a lower condition when caught in Leticia and Iquitos after the migration than those that had not yet migrated in the estuary.

Previously published information on *B. rousseauxii* growth and mortality parameters were obtained from both length frequency analyses (LFA) and otolith readings (Table V). Apart from one study (Alonso, 2002), which analysed age and growth patterns separately for both sexes, all the available information pooled females and males together, despite the existence of a sex dimorphism in growth. Keeping in mind that when L_∞ increases K tends to decrease and inversely, the growth parameters were remarkably similar among studies and over a considerable geographical area. The notable exception was a surprisingly low estimate of K (0·08) in the Colombian waters, logically associated with the highest L_∞ value (176 cm L_S, Muñoz-Sosa, 1996). The explanation may lie in the short duration of the study (6 months) that did not allow a proper validation of annulus formation, which could have led to an erroneous interpretation. In the other studies, K ranged between 0·21 and 0·32, the highest estimates being associated with the lowest values of L_∞. This important difference cannot be attributed to the method used for estimating growth patterns, as both LFA and otolith readings were used in the other studies. It must be pointed out, however, that Muñoz-Sosa's (1996) estimate of K is surprisingly low, even when compared with other large pimelodid catfishes: K ranges from 0·10 (Barthem & Goulding, 1997) to 0·22 (Barthem, 1990) for *B. vallantii*, from 0·24 (Loubens & Panfili, 2000) to 0·33 (Ruffino & Isaac, 1995) for *Pseudoplatystoma fasciatum* (L.) and from 0·15 (Loubens & Panfili, 2000) to 0·26 (Ruffino & Isaac, 1995) for *Pseudoplatystoma tigrinum* (Valenciennes).

The estimates of M and Z were also relatively similar among studies (Table V), particularly the two based on the most extensive sampling (Alonso, 2002 and the present study). The main differences were the lower M values (*c.* 0·30 *v. c.* 0·50 in this study) and slightly higher Z values found by Alonso (2002). Therefore, Alonso's (2002) estimates of F, when considering the whole axis estuary–Iquitos, were higher than those observed during this study carried out only around Iquitos ($F = 0·99$ *v.* 0·64 in this study). This suggests that the highest fishing pressure is supported by the immature specimens in the Brazilian sector of the Amazon basin.

Overall, the growth parameters calculated in the present study from LFA were remarkably similar to Alonso's (2002) estimate, based on otolith readings. Alonso's (2002) slightly lower L_∞ and higher K values might be due to the fact that his sampling (going from the estuary to Iquitos) was not as extensive in the largest sizes as in the present study. The direct comparison of growth parameters (K and L_∞), at least when considered separately, among populations can lead to erroneous interpretations as these parameters do not only depend on growth, but also on reproductive or biometric traits (Živkov *et al*., 1999; Charnov, 2008). Nevertheless, the length-at-age estimates presented in Table IV correspond almost exactly to the values calculated from otoliths (Alonso, 2002; Alonso & Fabré, 2003). Both Alonso's (2002) and the present results, obtained from two different methods over part of the same sampling zones and periods, tend to validate each other.

