UNIVERSIDADE FEDERAL DO PARÁ
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PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA
CURSO DE DOUTORADO EM ZOOLOGIA

ECOLOGIA DO BAGRE *Ageneiosus ucayalensis* CASTELNAU, 1855 (SILURIFORMES: AUCHENIPTERIDAE) EM UMA RIA FLUVIAL DA AMAZÔNIA ORIENTAL

M.Sc. Valéria de Albuquerque Oliveira

Tese apresentada ao Programa de Pós-graduação em Zoologia, Curso de Doutorado, do convênio Museu Paraense Emílio Goeldi e Universidade Federal do Pará como requisito parcial para obtenção do grau de Doutora em Zoologia.

Orientador: Dr. **Luciano Fogaça de A. Montag**
Lab. de Ecologia e Conservação ICB/UFPA

Co-orientadora: Dra. **Rossineide Martins da Rocha**
Lab. de Ultraestrutura Celular ICB/UFPA

Belém - Pará
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VALÉRIA DE ALBUQUERQUE OLIVEIRA

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OLIVEIRA VA. (2015). **Ecologia do bagre A*geneiosus ucayalensis* Castelnau, 1855 (Siluriformes: Auchenipteridae) em uma ria fluvial da Amazônia Oriental**. Tese de Doutorado. Universidade Federal do Pará e Museu Paraense Emílio Goeldi.

Esta tese apresenta informações sobre a ecologia de *A. ucayalensis*, avaliando a influência da variação pluviométrica, sexual e interindividual na biologia reprodutiva e trófica da espécie, além da contribuição para o conhecimento anatômico e histológico do sistema reprodutor dos machos. Foram realizadas pescas experimentais mensais para a coleta dos espécimes, os quais tiveram seus aspectos ecológicos e morfológicos estudados conforme as análises de rotina para esses parâmetros. A variação pluviométrica influenciou a reprodução dessa espécie, que apresentou desova total e se reproduziu no período com maior intensidade de chuvas. A espécie apresentou hábito alimentar carnívoro com forte tendência a piscivoria e a sua ecologia trófica não foi influenciada pela variação pluviométrica ou pelo sexo, sofrendo influência apenas da especialização individual. A morfologia dos testículos de *A. ucayalensis* diferiu da registrada para outras espécies de Auchenipteridae e foi evidenciada a inseminação, que pode corresponder a uma associação gamética interna para garantir que os espermatozoides consigam fertilizar os oócitos quando liberados no meio aquático. Desta forma, o presente trabalho fornece importantes informações sobre a autoecologia e a morfologia do sistema reprodutor dos machos dessa espécie, que por ser carnívoro desenvolve um importante papel na cadeia alimentar.

APRESENTAÇÃO

A estratégia reprodutiva e o comportamento alimentar, associados às características morfológicas e comportamentais, são responsáveis por garantir o sucesso de diversas espécies de peixes em novos hábitats (Agostinho et al. 2008). Assim, o conhecimento do ciclo reprodutivo das espécies é fundamental porque a sua abundância, assim como sua conservação, dependem do sucesso da sua reprodução (Suzuki & Agostinho 1997). Por outro lado, a reprodução e o crescimento dos peixes requerem boa condição nutricional, que é obtida pela ingestão dos alimentos disponíveis no ambiente (Vismara et al. 2004). Assim, estudos de autoecologia são importantes porque têm implicações sobre a sobrevivência e sucesso reprodutivo (Navarro et al. 2010), além de permitirem conhecer a dinâmica das populações de peixes, refletindo o papel que cada espécie exerce no ecossistema (Sabino & Castro 1990).

Na bacia Amazônica, um dos fatores sazonais que exerce maior influência sobre a reprodução e a dieta de muitas espécies de peixes é o pulso de inundação (Ruffino & Isaac 1995; Fernandes 1997; Hahn et al. 1997; Resende 2000; Rezende & Mazzoni 2005; Queiroz et al. 2010; Freitas et al. 2011; Maciel et al. 2011). Tal fato se dá devido aos alagamentos regulares das planícies de inundações que aumentam a disponibilidade de recursos alimentares e formam micro hábitats, os quais são utilizados como áreas de desova e berçário por muitas espécies de peixes (Junk et al. 1989; Lowe-Mcconell 1999).

Dentre os ecossistemas aquáticos amazônicos, a região do baixo rio Anapu, na Amazônia Oriental (Fig. 1), se destaca por ser uma ria fluvial derivada do afogamento do rio Anapu, ocasionado pela barragem natural formada pela deposição de sedimentos do Amazonas durante o Holoceno (Behling & Costa 2000). Com isso, houve a perda de grande parte de suas planícies de inundação que junto ao efeito tamponante dos seus rios e da maré fazem com que o nível da água se mantenha relativamente estável ao longo do ano (Costa et al. 2002). Tais características, mais o fato deste rio ter suas bordas delimitadas por áreas de terra firme, fizeram com que esse sistema hidrográfico adquirisse características de um lago (Costa et al. 2002).

Uma das espécies de peixes mais abundantes dessa região é o bagre *Ageneiosus ucayalensis* Castelnau, 1855 (Montag 2006) (Fig. 2). Essa espécie possui ampla distribuição, ocorrendo ao longo das bacias dos rios Amazonas, Orinoco, drenagens das Guianas e no alto rio Paraná (Ferraris-Jr 2003), e apresenta hábito alimentar carnívoro (), podendo exercer impacto direto ou indireto sobre a biota e/ou a qualidade da Sá-Oliveira et al. 2014água, por meio do efeito cascata trófica (Hodgson 2005).

Fig. 1 Ria fluvial, Baía de Caxiuanã, situada na região do baixo rio Anapu na Amazônia Oriental.

Embora *A. ucayalensis* apresente ampla distribuição nos rios amazônicos e desempenhe um importante papel no ecossistema aquático, poucos estudos sobre sua autoecologia foram realizados. Não se conhece aspectos básicos da sua biologia reprodutiva ou alimentar. Informações biológicas essas que são consideradas essenciais para o entendimento da capacidade de uma espécie ser bem sucedida em ambientes com características hidrológicas bem distintas.

Fig. 2 Exemplar de fêmea *Ageneiosus ucayalensis* (Siluriformes: Auchenipteridae) (Foto: Leandro Souza).

Diante da carência de informações da espécie, e da peculiaridade e importância da região de Caxiuanã, por ser unidade de conservação (FLONA), esta tese apresenta dados sobre a ecologia reprodutiva e alimentar do bagre *A. ucayalensis* em uma ria fluvial da Amazônia Oriental. Para tal, a tese foi dividida em três capítulos, os quais serão submetidos à revistas científicas de alto impacto.

No primeiro capítulo intitulado, “Influência da variação pluviométrica no padrão reprodutivo do bagre *Ageneiosus ucayalensis* Castelnau em uma ria fluvial da Amazônia Oriental”, abordamos o efeito da chuva local na razão sexual, tipo de crescimento, fator de condição, período reprodutivo, tipo de desova e tamanho de primeira maturação sexual desse bagre. No segundo capítulo, intitulado “Influência da sazonalidade de chuva, sexo e da especialização individual na ecologia trófica de um bagre (Auchenipteridae) em rios afogados, Amazônia Oriental”, abordamos o efeito da chuva e do sexo na sua ecologia alimentar e no último capítulo, intitulado “Anatomia e histologia do sistema reprodutor de machos de um bagre amazônico, evidências de inseminação” abordamos de forma descritiva a função do gonopódio, morfologia funcional dos testículos e o papel da inseminação na estratégia reprodutiva dos auchenipterídeos.

As referências, figuras e tabelas dos capítulos estão de acordo com as normas das revistas as quais serão submetidos, sendo que os dois primeiros já estão no idioma exigido pela revista.

CAPÍTULO I

INFLUÊNCIA DA VARIAÇÃO PLUVIOMÉTRICA NO PADRÃO REPRODUTIVO DO BAGRE *AGENEIOSUS UCAYALENSIS* CASTELNAU EM UMA RIA FLUVIAL DA AMAZÔNIA ORIENTAL

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Influence of the variation in rainfall levels on reproductive patterns in the duck catfish, *Ageneiosus ucayalensis* Castelnau, in a ria system of the eastern Amazon

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Abstract

Rainfall intensity is one of the principal factors that influence the reproductive biology of many Neotropical fish species. The present study evaluated the influence of the variation in rainfall levels on the condition factor and reproductive biology of the duck catfish, *Ageneiosus ucayalensis*, in a ria system of the eastern Amazon. A total of 1006 specimens were collected between May, 2012, and April, 2013, on the lower Anapu River in the state of Pará, Brazil. The sex and the maturation phase of the specimens were classified macroscopically and confirmed histologically. The sex ratio, mass-length relationship, condition factor (K), Gonadosomatic Index (GSI), relative frequency of the different stages of maturity, and the mean size at first gonadal maturity were estimated and analyzed in the context of the variation in local rainfall rates. In this study, 733 female specimens and 273 males were collected. Both sexes were characterized by negative allometric growth. The condition factor was weakly related to the breeding season. The GSI and the relative frequency of mature specimens indicate that the breeding season is short, and coincides with the region's rainy season. Males reach sexual maturity, on average, at a standard length of 11.75 cm, and females at a length of 12.85 cm. Overall, the results indicate that the reproductive biology of *A. ucayalensis* is influenced primarily by rainfall intensity in the study area.

Key words Gonadal development; first maturity; precipitation.

Introduction

In fish species, reproductive strategies are related to the constant variation found in environmental factors, such as the type of habitat, temperature, photoperiod, precipitation rates, and fluvial hydrology (Barbieri et al. 2004; Suzuki et al. 2004; Guerrero et al. 2009; Godinho et al. 2010). In tropical rivers, seasonal variation is determined primarily by hydrological fluctuations, which lead to the regular inundation of the floodplain, increasing the availability of feeding resources and forming new microhabitats, used as spawning grounds and nurseries by many fish species (Junk et al. 1989, Lowe-McConnell 1999).

The effects of the flood pulse on reproductive patterns have been investigated in a number of Amazonian fish species (Goulding 1980; Ruffino and Isaac 1995; Fernandes 1997; Queiroz et al. 2010; Freitas et al. 2011; Maciel et al. 2011). However, the considerable heterogeneity of environments found within the Amazon basin, which reflects variation in climatic patterns and the configuration of drainage basins, related to their geomorphology and vegetation cover, has a direct influence on the composition of local fish communities and their ecological characteristics (Lowe-McConnell 1999; Prudente et al. 2014).

The lower Anapu basin in eastern Amazonia forms a ria system, characterized by the “drowning” of its rivers and streams, where the buffering effect of the tides and the fluvial discharge has resulted in the loss of most of the floodplain area and a very discreet annual flood pulse (Hida et al. 1999; Behling and Costa 2000; Costa et al. 2002). The fact that water levels remain relatively stable during the course of the year, together with the reduction in current velocity, confers lentic characteristics on the region’s aquatic systems (Costa et al. 2002). The catfish *Ageneiosus ucayalensis* Castelnau, 1855 is one of the more abundant of the 111 fish species found on the lower Anapu (Montag 2006).

In this context, understanding the reproductive patterns of *Ageneiosus ucayalensis* Castelnau, 1855 in this ria system may provide important insights into the adaptability of the life cycle of this species, which is amply distributed in the Amazon and Orinoco basins, as well as the Guianas and the upper Paraná River (Ferraris-Jr 2003).

Given these considerations, the present study focused on the question: what is the influence of the variation in rainfall rates on the reproductive pattern of *A. ucayalensis* in a ria system of the eastern Amazon? This is based on the fact that the precipitation cycle in the Amazon basin appears to have a fundamental influence on the ecology and reproductive biology of many fish species, given that periods of high rainfall tend to have a positive effect on the availability of resources in the aquatic environment and the physical-chemical conditions of the water, which become more appropriate for spawning (Sánchez-Botero and Araújo-Lima 2001; Leite et al. 2006, Filho et al. 2012). Given this, the present study investigates whether increasing rainfall levels act as a trigger for the onset of the reproductive process in *A. ucayalensis*, even in environments where there is little annual variation in water levels.

Material and methods

Study area

The region of the lower Anapu River, in eastern Amazonia, can be characterized as a ria system, which is distinguished from other Amazonian ecosystems by the "drowning" of its rivers and streams (Costa et al. 2002). Caxiuanã Bay is located at the lower end of the Anapu, between the Tocantins and Xingu rivers, in the municipalities of Melgaço and Portel, in the state of Pará, Brazil. The Caixuanã National Forest (1º42'30" S, 51º31'45" W), located on the left bank of the lower Anapu (Fig. 1), is one of the largest federal conservation units in the state of Pará.

The region's climate is hot tropical, with annual precipitation of approximately 2020 mm (Moraes et al. 2009). Based on precipitation data for the Caxiuanã National Forest for the period between April, 2012, and May, 2013, obtained from the ESECAFLOR/LBA/TEAM project, the climatic seasons were classified as rainy-dry transition (May–July), dry season (August–October), dry-rainy transition (November–January), and rainy season (February–April). The local rivers are typical black-water bodies of water, with only discreet fluctuation in river levels, rarely exceeding one meter (Sioli 1984; Hida et al. 1999).

Caxiuanã Bay is characterized by a gradient of one meter per kilometer, sloping down gradually from the left margin to the center and then to near the right margin, where it attains a depth of 6 m to7 m. Here, there is a submerged valley with submerged cliffs, known locally as wells, which may reach depths of around 20 m (Costa et al. 2002).

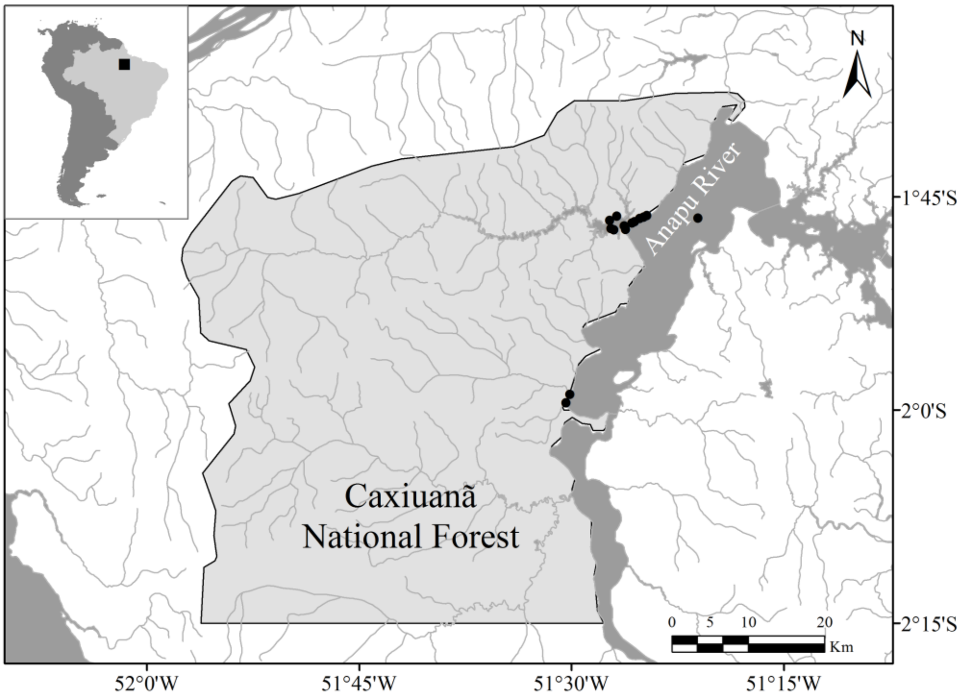


Fig. 1 Region of the lower Anapu River, showing the Caxiuanã National Forest and the collecting localities (black points) in Caxiuanã Bay.

Data collection and analysis

Specimens of *A. ucayalensis* were collected each month between May, 2012, and April, 2013 in standardized 10 m x 1.5 m gillnets of different mesh sizes (15, 20, 25, 30, 35, and 40 mm between opposing knots). The nets were set close to the margin of the water at dusk, and left for four hours. During the day, the nets were used to collect specimens at specific sites (wells) for 10 minutes, with lead weights being attached to each extremity of the set of nets, which were attached to sets of buoys with a 5-m long line, in order to guarantee finding the nets so that they could be retrieved at the allocated time.

Once collected, the *A. ucayalensis* specimens were sexed, their standard length (L_S: the distance between the tip of the snout and the caudal peduncle) was measured in centimeters and they were weighed (in grams) before being eviscerated. The viscera were removed through a longitudinal incision made from the urogenital opening to the head, for the extraction of the gonads, which were weighed. Sexing was based on the observation of the gonads.

The median third of the gonads of each specimen was fixed in Bouin's solution for 24 hours before routine histological processing for fixing in paraffin (Prophet et al. 1995), and the preparation of sections with a thickness of five micrometers. The slides were stained in hematoxylin and eosin for observation under a photomicroscope. The gonadal maturation stage was defined in both males and females according to the classification scheme proposed by Núnez and Duponchele (2009).

The sex ratio (females:males) was calculated from the absolute frequency of male and female specimens collected during each season and in each standard length class. The significance of deviations in the sex ratio, based on the null hypothesis that a 1:1 ratio would be expected, irrespective of the season, was tested using Chi-square (Sokal and Rohlf 1981). Differences between males and females in body size (standard length) were analyzed using Student's *t* for separate variances (Zar, 1999).

The mass-length relationship was calculated for the *A. ucayalensis* specimens in order to characterize growth patterns and identify possible differences between males and females. The relationship was described for the two sexes separately, based on the equation proposed by Huxley (1924): $\boldsymbol{M_t = a.L_S^b}$, where M_t = total mass, L_S = standard length, a = the coefficient of proportionality, and b = the coefficient of allometry. To test possible differences between the sexes, the residual values for males and females were compared using a *t* test, with a 5% significance level.

The proportional residuals ([observed mass - expected mass] / observed mass) were then plotted against body length, in order to verify any tendency for polyphasic growth

(Bervian et al. 2006). These residuals were used rather than absolute values in order to avoid any possible bias derived from the heteroscedasticity of the data. To test for possible tendencies in the residuals, they were analyzed against standard lengths in a linear regression (Bervian et al. 2006).

