Variations in reproductive strategy of the silver Arowana, Osteoglossum bicirrhosum Cuvier, 1829 from four sub-basins of the Peruvian Amazon

F. Duponchelle, A. Ruiz Arce, A. Waty, A. Garcia-Vasquez, J.-F. Renno, F. Chu-Koo, C. Garcia-Davila, G. Vargas, S. Tello, A. Ortiz, et al.

To cite this version:

F. Duponchelle, A. Ruiz Arce, A. Waty, A. Garcia-Vasquez, J.-F. Renno, et al.. Variations in reproductive strategy of the silver Arowana, Osteoglossum bicirrhosum Cuvier, 1829 from four sub-basins of the Peruvian Amazon. Journal of Applied Ichthyology, 2015, 31 (S4), pp.19-30. 10.1111/jai.12973 . hal-01292011

HAL Id: hal-01292011
https://hal.sorbonne-universite.fr/hal-01292011v1

Submitted on 22 Mar 2016

Variations in reproductive strategy of the silver Arowana, *Osteoglossum bicirrhosum* Cuvier, 1829 from four sub-basins of the Peruvian Amazon

F. Duponchelle[1,2], A. Ruiz Arce[1,3], A. Waty[3], A. Garcia-Vasquez[1,3], J.-F. Renno[1,2], F. Chu-Koo[1,3,4], C. Garcia-Davila[1,3], G. Vargas[1,3], S. Tello[1,3], A. Ortiz[5], R. Pinedo[5], R. Manzanares Vásquez[5], and J. Nuñez Rodriguez[1,2]

1 Laboratoire Mixte International - Evolution et Domestication de l'Ichtyofaune Amazonienne (LMI – EDIA).
2 Institut de Recherche pour le Développement (IRD), Unité Mixte de Recherche Biologie des Organismes et Ecosystèmes Aquatiques (UMR BOREA - MNHN, CNRS-7208, UPMC, UCBN, IRD-207), F-34394, Montpellier, France.
3 Instituto de Investigación de la Amazonía Peruana (IIAP), Iquitos-Quistococha, Perú.
4 Universidad Nacional Intercultural de la Amazonía - UNIA. Facultad de Ingeniería y Ciencias Ambientales
5 Instituto Nacional de Desarrollo (INADE). Proyecto Especial de Desarrollo Integral de la Cuenca del Putumayo (PEDICP). Iquitos, Peru.

Summary

The aim of this study was to assess the variability of reproductive characteristics of the silver Arowana, *Osteoglossum bicirrhosum*, in four sub-basins of the Peruvian Amazon: the Amazonas, Ucayali, Napo and Putumayo rivers. An illustrated, detailed gonadal maturation scale is proposed for a clearer determination of the reproductive status of male and female Arowana. The breeding season occurred during the dry season and early rising waters in the Amazonas and Ucayali, whereas it was restricted to the dry season in the Napo and Putumayo. A same female can reproduce more than once during the breeding season. Age at maturity was reached during the second year, at sizes varying between 43-45cm for males and 46-50 cm for females. Important variations in fecundity were observed between fish of the four sub-basins, whereas mean oocytes diameter and mass did not vary significantly, suggesting differences in reproductive investment. Together with previously reported variations of growth patterns in the same sub-basins, these results suggest the existence of distinct populations in the Peruvian Amazon, with important consequences for management and conservation, but also for future aquaculture development programs.

Introduction

The silver Arowana, *Osteoglossum bicirrhosum*, is a relatively large (>1 m length), laterally compressed fish of the archaic bony-tongued fish Order Osteoglossiforms (Goulding, 1980), comprising, in South America, the blue Arowana, *Osteoglossum ferreirai* Kanazawa 1966, and the species of the genus *Arapaima* spp., known as pirarucu in Brazil and paiche in the other Amazonian countries. The silver Arowana preferentially inhabits lentic waters of the Amazon, Rupununi and Oyapock rivers (Goulding, 1980; Bayley and Petrere, 1989; Reis et al., 2003; Saint-Paul et al., 2000). This species occupies a particular place in Amazonian fisheries as it is heavily harvested both as an adult for human consumption and as a small juvenile (usually still with its yolk sac) for the ornamental trade (Moreau and Coomes, 2006; Alcantara et al., 2007). The Asian Arowanas (*Sleropages* spp.) or dragon fish, closely resemble the Amazonian silver Arowana. These are very popular and sought for pet fish in Asian markets, which has lead natural populations to be so dramatically depleted that they have been listed under the Convention on

International Trade in Endangered Species (CITES) Appendix I in 1975 (Moreau and Coomes, 2006). Since then, the Amazonian cousin, *O. bicirrhosum*, has replaced them in Asian markets and its exportation has increased alarmingly since the 1990s (Tello and Canepa, 1991; Moreau and Coomes, 2006, 2007). Owing to its increasing exploitation in Amazonia for ornamental purposes, the species is considered threatened in Peru (Moreau and Coomes, 2006), it has already been placed on the Red Book of Colombia (Mojica et al., 2002) and its trade for ornamental purposes is prohibited in Brazil (Lima and Prang, 2008; Prang, 2008).

The reproductive biology of the silver Arowana is relatively well described since the early studies of Goulding (1980, 1990) and Aragao (1989). Recently, patterns of reproductive investment were further investigated in the Mamirauá Reserve (Queiroz, 2008) and the potential role of male aggregations was explored (Verba et al., 2014). In Peru, its reproductive characteristics were studied in one lake of the Putumayo River (Cortegano et al., 2014) and further information also exists from unpublished dissertations (Ayala, 2001; Tang and Gomez, 2005). Despite extensive ornamental fisheries in almost all the distribution area of the species and growing concern about its conservation, however, no assessment of the geographic variability of reproductive traits has yet been attempted. Besides the obvious interest for conservation and fisheries management, the knowledge of whether geographic population may display significant variations in specific reproductive traits such as the timing of maturation and egg production would be determinant for future aquaculture development. Indeed, the production of Arowana juveniles in controlled conditions (aquaculture) appears to be the most immediate alternative to extraction of natural populations for ornamental purposes (Argumedo, 2005; Moreau and Coomes, 2006). Choosing breeders from a population with higher relative fecundity (egg production per unit body mass), for example, might increase chances of success. A recent study in the Peruvian Amazon demonstrated important variations in the growth patterns of the silver Arowana in four sub-basins, suggesting the existence of distinct populations, which might require independent management (Duponchelle et al., 2012). The aim of the present study is to assess whether reproductive characteristics also vary, and to which extent, between these four sub-basins of the Peruvian Amazon.

Material and Methods

Fish collection

Fish were collected monthly between November 2006 and April 2009 at the Iquitos and Requena markets for the Amazonas, Ucayali and Napo sub-basins (Figure 1). Requena is an important market located on the lower Ucayali River and Iquitos is the main landing market of the Peruvian Amazon, concentrating fishes from the Amazonas, Ucayali, Marañon, Napo, Huallaga, Tigre, Putumayo, Nanay, Yavari and Morona sub-basins (Garcia-Vasquez et al., 2009). For a better accuracy on specimen provenance, fish (of the largest possible size range) were bought from specific providers from each river basin for the Amazonas, Napo and Ucayali rivers. For the Putumayo River, fish were bought monthly, from March 2008 to April 2009, from local fishermen in El Estrecho and Huapapa communities (Figure 1). The sub-basins were chosen on the basis of their hydrological cycle: the Amazonas and Ucayali have very similar hydrological cycles; the Putumayo and Napo also have similar hydrological cycles, but lag from about three months from that of the

Amazonas-Ucayali. The availability and reliability of specimen's provenance was also taken into account. Monthly means of water levels were provided by the SO-HYBAM (Observation Service - Geodynamical, hydrological and biogeochemical control of erosion/alteration and material transport in the Amazon basin) and SENAMHI (Servicio Nacional de Meteolоría e Hidrología), Peru.

Biological sample analysis

A total of 951 specimens of *O. bicirrhosum* were analysed. On each fish, total length (T_L), standard length (S_L) and body mass were measured to the nearest mm and g, respectively. Gonads were photographed and macroscopically checked for maturity stage. On each fish, a gonad sample was preserved in Bouin's fluid for histological analyses. Fixed gonads were further processed under classical histological methods with Haematoxylin and Eosin staining for confirmation of macroscopic maturity stages. A gonadal maturation scale was then established, based on the macroscopic criteria detailed in Nuñez and Duponchelle (2009). Nevertheless, the proposed scale also provides the equivalence with Brown-Petersen et al. (2011)'s terminology, which was developed in an effort to standardize the confusing number of terms referring to key phases of the reproductive cycle in fisheries science' literature.

The breeding season was estimated from the monthly proportions of females' gonadal maturation stage "spawning capable" (Brown-Petersen et al., 2011). To obtain a better representation of the annual cycle, data collected over the study period were pooled for each river basin.