Brachyplatystoma rousseauxii has rapid growth during the first 2 to 3 years, reaching 50 cm in its first year. The growth rate gradually decreases afterwards: the yearly size increment is <10 cm in the fifth year and drops to <5 cm after 6 years. The important geographic separation between the adults in the head waters and the juveniles in the estuary is hypothesized to have evolved to reduce competition over food and space with other large catfish young stages (Barthem & Goulding, 1997). Besides the advantages of escaping specific predation windows and being better competitors over food and space, a fast growth during the first phases of life may be particularly important for migratory species (Lowe-McConnell, 1987; Lucas & Baras, 2001). It is probably particularly important for species, such as *B. rousseauxii* and its congeners, which live in the main river channels, where most predators are large catfishes and dolphins. Barthem & Goulding (1997) considered that after reaching 50 cm, the catfishes have no significant predators in the Amazon basin. The fact that *B. rousseauxii* reaches this size during its first year, as also observed by Alonso (2002), is probably not a coincidence. This threshold size suggests that juveniles are able to initiate their upstream migration with minimum predation risks during their second year of life, which is consistent with their estimated migration pattern, reconstructed from the age distribution across the axis estuary, Santarem, Manaus, Tefé, Leticia and Iquitos (Alonso & Fabré, 2003). As stomach content analyses revealed that nearly all the prey eaten by *B. rousseauxii* and other river channel catfishes are >10 cm (Barthem & Goulding, 1997), reaching large lengths quickly may also be critical for the migrating juveniles to exploit their large food prey. Large sizes also allow for faster swimming, which may be important to catch the schooling characids, which make up 89% of their diet in the estuary and the central part of the Amazon (Zuanon, 1990; Barthem & Goulding, 1997).

AGE AND SIZE AT MATURITY

The available information on L_{S50} of *B. rousseauxii* comes almost exclusively from the Colombian rivers, where most studies found L_{S50} values of *c*. 100 cm for females and 90 cm for males: 108 cm (Castro & Santamaria, 1993), 101 cm (Celis, 1994; Muñoz-Sosa, 1996), 107 cm (Salinas, 1994) and 103 cm (Gomez, 1996; Agudelo *et al*., 2000) for females, and 98 cm (Castro & Santamaria, 1993), 89 cm (Celis, 1994; Muñoz-Sosa, 1996) and 88 cm (Gomez, 1996) for males. Alonso's (2002) low value (70·62 cm for combined sex) can be explained by the method used. As Fabré *et al*. (2000) had considered that most earlier estimations of the size at maturity in *B. rousseauxii* were overestimated owing to the scarcity of young and pre-adult specimens in the sampling, (Alonso's 2002) chose to average the smallest L_{S50} observed by previous authors instead of the mean L_{S50}. In the present study, carried out with an appropriate number of juveniles and pre-adults, including during the height of the breeding season, the observed values (from 81 to 87 cm for males and from 88 to 95 cm for females) were only slightly lower than those from the Colombian rivers but larger than (Alonso's 2002), suggesting that earlier estimations were probably correct in the Colombian rivers.

So far, only two estimations of A_{50} have been proposed: 7–10 years (Muñoz-Sosa, 1996) and an averaged 2 years for males and females pooled together (Alonso, 2002; Alonso & Pirker, 2005). Again, this striking difference can be explained. Both studies calculated the age at maturity from the VBGF: in the first case, the very low estimation of K (0·08; Muñoz-Sosa, 1996) is responsible for the unrealistically high value, whereas in the second case (Alonso, 2002; Alonso & Pirker, 2005), the underestimation of L_{S50} (see explanation above) resulted in an optimistically low A_{50}. The A_{50} calculated in the present study, *c.* 2·5 and 2·7 years for males and females, respectively, actually correspond to a first reproduction at an age >3 years old. Indeed, it must be pointed out that the calculated A_{50} are the corresponding ages for the L_S at which 50% of the fish in the population present signs of sexual maturity (vitellogenic and spermatogenetic activity for females and males, respectively) and does not correspond exactly to the age at which the fish are actually going to breed for the first time (Nuñez & Duponchelle, 2009). Although in the Peruvian Amazon, *B. rousseauxii* theoretically reach sexual maturity between 2·5 and 2·7 years old, which corresponds roughly to February and March if August is considered as the mean spawning period, they cannot start reproducing before the onset of the breeding season, 5 to 6 months later. Therefore, *B. rousseauxii* are likely to breed for the first time at >3 years old, which is supported by the fact that the smallest ripe female caught in the Peruvian Amazon had a length of 100 cm (see Table IV). This is consistent with the current knowledge of the species life cycle: immature individuals start leaving the nursery in the estuary between their first and second years at $L_S > 50$ cm (Barthem & Goulding, 1997; Alonso, 2002; present study) and start their upstream migration. They are known to feed heavily in the central Amazon and reach a large size before arriving at Leticia or at the Madeira and Caqueta rapids (Arboleda, 1989; Barthem & Goulding, 1997; Alonso, 1998). The mean catch L_S at Leticia and upstream is *c.* 90–100 cm (Barthem & Goulding, 1997; Alonso & Fabré, 2003), which corresponds to mature individuals. The upstream migration of pre-adults *B. rousseauxii* would take between 1 and 2 years, during which they would feed in the central Amazon, as hypothesized by Barthem & Goulding (1997) and grow larger before starting their sexual maturation when they reach the western part of the Amazon basin *c.* 3 years old.

