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

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34 second year, at sizes varying between 43-45cm for males and 46-50 cm for females.  
35 Important variations in fecundity were observed between fish of the four sub-basins,  
36 whereas mean oocytes diameter and mass did not vary significantly, suggesting  
37 differences in reproductive investment. Together with previously reported variations  
38 of growth patterns in the same sub-basins, these results suggest the existence of  
39 distinct populations in the Peruvian Amazon, with important consequences for  
40 management and conservation, but also for future aquaculture development  
41 programs.

42

### 43 **Introduction**

44

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

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

67 The reproductive biology of the silver Arowana is relatively well described since the  
68 early studies of Goulding (1980, 1990) and Aragao (1989). Recently, patterns of  
69 reproductive investment were further investigated in the Mamirauá Reserve  
70 (Queiroz, 2008) and the potential role of male aggregations was explored (Verba et  
71 al., 2014). In Peru, its reproductive characteristics were studied in one lake of the  
72 Putumayo River (Cortegano et al., 2014) and further information also exists from  
73 unpublished dissertations (Ayala, 2001; Tang and Gomez, 2005). Despite extensive  
74 ornamental fisheries in almost all the distribution area of the species and growing  
75 concern about its conservation, however, no assessment of the geographic variability  
76 of reproductive traits has yet been attempted. Besides the obvious interest for  
77 conservation and fisheries management, the knowledge of whether geographic  
78 population may display significant variations in specific reproductive traits such as  
79 the timing of maturation and egg production would be determinant for future  
80 aquaculture development. Indeed, the production of Arowana juveniles in controlled  
81 conditions (aquaculture) appears to be the most immediate alternative to extraction  
82 of natural populations for ornamental purposes (Argumedo, 2005; Moreau and  
83 Coomes, 2006). Choosing breeders from a population with higher relative fecundity

84 (egg production per unit body mass), for example, might increase chances of success.  
85 A recent study in the Peruvian Amazon demonstrated important variations in the  
86 growth patterns of the silver Arowana in four sub-basins, suggesting the existence of  
87 distinct populations, which might require independent management (Duponchelle et  
88 al., 2012). The aim of the present study is to assess whether reproductive  
89 characteristics also vary, and to which extent, between these four sub-basins of the  
90 Peruvian Amazon.

91

## 92 **Material and Methods**

93

### 94 **Fish collection**

95

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

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

114

### 115 **Biological sample analysis**

116

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

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

132 The average size at first sexual maturity ( $L_m$ ) is defined as the standard length  
133 at which 50% of the individuals are at an advanced stage of the first sexual cycle

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

$$140 \quad \%M = \frac{100}{1 + e^{(-a \times (L - L_m))}} \quad (1)$$

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

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

$$145 \quad A_m = (-\ln(1 - (L_m/L_\infty)) / K) + t_0 \quad (2)$$

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

149 Batch fecundity (number of eggs to be potentially laid per spawning event,  
150 resulting from the maturation of fully developed intra-follicular oocytes) and oocyte  
151 diameter were estimated by image analysis (using NIH Image J software) from  
152 whole gonads in final maturation stage (stage 3). As the oocytes were not exactly  
153 circular in shape, the mean arithmetic diameter was used:  $\sqrt{d \cdot D}$ , where d is the  
154 minimum diameter and D the maximum diameter of each oocyte. Oocyte mean mass  
155 was calculated from each stage 3 gonads, by weighing 30 oocytes to the nearest  
156 0.001 g.

157

158 **Statistical analyses**

159

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

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

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

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

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

177

## 178 **Results**

179

180 A total of 290 specimens of *O. bicirrhosum* were analysed for the Amazonas, 276 for  
181 the Ucayali, 145 for the Napo and 240 for the Putumayo (Figure 2a). Mean standard  
182 lengths ( $S_L$ ) and masses did not differ among sexes in any population. There were,  
183 however, significant differences in mean length (Kruskal-Wallis One Way ANOVA

184 on Ranks,  $H = 83.4$ ,  $P < 0.001$ ) and mass ( $H = 79.3$ ,  $P < 0.001$ ) between populations  
185 when females and males were pooled: the Ucayali population differed from all the  
186 others in both mean length ( $Q = 8.6$ ,  $P < 0.05$  with the Putumayo,  $Q = 6.7$ ,  $P < 0.05$   
187 with the Amazonas and  $Q = 4.8$ ,  $P < 0.05$  with the Napo) and mass ( $Q = 8.3$ ,  $P < 0.05$   
188 with the Putumayo,  $Q = 6.8$ ,  $P < 0.05$  with the Amazonas and  $Q = 4.5$ ,  $P < 0.05$  with  
189 the Napo), whereas the other populations did not differ between each other in mean  
190 length nor in mean mass. Maximum lengths and even more masses, however, did  
191 vary considerably between populations, reaching barely 80 cm and about 3.8 kg in  
192 the Putumayo and more than 90 cm and 8 kg in the Amazonas (Figure 2a). In the  
193 Amazonas, maximum observed body mass for the silver Arowana was 49, 75 and  
194 113% heavier than in the Napo, Ucayali and Putumayo, respectively. These  
195 important differences in body mass, however, are not a mere reflection of the larger  
196 maximum lengths in the Amazonas. Indeed, although mass-at-length is relatively  
197 similar between populations until about 50 cm (~ size at first sexual maturity, see  
198 below), afterwards fish start to become progressively heavier at a given length in the  
199 Amazonas than in the Ucayali, Napo and Putumayo, in order of increasing difference  
200 (Fig. 2b). These differences reached ~ 500 g and ~1000 g at 70 and 80 cm,  
201 respectively, between the Amazonas and Putumayo sub-basins (Fig. 2b).  
202 For comparison purposes with other studies, a relationship between standard length  
203 (SL) and total length (TL) is provided, calculated from all individuals in Figure 2a,  
204 giving:  $SL = 0.9345 TL + 0.102$ .