A *t* test was also applied to determine whether the *b* value estimated for each sex was significantly different from three, with a 5% significance level (Zar, 1999). This analysis is based on the fact that, when $b = 3$, growth is isometric, that is, body length increases at the same rate as mass, whereas all other values reflect allometric growth, that is, body length and mass increasing at different rates.

The allometric condition factor was also estimated for the male and female specimens of *A. ucayalensis*, based on the observed values for the coefficient of allometry (*b*), based on the equation: $K = M_t/L_S{}^b$, where K = the condition factor, M_t = total mass, L_S = standard length, and b = the coefficient of allometry obtained for the mass-length relationship (Braga, 1986). Differences between males and females in the condition factor were tested using *t*, with a 5% significance level. As the *K* values did not satisfy the assumptions for a parametric test, variation among seasons (rainy, rainy-dry transition, dry, and dry-rainy transition) was evaluated using the Kruskal-Wallis nonparametric analysis of variance (*H*) with a 5% significance level, followed by a Nemenyi post hoc test for the evaluation of pairwise differences (Zar, 1999).

The period with the highest level of reproductive activity was estimated for male and female *A. ucayalensis* (excluding immature specimens) using the gonadosomatic index (GSI), which is calculated by GSI = $M_g/M_t.100$, where GSI = gonadosomatic index, M_g = mass of the gonads, and M_t = total mass of the specimen (Nikolsky 1969). The GSI values were evaluated in relation to the assumptions for statistical testing and the variation among seasons (rainy, rainy-dry transition, dry, and dry-rainy transition) was evaluated using the Kruskal-Wallis test (*H*) with a 5% significance level, followed by the Nemenyi post hoc test (Zar, 1999).

The relationship between energetic expenditure and the breeding season was evaluated by calculating the Spearman rank correlation coefficient for the *K* and GSI values, with a 5% significance level. This nonparametric coefficient was selected because the data did not satisfy the assumptions for a parametric analysis. The correlation was considered high when the *r* value was above 0.6. Reproductive activity was also evaluated in terms of the relative frequency of the different gonadal stages recorded during the course of the study period (Prudente et al. 2014).

The mean size of *A. ucayalensis* at first sexual maturation (L_{50}) was calculated for males and females based on the frequency of reproductive and non-reproductive individuals found in 1 cm classes of standard length, based on the logistic equation: $F = \frac{1}{(1+ exp\,(-tax*(Ls-L50)))}$, where: F = proportion of mature individuals per length class, tax = rate of change from the non-reproductive to the reproductive phase, L_S = standard length (cm), L_{50} = body length at first sexual maturation (cm). The values were adjusted using the non-linear least-squares tool in the Solver package in Microsoft Office Excel® 2007.

The adjustment of the function and the estimate of the 95% confidence interval were obtained using Marquardt's Levenberg algorithm, run in SPSS® 17.5. The mean length at first sexual maturation corresponds to the standard length at which 50% of the individuals are sexually mature (Vazzoler 1996).

Results

A total of 1006 *A. ucayalensis* specimens were collected during the study period, of which, 733 were female, and 273, male, with a sex ratio significantly biased towards females, 2.69:1 ($\chi^2 = 10.45$; $p < 0.05$). The mean standard length of the females was 1.4 cm greater than that of the males, a significant difference (Student's *t* for separate variances: $t = 12.179$; d.f. = 1004; $p < 0.001$). Mean L_S in the females was 15.13 cm (range: 9.9–21.8 cm), while in the males, it was 13.99 cm (9.5–18.1 cm). Females were more abundant than males in all the months of the study period, irrespective of rainfall levels (Fig. 2).

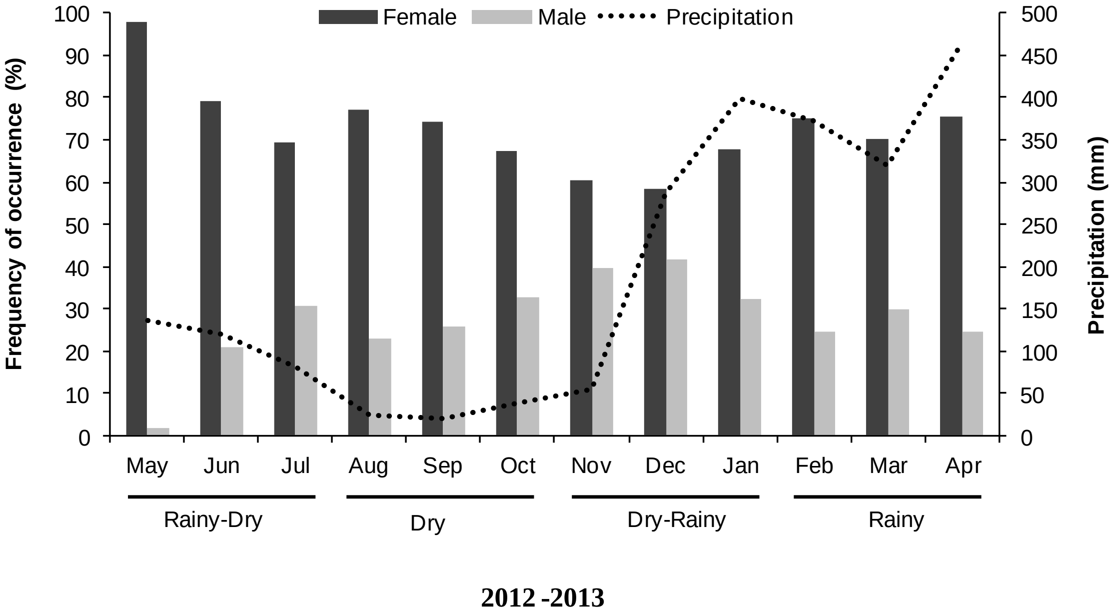


Fig. 2 Proportion of female and male *A. ucayalensis* specimens collected in the Anapu ria in the eastern Amazon between May 2012 and April 2013.

The females also predominated in all body size classes (Fig. 3). All individuals in the largest size classes were females.

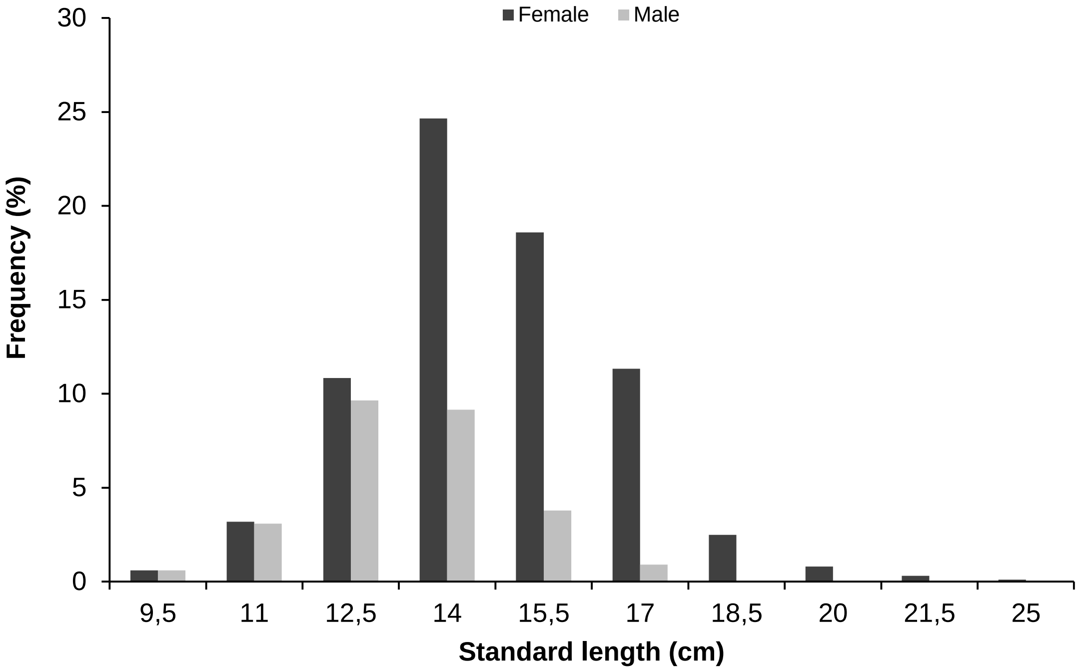


Fig. 3 Frequency by size class of female and male *A. ucayalensis* specimens captured in the Anapu ria in the eastern Amazon between May 2012 and April 2013.

Female and male *A. ucayalensis* had distinct patterns of growth (t = 1.962; d.f. = 1002; p < 0.001), although both females (b = 2.18; t = 18.088; d.f. = 636; p < 0.001) and males (b = 2.00; t = 14.391; d.f. = 243; p <0.001) presented negative allometric growth (Fig. 4a, 5a). The lack of any significant trend in the proportional residuals confirms the adequacy of the standard mass-length model for both females (Fig. 4a; p = 0.233) and males (Fig. 5b; p = 0.921), with no evidence of polyphasic growth in either sex.

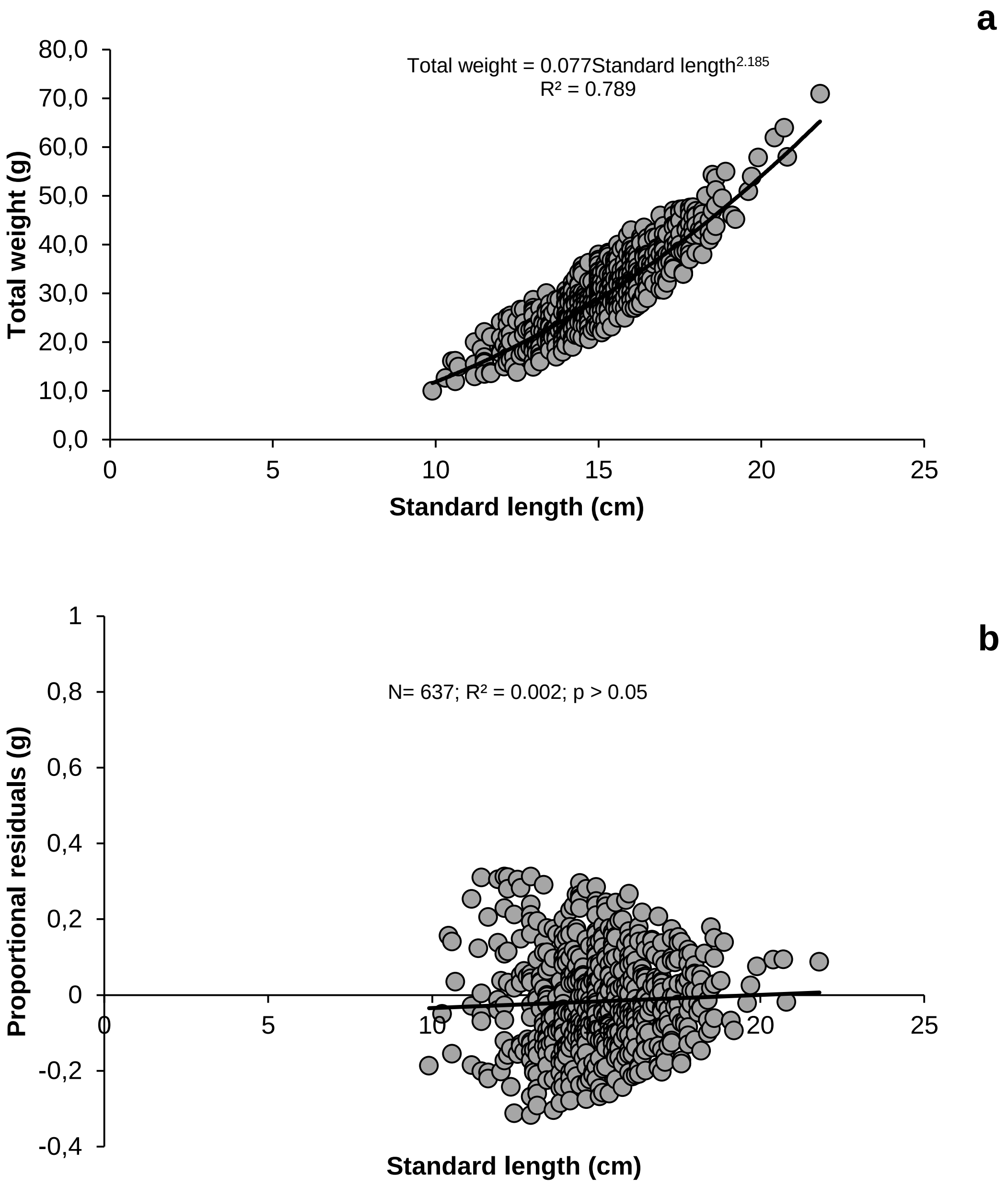


Fig. 4 Mass-length relationship (a) and distribution of the proportional residuals (b) for the female *A. ucayalensis* specimens captured in the Anapu ria in the eastern Amazon between May 2012 and April 2013.

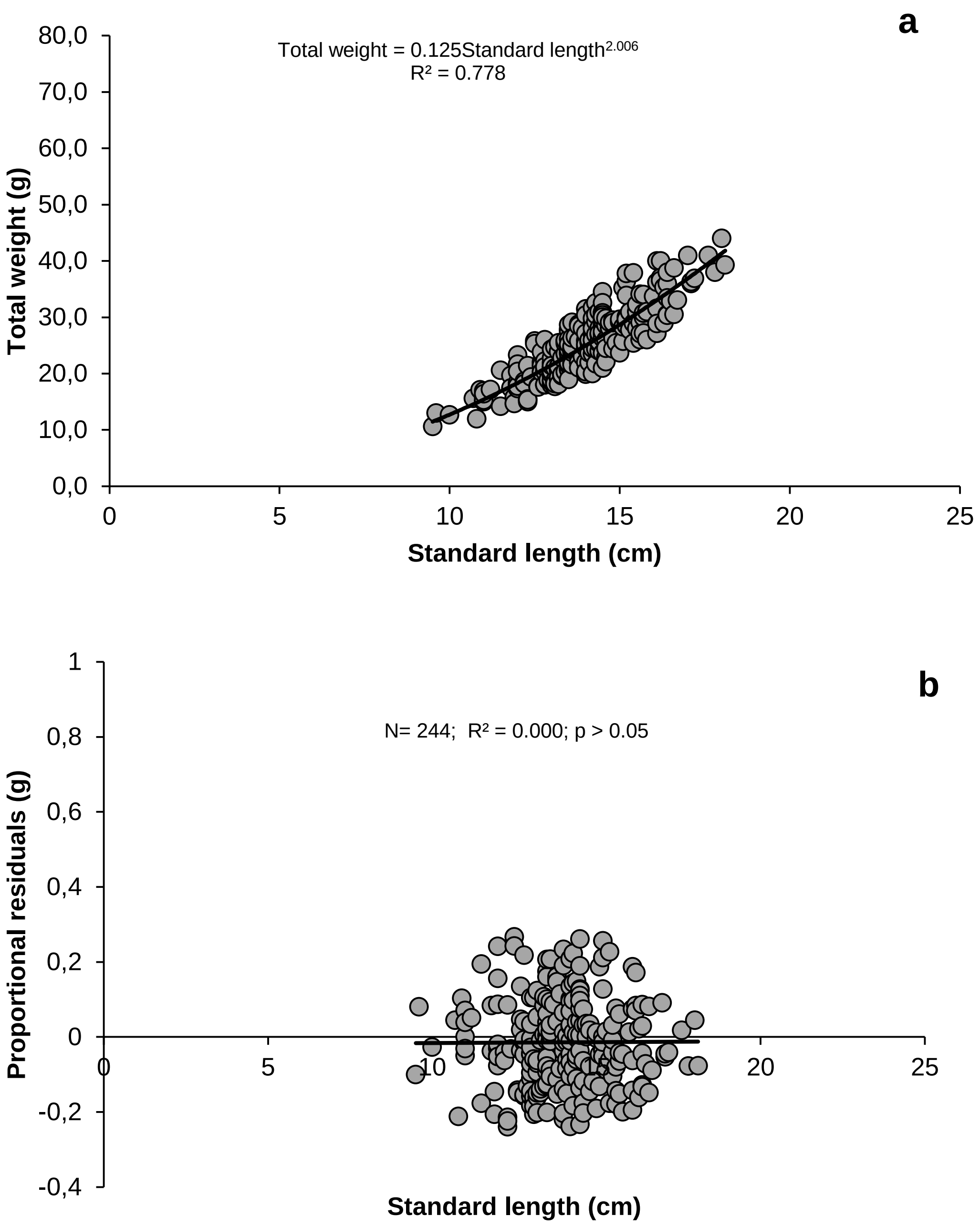


Fig. 5 Mass-length relationship (a) and distribution of the proportional residuals (b) for the male *A. ucayalensis* specimens captured in the Anapu ria in the eastern Amazon between May 2012 and April 2013.

The analysis of the condition factor (*K*) indicated a similar pattern for males and females. However, the values recorded for the males were higher than those recorded for the females throughout the study period (t = 63.293; d.f.= 1002; p < 0.001).

Significant seasonal variation was found in females (Fig. 6a: $H_{(3,729)} = 225.923$; $p < 0.001$) and males (Fig. 6b: $H_{(3,\ N=272)} = 77.490$; $p < 0.001$). In both sexes, significantly lower values ($p < 0.001$) were recorded in the dry season and the rainy-dry transition period in comparison with the rainy season and dry-rainy transition.