FECUNDITY

The available information about the fecundity of *B. rousseauxii* is even scarcer than for its other life-history traits and comes from the Colombian rivers. Celis (1994) calculated the fecundity of several females, but unfortunately his regression coefficients were incorrect, so only the extreme values of the observed range could be used: 81 270 eggs for a 10 kg and 709 840 eggs for a 22·5 kg fish. Gomez (1996) estimated a fecundity of 98 550 eggs for a 10 kg and 758 800 eggs for a 24 kg fish. The females for which fecundity was estimated in the present study were between 22 and 34 kg, barely overlapping with Celis's (1994) and Gomez's (1996) females W_t. Nevertheless, the fecundities of *B. rousseauxii* females of 22·5 or

24 kg in the Caqueta River (Celis, 1994; Gomez, 1996) were higher than the highest values observed in the Iquitos region for females of similar sizes (Fig. 7) and were *c*. 46 and 38% higher, respectively, than the mean fecundities of 22·5 and 24·0 kg females calculated from the fecundity and W_t relationship. Both Celis (1994) and Gomez (1996) found 10 kg females (85 cm, Celis, 1994) with full gonads, whereas in the present study, the smallest ripe female was *c*. 14 kg and 100 cm. Despite the fact that the mean L_{S50} observed by Celis (1994) and Gomez (1996) were slightly larger than in the present study, which were all carried out at comparable periods, females seem to be able to breed at slightly smaller sizes and possibly with higher fecundities in the Caqueta River, Colombia, than in the Peruvian Amazon around Iquitos.

This study provides important new information about *B. rousseauxii* life-history characteristics in the Peruvian Amazon and contributes to a better understanding of its complex life cycle. As new information become available, however, this seems to grow more complex. It was believed that only adult individuals lived in the western part of the Amazon basin and that juveniles were encountered only in the eastern and central parts (Barthem & Goulding, 1997; Agudelo *et al*., 2000). The present results show that large numbers of immature specimens are present in the Iquitos region. It was demonstrated that the breeding season coincided with falling waters in the Iquitos region, and probably also in the Colombian rivers, which probably improves the chances of larvae to reach the estuary. Nevertheless, the possibility remains that some populations breed during the high-water season and that large numbers of larvae never make it to the estuary and instead develop in adjacent floodplains or tributaries in the western Amazon. This would explain the increasingly reported presence of small and young (1·5 years, this study) specimens close to the breeding grounds or of specimens <30 cm in Leticia, Téfé and Manaus (Agudelo *et al*., 2000; Alonso, 2002; Alonso & Pirker, 2005).

It should also be pointed out that the present results, as well as most results concerning the Colombian rivers, are based on sampling carried out about a decade ago. Since then, human exploitation has steadily increased (Petrere *et al*., 2004; Garcia *et al*., 2009) and has probably further affected the life-history traits of *B. rousseauxii*. Effective management strategies for the conservation of this species are in urgent need of recent data, as well as data from the Madeira and its headwaters, which represent *c*. 20% of the Amazon waters (Goulding *et al*., 2003) and from which virtually no information about this species exist, apart from preliminary molecular analyses (Coronel *et al*., 2004).