205

206 *Gonadal maturity scale*

207

208 Females and males silver Arowana only have one functional gonad, the left one. The  
209 right gonad is atrophied. An illustrated, detailed gonadal maturity scale is presented  
210 in Figure 3 for both females and males. It allows for a clear determination of the  
211 breeding season, size / age at maturity and fecundity.  
212 The precise description of the gonadal cycle also allowed identifying that the silver  
213 Arowana is a multiple-spawner (sensu Nuñez and Duponchelle 2009). Indeed, the  
214 presence of small, vitellogenic oocytes in between large oocytes in “spawning  
215 capable” ovaries, both in stage 3 or 4 (Figure 4a) and in stage 5-2 (recently spawned)  
216 ovary initiating another vitellogenic cycle (Figure 4b), observed in all four sub-  
217 basins, proves that a same female can reproduce at least twice during a breeding  
218 season. Further evidences come from the size frequency distribution of oocytes in  
219 “spawning capable” ovaries from the Putumayo sub-basin, showing two clearly  
220 separated modes of vitellogenic oocytes: the largest (of 244 oocytes) that will be  
221 spawned shortly and a smaller one (of 221 oocytes) that will likely be released in  
222 another spawning bout during the same breeding season (Fig. 5).

223

#### 224 *Breeding season*

225

226 There exists a relationship, albeit not a direct one, between the reproductive cycle of  
227 the silver Arowana (estimated from the monthly proportions of females in “spawning  
228 capable” phase of the gonadal maturation scale) and the hydrological cycle (Figure  
229 6). In the Amazonas and Ucayali rivers, which have comparable hydrological cycles,  
230 females have similar breeding seasons. Although sampling could not be completed at  
231 some months, it can nevertheless be observed that the breeding season started during  
232 the dry season (August-September) and ended before the water level reaches its

233 maximum in both rivers. Some residual reproductive activity could be observed in  
234 the Ucayali at almost every month outside the main breeding season. Again, in the  
235 Napo and Putumayo rivers, which have comparable hydrological periodicity, the  
236 breeding season of the silver Arowana also tended to be similar (Figure 6). Although  
237 sampled could not be obtained in December and January in the Putumayo, it is likely  
238 that, as in the Napo, the breeding season initiated in December to peak in February-  
239 March. The breeding season in the Napo and Putumayo, however, did not last as  
240 long as in the Amazonas and Ucayali and was restricted to the low water period.

241

#### 242 *Size and age at sexual maturity*

243

244 Females tended to have slightly larger size at first sexual maturity (Figure 7) than  
245 males in every sub-basin, but these differences were not significant (t-test,  $t=0.292$ ,  
246  $df=24$ ,  $p=0.773$  for the Amazonas;  $t=0.226$ ,  $df=24$ ,  $p=0.823$  for the Ucayali;  $t=0.630$ ,  
247  $df=18$ ,  $p=0.536$  for the Napo; and  $t=0.327$ ,  $df=24$ ,  $p=0.746$  for the Putumayo).

248 The size at maturity did not differ significantly between sub-basins for females nor  
249 males.

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

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

254

#### 255 *Fecundity*

256

257 The number of oocytes per spawning event (batch fecundity) significantly varied  
258 (ANCOVA,  $D_{3,41} = 6.610$ ,  $P < 0.001$ ) between fish of the four sub-basins (Figure 8,  
259 Table 1). Batch fecundity ranged from 93 to 256 oocytes for females of 1300 and  
260 4960 g, respectively in the Amazonas, from 94 to 311 oocytes for females of 2080  
261 and 3480 g, respectively in the Ucayali, from 92 to 197 oocytes for females of 1460  
262 and 3220 g, respectively in the Napo and from 125 to 360 oocytes for females of  
263 1770 and 2980 g, respectively in the Putumayo.

264 The Putumayo population differed significantly from the Amazonas (ANCOVA,  
265  $D_{1,32} = 25.9$ ,  $P < 0.0001$ ), Napo ( $D_{1,30} = 9.7$ ,  $P < 0.05$  with Napo) and Ucayali ( $D_{1,33} =$   
266  $53.9$ ,  $P < 0.001$ ) populations, whereas the Amazonas, Ucayali and Napo populations  
267 did not significantly differ between each other ( $D_{2,12} = 1.4$ ,  $P > 0.05$ ).

268 Relative fecundity (batch fecundity per unit body mass), oocyte diameter and oocyte  
269 mass are presented in Table 2. Relative fecundity differed significantly between fish  
270 of the four sub-basins (One-way ANOVA,  $F_3 = 11.6$ ,  $P < 0.001$ ). Holm-Sidak post-  
271 hoc test indicated that fish from the Putumayo significantly differed from the  
272 Amazonas ( $t = 4.812$ ,  $P < 0.001$ ), the Ucayali ( $t = 3.614$ ,  $P = .0004$ ) and the Napo ( $t$   
273  $= 2.732$ ,  $P = 0.037$ ), whereas fish from the Amazonas, Ucayali and Napo did not  
274 differ significantly between each other.