The average size at first sexual maturity (L_m) is defined as the standard length at which 50% of the individuals are at an advanced stage of the first sexual cycle during the breeding season (Legendre and Ecoutin, 1989). Practically, this is the size at which 50% of the fish have reached stage 2 of the maturity scale for females and males (Nuñez and Duponchelle, 2009). The mean SL at first maturity (L_m) was estimated by fitting the fraction of mature individuals per 50 mm S_L intervals to a logistic regression function weighted by the total number of individuals in each size class (Barbieri et al., 1994; Duponchelle and Panfili, 1998):

$$\%M = \frac{100}{1 + e^{\left(-a\times\left(L-Lm\right)\right)}} \quad (1)$$

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

The age at first sexual maturity (A_m) was calculated from the von Bertalanffy growth function (VBGF) as follows:

$$A_m = (-\ln(1-(L_m/L_\infty)) / K) + t_0 \qquad (2)$$

where L_m is the size at first sexual maturity previously calculated and t, L_∞, K and t_0 the parameters of the VBGF obtained from Duponchelle et al. (2012) on the same samples.

Batch fecundity (number of eggs to be potentially laid per spawning event, resulting from the maturation of fully developed intra-follicular oocytes) and oocyte diameter were estimated by image analysis (using NIH Image J software) from whole gonads in final maturation stage (stage 3). As the oocytes were not exactly circular in shape, the mean arithmetic diameter was used: √d.D, where d is the minimum diameter and D the maximum diameter of each oocyte. Oocyte mean mass was calculated from each stage 3 gonads, by weighing 30 oocytes to the nearest 0.001 g.

Statistical analyses

Differences in mean standard length and mass between sexes within each sub-basin were tested with a t-test. Differences of mean standard length or mass between sub-basins were tested with Kruskal-Wallis One Way Anova on ranks and Dunn's all pairwise post-hoc tests.

For each sub-basin, logistic regression models provided an estimate of the L_m ± standard deviation (equation 1). Therefore, sizes at maturity between sexes or geographic locations were compared using a classical Student t-test (degrees of freedom calculated from the number of size classes).

Analysis of covariance (ANCOVA) was used to test for differences in the fecundity-body mass relationships between geographic populations, using fecundity as the dependent variable, body mass as the covariate, and geographic population as categorical variable.

Comparisons of mean oocyte diameter and mass between geographic populations were carried out using one-way ANOVA.

For all comparisons, when more than two pairwise-tests were performed, the Bonferroni correction was applied to keep the experiment-wide error rate at the desired α (0.05, 0.01 or 0.001).

Results

A total of 290 specimens of *O. bicirrhosum* were analysed for the Amazonas, 276 for the Ucayali, 145 for the Napo and 240 for the Putumayo (Figure 2a). Mean standard lengths (S_L) and masses did not differ among sexes in any population. There were, however, significant differences in mean length (Kruskal-Wallis One Way ANOVA on Ranks, H = 83.4, $P<0.001$) and mass (H = 79.3, $P<0.001$) between populations when females and males were pooled: the Ucayali population differed from all the others in both mean length (Q = 8.6, $P<0.05$ with the Putumayo, Q = 6.7, $P<0.05$ with the Amazonas and Q = 4.8, $P<0.05$ with the Napo) and mass (Q = 8.3, $P<0.05$ with the Putumayo, Q = 6.8, $P<0.05$ with the Amazonas and Q = 4.5, $P<0.05$ with the Napo), whereas the other populations did not differ between each other in mean length nor in mean mass. Maximum lengths and even more masses, however, did vary considerably between populations, reaching barely 80 cm and about 3.8 kg in the Putumayo and more than 90 cm and 8 kg in the Amazonas (Figure 2a). In the Amazonas, maximum observed body mass for the silver Arowana was 49, 75 and 113% heavier than in the Napo, Ucayali and Putumayo, respectively. These important differences in body mass, however, are not a mere reflection of the larger maximum lengths in the Amazonas. Indeed, although mass-at-length is relatively similar between populations until about 50 cm (~ size at first sexual maturity, see below), afterwards fish start to become progressively heavier at a given length in the Amazonas than in the Ucayali, Napo and Putumayo, in order of increasing difference (Fig. 2b). These differences reached ~ 500 g and ~1000 g at 70 and 80 cm, respectively, between the Amazonas and Putumayo sub-basins (Fig. 2b).

For comparison purposes with other studies, a relationship between standard length (SL) and total length (TL) is provided, calculated from all individuals in Figure 2a, giving: SL = 0.9345 TL + 0.102.

Gonadal maturity scale

Females and males silver Arowana only have one functional gonad, the left one. The right gonad is atrophied. An illustrated, detailed gonadal maturity scale is presented in Figure 3 for both females and males. It allows for a clear determination of the breeding season, size / age at maturity and fecundity.

The precise description of the gonadal cycle also allowed identifying that the silver Arowana is a multiple-spawner (sensu Nuñez and Duponchelle 2009). Indeed, the presence of small, vetelogenic oocytes in between large oocytes in “spawning capable” ovaries, both in stage 3 or 4 (Figure 4a) and in stage 5-2 (recently spawned) ovary initiating another vitellogenic cycle (Figure 4b), observed in all four sub-basins, proves that a same female can reproduce at least twice during a breeding season. Further evidences come from the size frequency distribution of oocytes in “spawning capable” ovaries from the Putumayo sub-basin, showing two clearly separated modes of vitellogenic oocytes: the largest (of 244 oocytes) that will be spawned shortly and a smaller one (of 221 oocytes) that will likely be released in another spawning bout during the same breeding season (Fig. 5).

Breeding season

There exists a relationship, albeit not a direct one, between the reproductive cycle of the silver Arowana (estimated from the monthly proportions of females in “spawning capable” phase of the gonadal maturation scale) and the hydrological cycle (Figure 6). In the Amazonas and Ucayali rivers, which have comparable hydrological cycles, females have similar breeding seasons. Although sampling could not be completed at some months, it can nevertheless be observed that the breeding season started during the dry season (August-September) and ended before the water level reaches its maximum in both rivers. Some residual reproductive activity could be observed in the Ucayali at almost every month outside the main breeding season. Again, in the Napo and Putumayo rivers, which have comparable hydrological periodicity, the breeding season of the silver Arowana also tended to be similar (Figure 6). Although sampled could not be obtained in December and January in the Putumayo, it is likely that, as in the Napo, the breeding season initiated in December to peak in February-March. The breeding season in the Napo and Putumayo, however, did not last as long as in the Amazonas and Ucayali and was restricted to the low water period.

Size and age at sexual maturity

Females tended to have slightly larger size at first sexual maturity (Figure 7) than males in every sub-basin, but these differences were not significant (t-test, t=0.292, df=24, p=0.773 for the Amazonas; t=0.226, df=24, p=0.823 for the Ucayali; t=0.630, df=18, p=0.536 for the Napo; and t=0.327, df=24, p=0.746 for the Putumayo). The size at maturity did not differ significantly between sub-basins for females nor males.

Age at first sexual maturity was reached during the second year for both males and females in all four sub-basins (Figure 7).

In all four sub-basins, the size at which 100% of both males and females were sexually mature was slightly before 60 cm S_L (Figure 7).

Fecundity

The number of oocytes per spawning event (batch fecundity) significantly varied (ANCOVA, $D_{3,41}$= 6.610, P<0.001) between fish of the four sub-basins (Figure 8, Table 1). Batch fecundity ranged from 93 to 256 oocytes for females of 1300 and 4960 g, respectively in the Amazonas, from 94 to 311 oocytes for females of 2080 and 3480 g, respectively in the Ucayali, from 92 to 197 oocytes for females of 1460 and 3220 g, respectively in the Napo and from 125 to 360 oocytes for females of 1770 and 2980 g, respectively in the Putumayo.

The Putumayo population differed significantly from the Amazonas (ANCOVA, $D_{1,32}$= 25.9, P<0.0001), Napo ($D_{1,30}$= 9.7, P<0.05 with Napo) and Ucayali ($D_{1,33}$= 53.9, P<0.001) populations, whereas the Amazonas, Ucayali and Napo populations did not significantly differ between each other ($D_{2,12}$= 1.4, P>0.05).

Relative fecundity (batch fecundity per unit body mass), oocyte diameter and oocyte mass are presented in Table 2. Relative fecundity differed significantly between fish of the four sub-basins (One-way ANOVA, F3 = 11.6, P < 0.001). Holm-Sidak post-hoc test indicated that fish from the Putumayo significantly differed from the Amazonas (t = 4.812, P < 0.001), the Ucayali (t = 3.614, P = . 0.004) and the Napo (t = 2.732, P = 0.037), whereas fish from the Amazonas, Ucayali and Napo did not differ significantly between each other.

There was no significant difference in mean oocytes diameter or mass between fish of the four sub-basins (Table 2).

Discussion

Important length and even more important body mass differences were observed between the four sub-basins, as already pointed out while studying age and growth patterns of these same populations (Duponchelle et al., 2012). After reaching sexual maturity, fishes in the Amazonas become progressively heavier than those from the Ucayali, Napo and Putumayo, in order of increasing difference. Beside inter-basin differences, silver Arowana from the Peruvian Amazon grow relatively heavier than fish from the Mamirauá Reserve in Brazil. An individual of 80 cm T_L (~ 75 cm S_L) weighs ~ 3000 g in the Mamirauá Reserve (Cavalcante, 2008), whereas it weighs in average 3161 g in the Putumayo, 3369 g in the Napo, 3552 g in the Ucayali and 3702 g in the Amazonas. The better body condition of Arowana in the Peruvian Amazon might result from better trophic conditions than in the Mamirauá Reserve, which would have to be tested.