This study was carried out as part of the scientific collaborations between the Instituto de Investigaciones de la Amazonía Peruana (IIAP), the Institut français de Recherche pour le Développement (IRD) and the Instituto Amazónico de Investigaciones Cientificas (SINCHI) de Colombia, all part of the network RIIA (Red de Investigación sobre la Ictiofauna Amazónica; www.riiaamazonia.org).

References

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

Alonso, J. C. (1998). Pesca e esforço de pesca dos grandes bagres (Siluriformes: Pimelodidae) em um sector Colombiano do alto Amazonas. MSc Thesis, Instituto Nacional de Pesquisas do Amazonas, Manaus, Brazil.

Alonso, J. C. (2002). Padrão espaçao-temporal da estructura populacional e estado actual da exploração pesqueira da dourada *Brachyplatystoma flavicans*, Castelnau, 1855 (Siluriformes: Pimelodidae), no sistema estuário-Amazonas-Solimões. In *Ciências Biologicas*, p. 217. PhD Thesis, UFAM/INPA, Manaus, Brazil.

Alonso, J. C. & Fabré, N. N. (2003). Spatial and temporal pattern of the population structure and current state of fishing exploitation of the dourada (*Brachyplatystoma flavicans*, Lichtenstein, 1819) along the system estuary Amazonas–Solimões. Abstract in *Second International Symposium on the Management of Large Rivers for Fisheries: Sustaining Livelihoods and Biodiversity in the New Millennium* (Welcomme R. L. & Petr T., eds). Phnom Penh: FAO & Mekong River Commission.

Alonso, J. C. & Pirker, L. E. M. (2005). Dinâmica populacional e estado actual da exploração de piramutaba e de dourada In *O manejo da pesca dos grandes bagres migradores: Piramutaba e dourada no eixo Solimões-Amazonas. Coleção Documentos Técnicos: Estudos estratégicos* (Fabré, N. N. & Barthem, R. B., eds), pp. 21–28. Manaus: IBAMA, ProVárzea.

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

Barthem, R. (1990). Ecologia e pesca da piramutaba (*Brachyplatystoma vallantii*). PhD Thesis, Universidade de São Paulo, Rio Claro, São Paulo, Brazil.

Barthem, R. B. & Fabré, N. N. (2004). Biologia e diversidade dos recursos pesqueiros da Amazônia. In *A pesca e os recursos pesqueiros na Amazônia brasileira* (Ruffino, M. L., ed.), pp. 17–62. Manaus: IBAMA/Provárzea.

Barthem, R. & Goulding, M. (1997). *The Catfish Connection. Ecology, Migration and Conservation of Amazon Predators*. New York, NY: Columbia University Press.

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

Barthem, R. B. & Petrere, M. (1995). Fisheries and population dynamics of the freshwater catfish *Brachyplatystoma vaillantii* in the Amazon estuary. In *Proceedings of the World Fisheries Congress, Theme 1. Condition of the World's Aquatic Habitats* (Armantrout, N. B. & Wolotira, R., eds), pp. 329–340. New Delhi: Oxford and IBH Publishing Co. Pvt. Ltd.

Barthem, R. B., Ribeiro, M. C. L. D. B. & Petrere, M. J. (1991). Life strategies of some long-distance migratory catfish in relation to hydroelectric dams in the Amazon Basin. *Biological Conservation* **55,** 339–345.

Batista, J. S. & Gomes, J. A. (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.

Batista, J., Aquino, K. F., Farias, I. P. & Gomes, J. A. (2005). Variabilidade genética da dourada e da piramutaba na bacia amazônica. In *O manejo da pesca dos grandes bagres migradores: Piramutaba e dourada no eixo Solimões-Amazonas. Coleção Documentos Técnicos: Estudos estratégicos* (Fabré, N. N. & Barthem, R. B., eds), pp. 15–19. Manaus: IBAMA, ProVárzea.