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

277

## 278 **Discussion**

279

280 Important length and even more important body mass differences were observed  
281 between the four sub-basins, as already pointed out while studying age and growth

282 patterns of these same populations (Duponchelle et al., 2012). After reaching sexual  
283 maturity, fishes in the Amazonas become progressively heavier than those from the  
284 Ucayali, Napo and Putumayo, in order of increasing difference. Beside inter-basin  
285 differences, silver Arowana from the Peruvian Amazon grow relatively heavier than  
286 fish from the Mamirauá Reserve in Brazil. An individual of 80 cm  $T_L$  ( $\sim 75$  cm  $S_L$ )  
287 weighs  $\sim 3000$  g in the Mamirauá Reserve (Cavalcante, 2008), whereas it weighs in  
288 average 3161 g in the Putumayo, 3369 g in the Napo, 3552 g in the Ucayali and 3702  
289 g in the Amazonas. The better body condition of Arowana in the Peruvian Amazon  
290 might result from better trophic conditions than in the Mamirauá Reserve, which  
291 would have to be tested.

292

### 293 *Gonadal maturity scale*

294

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

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

307 This result, however, differs from other studies in the Brazilian Amazon, Aragao  
308 (1989) in Lake Janavaca and more recently Queiroz (2008) in the Mamirauá  
309 Reserve, who reported that this species probably spawns only once during the  
310 breeding season, but without providing demonstrating evidence.

311

312 *Breeding season*

313

314 In Central Amazonia, Brasil, where most published studies about the silver  
315 Arowana's breeding cycle were carried out, the species was reported to reproduce  
316 during the dry season and early rising waters (Goulding, 1980; Aragao, 1989;  
317 Queiroz, 2008; Cavalcante, 2008). This is consistent with the observations from the  
318 present study in the Amazonas and Ucayali sub-basins, or with previous observations  
319 in Peru, in the Pacaya Samiria Reserve (Tang and Gomez, 2005) and in the Ucayali  
320 River (Ayala, 2001). This pattern, however, does not seem to hold for all silver  
321 Arowana of the Peruvian Amazon, as the breeding season seemed restricted to the  
322 dry season in the Napo and Putumayo sub-basins. This shorter breeding season might  
323 be an adaptation to the much shorter flooding season in the Napo and Putumayo  
324 (Figure 5). Once females have spawned, males guard the eggs and then the fry in  
325 their mouth for five to seven weeks (Goulding, 1990; Argumedo, 2005; Queiroz,  
326 2008), after which free swimming juveniles of over 6 cm are released from parental  
327 care and have to fend for themselves. It is well known that in Amazonian  
328 environments, the high water season with its extended floodplains and inundated  
329 vegetation, providing food and shelter from predators is particularly advantageous  
330 for the development and survival of fish's young stages (Lowe-McConnell, 1964,  
331 1987; Goulding, 1980). In order for males to release their free-swimming young in

332 time to make the most of these advantageous environmental conditions - which  
333 barely last three months in the Napo and Putumayo sub-basins (Figure 5) -, while  
334 allowing for the long incubation, the spawning period might have to be finished  
335 when the water starts to rise. Nevertheless, size frequency distribution of oocytes in  
336 ripe gonads (Figure 4c) and the presence of small vitellogenic oocytes in all stages of  
337 “spawning capable” ovaries support the idea that individual females may have time  
338 to produce a second brood during the spawning period, despite its shorter duration in  
339 the Putumayo. This suggests that the time needed for the small vitellogenic oocytes  
340 (Fig. 4a-b) to complete their growth is relatively short (a few weeks). These results  
341 also imply polyandry in the species: indeed, the short breeding season in the  
342 Putumayo and Napo and the long paternal mouthbrooding period do not allow for a  
343 same male to carry successively two broods of a same female. On the other hand, in  
344 the Amazonas and Ucayali sub-basins, where the high water season lasts nearly  
345 twice as much (December to May), females that spawn when the water has already  
346 started to rise may still ensure their progeny will find favourable environmental  
347 conditions long enough to survive, hence ensure reproductive success. This  
348 hypothesis could be tested by additional studies on these two specific sub-basins and  
349 others with similarly short high water seasons. As Arowana do not live in rivers, but  
350 instead in adjacent lakes and lagoons, testing this hypothesis would also require  
351 having water level data in specific lakes where Arowana concentrations are high.

352

### 353 *Age and size at maturity*

354

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

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

377  
378 It is worth noting that while the other reproductive traits (breeding season and  
379 fecundity) largely varied between sub-basins, size at maturity was relatively  
380 conserved and that the slight differences observed were not significant. This is  
381 particularly surprising as size at maturity is a plastic trait that readily responds to  
382 environmental variation (Stearns and Crandall, 1984; Stearns and Koella, 1986;

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

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

401

#### 402 *Fecundity*

403

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

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

433 the four the sub-basins. These hypotheses, however, will need to be further validated  
434 with an increased number of ripe gonads analysed in the Amazonas, Napo and  
435 Ucayali sub-basins.

436 As a comparison, in the Mamirauá Reserve females of 65 cm  $T_L$  (~ 61 cm  $S_L$  and  
437 1500 g) and 75 cm  $T_L$  (~ 70 cm  $S_L$  and 2500 g) produce ~ 200 and 230 oocytes,  
438 respectively (Queiroz, 2008, using the length-mass relationship provided in  
439 Cavalcante, 2008). This would be approximately twice as much as the fecundity of a  
440 1500 g female in the Peruvian Amazon and in the range of the Putumayo fecundity  
441 for a 2500 g female (Table 1), suggesting a higher relative fecundity in small females  
442 progressively decreasing with length in the Mamirauá Reserve. Again, fish from the  
443 Mamirauá, which have lower body condition than fish from the Peruvian Amazon,  
444 also have higher relative fecundity, contrary to expectations. A surprising  
445 information comes from the mean diameter (9.75 mm) and mass (1.8 g) of oocytes in  
446 the Mamirauá Reserve, which are 25% smaller but a 100% heavier than the largest  
447 and heaviest oocytes in the Peruvian Amazon (12.2 mm and 0.98 g in the Putumayo),  
448 resulting in a density over 3.5 g/cm<sup>3</sup>, (vs 1.03 g/cm<sup>3</sup> in the Putumayo), which appears  
449 much too dense for an egg.