Gonadal maturity scale

The description of the different maturity stages were consistent with Aragao' (1989) descriptions, for both females and males, although the number of stages was reduced to fit Nuñez and Duponchelle' (2009) scale. This illustrated gonadal maturity scale provides a clear reference for comparative works on the reproductive biology of this species.

Previous studies had suggested, from the observation of different sizes of oocytes in ripe gonads (but without providing evidence) that a same female could reproduce more than once during the breeding season (Ayala, 2001; Tang and Gomez, 2005). In the present study, the presence of small, vitellogenic oocytes in all stages of "spawning capable" ovaries and the size frequency distribution of oocyte in "spawning capable" ovaries provide strong evidence that a same individual female can reproduce more than once during the breeding season in the Peruvian Amazon.

This result, however, differs from other studies in the Brazilian Amazon, Aragao (1989) in Lake Janavaca and more recently Queiroz (2008) in the Mamirauá Reserve, who reported that this species probably spawns only once during the breeding season, but without providing demonstrating evidence.

Breeding season

In Central Amazonia, Brasil, where most published studies about the silver Arowana's breeding cycle were carried out, the species was reported to reproduce during the dry season and early rising waters (Goulding, 1980; Aragao, 1989; Queiroz, 2008; Cavalcante, 2008). This is consistent with the observations from the present study in the Amazonas and Ucayali sub-basins, or with previous observations in Peru, in the Pacaya Samiria Reserve (Tang and Gomez, 2005) and in the Ucayali River (Ayala, 2001). This pattern, however, does not seem to hold for all silver Arowana of the Peruvian Amazon, as the breeding season seemed restricted to the dry season in the Napo and Putumayo sub-basins. This shorter breeding season might be an adaptation to the much shorter flooding season in the Napo and Putumayo (Figure 5). Once females have spawned, males guard the eggs and then the fry in their mouth for five to seven weeks (Goulding, 1990; Argumedo, 2005; Queiroz, 2008), after which free swimming juveniles of over 6 cm are released from parental care and have to fend for themselves. It is well known that in Amazonian environments, the high water season with its extended floodplains and inundated vegetation, providing food and shelter from predators is particularly advantageous for the development and survival of fish's young stages (Lowe-McConnell, 1964, 1987; Goulding, 1980). In order for males to release their free-swimming young in time to make the most of these advantageous environmental conditions - which barely last three months in the Napo and Putumayo sub-basins (Figure 5) -, while allowing for the long incubation, the spawning period might have to be finished when the water starts to rise. Nevertheless, size frequency distribution of oocytes in ripe gonads (Figure 4c) and the presence of small vitellogenic oocytes in all stages of "spawning capable" ovaries support the idea that individual females may have time to produce a second brood during the spawning period, despite its shorter duration in the Putumayo. This suggests that the time needed for the small vitellogenic oocytes (Fig. 4a-b) to complete their growth is relatively short (a few weeks). These results also imply polyandry in the species: indeed, the short breeding season in the Putumayo and Napo and the long paternal mouthbrooding period do not allow for a same male to carry successively two broods of a same female. On the other hand, in the Amazonas and Ucayali sub-basins, where the high water season lasts nearly twice as much (December to May), females that spawn when the water has already started to rise may still ensure their progeny will find favourable environmental conditions long enough to survive, hence ensure reproductive success. This hypothesis could be tested by additional studies on these two specific sub-basins and others with similarly short high water seasons. As Arowana do not live in rivers, but instead in adjacent lakes and lagoons, testing this hypothesis would also require having water level data in specific lakes where Arowana concentrations are high.

Age and size at maturity

In the Mamirauá Reserve, the size at first sexual maturity was about 52 cm T_L (~ 49 cm S_L) for both sexes and was reached during the second year (Cavalcante, 2008).

These values were relatively similar to those observed in the Peruvian Amazon, where silver Arowana also reached maturity during their second year at sizes varying between 43-45 cm for males and between 46-50 cm for females. These values were relatively smaller than the ~ 60 cm T_L (~ 56 cm S_L) reported in the El Dorado lake in the Pacaya Samiria Reserve, Peru (Tang and Gomez, 2005). In a preliminary study in the Ucayali River, Peru, Ayala (2001) reported sizes at first maturity of 65.9 and 73.9 cm T_L (~ 62 and 69 cm S_L) for females and males, respectively. These obviously over-estimated values, however, were likely due to the fact that the author erroneously considered individuals in vitellogenesis (stage II of his gonadal maturation scale) as still immature. Cortegano et al. (2014) reported sizes at maturity of ~58 and 62 cm for females and males, respectively in lake Grande, close to Huapapa in the Putumayo. These large differences with our results from the Putumayo (47 and 43 cm for females and males, respectively) are particularly surprising, as about a third of our own sampling also came from lake Grande. Most of the observed differences might result from the interpretation of what is considered as "sexual maturity" in Cortegano et al.' study, which was not properly defined. It is likely, when looking at their logistic curves that reach 100% only close to the maximum observed sizes, that they considered as "sexually mature" female at the end of stage 2 rather than at the beginning of stage 2 (Fig. 3a). Likewise, for males, they likely considered males in late stage 2 or stage 3 rather than in stage 2 (Fig. 3b).

It is worth noting that while the other reproductive traits (breeding season and fecundity) largely varied between sub-basins, size at maturity was relatively conserved and that the slight differences observed were not significant. This is particularly surprising as size at maturity is a plastic trait that readily responds to environmental variation (Stearns and Crandall, 1984; Stearns and Koella, 1986;

Duponchelle and Panfili, 1998; Duponchelle et al., 2007) or fishing pressure (Olsen et al., 2004). This observation will have to be confirmed on other geographic populations.

It is important to keep in mind that the size at first sexual maturity (L_m) is the size at which 50% of the individuals have reached maturity during the breeding season, which means the other 50% have not. Considering the size at first sexual maturity as the legal minimum size at capture, as is customary in Amazonian fisheries regulations, we implicitly allow that half the fish be caught as immature, hence before they could reproduce (growth-overfishing). In order to ensure a healthy spawning stock, however, fisheries should ensure that all captured individuals have had a chance to reproduce at least once (Myers and Mertz, 1998; Froese, 2004). This goal can only be attained by fixing the minimum size at capture not at the size at which 50% of the individuals in a population are mature (L_m), but at the size at which 100% are mature. The size at which 100% of the fish are mature, considering all four sub-basins of the Peruvian Amazon, was slightly below 60 cm S_L (Fig. 6). Therefore, considering the approximately 5 cm difference between total and standard lengths, we recommend that the minimum size at capture should be fixed at 60 cm T_L in the Peruvian Amazon.

Fecundity

The silver Arowana reputedly produces very few eggs for its size (Goulding, 1980; Aragao, 1989; Queiroz, 2008). Fecundity variations between geographical samples, however, have never been reported so far. In the present study, important differences in batch fecundity were observed between the silver Arowana of the four sub-basins.

The Putumayo population significantly differed from the other three populations, which in turn did not differed between each other's. The absence of significant difference between the Amazonas, Napo and Ucayali populations, however, was likely due to the low number of gonads analysed and to the large variance observed in the Ucayali population (Fig. 7). Such a large variance could result from the mixing of individuals from distinct populations within the Ucayali sub-basin. Indeed, fish were sampled from fishermen operating in large portions of the Ucayali basin and which could hold populations with distinct reproductive characteristics. This indicates that further studies on this species will need to be carried out with on-site sampling rather than market sampling. Nevertheless, as an illustration of the important fecundity variation between fish of the four sub-basins, despite the absence of statistical significance, the batch fecundity at two representative female body masses (1500 and 3500 g) was calculated for each sub-basin from the regressions among batch fecundity and body mass (Table 1). The differences of batch fecundity between populations ranged from 33 to 104 % for females weighing 1500 and 3500 g, respectively. Given the energetic cost of gamete production, food is considered one of the most important environmental factors involved in the regulation of fecundity (Wooton, 1979; Wooton, 1998). One would thus expect the fish with the better body condition (in decreasing order those of the Amazonas, then Ucayali, Napo and Putumayo, see Fig. 2b), which usually reflects better trophic conditions, to also display the highest relative fecundity. Yet, relative fecundity was inversely proportional to body condition (Table 2), suggesting contrasted energy allocation (towards body growth *vs* reproduction) strategies between fish of the four sub-basins. Additionally, these large variations in fecundity were not compensated by variations of oocyte size or mass, suggesting differences in reproductive effort between fish of the four the sub-basins. These hypotheses, however, will need to be further validated with an increased number of ripe gonads analysed in the Amazonas, Napo and Ucayali sub-basins.