Buitrago-Suarez, U. A. & Burr, B. M. (2007). Taxonomy of the catfish genus *Pseudoplatystoma* Bleeker (Siluriformes: Pimelodidae) with recognition of eight species. *Zootaxa* **1512,** 1–38.

Casselman, J. M. (1987). Determination of age and growth. In *The Biology of Fish Growth* (Weatherley A. H. & Gill H. S., eds), pp. 209–242. London: Academic Press.

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

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

Charnov, E. L. (2008). Fish growth: Bertalanffy k is proportional to reproductive effort. *Environmental Biology of Fishes* **83,** 185–187.

Coronel, J. S., Maes, G. E., Claus, S., Van Damme, P. A. & Volckaert, F. A. M. (2004). Differencial population history in the migratory catfishes *Brachyplatystoma flavicans* and *Pseudoplatystoma fasciatum* (Pimelodidae) from the Bolivian Amazon assessed with nuclear and mitochondrial DNA markers. *Journal of Fish Biology* **65,** 859–868.

Duponchelle, F. & Panfili, J. (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.

Duponchelle, F., Lino, F., Hubert, N., Panfili, J., Renno, J.-F., Baras, E., Torrico, J. P., Dugué, R. & Nuñez, J. (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.

Fabré, N. N., Donato, J. C. & Alonso, J. C. (2000). *Bagres de la Amazonia Colombiana: Un recurso sin fronteras*. Bogota: Instituto Amazónico de Investigaciones Científicas SINCHI, Editorial Scripto.

Fabré, N. N., Barthem, R. B., Carvalho, A. & Angelim, R. (2005). Sistema integrado para o manejo dos grandes bagres migradores. In *O manejo da pesca dos grandes bagres migradores: Piramutaba e dourada no eixo Solimões-Amazonas. Coleção Documentos Técnicos: Estudos estratégicos* (Fabré, N. N. & Barthem, R. B., eds), pp. 75–93. Manaus: IBAMA, ProVárzea.

Froese, R. (2006). Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* **22,** 241–253.

Froese, R. & Binohlan, C. (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.

Fryer, G. & Iles, T. D. (1972). *The Cichlid Fishes of the Great Lakes of Africa*. London: Oliver & Boyd.

Garcia, A., Rodriguez, R. & Montreuil, V. (1996). Longitud de primera maduracion y epoca de desove de Dorado (*Brachyplatystoma flavicans*) en la amazonia Peruana. *Boletin Cientifico INPA. Santa Fé* **4,** 5–17.

Garcia, A., Montreuil, V. & Rodriguez, R. (2001). Talla de primera maduracion y epoca de desove de la "Doncella", *Pseudoplatystoma fasciatum* (Linnaeus), y del "Tigre zungaro", *Pseudoplatystoma tigrinum* (Valenciennes), en la amazonia Peruana. *Boletin del Museo Paraense Emilio Goeldi, séria Zoologia* **17,** 3–13.

Garcia, A., Tello, S., Vargas, G. & Duponchelle, F. (2009). 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. J. & Pauly, D. (1997). *The FAO-ICLARM Stock Assessment Tool (FiSAT) Reference Manual*. Rome: FAO.

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

Gil, B. D. (2008). Aspectos de la biología reproductiva del Dorado *Brachyplatystoma rousseauxii* Castelnau, 1855 (Pises: Pimelodidae), en la frontera Brasil – Colombia – Perú del rió Amazonas como instrumento de manejo y conservación. BSc Thesis, Facultad de Ciencias Naturales, Universidad de Bogota Jorge Tadeo Lozano, Bogota, Colombia.

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. BSc Thesis, Universidad de Bogota Jorge Tadeo Lozano, Santafé de Bogota, Colombia.

Goulding, M. (1980). *The Fishes and the Forest. Explorations in Amazonian Natural History*. Berkeley, CA: University of California Press.