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

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

463

#### 464 *Conclusions*

465 The important variability observed in reproductive characteristics and body condition  
466 of the silver Arowana from the four sub-basins is consistent with the important  
467 growth variations previously reported in these same localities (Duponchelle et al.,  
468 2012). This variability might result either from the phenotypic plasticity of the  
469 species due to environmental heterogeneity between the sub-basins or from the  
470 existence of several distinct genetic populations within Peru, that may need to be  
471 further characterized and managed independently. The important differences in  
472 breeding season, condition, growth and fecundity, however, strongly suggest that fish  
473 from the different sub-basins are distinct populations. The different breeding season  
474 and sedentary nature of the species should result in reduced gene flow between sub-  
475 basins, hence inducing genetic structuring. Although microsatellites markers are  
476 available for the silver Arowana (Silva et al., 2009), they have only been used to test  
477 for multiple paternity in the species (Verba et al., 2014) and no population genetic  
478 study has been carried out so far. Yet, as previously pointed out (Duponchelle et al.,  
479 2012), the growing concerns about *O. bicirrhosum* conservation (Moreau and  
480 Coomes, 2006, 2007) emphasize the need for comparative life history and genetics  
481 studies at the inter- and intra-basin levels (with sampling carried out on-site) in order

482 to understand the population structuring of this species and to define appropriate  
483 management strategies.

484

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494

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620

621

## 622 **Figure legends**

623

624 Fig. 1. Map of the collection sites of *Osteoglossum bicirrhosum* in the Peruvian  
625 Amazon (black circles). A total of 711 specimens were collected between November  
626 2006 and April 2009 at the Iquitos and Requena markets for the Amazonas, Ucayali  
627 and Napo sub-basins. For the Putumayo, 240 fish were bought between March 2008  
628 and April 2009 from local fishermen at El Estrecho and Huapapa communities.

629

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

632 between 2006 and 2009 (a). Modelled regressions (M as a function of SL) between  
633 60 and 90 cm SL, to illustrate inter-basin differences (b).

634

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

638

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

643

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

647

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

650

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

654

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

657 0.875,  $P < 0.001$ ), Napo ( $N = 3$ ,  $F = 0.0578 * M + 18.547$ ,  $R^2 = 0.907$ ,  $P < 0.001$ ),  
658 Ucayali ( $N = 6$ ,  $F = 0.0708 * M - 9.1942$ ,  $R^2 = 0.537$ ,  $P < 0.001$ ) and Putumayo ( $N = 28$ ,  
659  $F = 0.1055 * M - 29.253$ ,  $R^2 = 0.714$ ,  $P < 0.001$ ) rivers, Peruvian Amazon.

