ASPECTS OF THE REPRODUCTIVE BIOLOGY OF *Aequidens tetramerus* (CICHLIDAE) IN VÁRZEA AREAS OF THE MIDDLE SOLIMÕES RIVER, BRAZILIAN AMAZON

ASPECTOS DA BIOLOGIA REPRODUTIVA DE *Aequidens tetramerus* (CICHLIDAE) NAS VÁRZEAS DO MÉDIO SOLIMÕES, AMAZÔNIA BRASILEIRA

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KEY WORDS:

White waters;

Várzea;

Fertility;

Partial spawning;

Sexual maturation.

ABSTRACT

This work investigates life strategy elements of the neotropical cichlid *Aequidens tetramerus* in the lakes of Central Amazon várzea, predominated by white waters. During the 2011 hydrological cycle, fish were captured monthly from banks of aquatic macrophytes present in the lakes studied. The animals found had total maximum lengths of 18.5 cm and 20 cm for females and males, respectively. The average length recorded for their first sexual maturation was 6.49 cm and 8.35 cm for females and males, respectively. Species reproduction occurred throughout the hydrological cycle, but the peak of the reproductive activity was observed during the period of rising water. The average fertility was 1,477 oocytes. The diametric distribution of these oocytes showed synchronous development in more than two groups, suggesting partial spawning. It seems that *A. tetramerus* reaches sexual maturation early in its life time. Based on the reproductive attributes unveiled in this study and on the fact that the species performs parental care, it is suggested that this is a predominantly K-strategist species.

PALAVRAS - CHAVE:

Águas brancas;

Várzea;

Fecundidade;

Desova parcelada;

Maturação sexual.

RESUMO

Este trabalho investiga aspectos da estratégia de vida do ciclídeo neotropical *Aequidens tetramerus* em lagos de várzea na Amazônia Central, ambientes dominados por águas brancas. Os peixes foram capturados mensalmente durante todo o ciclo hidrológico de 2011 em bancos de macrófitas aquáticas presentes nos lagos estudados. Foram encontrados animais com comprimentos totais máximos de 18,5 cm e 20 cm para fêmeas e machos, respectivamente. O comprimento médio encontrado para a primeira maturação sexual foi de 6,49 cm e 8,35 cm para fêmeas e machos, respectivamente. A reprodução da espécie ocorreu durante todo o ciclo hidrológico, mas foi observado um pico de atividade reprodutiva no período da enchente. A fecundidade média foi de 1.477 oócitos. A distribuição diamétrica destes oócitos evidenciou um desenvolvimento sincrônico em mais de dois grupos, sugerindo uma desova parcelada. Aparentemente A. tetramerus atinge precocemente a sua maturação sexual. As maiorias dos atributos reprodutivos levantados neste estudo, e o fato da espécie apresentar cuidado parental, indicam que ela seja predominantemente uma espécie K-estrategista.

INTRODUCTION

The neotropical freshwater bodies are home to almost 24% of the known fish species (VARI; MALABARBA, 1998). Among this great diversity, the Cichlidae family stands out with approximately 1,350 known species around the world. The Neotropical Region is home to almost 400 species of this family, of which at least 287 appear in South America, where it is estimated that this group could be as large as 450 species. More than half of them can be found in the Amazon basin (KULLANDER, 2003).

The Cichlidae family is fundamentally comprised of freshwater fish, and even when they are associated with marine environments, they remain confined to continental habitats, such as estuaries (REIS, 2013). The members of this family exhibit very diverse reproductive strategies in order to ensure higher survival rates for their descendents (KEENLEYSIDE, 1991). The species which is the focus of this study, *Aequidens tetramerus*, reaches a maximum total length of 25 centimetres and has striking colouration, particularly during its reproductive period. It feeds primarily on insects, fish and vegetable material (SANTOS et al., 2006). It exhibits intense territorial behaviour and strong parental care (REIS; KULLANDER; FERRARIS JR., 2003).

Keenleyside (1979) points out that a large portion of the species of the genus *Aequidens* performs oral incubation. Due to these and other behavioural attributes, and due to its colouration patterns, this species attracts the attention of aquarists and is important in the ornamental fish market (PRANG, 2007). The viability of fish populations depends in large part on the success of reproductive activity and to their capacity to adapt to different environmental conditions (VAZZOLER, 1996; SUZUKI; AGOSTINHO, 1997).

The reproductive success of fish depends on the variety of reproductive strategies developed by the group. This success will depend on the location and period in which the species reproduces, and on the resources it allocates to reproduction (WOOTTON, 1984). In any studied environment, one school of fish may have many very different reproductive patterns which are comprised of the reproductive strategies and tactics of each species of the school (WINEMILLER, 1989).