As a comparison, in the Mamirauá Reserve females of 65 cm T_L (~ 61 cm S_L and 1500 g) and 75 cm T_L (~ 70 cm S_L and 2500 g) produce ~ 200 and 230 oocytes, respectively (Queiroz, 2008, using the length-mass relationship provided in Cavalcante, 2008). This would be approximately twice as much as the fecundity of a 1500 g female in the Peruvian Amazon and in the range of the Putumayo fecundity for a 2500 g female (Table 1), suggesting a higher relative fecundity in small females progressively decreasing with length in the Mamirauá Reserve. Again, fish from the Mamirauá, which have lower body condition than fish from the Peruvian Amazon, also have higher relative fecundity, contrary to expectations. A surprising information comes from the mean diameter (9.75 mm) and mass (1.8 g) of oocytes in the Mamirauá Reserve, which are 25% smaller but a 100% heavier than the largest and heaviest oocytes in the Peruvian Amazon (12.2 mm and 0.98 g in the Putumayo), resulting in a density over 3.5 g/cm^3, (*vs* 1.03 g/cm^3 in the Putumayo), which appears much too dense for an egg.

In the Pacaya-Samiria Reserve, Peru, Tang and Gomez (2005) observed that females of 1500 and 2500 g would produce in average 215 and 266 oocytes, respectively, which is above the mean values observed in the present study. A recent study in lake Grande on the Putumayo River, reported batch fecundities ranging from 115 oocytes for a female weighing 1100 g to ~240 oocytes for a female of ~3000 g (Cartegano et al., 2014), within the range of the values observed for the Putumayo in the present study.

The only other available information about the silver Arowana's fecundity comes from Aragao (1989) in the Solimões River basin (lake Janauacá), but the range of female body masses he worked with (551 – 1750 g, with only 2 females above 1500 g) barely overlap with ours, hampering a direct comparison. Nevertheless, a 1500 g female would produce approximately 182 oocytes, which is also above the mean values observed in the present study.

Conclusions

The important variability observed in reproductive characteristics and body condition of the silver Arowana from the four sub-basins is consistent with the important growth variations previously reported in these same localities (Duponchelle et al., 2012). This variability might result either from the phenotypic plasticity of the species due to environmental heterogeneity between the sub-basins or from the existence of several distinct genetic populations within Peru, that may need to be further characterized and managed independently. The important differences in breeding season, condition, growth and fecundity, however, strongly suggest that fish from the different sub-basins are distinct populations. The different breeding season and sedentary nature of the species should result in reduced gene flow between sub-basins, hence inducing genetic structuring. Although microsatellites markers are available for the silver Arowana (Silva et al., 2009), they have only been used to test for multiple paternity in the species (Verba et al., 2014) and no population genetic study has been carried out so far. Yet, as previously pointed out (Duponchelle et al., 2012), the growing concerns about *O. bicirrhosum* conservation (Moreau and Coomes, 2006, 2007) emphasize the need for comparative life history and genetics studies at the inter- and intra-basin levels (with sampling carried out on-site) in order to understand the population structuring of this species and to define appropriate management strategies.

Acknowledgements

Financial support was provided by INCAGRO (Subproyecto "Bases para el manejo sostenible y el cultivo de la arowana *Osteoglossum bicirrhosum* en la amazonía peruana", presentado al Concurso Público Nacional Nº 03– 2007 – PIEA – INCAGRO) and IRD. Special thanks go to the Proyecto Especial Desarrollo Integral de la Cuenca del Río Putumayo (PEDICP), particularly to Luis Alberto Moya Ibanez, for ensuring the sampling in the Putumayo. We would also like to thank Etienne Baras for discussions on some aspect on the manuscript and Jérémie Subrini for producing the size frequency distribution of oocytes.

References

Alcántara, B. F.; Chu-Koo, F.; Chávez, V. C. A.; Tello, S.; Bances, C. K. C.; Torrejón, M. M.; Gómez, N. J. L. ; Noriega, M. J., 2007: Notas sobre la pesquería ornamental de la arahuana *Osteoglossum bicirrhosum* (Osteoglossidae) en Loreto, Perú y posibilidades de su cultivo. Folia Amaz. **16**, 55-61.

Aragao, L. P., 1989: Contribuição ao estudo da biologia do Aruanã, *Osteoglossum bicirrhosum* Vandelli, 1829, no Lago Janauacá - Estado do Amazonas, Brasil. III-Reprodução e relações biometricas. Cienc. Agronom. **20**, 59-72.

Argumedo, T. E. G., 2005: Arawanas: manual para la cria comercial en cautiverio. ACUICA, Fondo para la Accion Ambiental, Florencia, Colombia.

Ayala, I., 2001: Ecologia reproductiva de Ostoglossum bicirrhossum Vandelli, 1829 "arahuana" en la cuenca del rio Ucayali, Ciencias en Conservacion de Recursos Forestales. MSc. Thesis, Universidad Nacional Agraria La Molina, Lima.

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

Bayley, P. B. ; Petrere , M., 1989: Amazon Fisheries: Assessment methods, current status and management options. in: Proceedings of the International Large River Symposium. D. P. Dodge (Ed.). Canadian Special Publication of Fisheries and Aquatic Sciences, pp. 385-398.

Brown-Peterson, N. J.; Wyanski, D. M.; Saborido-Rey, F.; Macewicz, B. J. ; Lowerre-Barbieri, S. K., 2011: A standardized terminology for describing reproductive development in fishes. Mar. Coast. Fish. **3**, 52-70.

Lima, A. C. ; Prang, G., 2008: Demandas para o manejo e conservação do Aruanã branco, *Osteoglossum bicirrhosum* (Cuvier, 1829), na região do Medio Solimões. in: Biologia, Conservação e Manejo dos Aruanãs na Amazônia Brasileira. H. L. Queiroz, M. Camargo (Eds.). Instituto de Desemvolvimento Sustentavel de Mamirauá, Téfé, Brasil, pp. 15-26.

Cavalcante, D., 2008: Crescimento e maturação sexual de Aruanãs brancos (*Ostoglossum bicirrhosum*) em Mamirauá. in: Biologia, Conservação e Manejo dos Aruanãs na Amazônia Brasileira. H. L. Queiroz, M. Camargo (Eds.). Instituto de Desemvolvimento Sustentavel de Mamirauá, Téfé, Brasil, pp. 105-117.

Cortegano, C. A. A.; Pinedo, L. A. M.; Ibanez, L. A. M.; Vásquez, M. R. ; Ruiz, P. S., 2014: Productivity and reproductive characteristics of silver arowana *Osteoglossum bicirrhosum* (Osteoglossiformes: Osteoglossidae) at Grande lake, Putumayo basin, Peru. Biota Amaz. 4, 21-26.

Silva, T. J.; Hrbek, T. ; Farias, I. P., 2009: Microsatellite markers for the silver arowana (*Osteoglossum bicirrhosum*, Osteoglossidae, Osteoglossiformes). Mol. Ecol. Resour. **9**, 1019-1022.

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. Environ. Biol. Fish. **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. J. Fish Biol. **71**, 1113-1134.

Duponchelle, F.; Ruiz Arce, A.; Waty, A.; Panfili, J.; Renno, J.-F.; Farfan, F.; Garcia-Vasquez, A.; Chu-Koo, F.; Garcia-Davila, C.; Vargas, G.; Ortiz, A.; Pinedo, R. ; Nuñez, J., 2012: Contrasted hydrological systems of the Peruvian Amazon induce differences in growth patterns of the silver arowana, Osteoglossum bicirrhosum. Aquat. Living Resour. **25**, 55-66.

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

Garcia-Vasquez, A.; Tello, S.; Vargas, G. ; Duponchelle, F., 2009: Patterns of commercial fish landings in the Loreto region (Peruvian Amazon) between 1984 and 2006. Fish Physiol. Biochem. **35**, 53-67.

Goulding, M., 1980: The fishes and the forest. Explorations in Amazonian natural history. University of California Press, Berkeley.

Goulding, M., 1990: Amazon: The Flooded Forest. Sterling Publishing,, New York, USA.

Legendre, M. ; Ecoutin, J-M., 1989: Suitability of brackish water tilapia species from the Ivory Coast for lagoon aquaculture 1 - Reproduction. Aquat. Living Resour. **2**, 71-

79.

Lowe-McConnell, R. H., 1964: The fishes of the Rupununi savanna district of Bristish Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. J. Linn. Soc. (Zool.). **45**, 103-144.

Lowe-McConnell, R. H., 1987: Ecological studies in tropical fish communities. Cambridge University Press, Cambridge.

Mojica, J. I.; Castellanos, C.; Usma, J. S. ; Álvarez, R., 2002: Libro rojo de peces dulceacuícolas de Colombia. Instituto de Ciências Naturales - Universidad Nacional de Colômbia y Ministério del Médio Ambiente, Bogotá, Colômbia.

Moreau, M.-A. ; Coomes, O. T., 2006: Potential threat of the international aquarium fish trade to silver arawana *Osteoglossum bicirrhosum* in the Peruvian Amazon. Oryx. **40**, 152-160.

Moreau, M.-A. ; Coomes, O. T., 2007: Aquarium fish exploitation in western Amazonia: conservation issues in Peru. Environ. Conserv. **34**, 12-22.