660

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

664

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

668

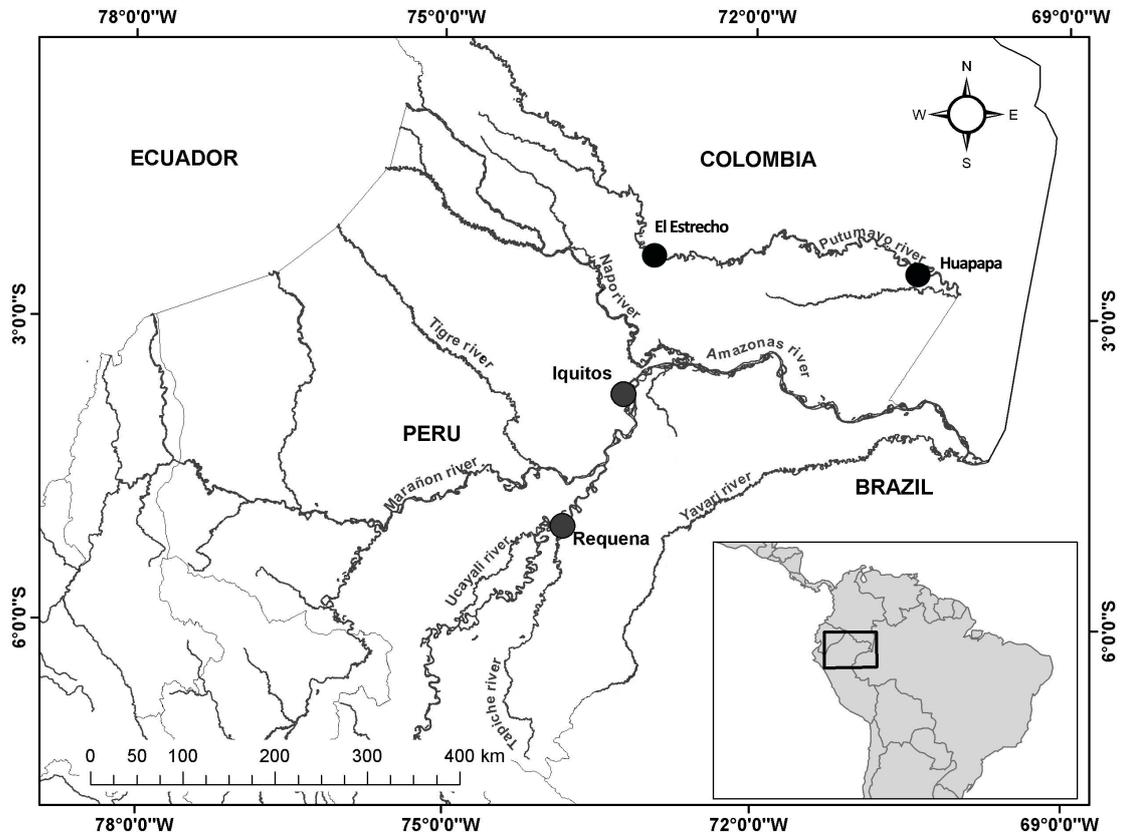
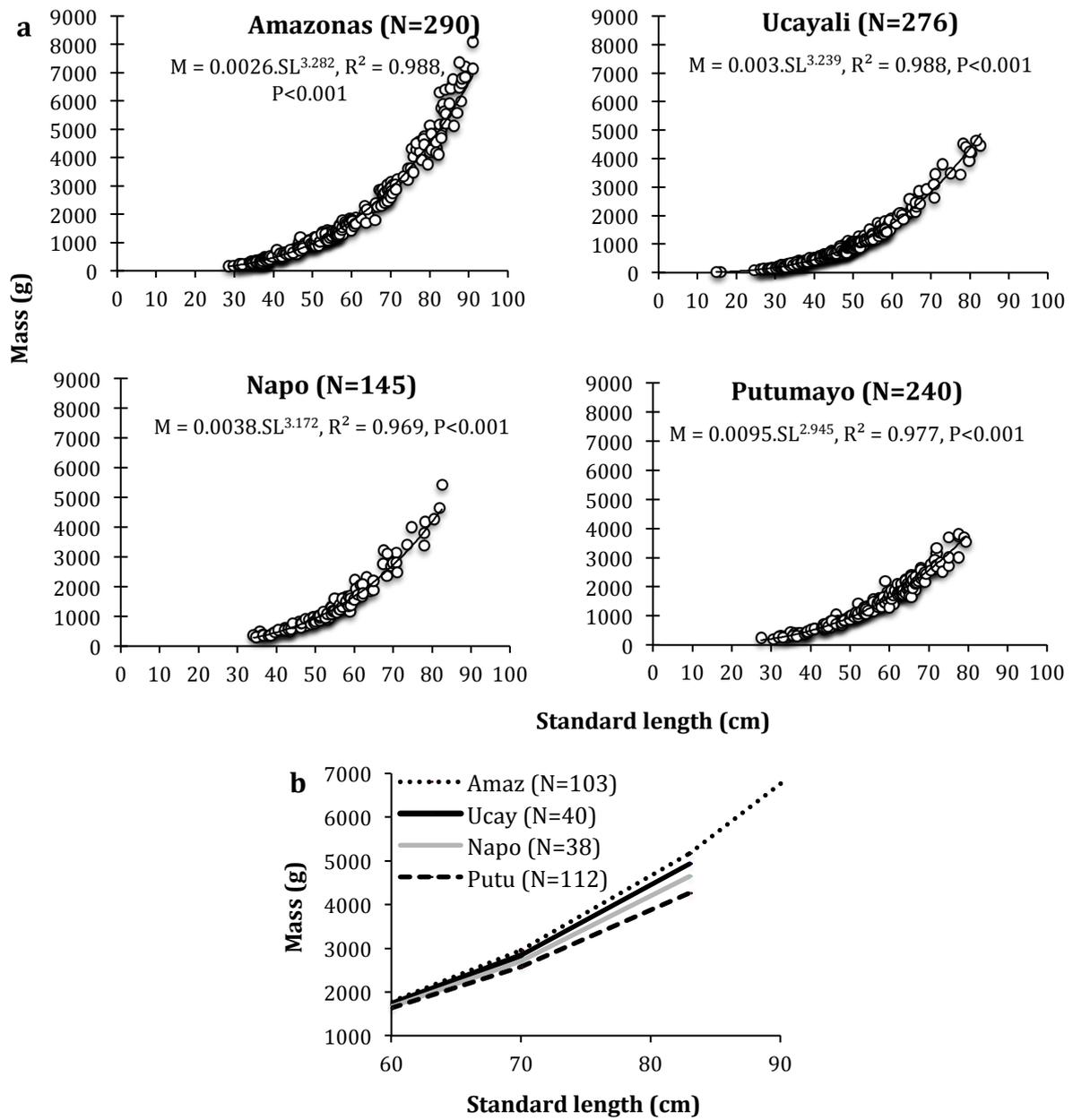
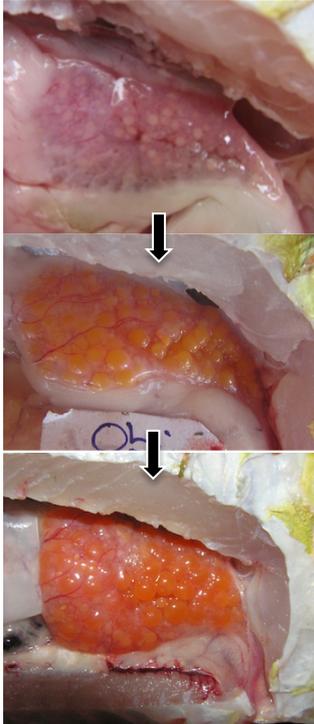
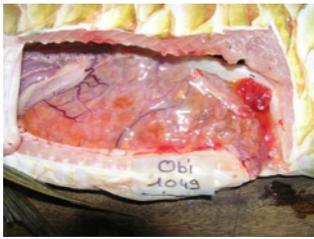
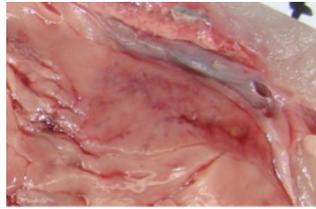