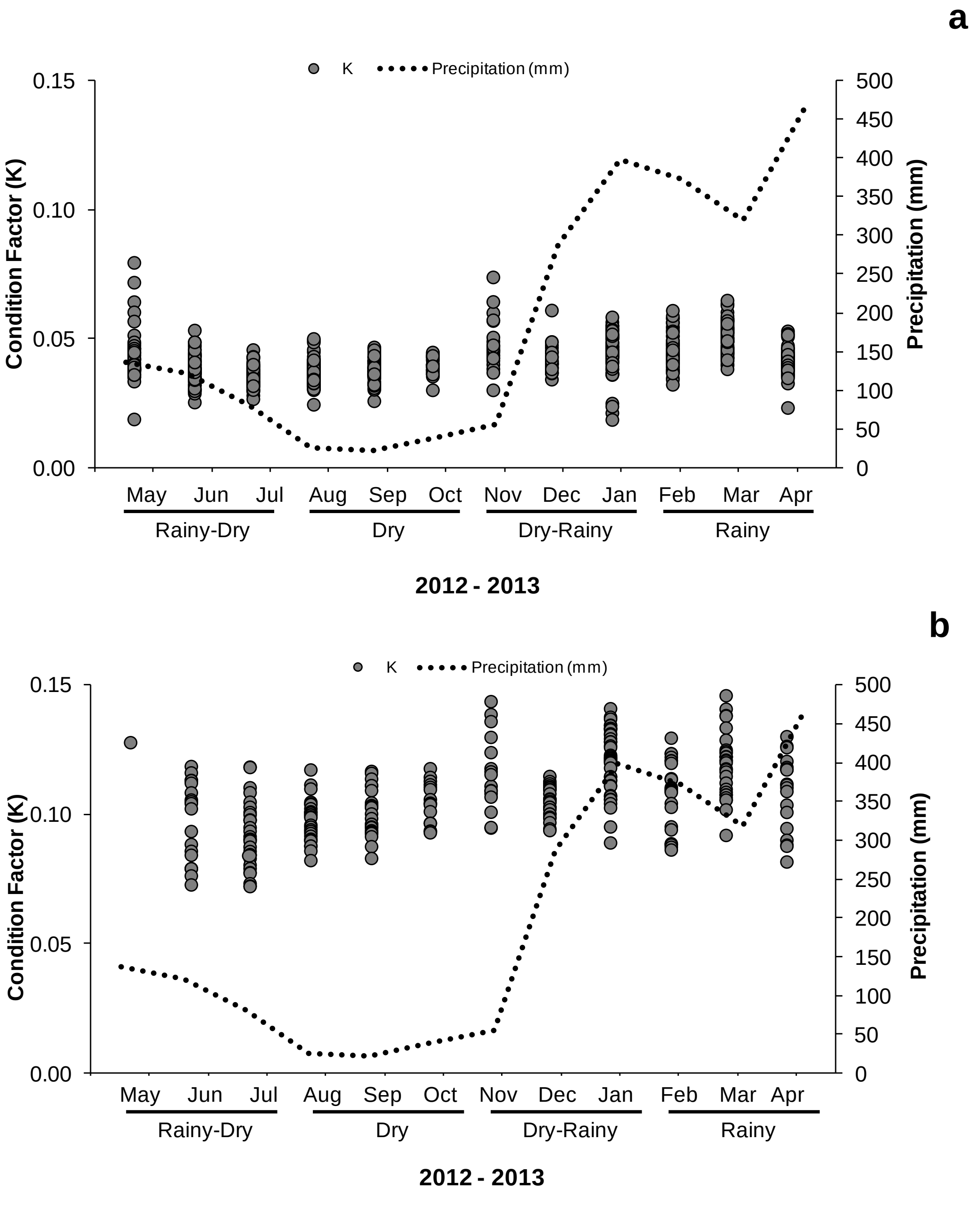


Fig. 6 Variation in the condition factor (*K*) of the female (a) and male (b) *A. ucayalensis* specimens captured in the Anapu ria in the eastern Amazon between May 2012 and April 2013.

The gonads of *A. ucayalensis* were paired structures of approximately the same size. The ovaries were tubular in shape, while the testes were fringed. In both sexes, the gonads present a distinct pattern of size, color, consistency, and vascularization, according to the phase of the reproductive cycle.

Based on the microscopic analysis, five stages of gonadal development were defined for the females: (i) immature, (ii) maturing, (iii) mature, (iv) spent, and (v) resting. In the males, only three stages were defined: (i) immature, (ii) maturing, and (iii) mature. The histological analyses indicate that the immature ovaries contained oogonia, numerous stage I oocytes, and a few stage II oocytes. The type I oocytes correspond to the pre-vitellogenic oocytes, and were identified based on their small size, basophil, homogeneous cytoplasm, and central or peripheral nuclei. The type II oocytes (undergoing vitellogenesis) were characterized by the presence of cortical alveoli and small yolk granules, with the nucleolus peripheral to the nucleus (Fig. 7a). The maturing ovaries contained oocytes of types I, II, and III. In the type III oocytes (vitellogenic), the zona radiata was clearly visible and the cytoplasm was filled completely with yolk granules (Fig. 7b). The nucleus was still visible and located in a central position. The mature ovaries contained primarily type IV (vitellogenic) oocytes (Fig. 7c), which have acidophilic cytoplasm, filled with granules of yolk, and a fragmented nucleus, migrated to the periphery of the cell. The spent ovaries contained atretic oocytes and post-ovulatory follicles (Fig. 7d). The rest phase differs from the immature phase only in having a more open lumen and the reticular arrangement of the oocytes (Fig. 7e).

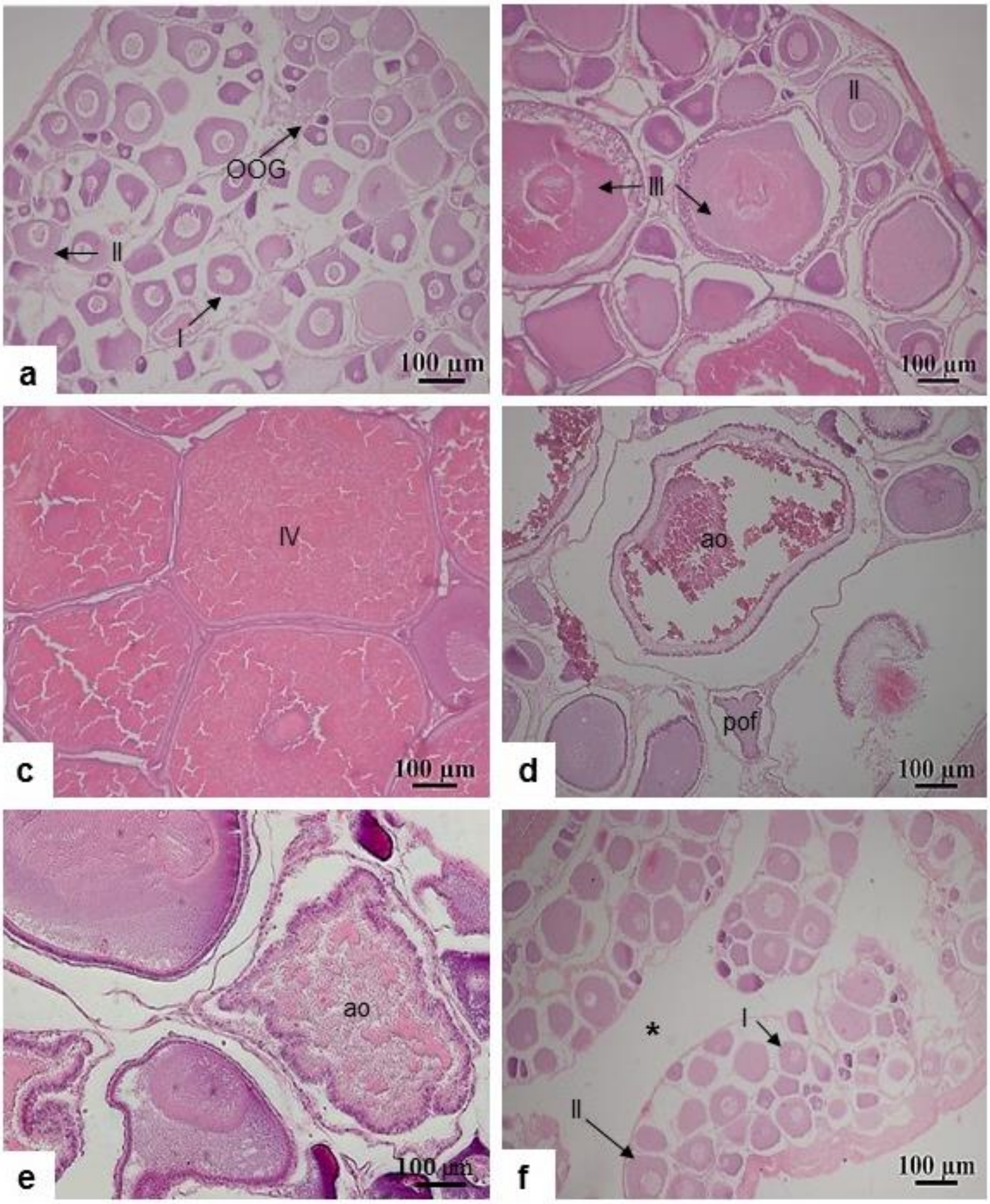


Fig. 7 Ovarian maturation stages the *A. ucayalensis*: (a) immature; (b) maturing; (c) mature; (d, e) spent; (f) resting. I: phase I oocyte; II: phase II oocyte; III: phase III oocyte; IV: phase IV oocyte; OOG: oogonia; pof: postovulatory follicle; ao: atretic oocyte; *: open lumen.

Histologically, the testes are coated by the tunica albugina, tissue conjunctive, which emits septa into the spermatogenic fringes (Fig. 8a). The immature testes have seminiferous tubules filled with spermatogonia, the only type of cell present in this phase (Fig. 8b). In the maturing testes, the tubules increase in size and the presence of spermatogonia, spermatocytes, spermatid, and spermatozoa can be observed (Fig. 8c). In the mature testes, the tubules are filled with sperm, although some spermatids and spermatocytes can still be observed (Fig. 8d).

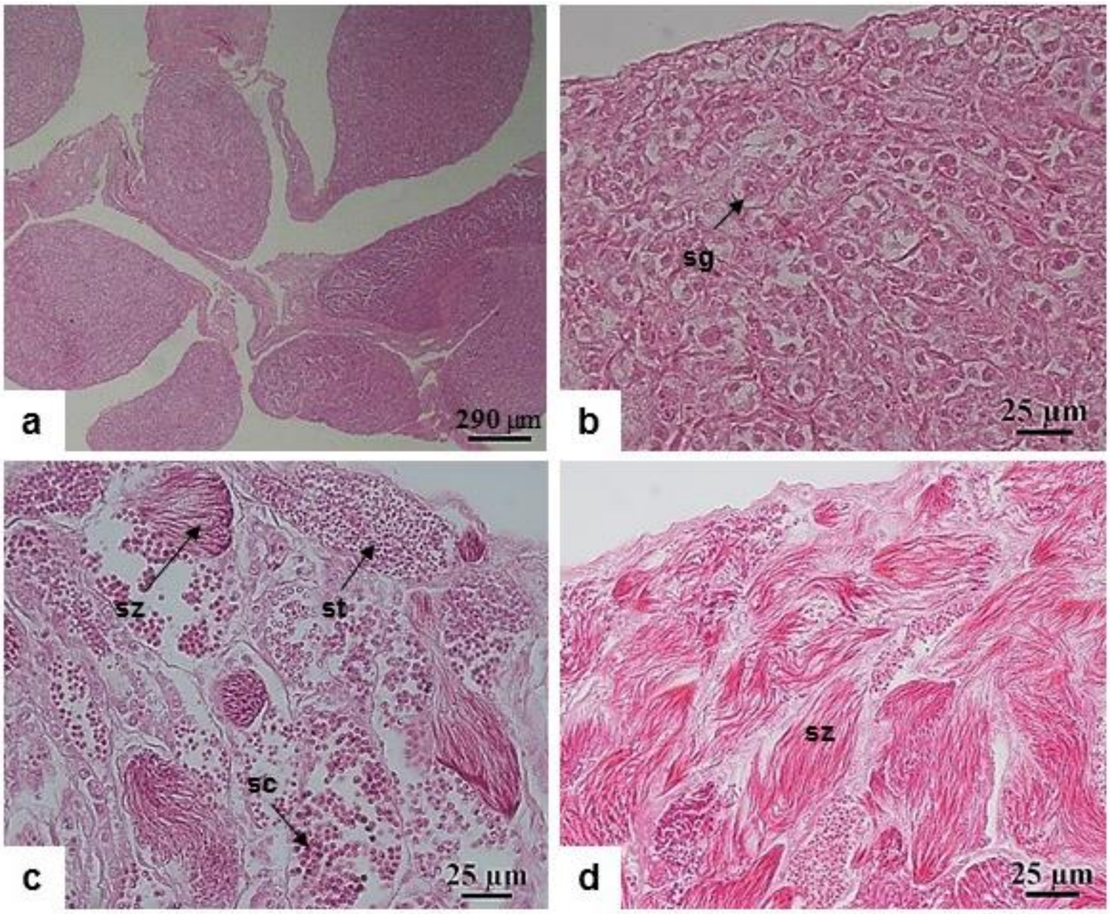


Fig. 8 Testes maturation stages in *A. ucayalensis*: (a) testicular fringes; (b) immature; (c) maturing; (d) mature. sg: spermatogonia; sc: spermatocyte; st: spermatid; sz: spermatozoa.

The variation in the GSI scores indicated higher levels of reproductive activity in *A. ucayalensis* during the dry-rainy transition period and rainy season (Fig. 9). The highest values were recorded in January (end of the dry-rainy transition), and February and March (rainy season) in both females ($H_{(3;\ 598)}$ = 29.285; $p < 0.001$) and males ($H_{(3;242)}$ = 77.742; $p < 0.001$). In the females, the values recorded in the dry-rainy transition differed significantly from those registered in the rainy-dry transition ($p < 0.001$), dry ($p = 0.043$), and rainy seasons ($p < 0.001$). In the males, the rainy season was significantly different from all other periods ($p < 0.001$).

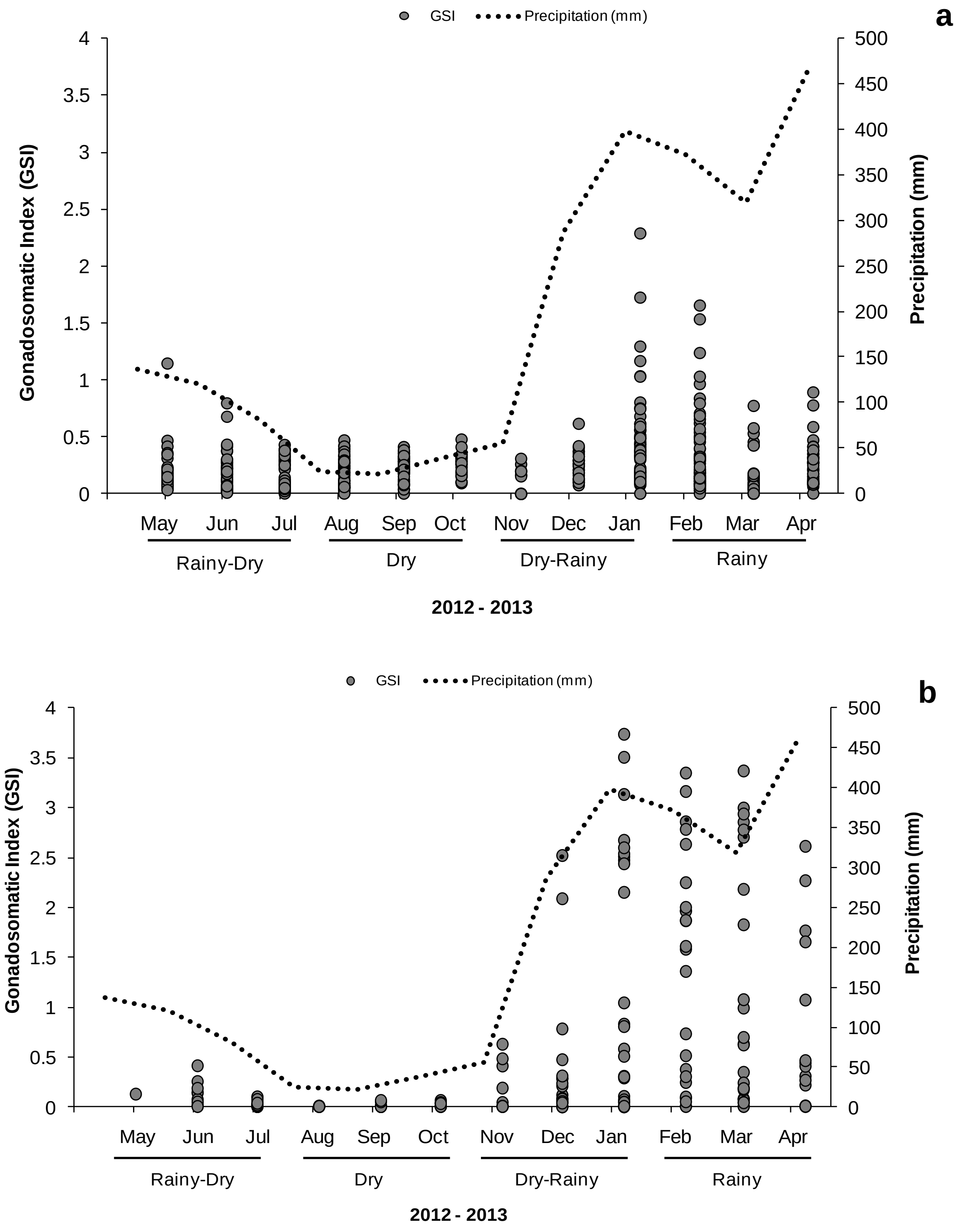
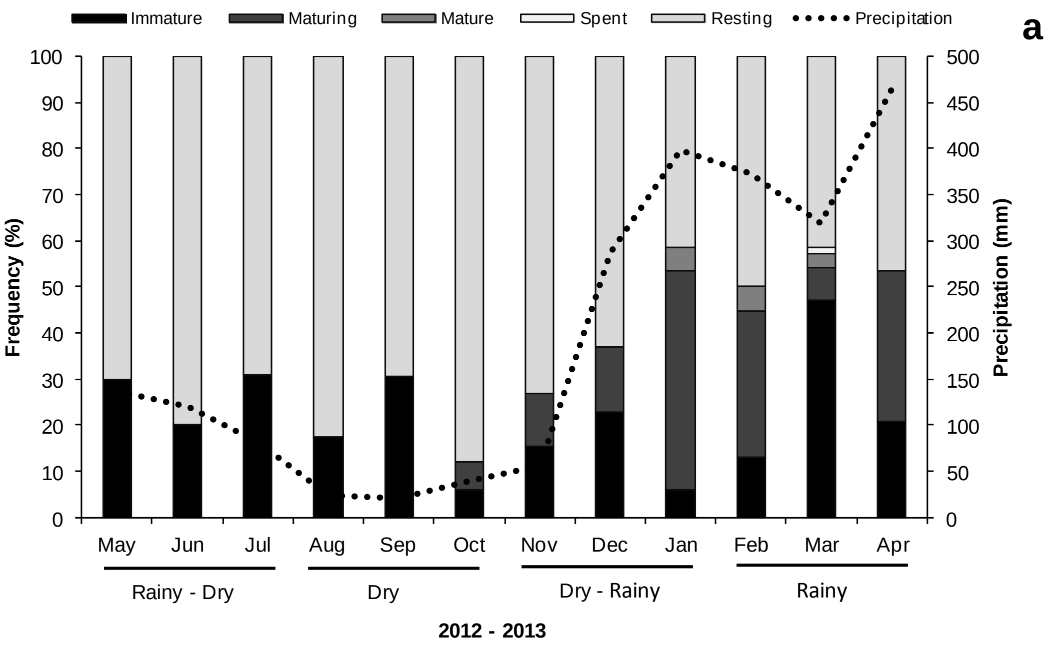


Fig. 9 Monthly variation in the Gonadosomatic Index (GSI) in the female (a) and male (b) *A. ucayalensis* specimens captured in the Anapu ria of the eastern Amazon between May 2012 and April 2013.