Goulding, M., Barthem, R. & Ferreira, E. J. G. (2003). *The Smithsonian Atlas of the Amazon*. Washington, DC: Smithsonian Institution.

Guerra Flores, H. (1995). *Estado actual del conocimiento de la pesqueria en la Amazonia Peruana*. Iquitos, Peru: IIAP.

Hoeinghaus, D. J., Winemiller, K. O., Layman, C. A., Arrington, D. A. & Jepsen, D. B. (2006). Effects of seasonality and migratory prey on body condition of Cichla species in a tropical floodplain river. *Ecology of Freshwater Fish* **15,** 398–407.

King, M. (1995). *Fisheries Biology, Assesment and Management*. Oxford: Fishing News Books.

Loubens, G. & Panfili, J. (2000). Biologie de *Pseudoplatystoma fasciatum* et *P. tigrinum* (Teleostei: Pimelodidae) dans le bassin du Mamoré. *Ichthyological Exploration of Freshwaters* **11,** 13–34.

Lowe-McConnell, R. H. (1987). *Ecological Studies in Tropical Fish Communities*. Cambridge: Cambridge University Press.

Lucas, M. C. & Baras, E. (2001). *Migration of Freshwater Fishes*. Oxford: Blackwell Science Ltd.

Moreau, J. & Nyakageni, B. (1992). *Luciolates stapperssi* in Lake Tanganyika. Demographical status and possible recent variations assessed by length frequency distributions. *Hydrobiologia* **232,** 57–64.

Moreau, J., Munyandorero, J. & Nyakageni, B. (1991). Evaluation des paramètres démographiques chez *Stolothrissa tanganyikae* et *Limnothrissa myodon* du lac Tanganyika. *Verhandlungen der Internationalen Vereinigung fuer Limnologie* **24,** 2552–2558.

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

Muñoz, H. & Van Damme, P. A. (1998). Parametros de reproduction de 4 especies de peces comerciales (*Pseudoplatystoma fasciatum*, *P. trigrinum*, *Colossoma macropomum* y *Piaractus brachypomum*) en la cuenca del Rio Ichilo (Bolivia). *Revista Boliviana de Ecologia y Conservacion Ambiantal* **4,** 39–54.

Muñoz-Sosa, D. L. (1996). Age structure and exploitation of giant catfish populations (*Brachyplatystoma* spp.) in the Lower Caqueta River, Colombia. MSc Thesis, College of Environmental Science and Forestry, State University of New York, Syracuse, NY, USA.

Nuñez, J. & Duponchelle, F. (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.

Parente, V. D. M., Vieira, E. F., Carvalho, A. R. & Fabré, N. N. (2005). A pesca e a economia da pesca de bagres no eixo Solimões-Amazonas. In *O manejo da pesca dos grandes bagres migradores: Piramutaba e dourada no eixo Solimões-Amazonas. Coleção Documentos Técnicos: Estudos estratégicos* (Fabré, N. N. & Barthem, R. B., eds), pp. 47–66. Manaus: IBAMA, ProVárzea.

Pauly, D. (1979). Theory and management of tropical multiespecies stocks. *ICLARM Studies and Reviews* **1,** 35.

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). The length converted catch curves. A powerful tool for fisheries research in the tropics. *Fishbyte* **1,** 9–13.

Pauly, D. (1987). A review of the ELEFAN system for analysis of length frequency data in fish and aquatic invertebrates. In *Length-based Methods in Fisheries Research* (Pauly, D. & Morgan, G. R., eds), pp. 7–34. *ICLARM Conference Proceedings* **13**.

Petrere, M., Jr, Barthem, R. B., Cordoba, E. A. & Gomez, B. C. (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.

Reis, R. E., Kullander, S. O. & Ferraris, C. J. (2004). *Checklist of Freshwater Fishes of South and Central America*. Porto Alegre: Edipucrs.