Fig. 1

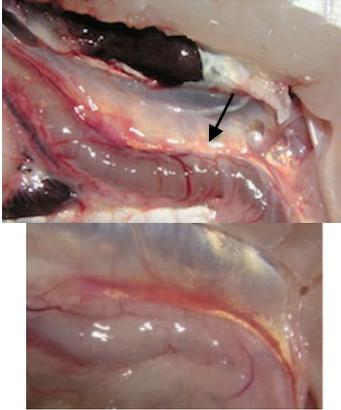


**Fig. 2**

Description	Illustration (females)	with Brown-Petersen et al. (2011)'s terminology
<p><b>Stage 1: immature individuals</b> 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.</p>		Immature
<p><b>Stage 2: maturing individuals</b> 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.</p>		Developing
<p><b>Stage 3: individuals in final maturation</b> The ovary now occupies about <math>\frac{3}{4}</math> 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.</p>		
<p><b>Stage 4: individuals ready to spawn / ripe</b> 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 follicles) in the ovary.</p>		Spawning capable
<p><b>Stage 5-2: recently spawned individuals initiating another cycle</b> 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.</p>		

<p><b>Stage 5: individuals that have just spawned</b> 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.</p>		<p>Regressing</p>
<p><b>Stage 5-1: resting individuals</b> 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.</p>		<p>Regenerating</p>

**Fig. 3a.**

<p><b>Description</b></p>	<p><b>Illustration (males)</b></p>	<p><b>Equivalence with Brown-Petersen et al. (2011)'s terminology</b></p>
<p><b>Stage 1: immature individuals:</b> 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.</p>		<p>Immature</p>
<p><b>Stage 2: maturing or resting individuals:</b> 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.</p>		<p>Developing / Regenerating</p>
<p><b>Stage 3: ripe individuals:</b> Testis even larger, wider and really thick, with dark red opaque appearance. The golden colour is usually not visible at this stage.</p>		<p>Spawning capable</p>
<p><b>Stage 4: individuals after ejaculation:</b> Testis of a similar size to stage 3, but with a flaccid, more translucent appearance.</p>		<p>Regressing</p>

**Fig. 3b.**

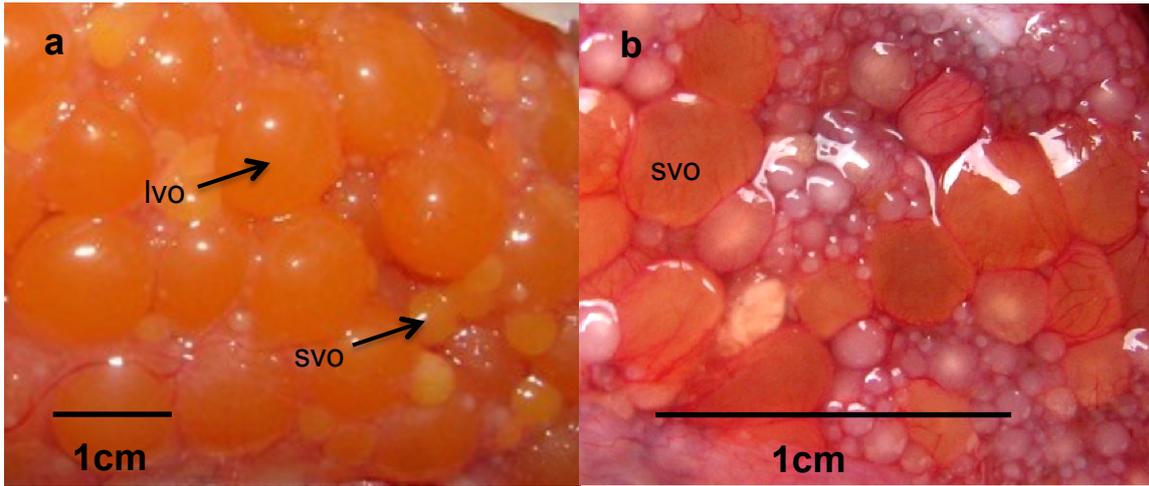
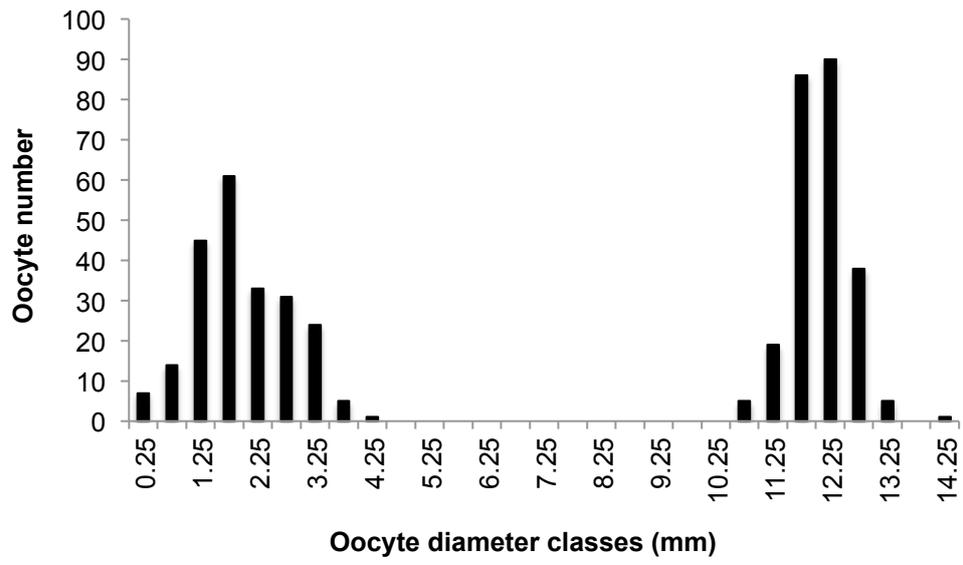