Only a weak correlation was found between the GSI scores and the *K* values in females ($r = 0.124$; $p < 0.01$) and males ($r = 0.285$; $p < 0.01$). Sexually mature females were captured only between January and March (Fig. 10 a), the period with the highest rainfall rates. In the males, most individuals were immature (69%) throughout the study period, although mature males were captured from October onwards, and were most common during the same period (January–March) when mature females were found in the population (Fig. 10b).



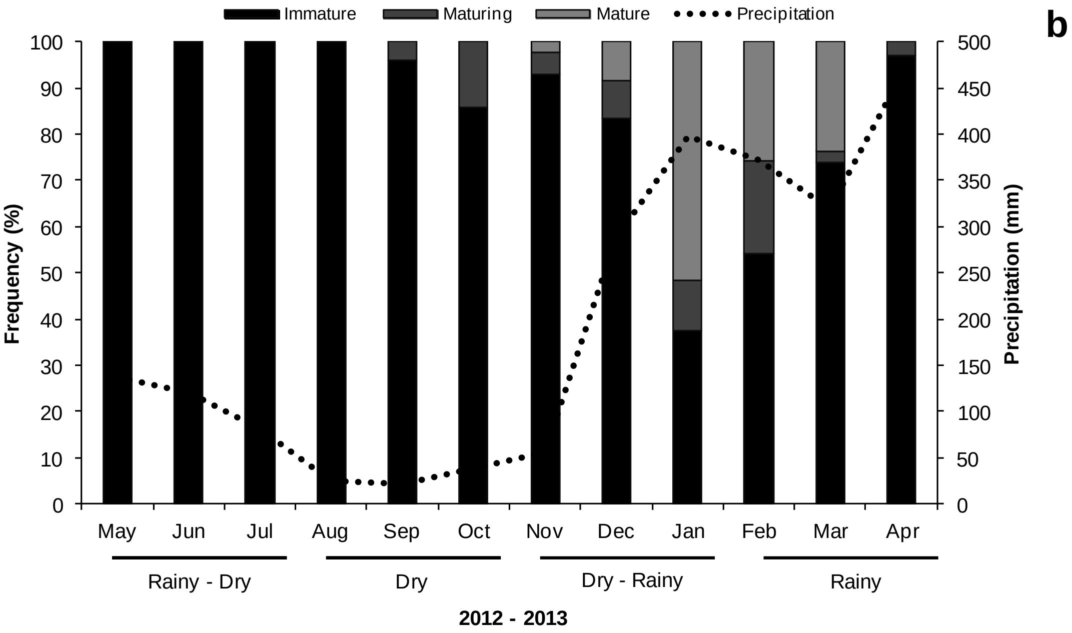


Fig. 10 Monthly variation in the gonadal maturity phases of the female (a) and male (b) *A. ucayalensis* specimens captured in the Anapu ria of the eastern Amazon between May 2012 and April 2013.

The mean length at first sexual maturity was estimated at 12.84 cm (12.53–13.20 cm) for females (Fig. 11a), more than 1.0 cm longer than the value estimated for the males (Fig. 11b), i.e., 11.75 cm (11.67–11.86 cm).

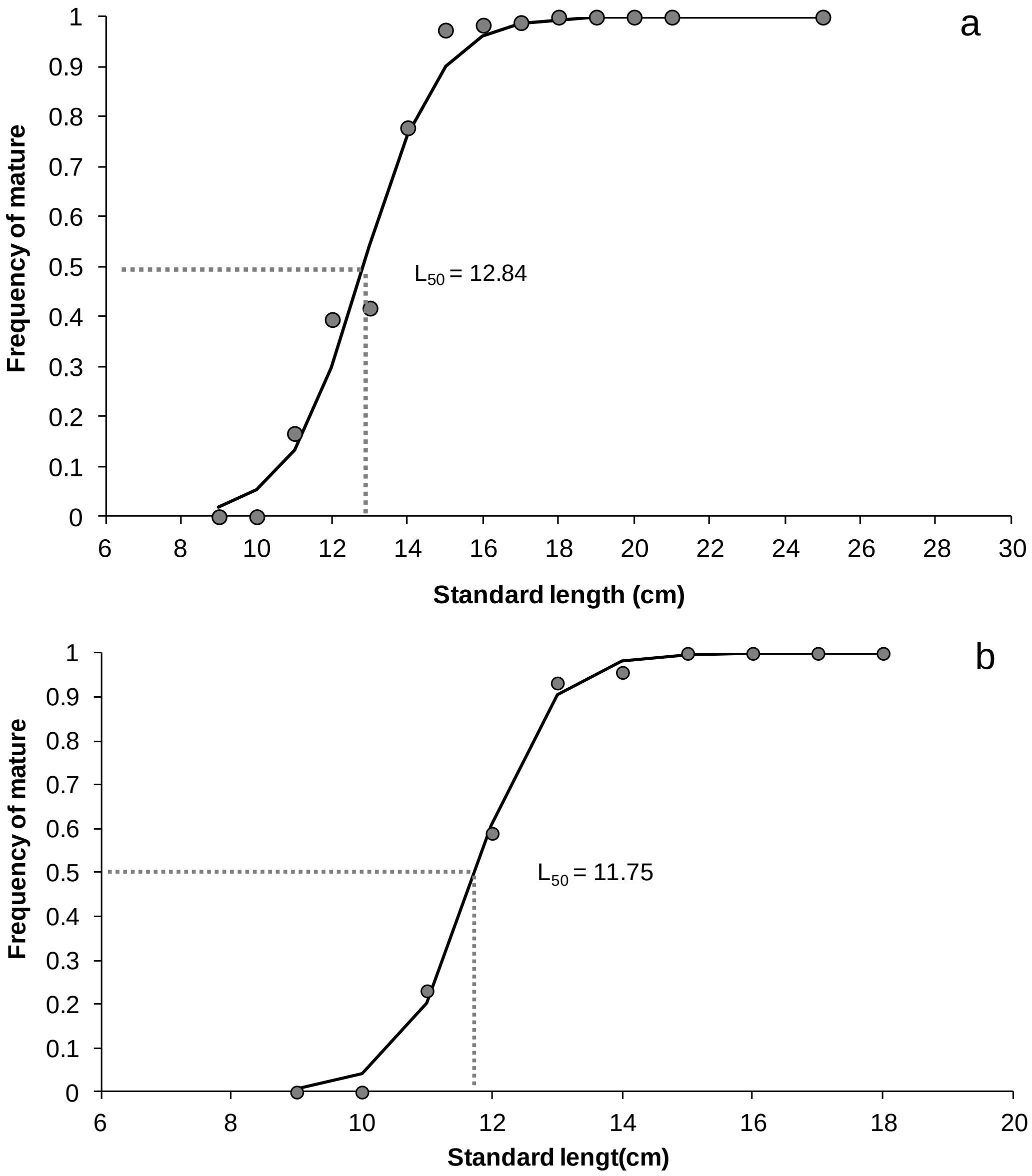


Fig. 11 Estimates of the mean length at first sexual maturity (L_{50}) in the female (a) and male (b) *A. ucayalensis* specimens captured in the Anapu ria of the eastern Amazon between May 2012 and April 2013.

Discussion

The gonadal morphology and internal insemination of the auchenipetid catfish are relatively well known (Meisner et al. 2000; Santos et al. 2014), although the reproductive process has been studied in detail in only a few species (Becker 2001; Freitas et al. 2011; Maia et al. 2013), and little is known of the phenomenon in most

Ageneiosus species. In the present study, the predominance of female *A. ucayalensis* in all size classes, and during all months of the study period may reflect a population-level strategy for the optimization of reproductive success, in which the males fertilize more than one female (Burgess 1989; Prudente et al. 2014).

A predominance of females associated with a pattern of sexual segregation during the spawning period has also been observed in the auchenipterid *Auchenipterichthys longimanus* in the same region as the present study (Freitas et al. 2011). Maia et al. (2013) suggested that the predominance of females in the *Trachelyopterus lucenae* populations of lakes in the southern Brazilian state of Rio Grande do Sul, is a result of the competition between males for access to mature females.

The larger size of the females in comparison with the males in *A. ucayalensis* is a typical pattern in siluriform species (Gomiero and Braga 2007). As larger females are capable of producing larger numbers of oocytes, this would increase fecundity in the population as a whole, and thus the reproductive success of the species (Mai et al. 2007), which may also be enhanced by the internal inssemination characteristic of the auchenipterids (Bailly et al. 2008).

The mass-length relationship indicated negative allometric growth for both male and female *A. ucayalensis*, that is, that body length grows increases at a faster rate than mass. The fact that the allometric relationship was even more negative in the males in comparison with the females may reflect a male strategy for rapid sexual maturation with the aim of gaining access to reproductive females. The variation observed in this parameter may be related to the varying environmental conditions encountered by different populations (Le Cren 1951), or to distinct reproductive strategies.

The variation in the condition factor observed over the course of the study period indicates that it may represent a useful additional parameter for the study of seasonal patterns in the reproductive process in fish (Lima-Júnior et al. 2002; Gomiero and Braga 2007; Braun and Fontoura 2004). No clear correlation was found between the values of *K* and GSI recorded for either female or male *A. ucayalensis* during the study period, contrasting with the pattern found in other auchenipterids, where the two values were inversely proportional (Araújo et al. 1999; Freitas et al. 2011). Santos et al. (2006) found that, in some fish species, the condition factor may vary according to the availability of feeding resources and the exploitation of these resources by the individuals in the population over the course of the year, with no seasonal variation in the growth and development of the ovaries, in contrast with the pattern observed in the present study.

The histological evidence of synchronous oocyte development in *A. ucayalensis* indicates a total spawning pattern in this species (Wallace and Selman 1981; Murua 2003), which is characterized by the synchronized release of the mature oocytes (Vazzoler 1996), and is typical of fishes of large size, migratory habits and/or that spawn on the river bottom. This spawning pattern is consistent with the GSI scores and the observed distribution of the different gonadal phases, which both indicate that reproductive activity is restricted to the rainiest part of the year. This implies that the environmental conditions encountered during this period are the most favorable for the reproductive process. A similar pattern has been described in three other auchenipterids, *Parachenioptterus striatulus, Parachenioptterus galeatus* and *Trachelyopterus lucenai* (Araújo et al. 1999; Medeiros et al. 2003; Maia et al. 2013). Even in species such as *A. longimanus*, which reproduces throughout the year, spawning becomes more intense during the high water period, when conditions are most appropriate for breeding (Freitas et al. 2011).

The annual flood pulse is considered to be the principal environmental factor influencing reproductive patterns in a number of different Amazonian fish species (Bailly et al. 2008). However, in environments such as the lower Anapu River, or ria, where there is little inundation, local rainfall has the greatest influence on water levels, and in turn, on the reproductive pattern observed in many aquatic species.

In environments with a discreet annual flood pulse and well-defined rainy and dry seasons, the spawning period in *Parachenioptérus galeatus* coincided with that of the highest rainfall (Medeiros et al. 2003), as observed in the present study. This may be because, in tropical freshwater systems, fluctuations in precipitation rates constitute the principal abiotic factor affecting ecosystems, due principally to the runoff of nutrients from terrestrial systems, contributing to the increase in feeding resources and the overall enrichment of the aquatic ecosystems during this period (Filho et al. 2012). The levels of dissolved oxygen also increase, and the activity patterns of resident organisms, in particular reproductive processes, are regulated by the proliferaton of microhabitats for nesting and feeding the larvae through the inundation of the floodplain (Agostinho and Júlio 1999; Sánchez-Botero and Araújo-Lima 2001; Leite et al. 2006), even when this process is relatively subtle.

In Amazonian systems with a strong annual flood pulse, the occurrence of *A. ucayalensis* has been associated with the local flood period (Cox-Fernandes and Merona 1988; Sousa and Freitas 2008). On the lower das Mortes River in the Brazilian state of Mato Grosso, Melo et al. (2012) observed that the local auchenipterids undertake lateral migrations to breed, moving into seasonally flooded habitats. However, the reduced numbers of mature females and the absence of spermiated males observed in the present study suggests that, in environments with little seasonal flooding, the local migration in

A. ucayalensis may not be towards the margin, as in other regions, given that mature individuals were captured only in the deep “wells” of Caixuanã Bay.

The estimates of the first sexual maturation for the study species ere consistent with the pattern found in most tropical fish species, in which the males mature at a smaller body size than the females (Barbieri et al. 2004; Nunes et al. 2004; Gomiero et al. 2007; Freitas et al. 2011). This pattern may be related to the greater energy requirements of the reproductive process for the females, in comparison with the males, including gonadal maturation (Bromley 2003). Mean size at first sexual maturity is considered to be an important parameter for the understanding of population dynamics, and the establishment of effective measures for the conservation of natural fish stocks. This parameter is widely used for the definition of the minimum size for the harvesting of the stocks of a given species (Barbieri et al. 2004).

Overall, then, the results of the present study indicates that the intensity of the rainfall on the lower Anapu River, in particular in Caxiuanã Bay, influences the reproduction of *A. ucayalensis*, leading to an increase in the GSI between January and March, when the most intensive rainfall is recorded in the region. The data also indicate that the lateral breeding migration of this species in environments with a negligble floodplain area occurs not in the direction of the margin, but towards the main channel of the river. With these findings, the present study has provided important new data for the understanding of the reproductive biology of the auchenipterids.

Acknowledgments

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CAPÍTULO II

INFLUÊNCIA DA SAZONALIDADE DE CHUVA, SEXO E DA ESPECIALIZAÇÃO INDIVIDUAL NA ECOLOGIA TRÓFICA DE UM BAGRE (AUCHENIPTERIDAE) EM RIOS AFOGADOS, AMAZÔNIA ORIENTAL

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Influence of rainfall seasonality, sex, and individual specialization on the feeding ecology of the duck catfish (Auchenipteridae) in a drowned river system of the eastern Amazon region

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Abstract

A number of studies have shown that the feeding ecology of animal populations may be influenced by both environmental factors and the behavioral, morphological, sexual or ontogenetic characteristics of the species. In this context, the present study investigated the influence of rainfall seasonality, sex, and individual specialization on the feeding ecology of *Ageneiosus ucayalensis* in a drowned river system (ria) of the eastern Amazon region. A total of 919 specimens were collected in monthly captures conducted between May, 2012, and April, 2013, encompassing four distinct rainfall periods (rainy-dry transition, dry season, dry-rainy transition, rainy season). The composition of the diet, feeding intensity, and niche breadth were analyzed in relation to these seasons, sex, and individual specialization. A total of 13 different food items were identified, which were grouped in seven categories. The predominance of fish in the diet and the presence of plant material in the stomach contents led to the classification of the species' diet as carnivorous, with a strong tendency for piscivory. While no significant variation in the composition of the diet was found in relation to rainfall levels or the sex of the specimens, feeding patterns were more variable during the rainy season. Feeding intensity was higher during both the dry and the rainy season, but did not vary between the sexes. In general, niche breadth was consistent with a pattern of specialist feeding behavior, varying discreetly over the course of the year. A high degree of individual specialization was observed in the exploitation of feeding resources. Overall, the results of the present study indicate that, while the feeding ecology of *A. ucayalensis* was unaffected by rainfall patterns or sex, it was influenced by individual specialization.

Key words: Niche breadth; precipitation; individual specialization; catfish.

Introduction

Studies of feeding ecology in natural environments provide data on basic parameters of the biology of a species, providing a baseline for the understanding of the trophic organization of the ecosystem and the quantitative analysis of the mechanisms of interspecific interactions such as predation and competition (Zavala-Camin 1996). A number of studies have shown that the feeding ecology of a species may be influenced by environmental factors, which can provoke both qualitative and quantitative modifications in the availability of resources over the course of the year (Hahn et al. 1997; Abelha et al. 2001; Ximenes et al. 2011), in addition to the biology of the species, given that its behavioral and morphological characteristics are fundamental determinants of its ability to exploit specific types of feeding resource (Ehlinger 1990; Wootton 1998).

The composition of the diet may vary considerably during the life cycle in many fish species, especially during growth and development (Hahn et al. 2000; Ortêncio-Filho et al. 2001; Lima-Junior and Goiten 2003), or when different types of feeding resource become available (Lowe-McConnell 1987; Abelha et al. 2001), resulting in seasonal (Hahn et al. 1997) and/or spatial (Abujanra et al. 1999) differences in the diet of the species. Variation in the feeding behavior of different individuals may also contribute to the diversity of feeding patterns within a given population, with different individuals or groups exploiting distinct subsets of the resources available in the environment (Bolnick et al. 2003), irrespective of their sex or age class, and even at the same site and during the same period. This variation among individuals is known as individual specialization and may have important implications for the development of resource-sharing mechanisms (Bolnick et al. 2003, 2011; Araújo et al. 2005).

Variation in rainfall rates is also considered to be an important factor determining feeding ecology patterns in tropical species, given that resources tend to increase during the rainy season in most aquatic systems, as the adjacent forests are flooded with waters carrying allochthonous material (Prejs and Prejs 1987; Hahn et al. 1997; Resende 2000; Rezende and Mazzoni 2005). Variation in habitat structure may also influence feeding strategies by determining the spatial distribution of different resources (Hajisamae et al. 2003), which in turn will influence the availability of resources for a species in a given type of habitat (Hajisamae 2009).