Myers, R. A. ; Mertz, G., 1998: The Limits of Exploitation: A Precautionary Approach. Ecol. Appl. **8**, S165-S169.

Nuñez, J. ; Duponchelle, F., 2009: Towards a universal scale to assess sexual maturation and related life history traits in oviparous teleost fishes. Fish Physiol. Biochem. **35**, 167-180.

Olsen, E. M.; Heino, M.; Lilly, G. R.; Joanne Morgan, M.; Brattey, J.; Ernande, B.; Dieckmann, U., 2004: Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature. **428**, 932-935.

Prang, G., 2008: An industry analysis of the freshwater ornamental fishery with particular reference to the supply of Brazilian freshwater ornamentals to the UK market. Uakari. **3**, 7-51.

Queiroz, H. L., 2008: Investimento parental e reprodução do Aruanã branco, *Osteoglossum bicirrhosum*, na Reserva Mamirauá. in: Biologia, Conservação e Manejo dos Aruanãs na Amazônia Brasileira. H. L. Queiroz, M. Camargo (Eds.).Instituto de Desemvolvimento Sustentavel de Mamirauá, Téfé, Brasil, pp. 119-132.

Reis, R. E.; Kullander, S. O. ; Ferraris, C. J., 2003: Checklist of freshwater fishes of South and Central America. Edipucrs, Porto Alegre.

Saint-Paul, U.; Zuanon, J.; Villacorta Correa, M.A.; Garcia, M.; Noemi Fabre, N.; Berger, U. ; Junk, W.J., 2000: Fish communities in central white- and blackwater floodplains. Environ. Biol. Fish. **57**, 235-250.

Stearns, S. C.; Crandall, R. E., 1984: Plasticity for age and size at sexual maturity: a life history response to unavoidable stress. in: Fish Reproduction : strategies and tactics. G. W. Potts, R. J. Wootton (Eds.). Academic press, London, pp. 13-33.

Stearns, S. C.; Koella, J. C., 1986: The evolution of phenotypic plasticity in life history traits: predictions of reaction norms for age and size at maturity. Evolution **40**, 893-913.

Stewart, D. J., 2013b: A new species of *Arapaima* (Osteoglossomorpha, Osteoglossidae) from the Solimões River, Amazonas State, Brazil. Copeia **3**, 470-476.

Stewart, D. J., 2013a: Re-description of *Arapaima agassizii* (Valenciennes), a rare fish from Brazil (Osteoglossomorpha, Osteoglossidae). Copeia **1**, 38–51.

Tang , M. ; Gomez Noriega, J. L., 2005: Biologia y aprovechamiento del Arahuana, *Osteoglossum bicirrhosum* en la micro cuenca de lacocha El Dorado, Reserva Nacional Pacaya Samiria, Facuiltad de Ciencias Biologiacas. Universidad Nacional de la Amazonia Peruana, Iquitos.

Tello, M. S. ; Cánepa, J. R. L. S., 1991: Estado actual de la explotación de los principales peces ornamentales de la Amazonía Peruana. Folia Amaz. - IIAP. **3**, 109-128.

Verba, J. T.; Rabello Neto, J. G.; Zuanon, J. ; Farias, I. P., 2014: Evidence of multiple paternity and cooperative parental care in the so called monogamous silver arowana *Osteoglossum bicirrhosum* (Osteoglossiformes: Osteoglossidae). Neotrop. Ichtyol. **12**, 145-151.

Wootton, R. J., 1979: Energy cost of egg production and environmental determinants of fecundity in teleost fishes. Symp. Zool. Soc. Lond. 44, 133-159.

Wootton, R. J., 1998: The ecology of teleost fishes, Second Edition. Kluwer Academic Publisher, Dordrecht, The Netherlands.

Author’s address: Institut de Recherche pour le Développement (IRD), Unité Mixte de Recherche Biologie des Organismes et Ecosystèmes Aquatiques (UMR BOREA - MNHN, CNRS-7208, UPMC, UCBN, IRD-207), F-34394, Montpellier, France.

E-mail: fabrice.duponchelle@ird.fr, tel: (33) 04 67 63 64 28

Figure legends

Fig. 1. Map of the collection sites of *Osteoglossum bicirrhosum* in the Peruvian Amazon (black circles). A total of 711 specimens were collected between November 2006 and April 2009 at the Iquitos and Requena markets for the Amazonas, Ucayali and Napo sub-basins. For the Putumayo, 240 fish were bought between March 2008 and April 2009 from local fishermen at El Estrecho and Huapapa communities.

Fig. 2. Relationships between standard length (SL) and total body mass (M) of *Osteoglossum bicirrhosum* caught in four sub-basins of the Peruvian Amazon

between 2006 and 2009 (a). Modelled regressions (M as a function of SL) between 60 and 90 cm SL, to illustrate inter-basin differences (b).

Fig. 3. Macroscopic gonadal maturity scale for females (a) and males (b) *Osteoglossum bicirrhosum*, following Nuñez and Duponchelle (2009). Equivalence with Brown-Petersen et al. (2011)'s terminology is provided.

Fig. 4. Small vitellogenic oocytes (svo) in "spawning capable" ovaries of female *Osteoglossum bicirrhosum*: (a) in between large vitellogenic oocytes (lvo) in a ripe - stage 4 - gonad and (b) in a post-spawning gonad reinitiating another vitellogenic cycle – stage 5-2.

Fig. 5. Size frequency distribution of oocytes in a "spawning capable" ovary of *Osteoglossum bicirrhosum* from the Putumayo River showing two clearly separated modes of vitellogenic oocytes.

Fig. 6. Proportions of breeding *Osteoglossum bicirrhosum* females in relation to the mean water level in four sub-basins of the Peruvian Amazon.

Fig. 7. Age (Am) and size (Lm) at first sexual maturity of both males (black circles and solid lines) and females (white triangles and dashed lines) *Osteoglossum bicirrhosum* in four sub-basins of the Peruvian Amazon.

Fig. 8. Linear regressions between batch fecundity and total female body mass of *Osteoglossum bicirrhosum* in the Amazonas ($N = 5$, $F = 0.0307*M + 60.922$, $R^2 =$

0.875, $P<0.001$), Napo ($N = 3$, $F = 0.0578*M + 18.547$, $R^2 = 0.907$, $P<0.001$), Ucayali ($N = 6$, $F = 0.0708*M – 9.1942$, $R^2 = 0.537$, $P<0.001$) and Putumayo ($N=28$, $F = 0.1055*M – 29.253$, $R^2 = 0.714$, $P<0.001$) rivers, Peruvian Amazon.

Table 1. Comparison of *Osteoglossum bicirrhosum*'s batch fecundity at a given female body mass in four sub-basins of the Peruvian Amazon (calculated from the regressions between batch fecundity and total body mass presented in Figure 8).

Table 2. Mean relative fecundity (oocytes per kg total body mass), oocytes diameter (mm) and oocytes mass (g) ± SD of *Osteoglossum bicirrhosum* in four sub-basins of the Peruvian Amazon.

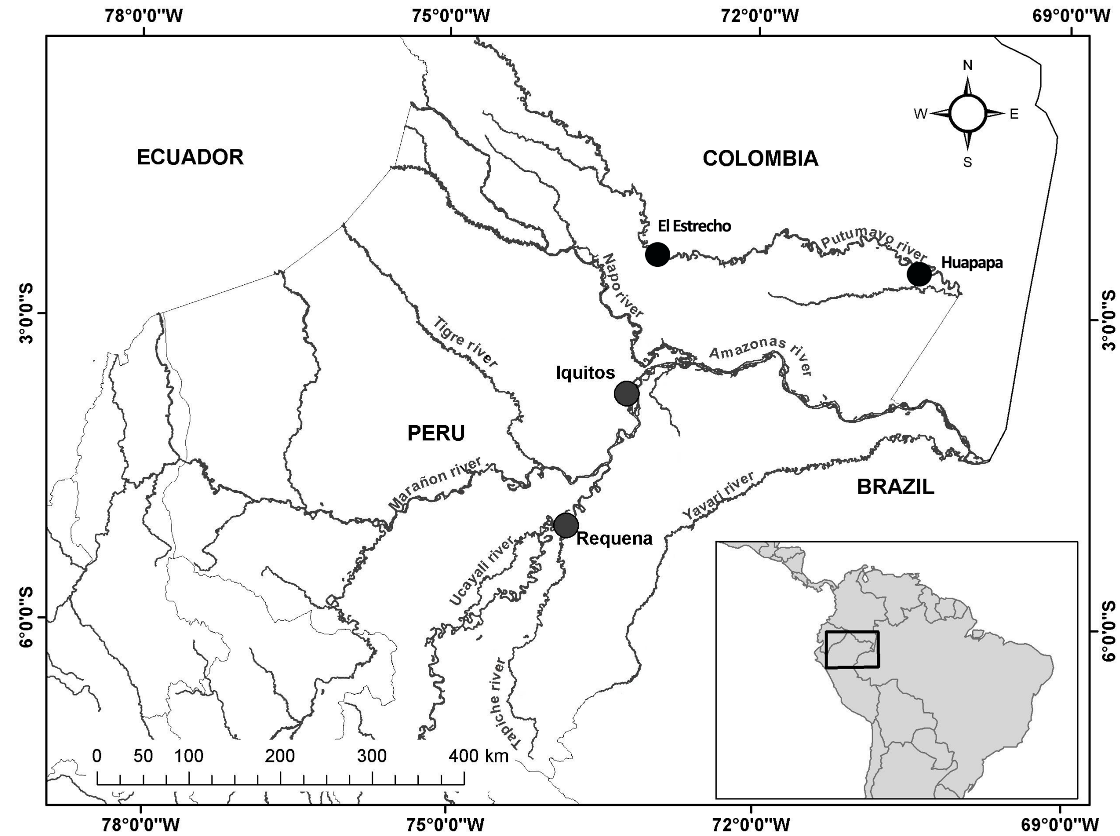

78°0'0"W
75°0'0"W
72°0'0"W
69°0'0"W
3°0'0"S
6°0'0"S
N
W
E
S
ECUADOR
COLOMBIA
El Estrecho
Putumayo river
Huapapa
Napo river
Tigre river
Amazonas river
Iquitos
PERU
Marañon river
BRAZIL
Yavari river
Requena
Ucayali river
Tapiche river
0
50
100
200
300
400 km