Fig. 4



**Fig. 5**

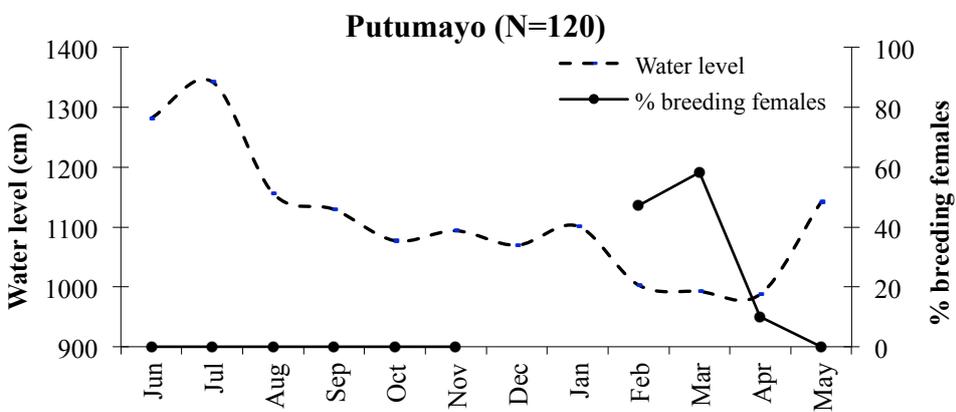
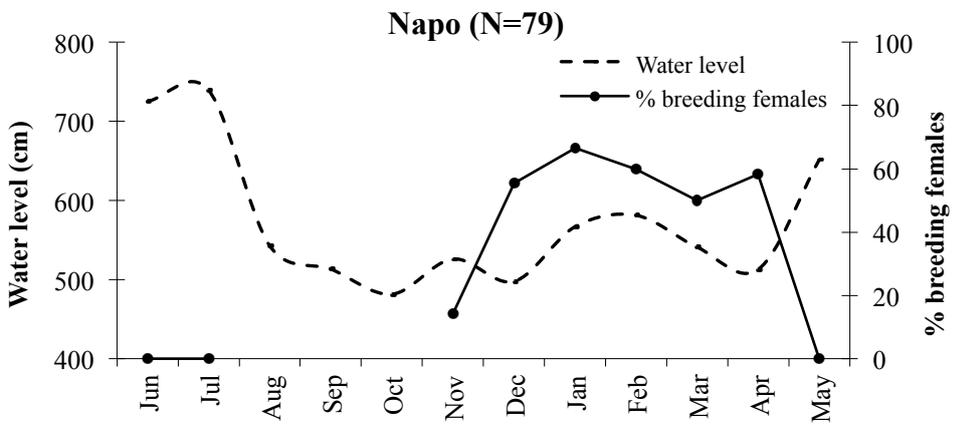
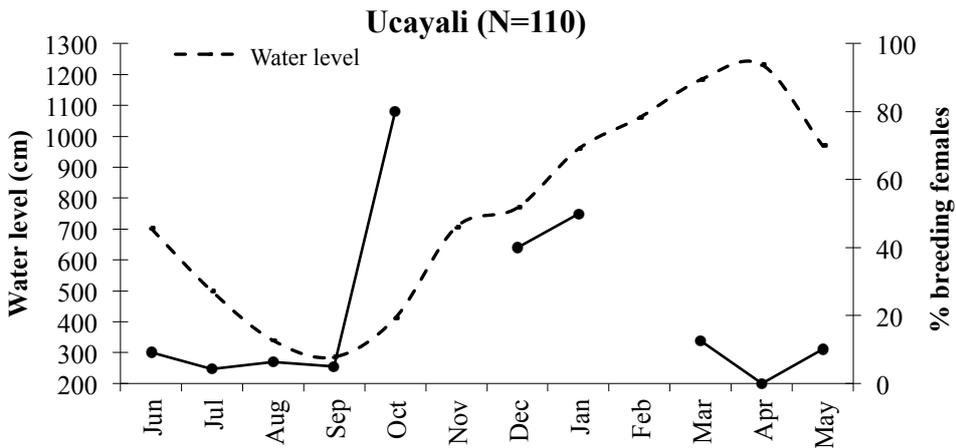
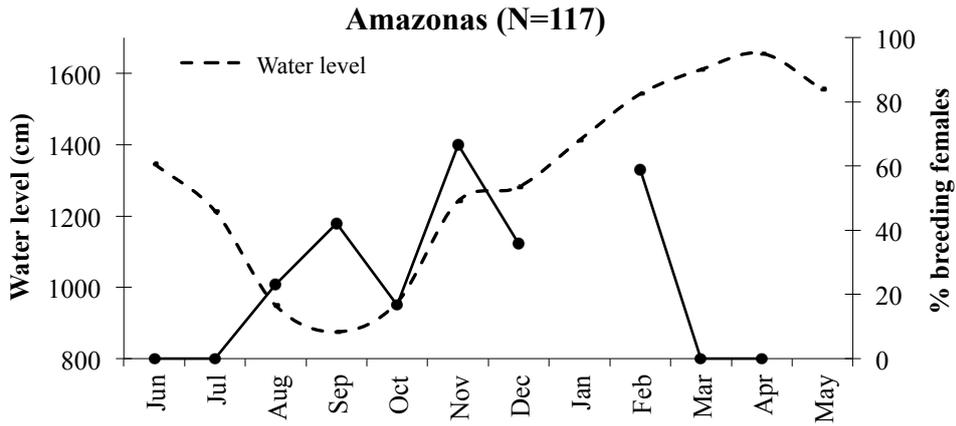