The region of the lower Anapu River, in the eastern Amazon basin, is a drowned river valley or ria, unique among Amazonian ecosystems, which is characterized by the loss of most of its floodplain area, and a barely noticeable annual flood pulse (Costa et al. 2002). The duck catfish *Ageneiosus ucayalensis* Castelnau, 1855 is one of the most abundant fish species in this region (Montag, 2006). This species is widely distributed in South America, being found throughout the Amazon and Orinoco basins, as well as the river systems of the Guianas, and the upper Paraná River (Ferraris-Jr 2003). The species has been classified as a carnivore (Sá-Oliveira et al. 2014).

Given the prominent role of carnivorous species in the food chain and the intrinsic characteristics of the region of the lower Anapu River, the present study focused on the feeding ecology of the local population of *A. ucayalensis* in the context of the annual variation in precipitation rates, the sex of the specimen, and individual specialization. Feeding intensity was predicted to increase during the rainy season. In addition, differences were predicted in the composition of the diet of males and females, and individual specializations were assumed to affect patterns of resource use. The present study provides important new data on the feeding ecology and bionomics of *A. ucayalensis*, essential information for the conservation of the species and the ecosystems it inhabits.

Material and methods

Study area

The specimens of *A. ucayalensis* were collected in Caxiuanã Bay, on the lower Anapu River, between the Tocantins and Xingu rivers, in the municipalities of Melgaço and Portel, in Pará, Brazil. The Caxiuanã National Forest (Figure 1) – one of the largest federal conservation units in the state of Pará – is located on the left margin of the lower Anapu (1º42’30” S, 51º31’45” W).

The region’s climate is humid tropical, with mean annual precipitation of approximately 2020 mm (Moraes et al. 2009). Precipitation data from the Caxiuanã National Forest for the period between April, 2012, and May, 2013, were collected during the ESECAFLOR/LBA/TEAM project. These data were used to classify the climatic seasons as rainy-dry transition (May–July), dry season (August–October), dry-rainy transition (November–January), and rainy season (February–April). The region's rivers are typical black-water bodies of water, with little fluctuation in river levels, which rarely exceed one meter (Sioli 1984; Hida et al. 1999).

Caxiuanã Bay has a gradient of one meter per kilometer, sloping gently down from the left margin to the center of the bay and then closer to the right margin, where it attains a depth of 6 m to7 m. At this point, there is a submerged valley, known locally as "wells", which may reach a depth of approximately 20 m (Costa et al. 2002).

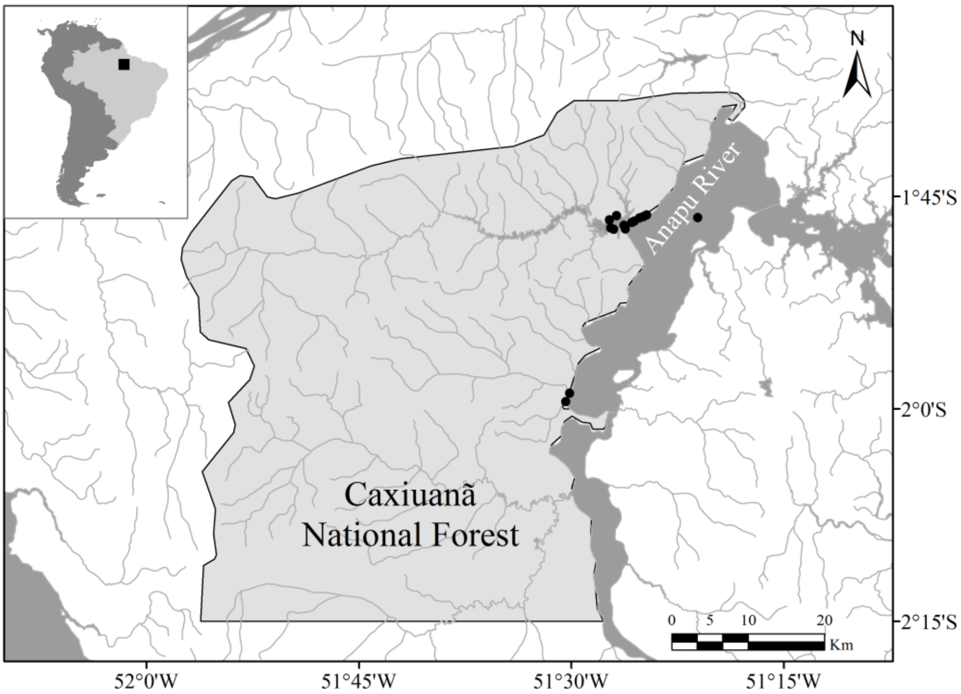

Fig.1 Region of the lower Anapu River, showing the Caxiuanã National Forest and the collecting localities (black circles) in Caxiuanã Bay.

Data collection and analysis

Specimens of *A. ucayalensis* were collected each month between May, 2012, and April, 2013 in gillnets of different mesh sizes (15, 20, 25, 30, 35, and 40 mm between opposing knots), with standard dimensions of 10 m in length by 1.5 m in height. The nets were set close to the margin of the bay or river at dusk, and left for four hours. During the day, the nets were set at specific sites (wells) for 10 minutes, with lead weights being attached to each extremity of the set of nets, which were attached to buoys with a 5-m long line, in order to facilitate the identification of the position of the nets so that they could be found and removed at the allocated time.

Following collection, all the specimens of *A. ucayalensis* were sexed, their standard length (L_S): the distance between the tip of the snout and the caudal peduncle was measured in centimeters and they were weighed (in grams) before being eviscerated. The viscera were removed through a longitudinal incision made in the ventral region of each specimen, for the extraction of the stomach and the gonads (for the identification of the sex of the specimen). The mass of each stomach (M_s) was determined in grams and the organ was conserved in 70% ethanol for the subsequent analysis of its contents.

The stomach contents were analyzed under a stereomicroscope and the items were identified to the lowest possible taxonomic level based on the specialist literature (Ruppert and Barnes 2005; Costa et al. 2006) and through consultation with specialists. The items were weighed on a precision balance with an accuracy of 0.001 g.

Each item found in the stomach contents was analyzed in terms of its frequency of occurrence, $\mathrm{FO_i}\%$ (Hyslop 1980), and mass, $\mathrm{M_i}\%$ (Hynes 1950). These parameters were used to obtain the Alimentary Importance index, $\mathrm{AI_i}\%$ (Kawakami and Vazzoler 1980), which is given by the equation $AI_i\ \% = (FO_i\% * FM_i\%/\sum FO_i\% * FM_i\%) * 100$**,** where: $AI_i\%$ = the alimentary importance of item *i*, $FO_i\%$ = the frequency of occurrence of item *i*, and $M_i\%$ = the mass of item *i*.

In order to evaluate the seasonal variation in the composition of the diet of *A. ucayalensis*, and possible differences between males and females, the feeding items were grouped into seven categories – allochthonous arthropods, plant fragments (non-reproductive), seed, autochthonous insects, crustaceans, other invertebrates, and fish. This adjustment was applied in order to guarantee the robustness of the analyses, given the extremely low frequency of some items.

The data were analyzed and organized using a non-metric multidimensional scaling (NMDS) approach (Clarke and Warwick 2001). For this, the values of the alimentary indices for each feeding category were log-transformed for the establishment of a similarity matrix based on the Bray-Curtis coefficient of similarity and then grouped using a cluster analysis. This analysis evaluated the distortion or stress between the similarity matrix and the clustering pattern found in the graphic representation of the axes, providing a measure of reliability for the interpretation of its results (Clarke and Warwick 2001).

A Permutational Multivariate Analysis of Variance (PERMANOVA, based on the Bray-Curtis index with 9999 random permutations) was used to test the hypotheses that precipitation levels or the sex of the individual influenced the composition of the diet of *A. ucayalensis*. This nonparametric approach tests the differences among predefined multivariate groups (Anderson 2001).

In order to assess feeding intensity, the stomach repletion index (*RI%*) was calculated for each specimen, based on the equation presented by Santos (1978): $IR\% = (M_s/M_t) * 100$, where M_s = mass of the stomach and M_t = total mass of the individual (Zavala-Camin 1996).

To test the hypothesis that the feeding intensity of *A. ucayalensis* varied seasonally, the *RI%* values were analyzed using a one-way ANOVA, followed by Tukey’s post hoc test for pairwise comparisons. Variation in feeding intensity related to the sex of the specimens was tested using Student's *t*. In all cases, the data were tested prior to analysis to determine whether they adhered to the assumptions required for each procedure (Zar 1999). Values identified as outliers were excluded from the analyses, all of which were based on a 5% significance value.

Niche breadth (dietary amplitude) was calculated using Levin's standardized index (Hurlbert 1978), which varies from 0, when the species consumes only a single type of item, to 1, when a number of different items are exploited in equal quantities. Niche breadth (*Ba*) is found by $Ba = [(\sum_j P^2_{ij})^{-1} - 1]\ (n - 1)^{-1}$, where *Ba* = feeding niche breadth, P_{ij} = the proportion of item *j* in the diet of species *i*, and n = the total number of feeding items (categories). The observed variation in niche breadth was evaluated descriptively in the context of the observed variation in rainfall levels. A simple linear regression was used to determine whether there was a relationship between the degree of feeding specialization and the number of individuals.

Variation in the diet within the population was determined by comparing the distribution of resource use by each individual with that of the population as a whole using a Proportional Similarity Index, or PS_i (Bolnick et al. 2002). The overlap between the diet of an individual and that of the population was defined by $PS_i = 1 - 0.5\ \Sigma_j \mid p_{ij} - q_j \mid = \Sigma_j\ min(p_{ij} - q_j)$, where p_{ij} = the frequency of item *j* in the diet of individual *i*, and *qj* = the frequency of item *j* in the diet of the population as a whole. When an individual specializes in a single item (*j*), the PS_i is equal to the value of *qj*. When PS_i is equal to 1, individual specialization is low, and when it is equal to 0, specialization is high. For the purposes of the present study, PS_i values of less than 0.6 were considered to represent high levels of individual specialization.

Trophic connections were visualized by constructing bipartite networks between individuals and dietary items for each seasonal period. The links identified by this analysis were used to calculate indices of connectivity (Dunne et al. 2002), niche overlap (Yodzis and Winemiller 1999), density of links, and the number of nodes (Vermaat and Dunne 2009). The networks and parameters were produced in the *bipartite* package (Dormann et al. 2008) of the R program (R Development Core Team 2011).

Results

The stomachs of 919 specimens were analyzed in the present study, of which, 672 were female, and 247, male. However, 75% (505) of the stomachs of the female specimens were empty, as were 68% (169) of those of the male specimens. These specimens were thus excluded from the analyses of dietary importance and niche breadth, although they were included in the analysis of feeding intensity. The standard length of the females varied from 9.9 cm to 21.8 cm, and that of the males, from 9.5 cm to 18.1 cm.

The diet of *A. ucayalensis* was made up of 13 items, of which six (46.15%) were of allochthonous origin, while the other seven (53.85%) were autochthonous. This catfish fed primarily on other fish (AI% = 69.49%), crustaceans (AI% = 18.36%), mainly crab and shrimp, and arthropods (AI% = 8.36%). All other categories (plant fragments, seeds, aquatic insects, and miscellaneous aquatic invertebrates) returned AI% values of less than 4% (Table 1). Given the degree of trituration and digestion of the items found in the stomach contents, it was not possible to identify the taxonomic order of the fish fragments found in the samples.

Table 1 – Alimentary Importance indices (AI%) for the food items in the diet of the catfish *Ageneiosus ucayalensis* captured in the Anapu ria of the eastern Amazon between May 2012 and April 2013.

Food Itens	**2012**								**2013**				**General**
	Rainy-Dry			**Dry**			**Dry-Rainy**			**Rainy**			
	May (N=25)	**Jun** (N=13)	**Jul** (N=12)	**Aug** (N=52)	**Sep** (N=25)	**Oct** (N=33)	**Nov** (N=2)	**Dec** (N=7)	**Jan** (N=4)	**Fev** (N=28)	**Mar** (N=21)	**Apr** (N=23)	
Allochthonous													
Arthropods	**0,86**	**0,44**	**-**	**2,22**	**2,61**	**10,28**	**-**	**-**	**82,41**	**59,82**	**78,05**	**1,20**	**8,36**
Aracnida (Araneae)	-	-	-	0,06	-	-	-	-	9,45	-	-	-	0,00
Coleoptera	0,42	-	-	-	0,11	5,54	-	-	-	0,18	0,32	-	0,82
Hemiptera (Naucoridae)	0,00	-	-	-	-	-	-	-	-	54,74	-	-	0,82
Terrestrial insects fragments	0,02	0,44	-	1,25	1,53	0,57	-	-	60,63	0,00	84,27	1,97	0,57
Plant	**-**	**0,07**	**1,43**	**62,10**	**13,65**	**0,05**	**-**	**0,00**	**-**	**0,01**	**-**	**0,07**	**0,42**
Plant fragments	-	0,07	2,62	62,67	13,78	0,06	-	0,00	-	0,02	-	0,12	0,51
Seed	-	6,33	-	1,29	0,05	-	-	0,00	-	-	0,24	-	**0,03**
Plant fragments (seed)	-	6,33	-	1,30	0,05	-	-	0,00	-	-	0,30	-	0,04
Autochthonous													
Aquatic insects	**2,09**	**25,43**	**6,42**	**22,93**	**78,76**	**0,32**	**-**	**0,00**	**17,59**	**5,46**	**18,59**	**-**	**3,34**
Aquatic insects fragments	0,08	25,43	11,81	23,14	79,54	0,43	-	0,00	29,92	2,18	7,86	-	1,34
Odonata larvae	0,83	-	0,00	-	-	-	-	0,00	-	1,11	3,41	-	0,33
Crustacea	**8,15**	**1,39**	**91,34**	**0,16**	**2,80**	**34,00**	**100,00**	**99,99**	**-**	**0,92**	**-**	**95,14**	**18,36**
Brachyura	3,73	-	-	0,16	-	14,16	-	99,99	-	-	-	72,25	7,85
Caridea	0,96	1,39	0,50	-	2,82	4,06	100,00	0,00	-	1,11	-	19,76	3,01
Isopoda	-	-	83,55	-	-	0,25	-	-	-	-	-	-	0,05
Other aquatic invertebrates	**-**	**0,02**	**-**	**-**	**0,01**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**0,00**

Annelida	-	0,02	-	-	0,01	-	-	-	-	-	-	-	0,00
Fish	**88,90**	**66,31**	**0,82**	**11,31**	**2,13**	**55,35**	**-**	**-**	**-**	**33,79**	**3,12**	**3,59**	**69,49**
Fish fragments	93,96	66,31	1,51	11,41	2,15	74,93	-	-	-	40,67	3,85	5,90	84,66

While neither the NMDS analysis nor the results of the PERMANOVA (Fig. 2) indicated any significant variation in the composition of the diet over the course of the year (Pseudo-F = 1.029; d.f. = 3; p = 0.426), there is a marked tendency for the exploitation of allochthonous arthropods during the rainy season (30.0%), plant fragments (33.9%) and aquatic insects (23.8%) during the dry season, and crustaceans (60.0%) during the dry-rainy transition. No significant difference was found between males and females in the composition of the diet (Pseudo-F = 1.777; d.f. = 1; p = 0.196).

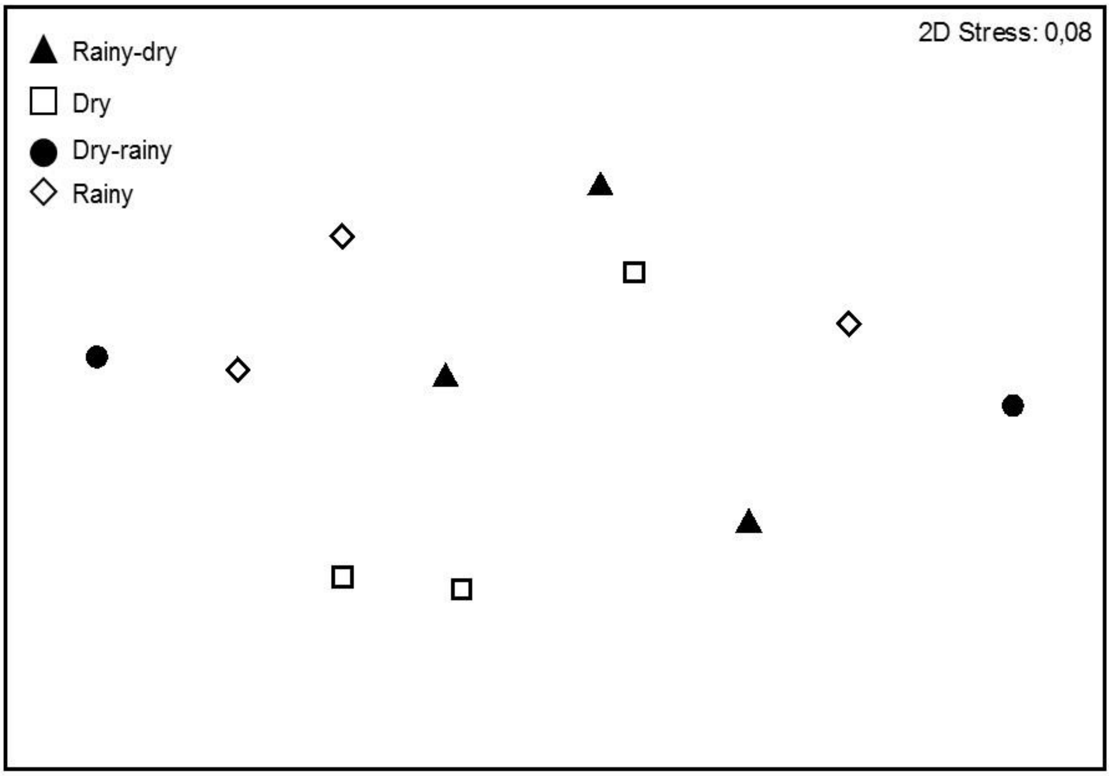

Fig. 2 Graphic representation of the non-metric multidimensional scaling analysis (NMDS) of the diet of the duck catfish *Ageneiosus ucayalensis* captured in the Anapu ria of the eastern Amazon in relation to the climatic season between May 2012 and April 2013.