Fig. 1

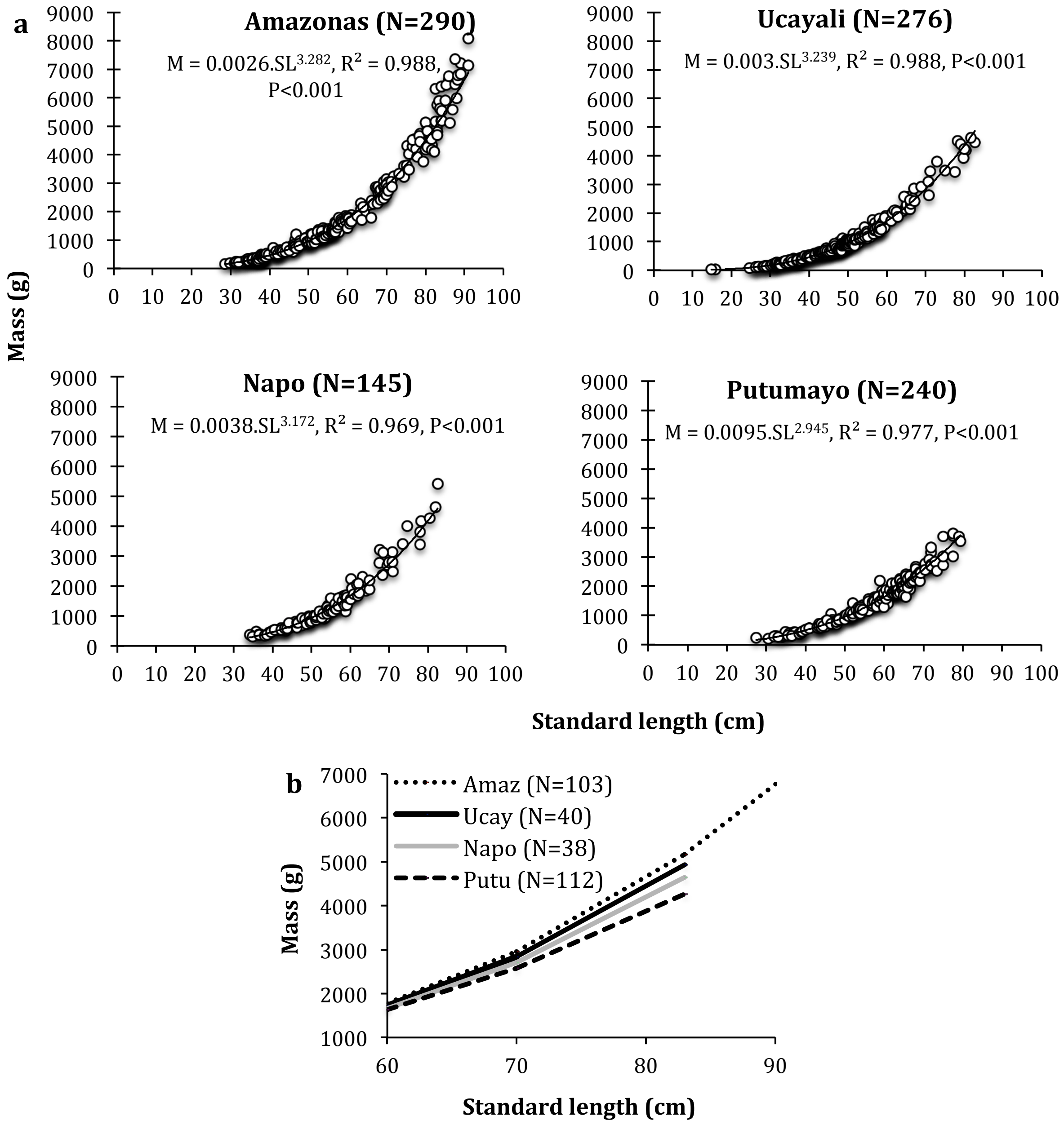
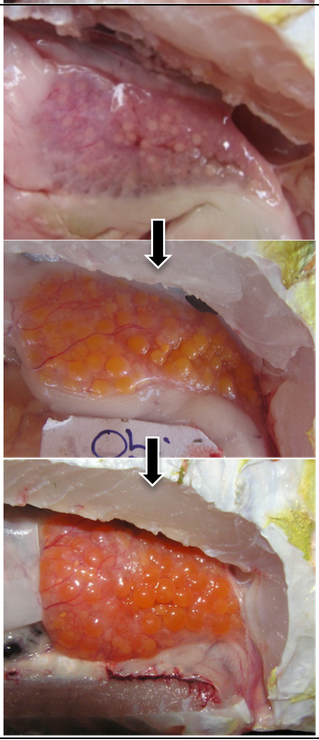
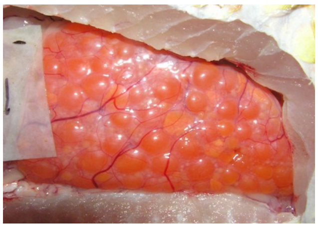
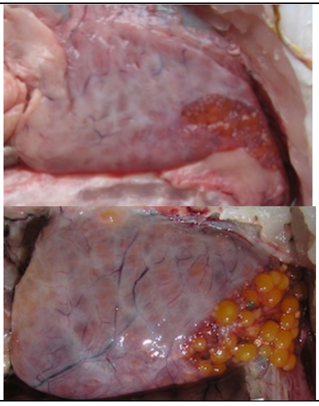

a
Amazonas (N=290)
M = 0.0026.SL$^{3.282}$, R^2 = 0.988, P<0.001
Ucayali (N=276)
M = 0.003.SL$^{3.239}$, R^2 = 0.988, P<0.001
Napo (N=145)
M = 0.0038.SL$^{3.172}$, R^2 = 0.969, P<0.001
Putumayo (N=240)
M = 0.0095.SL$^{2.945}$, R^2 = 0.977, P<0.001
Mass (g)
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
0 10 20 30 40 50 60 70 80 90 100
Standard length (cm)
b
Amaz (N=103)
Ucay (N=40)
Napo (N=38)
Putu (N=112)
Mass (g)
1000
2000
3000
4000
5000
6000
7000
60 70 80 90
Standard length (cm)

Fig. 2

Description	**Illustration (females)**	**with Brown-Petersen et al. (2011)'s terminology**
Stage 1: immature individuals Ovaries small and firm, opaque and whitish or slightly pinkish. No oocyte can be seen to the naked eye. A typical longitudinal canyon-type depression is clearly visible at the surface of the ovary.		Immature
Stage 2: maturing individuals Ovaries are larger with more important vascularisation and clearly visible oocytes. Oocytes are whitish and sparse at the beginning of stage 2, and the canyon-like depression is still visible. Progressively, the oocytes turn yellow and the canyon disappears. At the end of stage 2, the oocytes are orange and fill the ovary, but are not of a homogeneous size: all intermediaries between small whitish oocytes and large orange ones are visible. This last point is a clear distinction with stage 3.		Developing
Stage 3: individuals in final maturation The ovary now occupies about ¾ of the abdominal cavity. Most oocytes are large, circular, orange, and homogeneous in size. Small oocytes are still visible in between the larger ones, but there is now a very clear size difference between the large and small ones.		Spawning capable
Stage 4: individuals ready to spawn / ripe The ovary occupies almost the whole abdominal cavity and appears even fuller. The ovary's membrane is very thin and transparent. A slight pressure on the abdomen can expulse the ovules, that are now free (out of their follicules) in the ovary.		
Stage 5-2: recently spawned individuals initiating another cycle The appearance is close to that of a stage 2 gonad, but the ovary is still relatively flaccid, larger and more vascularised. Developing oocytes of all colours are filling the ovary and some remaining large atretic oocytes can sometimes be observed. This stage is characteristic of females that have just spawn and that are initiating a new reproductive cycle.		