Fig. 6

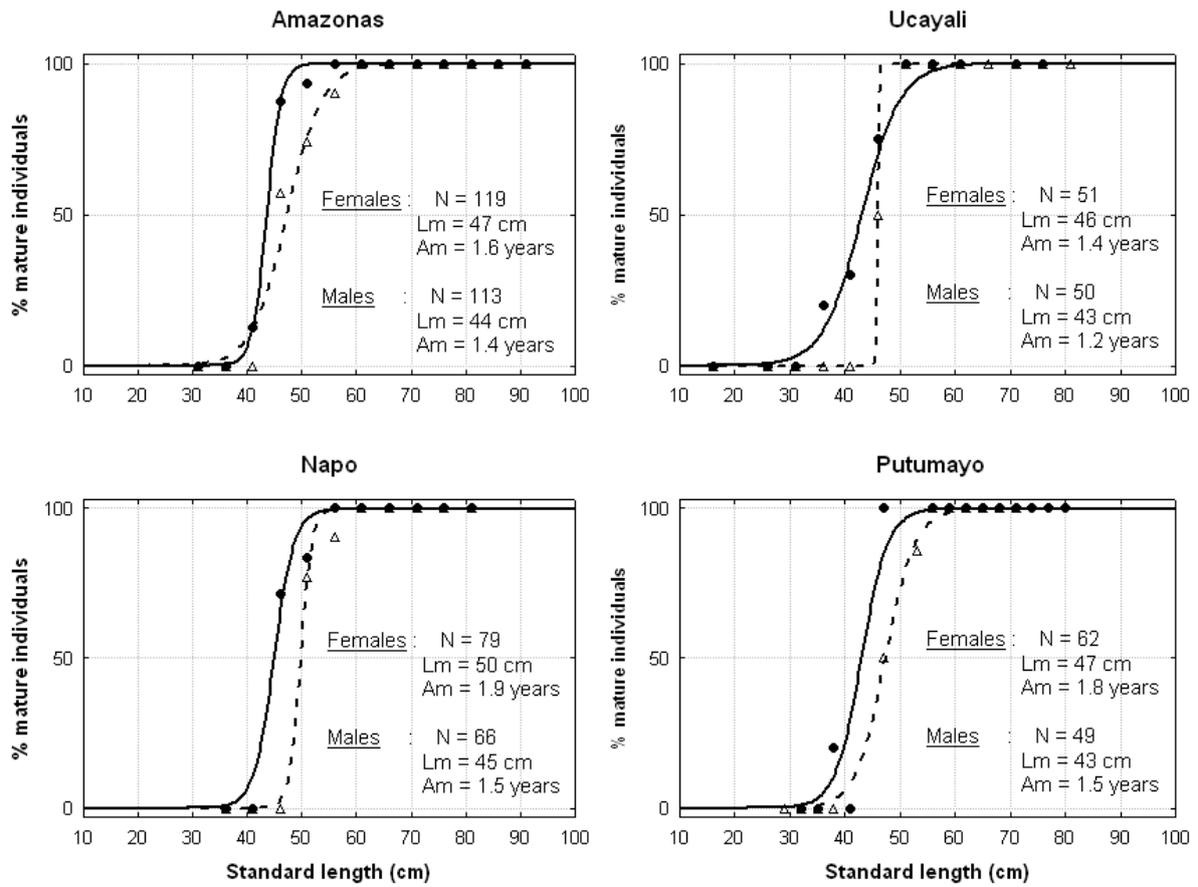


Fig. 7

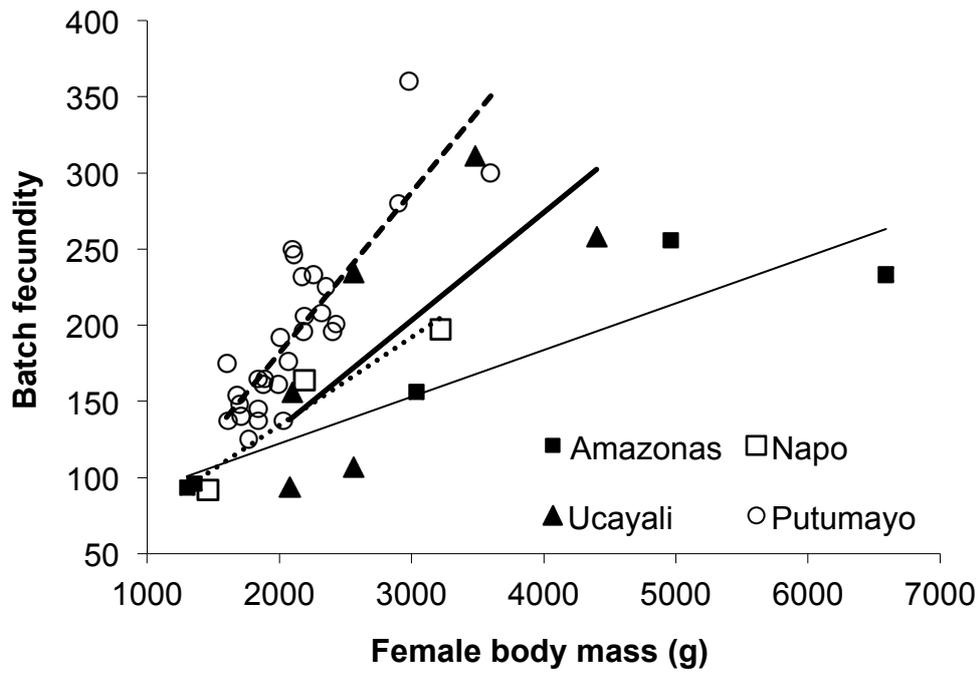


Fig. 8

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