The feeding intensity of *A. ucayalensis* varied significantly among seasons ($F_{(3, 904)}$= 47.559; p < 0.01) (Fig. 3). On average, the repletion index for the rainy-dry season transition was 0.5 lower than that recorded for the rainy-dry season transition (Tukey p < 0.001), 0.6 lower than that found during the dry season (Tukey; p < 0.001), and 0.7 lower than that recorded during the rainy season (Tukey; p < 0.001). The repletion index (RI%) for the dry-rainy season transition period was 0.4 higher, on average, than that recorded for the rainy-dry transition (Tukey; p < 0.001) and 0.2 lower than that recorded for the rainy season (Tukey; p < 0.005). However, the sex of the specimen did not affect feeding intensity (*t* = 0.713; d.f. = 917; p = 0.475).

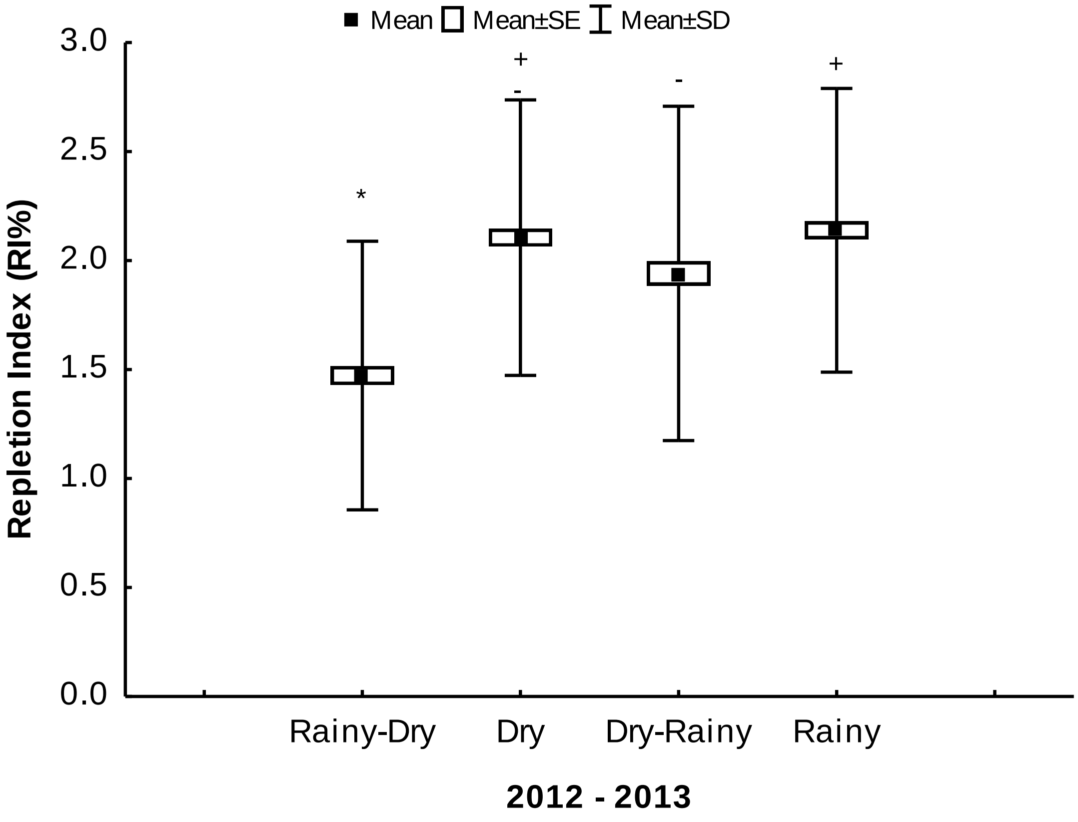

Fig. 3 Seasonal variation in the Repletion Index (RI%) of the duck catfish *Ageneiosus ucayalensis* captured in the Anapu ria of Eastern Amazon between May 2012 and April 2013. Values marked by different symbols are significantly different.

The diet of the *A. ucayalensis* population in the study area reflected the essentially specialist feeding behavior of the species, which is reflected in reduced levels of niche breadth (< 0.5). However, niche breadth did vary considerably over the course of the year (Fig. 4).

The diet of *A. ucayalensis* was less specialized during the dry (*Ba* = 0.50 in August) and rainy seasons (*Ba* = 0.32 in February), and the rainy-dry transition period (*Ba* = 0.32 in June). The lowest values of niche breadth were recorded during the dry-rainy transition period (*Ba* = 0.00 in November and December), with a diet composed exclusively of crustaceans (AI_i% = 100).

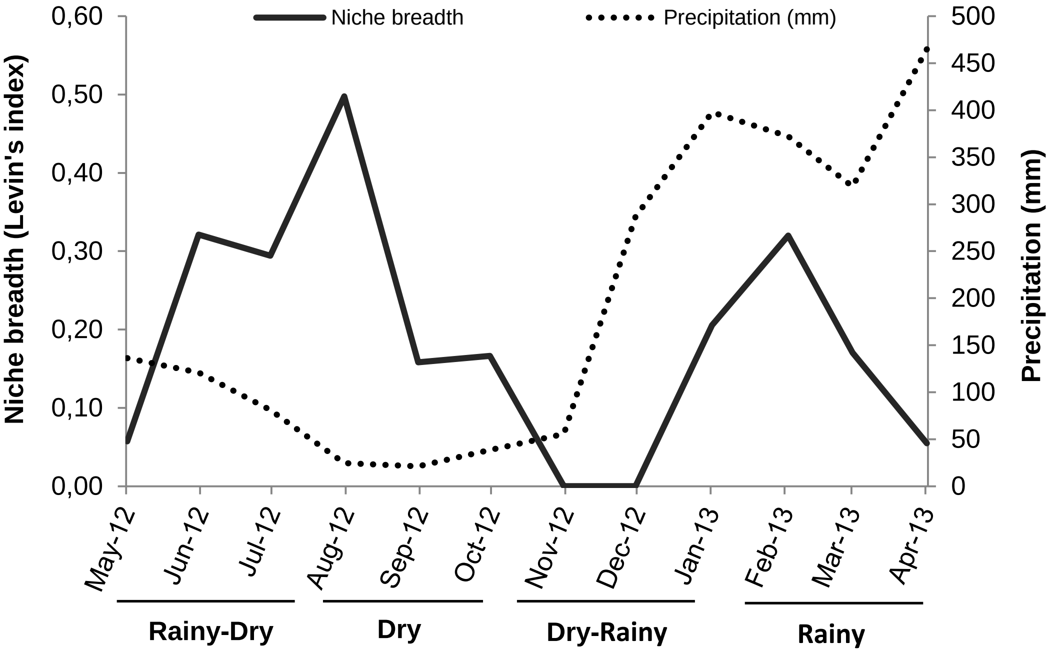

Fig. 4 Seasonal variation in feeding niche breadth in the duck catfish *Ageneiosus ucayalensis* captured in the Anapu ria of the eastern Amazon between May 2012 and April 2013.

In general, males and females presented the same pattern of variation in niche breadth during the course of the year. However, males tended to be less specialized (Ba = 0.24) than the females (Ba = 0.16).

The analysis of individual specialization indicated high levels of individual specialization in the population during the rainy-dry transition period ($PS_i = 0.20$), and the dry ($PS_i = 0.23$) and rainy seasons ($PS_i = 0.23$). These values reflect the greater intraspecific variation in the exploitation of items during these periods, in comparison with the dry-rainy transition, when $PS_i = 0.50$.

The trophic network in the dry season (Table 2) was the largest recorded in the study, with the highest number of nodes (115) and density of links (12.93) in comparison with the other periods sampled. The dry season presented the highest connectivity (0.22) and niche overlap (0.46).

Table 2 – Quantitative parameters of the bipartite networks produced for the four climatic periods covered by the present study. The highest values of each parameter are shown in bold type.

Period	Connectivity	Niche overlap	Linkage density	Number of nodes
Rainy-dry transition	0.16	0.17	5.11	55
Dry season	0.16	0.22	**12.93**	**115**
Dry-rainy transition	**0.22**	**0.46**	3.79	18
Rainy season	0.17	0.22	3.68	32

The graphic representations of the bipartite networks produced from the data on the *A. ucayalensis* population was composed of individual modules with low niche breadth (indicating specializations for different items), irrespective of the season analyzed. However, the rainy-dry transition (Fig. 5a) and the dry season (Fig. 5b) were the periods which had items with the largest numbers of links. These links were represented by the categories crustaceans, autochthonous insects, arthropods, other autochthonous invertebrates, seeds, and plant fragments. Only a single type of link was found in the dry-rainy transition (Fig. 6a) and rainy season (Fig. 6b), however, represented by the items crustaceans and plant fragments, in both periods.

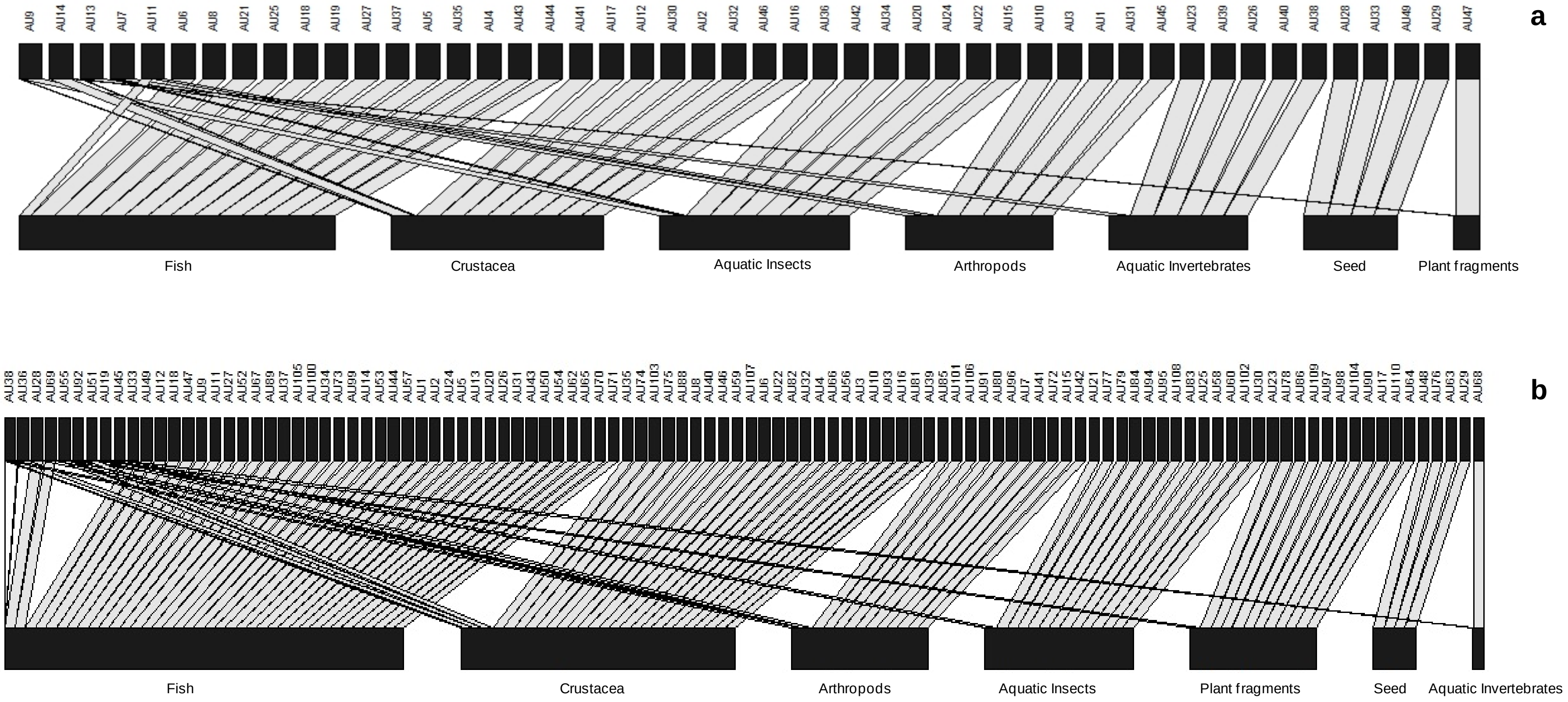

Fig. 5 - Graphical representations of the bipartite networks for the food items found in the diet of the *Ageneiosus ucayalensis* specimens captured in the (a) rainy-dry transition and (b) dry season in the Anapu ria of the eastern Amazon.

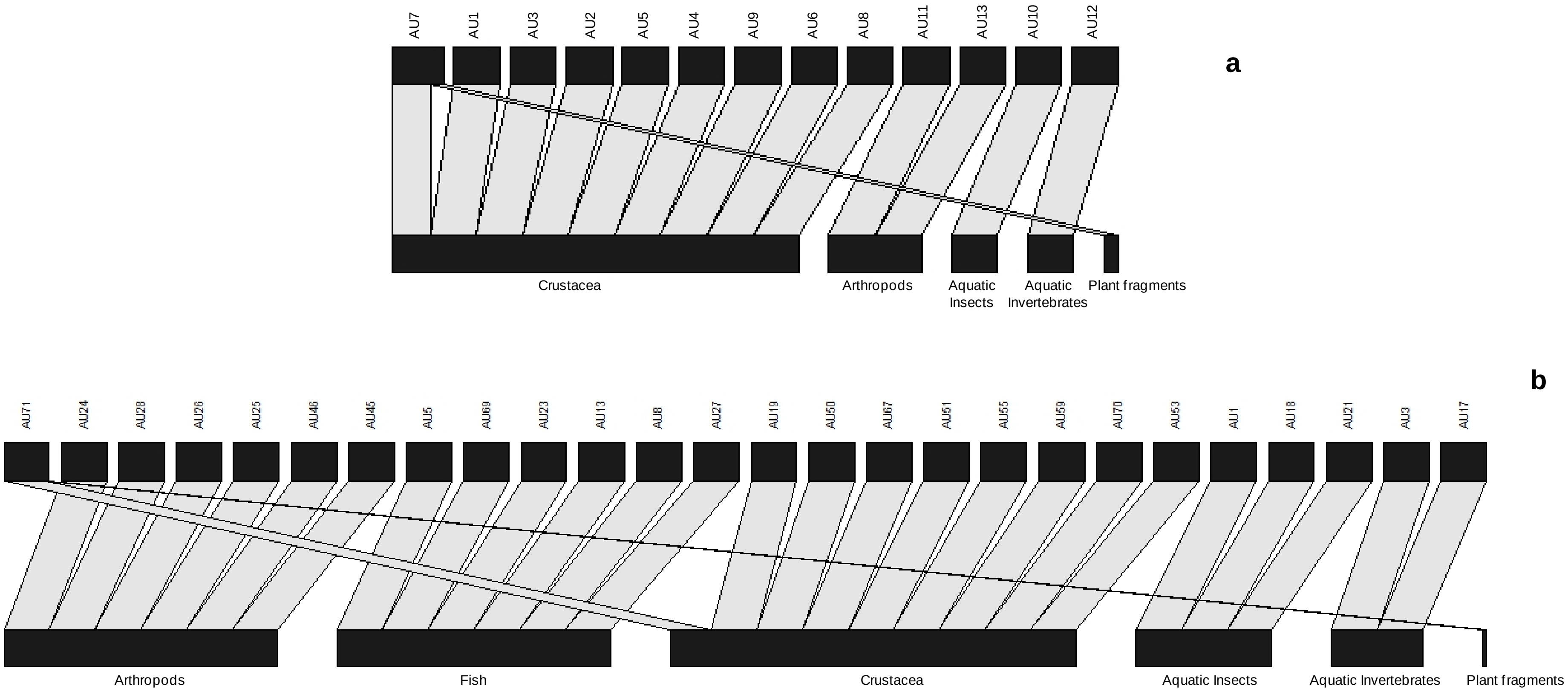

Fig. 6 - Graphical representations of the bipartite networks for the food items found in the diet of the *Ageneiosus ucayalensis* specimens captured in the (a) dry-rainy transition and (b) rainy season in the Anapu ria of the eastern Amazon.

Discussion

The *A. ucayalensis* population of Caxiuanã Bay was primarily piscivorous. However, the specimens had also consumed crustaceans, terrestrial arthropods, aquatic insects and other invertebrates. Considering this, the study population was characterized as carnivorous, with a strong tendency for piscivory. The plant fragments, including seeds, found in the stomach contents may have been ingested accidentally, already had low importance feed.

The composition of the diet of *A. ucayalensis* recorded in the present study is consistent with of auchenipterid species, although some variation was found in the relative contribution of fish and invertebrate items. Sá-Oliveira et al. (2014) classified the diet of the *A. ucayalensis* population of the Coaracy Nunes reservoir on the Araguari River as carnivorous, given that is diet was composed primarily of microcrustaceans of the order Isopoda, decapod crustaceans, and fragments of fish. However, a purely piscivorous diet was recorded for *Ageneiosus brevifilis* in Venezuela (Duque and Winemiller, 2003). Omnivory with a tendency for insectivory, has been recorded in *Parauchenipterus galeatus* by Andrian and Barbieri (1996), in *Trachelyopterus striatulus* by Dias et al. (2005), *Trachelyopterus lucenai* (Moresco and Bemvenuti, 2005; Maia et al., 2013), and in *Auchenipterichthys longimanus* by Freitas et al. (2011). This variation in the feeding behavior of the auchenipterids may be related to the morphological diversity of the species belonging to the subfamilies Auchenipterinae and Ageneiosinae, given that the morphology of a species determines the resources it can exploit, given that its capacity to feed on specific items will be related to its foraging strategy, mouthparts, and digestive adaptations (Wootton 1998; Araújo et al. 2005; Correa et al. 2009).

The composition of a fish's diet will be determined by the interaction between its alimentary preferences, and the availability and accessibility of different items in the environment (Wootton 1998; Abelha et al. 2001; Correa and Winemiller 2014). This will determine the trophic plasticity of a species in the context of variations in water levels (Claro-Jr et al. 2004; Luz-Agostinho et al. 2008; Freitas et al. 2011), rainfall intensity (Ballesteros et al. 2009), the availability of resources (Vidotto-Magnoni and Carvalho 2009), and intra- and interspecific competition (Fugi et al. 2008), all of which cause variations in the availability of feeding resources, especially in tropical environments.