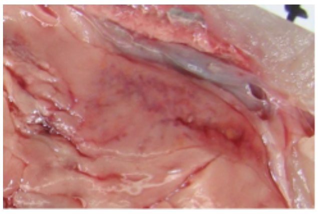
Stage 5: individuals that have just spawned The ovary is of similar size to a stage 4 ovary, but with an empty, flaccid appearance and well developed vascularisation. Some un-spawned, large oocytes can still be seen together with others already in re-absorption process (atresia) and early vitellogenic ones.		Regressing
Stage 5-1: resting individuals The ovary looks like a stage 1 ovary (with no visible oocyte), but is larger, with a thicker membrane, a more important vascularisation and a generally redder colour than a stage 1. This stage is characteristic of adult females resting in between two breeding seasons.		Regenerating

Fig. 3a.

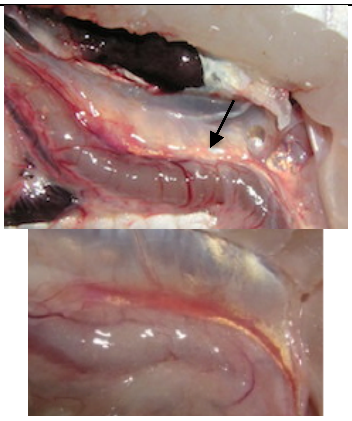
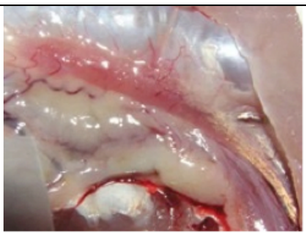
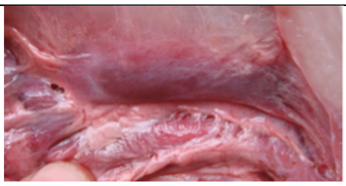
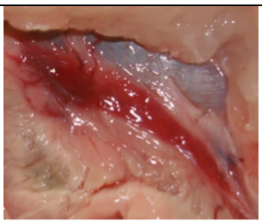
Description	**Illustration (males)**	**Equivalence with Brown-Petersen et al. (2011)'s terminology**
Stage 1: immature individuals: The testis is a pinkish, translucent curved tube, thinner and longer than stage 1 ovary. It is often bordered by a golden colour towards the genital pore.		Immature
Stage 2: maturing or resting individuals: Testis wider, thicker, of a more opaque pinkish to reddish colour. The golden colour towards the genital pore is often still visible. Resting adults are usually at this stage.		Developing / Regenerating
Stage 3: ripe individuals: Testis even larger, wider and really thick, with dark red opaque appearance. The golden colour is usually not visible at this stage.		Spawning capable
Stage 4: individuals after ejaculation: Testis of a similar size to stage 3, but with a flaccid, more translucent appearance.		Regressing

Fig. 3b.

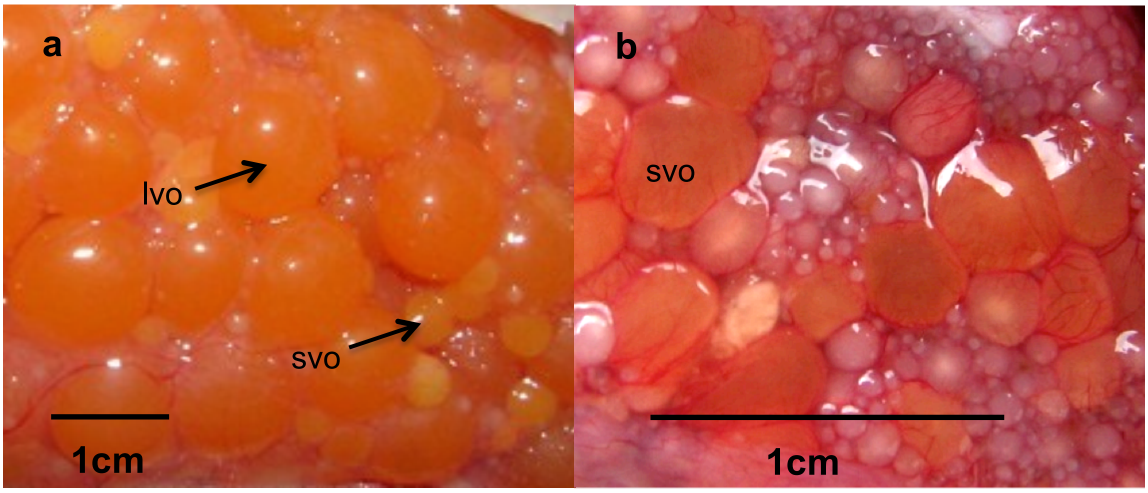


Fig. 4

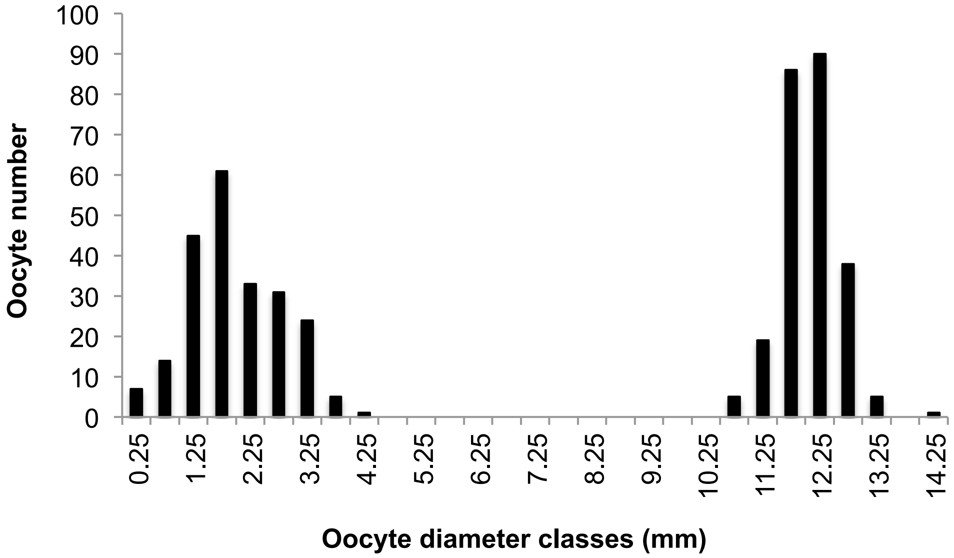
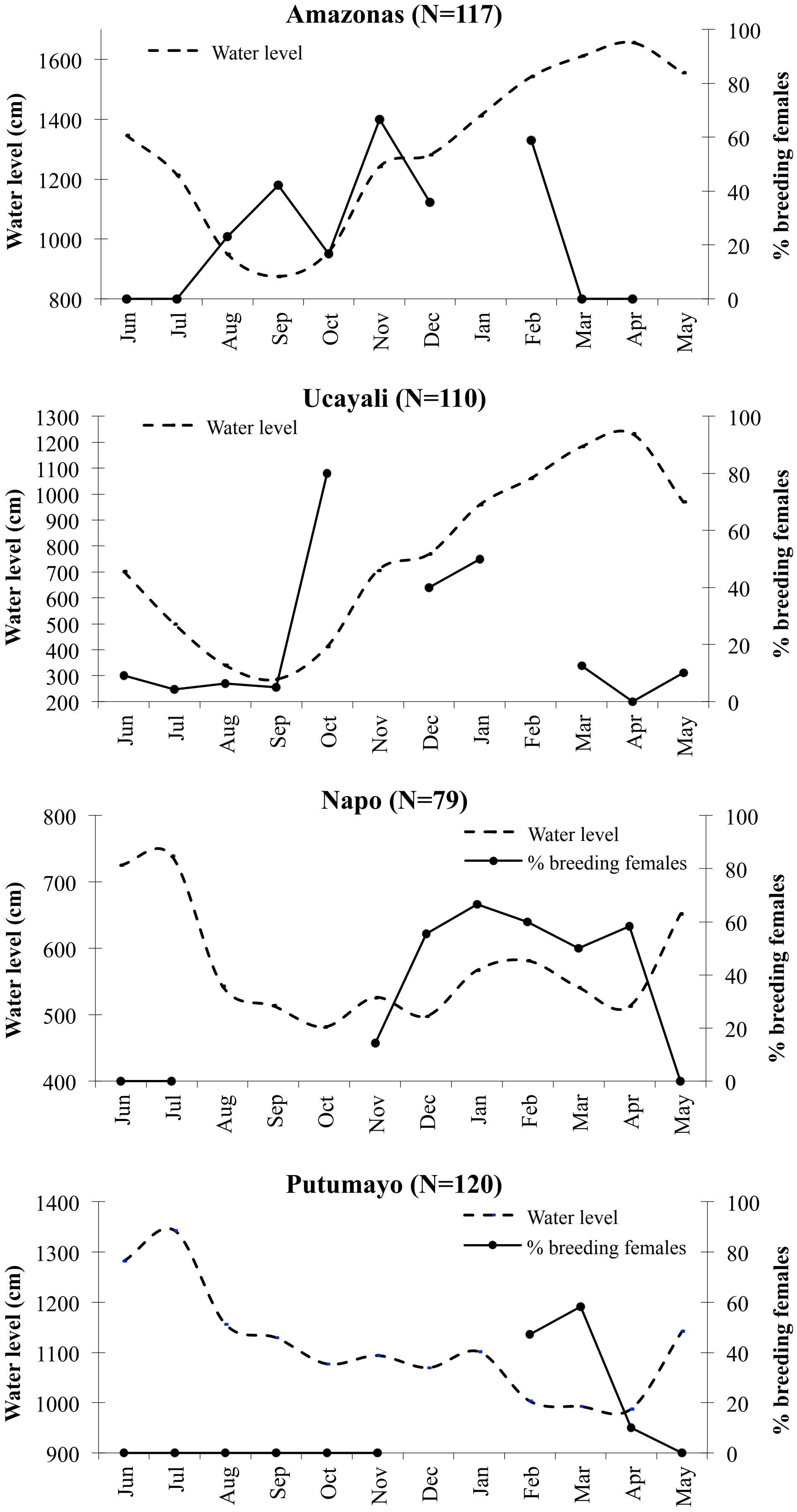