Rezende, L. F. B. (1999). Aspectos Biológicos e Pesqueiros da dourada (*Brachyplatystoma flavicans*) Pimelodidae – Siluroidei em um Trecho da Amazônia Central. MSc Thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**.

Ruffino, M. & Isaac, V. (1995). Reproductive strategies and biological parameters of several Brazilian Amazon fish species. *NAGA. The ICLARM Quaterly* **18,** 41–45.

Salinas, Y. S. (1994). Aspectos de la Biologia Pesquera de las Poblaciones de los Grandes Bagres (Ostariophysi: Siluriformes, Pimelodidae) en el Sector colombiano del Rio Amazonas. BSc Thesis, Universidad Pedagogica Nacional, Santafé de Bogota, Colombia.

Schnute, J. (1981). A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences* **38,** 1128–1140.

Stearns, S. C. (1992). *The Evolution of Life Histories*. New York, NY: Oxford University Press.

Taylor, C. C. (1958). Cod growth and temperature. *Journal du Conseil international pour l'Exploration de la Mer* **23,** 366–370.

Tedesco, P. A. & Hugueny, B. (2006). Life history strategies affect climate based spatial synchrony in population dynamics of West African freshwater fishes. *Oikos* **115,** 117–127.

Tedesco, P. A., Hugueny, B., Oberdorff, T., Dürr, H. H., Mérigoux, S. & de Mérona, B. (2008). River hydrological seasonality influences life history strategies of tropical riverine fishes. *Oecologia* **156,** 691–702.

Torres, R. M. (1974). Contenido estomacal de Dorado *Brachyplatystoma flavicans* (Castelnau, 1855). BSc Thesis, Bio-Medicas, Universidad Nacional de la Amazonia Peruana, Iquitos, Peru.

Torrico, J.-P., Hubert, N., Desmarais, E., Duponchelle, F., Nuñez Rodriguez, J., Montoya-Burgos, J., Garcia-Davila, C., Carvajal, F., Grajales, A. A., Bonhomme, F. & Renno, J.-F. (2009). Molecular phylogeny of the *Pseudoplatystoma* (Bleeker, 1862): biogeographic and evolutionary implications. *Molecular Phylogenetics and Evolution* **51,** 588–594.

Tressierra, A. & Culquichicón, Z. (1993). *Biología Pesquera*. Trujillo, Perú.: Editorial Libertad.

Vari, R. P. & Malabarba, L. R. (1998). Noetropical ichthyology: an overview. In *Phylogeny and Classification of Neotropical Fishes* (Malabarba, L. R., Reis, R. E., Vari , R. P., Lucena , Z. M. S. & Lucena, C. A. S., eds), pp. 1–11. Porto Alegre: Edipucrs.

Vazzoler, A. E. D. M. & Menezes, N. A. (1992). Sintese de conhecimentos sobre o comportamento reproductivo dos Characiformes da America do Sul (Teleostei, Ostariophysi). *Revista Brasiliera de Biologia* **52,** 627–640.

Winemiller, K. O. (1989). Patterns of variations in life history among south American fishes in seasonal environments. *Oecologia* **81,** 225–241.

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

Wootton, R. J. (1998). *The Ecology of Teleost Fishes*, 2nd edn. Dordrecht, The Netherlands: Kluwer Academic Publisher.

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

Zuanon, J. A. S. (1990). Aspectos da biologia, ecologia e pesca de grandes bagres (Pisces: Siluriformes, Siluroidei) na área da ilha da Marchantaria – rio Solimões, AM. MSc Thesis, Brazil Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

Electronic Reference

Tello, S., Guerra, H., Rodríguez , R. & García, A. (1995). La pesquería de grandes bagres en la región Loreto, con énfasis en Dorado (*B. flavicans*). *Informe del Instituto de Investigaciones de la Amazonia Peruana-IIAP.* Iquitos: IIAP. Available at www.iiap.org.pe