In the present study, a tendency was found for a reduction in the ingestion of autochthonous items (fish fragments) and an increase in that of allochthonous items (terrestrial arthropods) during the rainy season. This may have been a strategy adopted to optimize foraging, given the reduction in visibility caused by the increase in the turbidity of the water during this period (Abrahams and Kattenfeld 1997; Arcova and Cicco 1999), which would make the capture of fish prey relatively costly, in energetic terms. However, rising water levels during this period result in the flooding of the adjacent forest, albeit to a limited extent in the Caxiuanã region, as well as an increase in the input of resources, resulting in an expansion in the availability of allochthonous items (Abelha et al. 2001; Stoner 2004; Cenzano and Wurdig 2006; Winemiller et al. 2008).

Many fish species modify their diets – either partly or completely – over the course of the year and the different climatic seasons (Prejs and Prejs 1987; Mazzoni and Rezende 2003), with feeding intensity generally increasing during the rainy season, when the availability of prey tends to expand (Prejs and Prejs 1987). This pattern was not observed in the present study, however, where the feeding intensity of *A.*

ucayalensis was highest in both the rainy and dry seasons. This is probably related to the reduced area of floodplain forest found in this region (Costa et al. 2002), which may suppress the rainy season increase in the availability of resources typical of other Amazonian river systems.

As the male and female *A. ucayalensis* presented virtually the same diet and feeding intensity, it seems likely that the species does not segregate seasonally or spatially within the study area. Freitas et al. (2011) recorded a similar pattern in *A. longimanus* in the same area, that is, a lack of any significant variation in the composition of the diet between the sexes. It thus seems likely that the lack of sexual dimorphism in the auchenipterids is reflected in the adoption of the same foraging strategies, and that the energetic investment in the reproductive process is similar in males and females, given that the gonads of both sexes occupy a considerable portion of the abdominal cavity.

However, sexual differences in feeding strategies and the composition of the diet have been recorded in other fish species. In *Limanda limanda*, for example, Temming and Hammer (1994) observed differences between males and females in diurnal feeding rates. Oxenford and Hunte (1999) found that male *Coryphaena hippurus* ingested a higher proportion of fast-swimming prey than the females. Many of these differences may be associated with sexual dimorphism in both morphology and ecology (Magurran and Garcia 2000), as well as contrasts in the energetic requirements of the reproductive process (Belovsky 1978), given that the maturation of the oocytes tends to demand more energy than the gonadal development of the males (Jonsson et al. 1997; Huntingford et al. 2001). The results of the present study indicate that the morphological dimorphism found in *A. ucayalensis*, characterized by the presence of a gonopod and an aculeus on the dorsal fin in the males, does not influence the exploitation of feeding resources, in other words, that there is no sexual dimorphism in the feeding ecology of the species.

The general niche breadth recorded for *A. ucayalensis* was low due to the high levels of piscivory. A similar pattern has been recorded in other predominantly piscivorous fishes in swamp lakes in Bolivia and Brazil (Pouilly et al. 2004; Bozza and Hahn 2010), suggesting the niche breadth may be reduced when piscivorous feeding behavior predominates. It is important to note, however, that considerable fluctuations in niche breadth were recorded during the course of the present study period. This is consistent with optimal foraging theory, which predicts that, when resources are abundant, predators will concentrate on the items with the best benefit-cost ratio, and have narrower niches (Abelha et al. 2001). When these prey items become scarcer, other items will be added to the diet and the species will become more opportunistic (Claro-Jr et al. 2004; Ceneviva-Bastos and Casatti 2007). This will occur even in species with highly specialized diets (Abelha et al. 2001).

The fact that the diet of *A. ucayalensis* was composed almost entirely of brachyurans during the dry-rainy season transition (November and December) may have been a result of the low number of individuals with stomachs with food items or a response to fluctuations in the abundance of the resources available to this species. Warburton et al. (1998) recorded a similar pattern in *Bidyanus bidyanus*, which had a highly specialized diet during a period of two to four weeks, after which its feeding habit shifted in response to fluctuations in the abundance of resources. This reinforces the conclusion that alterations in the environment may provoke changes in the feeding ecology of a species. Novakowski et al. (2008) concluded that the exploitation of resources does not follow any universal pattern, but rather reflects the different behavioral strategies adopted by the species in response to fluctuations in the conditions encountered in each ecosystem.

The high degree of individual specialization recorded in the present study may reflect a population-level strategy for the reduction of the intensity of intraspecific competition. Svanbäck and Bolnick (2007) confirmed that competition for resources may lead to an increase in the variability of the composition of the diet in different individuals of the same population, with individual specialization being related positively with population density, as observed in the case of *A. ucayalensis*, which is extremely abundant in Caxiuanã Bay (Montag 2006) and presents a high degree of individual specialization. In addition, individuals that vary in their use of resources would be expected to suffer differential effects of interspecific competition (Bolnick et al. 2003), and thus tend to be more stable over time (Lomnicki 1992).

The graphic representations of the bipartite networks indicate that the population of *A. ucayalensis* is composed primarily of individuals specialized for the exploitation of different dietary items, reinforcing the high degree of individual specialization recorded for the species. It was also possible to confirm that the degree of overlap in the exploitation of different items varies in accordance with rainfall intensity. However, it was not possible to establishment a systematic comparison with other studies, given that bipartite networks have generally been used to analyze community-level trophic relationships (Rosa 2011).

Overall, then, the present study has provided a fundamental contribution to the understanding of the feeding ecology of the catfish *A. ucayalensis*, one of the most abundant fish species found in Caxiuanã Bay. The results of this study have shown that environments with lentic characteristics, in which abundance is high, the species may adopt a high degree of individual specialization in the exploitation of feeding resources as a strategy for the reduction of competition. The results also indicate that the species is carnivorous, with a strong tendency for piscivory in the study area, but that neither precipitation levels nor the sex of the individual have any marked effect on the composition of the diet.

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CAPÍTULO III

ANATOMIA E HISTOLOGIA DO SISTEMA REPRODUTOR DE MACHOS DE UM BAGRE AMAZÔNICO, EVIDÊNCIAS DE INSEMINAÇÃO

Oliveira, V. A., Gonçalves, L. A.B., Rocha, R. M., Montag, L. F. A.

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Anatomia e histologia do sistema reprodutor de machos de um bagre amazônico, evidências de inseminação

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Resumo

A morfologia testicular, espermatogênese e ocorrência de esperma no lúmen ovariano de *Ageneiosus ucayalensis* foi estudada, usando anatomia e técnicas histológicas. Foi coletado um total de 108 machos em diferentes estádios de maturação e 124 fêmeas em atividade reprodutiva. Esses espécimes foram coletados no rio Anapu, na Amazônia Oriental, com o uso de redes de emalhar com diferentes tamanhos de malha. Os machos adultos apresentaram gonopódio, que teve como função transferir o esperma para o interior da cavidade ovariana. Os testículos foram órgãos pareados, apresentando franjas na região cranial e um ducto espermático comum na região caudal. Histologicamente, as franjas craniais desenvolveram atividade espermática, enquanto o ducto desempenhou função secretora, evidenciada pela presença de espermatozoides e de secreção. A inseminação foi confirmada pela presença de espermatozoides no lúmen ovariano. A ausência de oócitos vitelogênicos fertilizados nos ovários indicou que a inseminação pode corresponder a uma estratégia da espécie para capacitar os espermatozoides, ou seja, a associação gamética interna pode aumentar a motilidade e tempo de sobrevivência do espermatozoide.

Palavras chaves: Auchenipteridae; Espermatogênese; Reprodução.

Introdução

Os Siluriformes apresentam uma diversidade morfológica do sistema reprodutor dos machos, o qual pode corresponder a um testículo totalmente franjado, ou parcialmente franjado com vesícula seminal, ou ainda plissado ou fusiforme (Legendre et al. 1996, Guimarães-Cruz and Santos 2004, Melo et al. 2011). Esses peixes também variam quanto ao tipo de fertilização, que pode ser interna ou externa (Nelson 1994, Mazzoldi et al. 2007, Quagio-Grazziotto et al. 2011). Devido a essas características, estudos recentes têm analisado a organização anatômica dos testículos, a fim de informar sobre sua morfologia, estratégia reprodutiva e subsidiar análises filogenéticas (Santos et al. 2001, 2010; Guimarães–Cruz and Santos 2004; Barros et al. 2007; Melo et al. 2011).

Dentre as espécies de Auchenipteridae tem sido demonstrado que o sistema reprodutor dos machos varia entre espécies do mesmo gênero (Araújo et al. 2000; Meisner et al. 2000; Santos et al. 2014) e está relacionado aos diferentes tipos de fertilização (Mazzoldi et al. 2007), embora a fertilização interna já tenha sido descrita para algumas espécies dessa família, pela presença do espermatozoide no lúmen ovariano (Loir et al. 1989, Meisner et. 2000, Santos et al. 2014). Alguns autores citam que a ausência de oócitos vitelogênicos fertilizados nessa região, caracteriza o processo de inseminação e não de fertilização interna. Assim, as espécies de Auchenipteridae não poderiam ser consideradas como fertilizadores internos e sim, inseminadores (Meisner et al. 2000, Santos et al. 2014).

Devido ao fato das espécies com inseminação apresentarem gonopódio, órgão copulador dos machos, muitos auchenipterideos têm sido considerados como inseminadores. Contudo, apenas *Trachelyopterus galeatus*, *Trachelyopetrus lucenai*, *Trachelyopterus striatulus*, *Auchenipterus nuchalis* e *Ageneiosus inermis* tiveram inseminação confirmada através de estudos anatômicos e histológicos dos testículos (Loir et al. 1989, Meisner et al. 2000, Mazzoldi et al. 2007, Parreira et al. 2009, Santos et al. 2014).

O bagre *Ageneiosus ucayalensis* Castelnau, 1988 ocorre ao longo das bacias dos rios Amazonas, Orinoco, drenagens das Guianas e no alto rio Paraná (Ferraris-Jr 2003). Embora essa espécie possua ampla distribuição, não se conhece o padrão morfofuncional testicular, o qual pode auxiliar no conhecimento da estratégia reprodutiva utilizada para garantir o seu sucesso em hábitats tão distintos. Desta forma, o presente estudo contribui para o conhecimento da estrutura testicular de *A. ucayalensis* e analisa a ocorrência de inseminação como estratégia reprodutiva.

Material e Métodos

Um total de 108 machos, em diferentes estádios de maturação gonadal, e 124 fêmeas, em atividade reprodutiva, foi coletado no rio Anapu, na Amazônia Oriental (1º42’30”S e 51º31’45”W). As fêmeas foram analisadas para verificar a inseminação e o estádio reprodutivo foi classificado de acordo com Núñez and Duponchelle (2009).

Os espécimes de *A. ucayalensis* foram coletados mensalmente, durante o período de maio de 2012 a abril de 2013. A captura foi realizada com redes de emalhar com diferentes tamanhos de malhas (15, 20, 25, 30, 35 e 40 mm entre nós opostos). Em seguida, as amostras foram acondicionadas em caixas isotérmicas, anestesiadas com benzocaína (0.1g.L^{-1}) e eutanaziados de acordo com as diretrizes do Conselho Nacional de Controle de Experimentação Animal (CONCEA). Após a eutanásia, todos os exemplares foram eviscerados para a sexagem e retirada das gônadas.

A anatomia dos testículos foi descrita em relação aos outros órgãos da cavidade celomática. Em seguida, fragmentos da porção cranial e caudal dos testículos, assim como porção mediana dos ovários foram fixados em Bouin por 24 horas e submetidos ao processamento histológico de rotina para inclusão em parafina (Prophet et al. 1995). Foram realizados cortes de 5 µm de espessura, os quais foram corados em Hematoxilina e Eosina, analisados e fotomicrografados em microscópio de luz (NIKON Eclipse Ci), acoplado a uma câmera digital (NIKON DS-Ri1).

Resultados

Os machos adultos de *A. ucayalensis* apresentaram um gonopódio (Fig. 1a), que correspondeu à unificação dos primeiros raios da nadadeira anal, que apresentou uma papila urogenital na sua extremidade. Este órgão foi mais evidente durante o período reprodutivo, quando ficava bastante avermelhado. Nas fêmeas essa estrutura foi ausente (Fig. 1b).

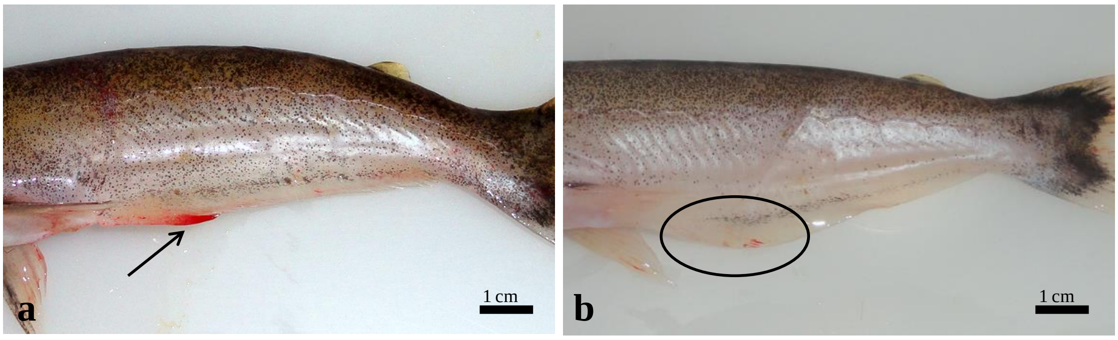

Fig. 1 – Anatomia da nadadeira anal em *A. ucayalensis*. **a**: nadadeira anal modificada em macho. **b**: nadadeira anal não modificada em fêmea. **Seta**: gonopódio; **Círculo**: ausência de gonopódio.

Os testículos de *A. ucayalensis* ocuparam a região mediana da cavidade abdominal e apresentaram um padrão distinto de tamanho, cor, consistência e vascularização, de acordo com a fase do ciclo reprodutivo em que se encontraram. Anatomicamente, estavam relacionados ventralmente com o estômago, e dorsalmente com os rins, intestino e bexiga natatória.

Estas gônadas corresponderam a órgãos pareados, aproximadamente do mesmo tamanho, com franjas ou lóbulos na porção cranial. As franjas se uniram sozinhas ou em pares, com o ducto espermático localizado na porção central de cada testículo. Os ductos espermáticos dos testículos direito e esquerdo se juntaram na porção caudal, formando o ducto espermático comum, que se estendeu até a papila urogenital, situada na extremidade do gonopódio (Fig. 2).

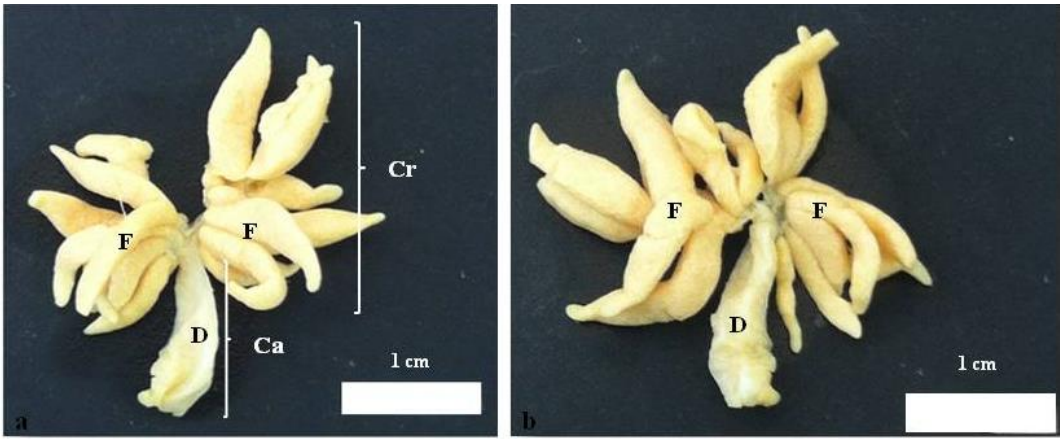

Fig. 2 – Testículo maturo de *A. ucayalensis*. **a**: vista ventral. **b**: vista dorsal. **F**: franjas. **D**: ducto espermático. **Cr**: região cranial. **Ca**: região caudal.

As franjas craniais dos testículos desempenharam função espermatogênica (Fig. 3a), enquanto o ducto espermático foi apenas secretor (Fig. 3b). Histologicamente, as franjas testiculares foram revestidas por uma túnica albugínea de tecido conjuntivo que emitiu septos para o interior do órgão, delimitando os túbulos seminíferos. Nos machos maturos, os túbulos seminíferos se ramificaram ao longo de todo lóbulo, formando uma rede anastomosada interconctada (Fig. 3c). Internamente, os túbulos seminíferos foram constituídos por cistos germinativos (Fig. 3d).