Oocyte number
100
90
80
70
60
50
40
30
20
10
0
0.25
1.25
2.25
3.25
4.25
5.25
6.25
7.25
8.25
9.25
10.25
11.25
12.25
13.25
14.25
Oocyte diameter classes (mm)

Fig. 5



Amazonas (N=117)
Water level
Water level (cm)
% breeding females
800
1000
1200
1400
1600
0
20
40
60
80
100
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Ucayali (N=110)
Water level
Water level (cm)
% breeding females
200
300
400
500
600
700
800
900
1000
1100
1200
1300
0
20
40
60
80
100
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Napo (N=79)
Water level
% breeding females
Water level (cm)
% breeding females
400
500
600
700
800
0
20
40
60
80
100
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Putumayo (N=120)
Water level
% breeding females
Water level (cm)
% breeding females
900
1000
1100
1200
1300
1400
0
20
40
60
80
100
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May

Fig. 6

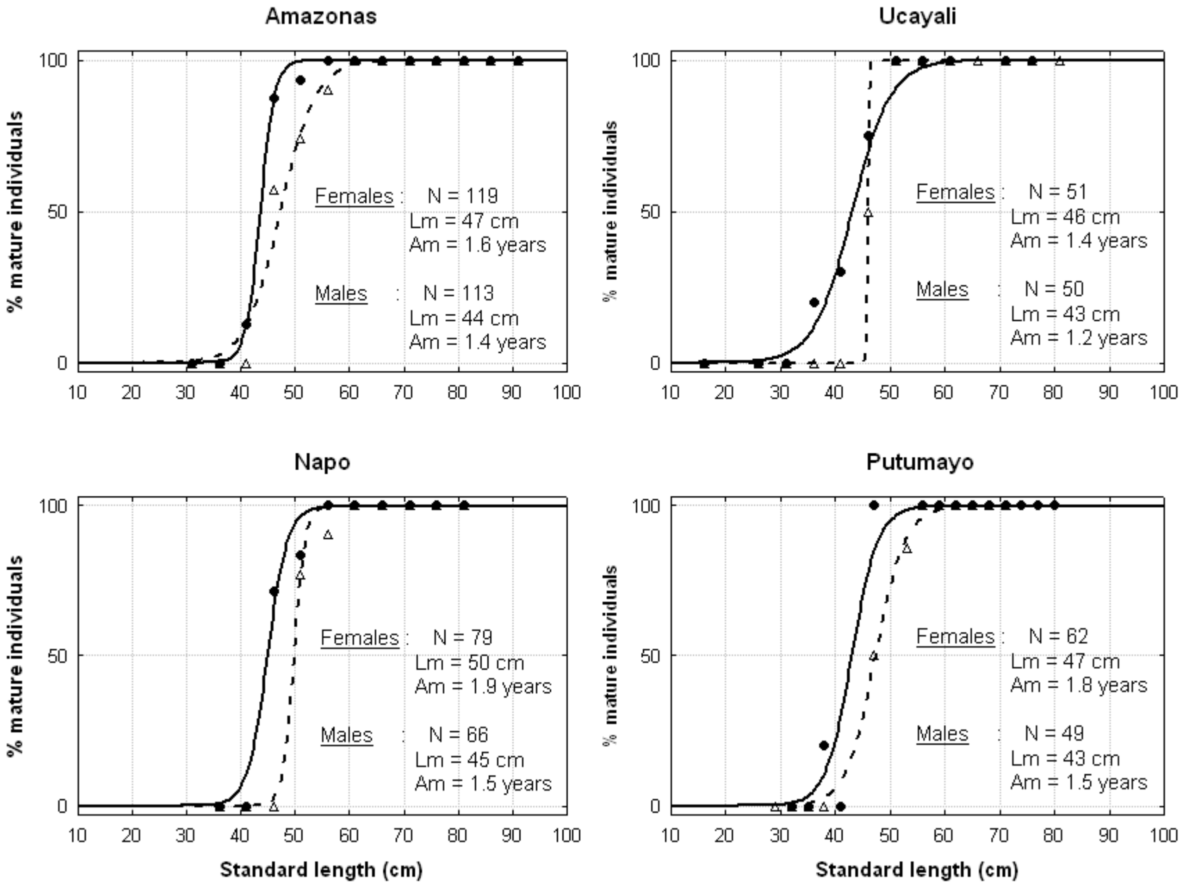

Amazonas
Ucayali
Napo
Putumayo
% mature individuals
Standard length (cm)
0
50
100
10
20
30
40
50
60
70
80
90
100
Females : N = 119
Lm = 47 cm
Am = 1.6 years
Males : N = 113
Lm = 44 cm
Am = 1.4 years
Females : N = 51
Lm = 46 cm
Am = 1.4 years
Males : N = 50
Lm = 43 cm
Am = 1.2 years
Females : N = 79
Lm = 50 cm
Am = 1.9 years
Males : N = 66
Lm = 45 cm
Am = 1.5 years
Females : N = 62
Lm = 47 cm
Am = 1.8 years
Males : N = 49
Lm = 43 cm
Am = 1.5 years

Fig. 7

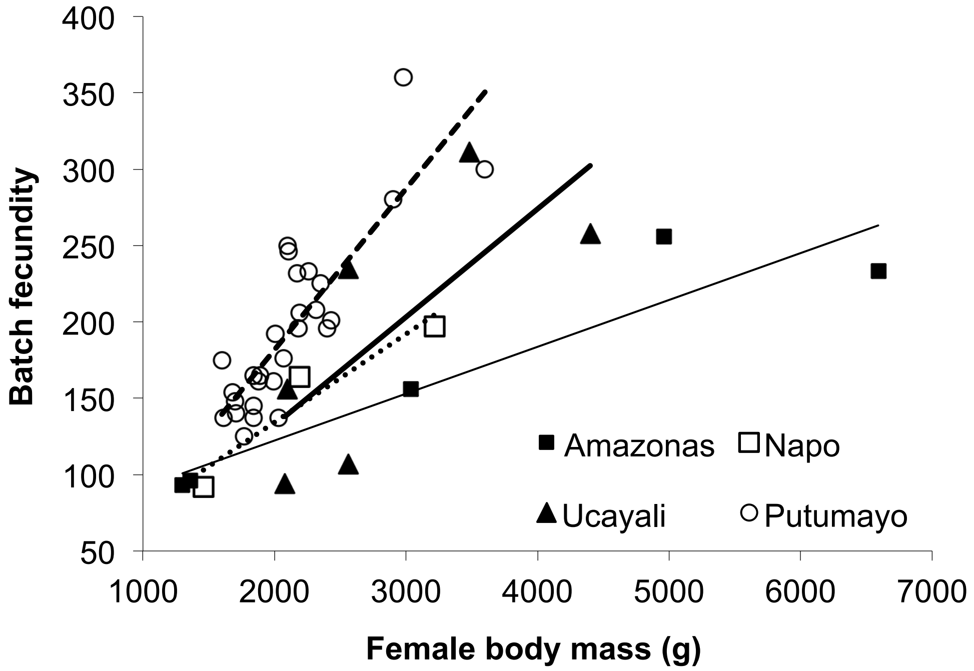

400
350
300
250
200
150
100
50
Batch fecundity
1000
2000
3000
4000
5000
6000
7000
Female body mass (g)
■ Amazonas
□ Napo
▲ Ucayali
○ Putumayo

Fig. 8

Table 1.

Female body mass (g)	**Batch fecundity**			
	Amazonas	Napo	Ucayali	Putumayo
1500	107	105	97	129
2500	138	163	168	234
3500	168	221	239	340

Table 2.

	Amazonas (N=5)	Napo (N=3)	Ucayali (N=6)	Putumayo (N=28)
Relative fecundity	56 ± 15	66 ± 7	67 ± 22	91 ± 14
Oocyte diameter	10.8 ± 0.29	10.6 ± 0.36	11.8 ± 1.46	12.2 ± 0.95
Oocyte mass	0.67 ± 0.05	0.64 ± 0.01	0.77 ± 0.17	0.89 ± 0.24