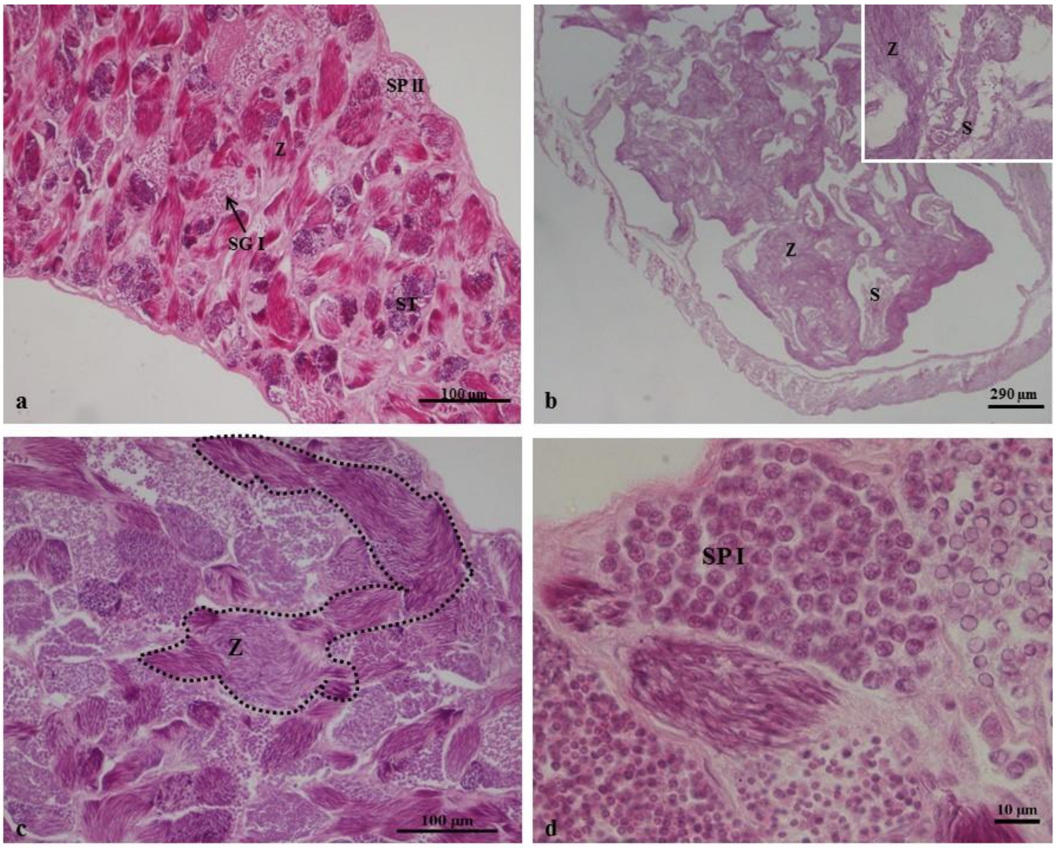

Fig. 3 – Histologia dos testículos de *A. ucayalensis*. **a:** franja cranial, contendo células da linhagem germinativa. **b**: ducto espermático comum da região caudal, contendo espermatozoides e secreção. Insert: espermatozoides e secreção. **c**: testículo maturo, ilustrando a anastomose do túbulo seminífero. **d**: testículos em maturação, com detalhe dos cistos germinativos. **SG I**: espermatogônias primárias. **SP I**: espermatócitos primários. **SP II**: espermatócitos secundários. **ST**: espermátides. **Z**: espermatozoides. **S**: secreção. **Seta**: secreção.

As células de Sertoli se encontravam na base dos cistos, apoiando a estrutura (Fig. 4a). Esses cistos continham células da mesma linhagem espermatogênica que foram descritos baseados na sua morfologia.

Espermatogônia primária (Fig. 4b): correspondeu a maior célula da linhagem espermatogênica, com citoplasma abundante e núcleo central. Essas células foram encontradas ao longo de todo o túbulo seminífero.

Espermatogônia secundária (Fig. 4c): apresentou citoplasma menor em relação a primária, núcleo esférico e central. Essas células foram observadas em grande quantidade dentro dos cistos.

Espermatócito primário (Fig. 4d): apresentou citoplasma escasso, núcleo esférico e central, e cromatina de aspecto granular.

Espermatócito secundário (Fig. 4e): apresentou citoplasma delgado, núcleo esférico e central, com ausência de nucléolo e heterocromatina em um dos polos do núcleo.

Espermátide (Fig. 4f): apresentou citoplasma delgado, núcleo denso e cromatina em diferentes graus de condensação.

Espermatozoide (Fig. 4g): foi a menor célula germinativa, ocorrendo em grande quantidade no lúmen dos túbulos seminíferos e dos ductos testiculares. Apresentaram núcleo alongado, flagelo bem desenvolvido e foram encontrados formando feixes.

Espermátide e espermatozoide foram encontrados em grande quantidade no lúmen do túbulo seminífero (Fig. 4h).

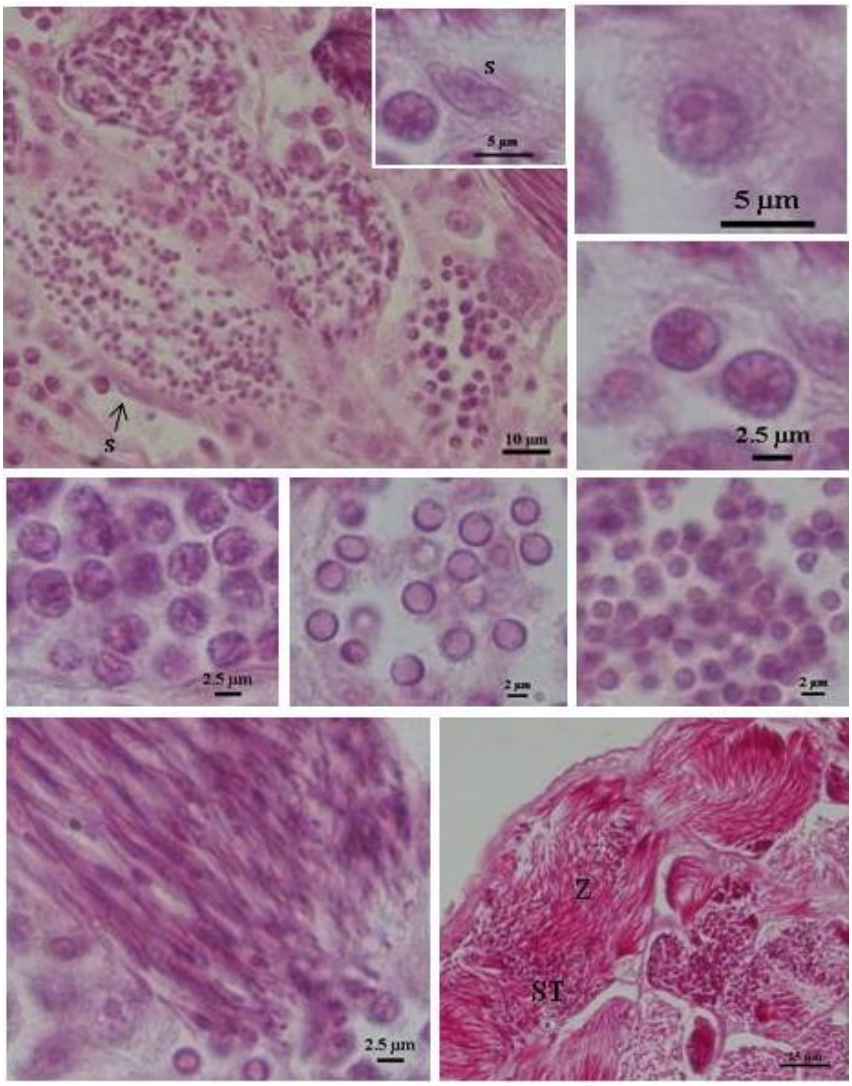

Fig. 4 – Células da linhagem espermatogênica de *A. ucayalensis*. **a**: cisto envolvido pela célula de Sertoli.Insert: célula de Sertoli. **b**: espermatogônia primária (SGI) com núcleo arredondado. **c**: espermatogônia secundária (SGII). **d**: espermatócitos primários (SPI). **e**: espermatócitos secundários (SPII). **f**: espermátides (ST). **g**: espermatozoides (Z). **h**: espermátides (ST) e espermatozoides (Z) livres no lúmen, caracterizando espermatogênese semicística.

Em fêmeas de *A. ucayalensis* no estágio em maturação foi observado espermatozoides no lúmen ovariano (Fig. 5), contudo não foi observado fertilização de oócitos vitelogênicos.

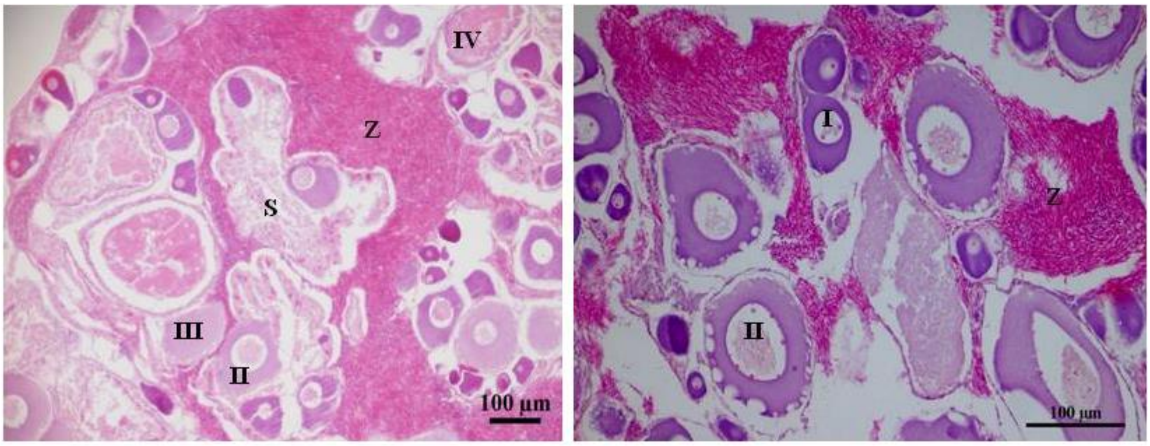

Fig. 5 – Secção do ovário de *A. ucayalensis* com a presença de espermatozoides no lúmen ovariano. Z: espermatozoides. S: secreção. I: oócito 1. II: oócito 2. III: oócito 3. IV: oócito 4.

Discussão

O presente estudo confirma que a presença do gonopódio nos machos de *A. ucayalensis* está associada com a inseminação. Estudos anteriores relataram que a inseminação em peixes requer não só a presença deste órgão, mas modificações na papila urogenital da fêmea e na morfologia dos espermatozoides (von Ihering 1937, Schaefer et al. 1989, Javonillo et al. 2009, Parreira et al. 2009). Em auchenipterídeos foi demonstrada a presença do gonopódio e relacionada com a fertilização interna/inseminação em *Auchenipterus nuchalis*, *T. galeatus* e *T. lucenai* (Meisner et al. 2000, Mazzoldi et al. 2007). Porém em *Tatia intermedia* o gonopódio estava ausente e foi sugerido que os animais que não apresentam esse órgão realizam fertilização externa (Mazzoldi et al. 2007).

Os testículos de *A. ucayalensis* apresentaram franjas somente na porção cranial, enquanto que a região caudal foi constituída apenas por um ducto espermático comum. Resultados similares foram observados em *Ageneiosus inermis* (Loir et al. 1989). Entretanto, a região caudal dos testículos de *A. ucayalensis* diferiu de *T. lucenai*, *T.*

galeatus, *T. striatulus*, *A. nuchalis* e *T. intermédia* (Meisner et al. 2000, Mazzoldi et al. 2007, Santos et al. 2014). Tal diversidade testicular pode ser útil no diagnóstico dessas espécies, assim como pode subsidiar estudos de relações filogenéticas das espécies de Auchenipteridae.

A presença de espermatozoides e secreção observados no ducto espermático caudal de *A. ucayalensis* sugere que essa estrutura está relacionada com a atividade secretora. A função secretora já foi atribuída para as estruturas acessórias da região caudal dos testículos de *T. galeatus*, *T. lucenai* e para *T. striatulus* (Meisner et al. 2000, Santos et al. 2014). Essa secreção desempenha importante papel na abertura do poro genital da fêmea, assim como previne a inseminação de novo esperma ou o refluxo dos espermatozoides pelo trato reprodutivo da fêmea, bem como, pode aumentar o volume do sêmen, nutrir e manter os espermatozoides e atrair as fêmeas (Parreira et al. 2009, Santos et al. 2014).

Histologicamente, a estrutura testicular de *A. ucayalensis* correspondeu ao tipo tubular anastomosado, evidenciada pela rede interconectada dos túbulos seminíferos nos testículos maturos. De acordo com Grier (1993), os testículos dos teleósteos podem ser tubular anastomosado, espermatogonial irrestrito ou espermatogonial restrito. Acredita-se que os testículos do tipo tubular anastomosado estão presentes nos peixes mais basais, enquanto os outros tipos estão presentes nos neoteleósteos (Grier and Aranzábal 2009). O presente estudo é o primeiro a classificar os testículos de um auchenipterídeo, quanto á sua organização estrutural. Mediante a diversidade morfológica dos testículos das espécies de Auchenipteridae, ressaltamos a importância de se fazer essa caracterização histológica como ferramenta para o melhor entendimento da evolução dessa família.

A espermiogênese de *A. ucayalensis* foi caracterizada como semi cística, pois as espermátides e os espermatozoides foram observadas no lúmen do túbulo seminífero. Esse tipo de espermatogênese diferiu do registrado para *T. striatulus*, onde a diferenciação do espermatozóide ocorreu no interior do cisto, liberando somente os espermatozoides maduros no lúmen do túbulo seminífero, caracterizando espermatogênese cística (Santos et al. 2014). Entretanto, espermatogênese semi cística já foi registrada para outros Siluriformes (Mattei et al. 1993, Quagio-Grassioto et al. 2011, Mattei et al. 1993, Quagio-Grassioto et al. 2011). Tais evidências nos levam a sugerir que nas espécies de Auchenipteridae, o tipo de espermatogênese pode estar relacionado com a morfologia dos testículos.

A distribuição e organização das células de Sertoli de *A. ucayalensis* foram similares às descritas para a maioria dos teleósteos (Pudney 1995). Em relação às características morfológicas da linhagem espermatogênica da espécie estudada, as espermatogônias primárias corresponderam as maiores células, apresentando o maior núcleo, o qual foi diminuindo gradativamente ao longo da diferenciação celular. Essa redução de tamanho ocorreu devido à condensação da cromatina até a formação dos espermatozoides (Santos et al. 2001), e seguiu o padrão encontrado para outros Siluriformes Neotropicais (Santos et al. 2001, Barros et al. 2007, Santos et al. 2014).

Em *A. ucayalensis*, as espermatogônias estiveram distribuídas ao longo de todo epitélio dos túbulos seminíferos, caracterizando desenvolvimento espermatogonial irrestrito. Esse tipo de desenvolvimento permite a produção potencial de células germinativas (Schulz and Miura 2002) e também já foi descrito para *T. striatulus* (Santos et al. 2014) e para os Siluriformes *Conorhynchos conirostris* (Lopes et al. 2004), *Lophiosilurus alexandri* (Barros et al. 2007) e *Pimelodella vittata* (Santos et al. 2010).

O fato dos espermatozoides de *A. ucayalensis* apresentarem o núcleo alongado confirma que essa característica é essencial para que a inseminação aconteça dentre as espécies de Auchenipteridae (Meisner et al. 2000, Parreira et al. 2009, Santos et al. 2014). Tal característica facilitaria o deslocamento do espermatozoide no lúmen ovariano e entre as lamellas ovígeras (Parreira et al. 2009).

No presente estudo, a inseminação foi confirmada pela presença de espermatozoides no lúmen ovariano. Contudo, não foi identificada a fertilização dos oócitos dentro do ovário, indicando que a inseminação em *A. ucayalensis* pode ser uma estratégia da espécie para capacitar os espermatozoides, ou seja, o contato com a secreção proteica do ovário pode aumentar sua motilidade e tempo de sobrevivência, para fertilizarem os oócitos quando liberados no ambiente aquático. Esse processo é conhecido como associação gamética interna (Javonillo et al. 2009) e foi evidenciado para outras espécies de peixes. Koya et al. (1993) demonstraram que os espermatozoides de algumas espécies marinhas de Cottidae, em associação gamética interna com o fluido ovariano, apresentaram maior motilidade nas condições ambientais apropriadas para seus respectivos modos de reprodução. No entanto, a fertilização só acontecia quando os espermatozoides entravam em contato com a água do mar, caracterizando fertilização externa. Elofson et al. (2006) demonstraram que a passagem dos espermatozoides pelo fluido ovariano de *Gasterosteus aculeatus* prolongou a motilidade de aproximadamente um minuto para várias horas, mas a fertilização só aconteceu no meio externo. Tais evidências mais a ausência de estudos registrando a fertilização dos oócitos, assim como a observação de oócitos fertilizados para as espécies de Auchenipteridae (Meisner et al. 2000, Parreira et al. 2009, Santos et al. 2014, Chiarini-Garcia et al. 2014), corrobora com a nossa hipótese de que a inseminação nos auchenipterideos pode corresponder a uma associação gamética interna, atuando na capacitação dos espermatozoides, mas que a fertilização pode ocorrer apenas quando a fêmea liberar os espermatozoides e os oócitos vitelogênicos no meio aquático.

Desta forma, o presente estudo registra a estratégia reprodutiva para *A. ucayalensis* e colabora para o conhecimento da diversidade morfofuncional do sistema reprodutor dos auchenipterideos, bem como fornece subsídios para futuros estudos sobre a evolução dessa família.

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CONSIDERAÇÕES FINAIS

O predomínio de fêmeas na população de *A. ucayalensis* estudada indica que um macho pode inseminar mais de uma fêmea e que os machos competem para ter acesso as fêmeas reprodutivas. A espécie apresentou desova total e curto período de atividade reprodutiva, que foi influenciado pela intensidade de chuvas. Além disso, acredita-se que em ambientes com pouca variação fluviométrica, *A. ucayalensis* realiza migração lateral reprodutiva em direção ao canal do rio, a fim de garantir maior sucesso reprodutivo.

Contudo, a hipótese de que a variação pluviométrica ou sexual influenciaria a ecologia trófica dessa espécie não foi corroborada. Acreditamos que o hábito alimentar carnívoro com forte tendência a piscivoria foi o principal responsável por não mudar a dieta conforme a intensidade de chuvas, e que a maturação gonadal de machos e fêmeas de *A. ucayalensis* demande gasto energético similar. Foi observado ainda, alto grau de especialização individual, indicando uma variação intraespecífica na utilização de recursos ao longo do ano, o que pode ser considerado como uma estratégia para evitar a competição por recursos alimentares, garantindo assim o seu sucesso no ambiente.

Em relação à morfologia do sistema reprodutor dos machos de *A. ucayalensis* podemos inferir que a presença do gonopódio nos adultos está relacionada com a inseminação. Os testículos foram do tipo anostomosado tubular e apresentaram desenvolvimento espermatogonial irrestrito, características que podem auxiliar no entendimento da evolução dessa família. Embora o processo de inseminação em *A. ucayalensis* tenha sido confirmado pela presença de espermatozoides no lúmen ovariano, a ausência de oócitos fertilizados neste local nos leva a sugerir que a inseminação pode corresponder a uma associação gamética interna para aumentar a taxa de motilidade ou de sobrevivência dos espermatozoides, para fertilizarem os oócitos vitelogênicos quando forem liberados no meio aquático.

Sendo assim, o presente trabalho apresenta importantes informações sobre as estratégias reprodutivas e alimentares utilizadas por *A. ucayalensis* que podem garantir seu sucesso na Amazônia Oriental.

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