The reproductive attributes were correlated by various authors with the different types of environments in which the fish live in order to identify the environmental trends for the ecological strategies adopted by the group (WINEMILLER, 1989; OLDEN et al., 2006; MIMS et al., 2010). One of the most accepted approaches in the study of this relationship (WINEMILLER, 1989) uses a model that is based on three significant strategies, seeking to explain the species' adaptive responses to environmental variations. The opportunistic strategy (*r*) is characterized by small species with fast reproductive maturation, relatively small number of eggs and multiple or partial spawning.

The seasonal strategy defines intermediate and large species with high fertility, short reproductive cycles and fast growth rate in the first year, as well as late maturation. In the third vertex of this triangular model, there is the equilibrium strategy (K), which defines dense-dependent species that practice parental care, have large eggs, produce few offspring, and generally live in habitats with limited resources (ZEUG; WINEMILLER, 2007).

Understanding the reproductive strategies and tactics of ornamental fish is the key to effectively managing their exploitation and to promoting the conservation of their stocks. Furthermore, this knowledge facilitates understanding the ecology and evolution of this species in the unusual whitewater environment of the Brazilian Amazon. This species has not been previously studied in the Médio Solimões region. The objective this study was to investigate the main aspects of the reproductive strategy of *A. tetramerus* in várzea lakes in this region as means to support its local sustainable use.

Figure 1 - Specimen of *Aequidens tetramerus* taken from Mamirauá

MATERIALS AND METHODS

The 209 specimens of *Aequidens tetramerus* (Figure 1), used in this study, were taken from várzea lakes in the Mamirauá Sustainable Development Reserve (MSDR) in the Central Brazilian Amazon (Figure 2). These are whitewater with Andean origin and influenced by the annual cyclical flood pulses that are very rich in nutrients and a neutral pH (SIOLI, 1984; AYRES, 1993; AFFONSO et al., 2011). The MDSR is a *protected area of várzea,* located between the Japurá and Solimões Rivers, and the Auati-Paraná River, near the city of Tefé, in the State of Amazonas (QUEIROZ; PERALTA, 2006). The Amazon várzea is a complex ecosystem of floodplain lakes, backwaters, canals, dikes and islands (IRION et al., 1997; JUNK, 1997; JUNK et al., 2011). The várzeas in the MSDR have morphological characteristics associated with the seasonal variation caused by the hydrological cycle, forming a complex of waterbodies and seasonally flooded forests (QUEIROZ, 2007).

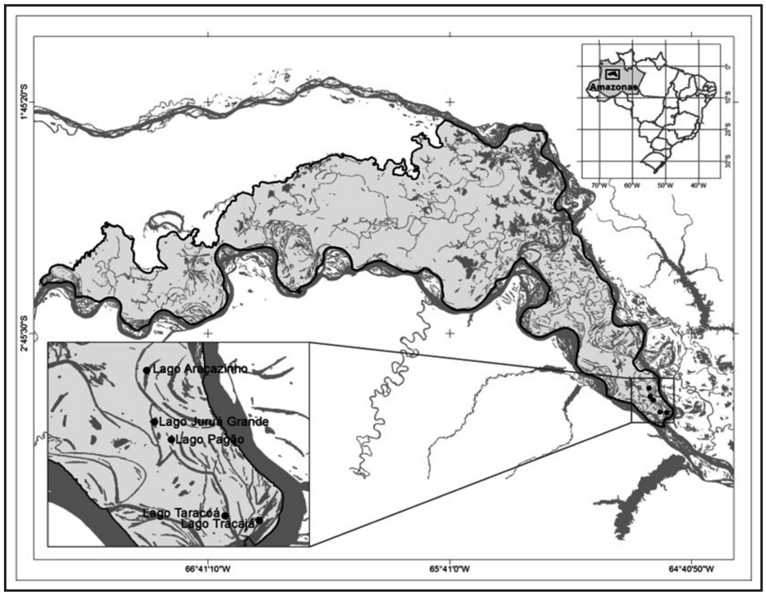

Figura 2 – Location of the várzea lakes sampled at Mamirauá Sustainable Development Reserve, MSDR.

The fish examined here were captured monthly during 2011 (including periods of rising water, high water, dropping water and draught), from five lakes in the MDSR (Araçazinho, Juruá Grande, Pagão, Tracajá and Taracoá (Figure 2). The number of individuals collected per month varied between 15 and 30. the collections were made with the due legal licences (15/2006 NRP, process 02005.002120/06-31). A drag net was used for the collection (30x6m, and mesh of 5 mm between opposite knots) at five random points in the banks of aquatic macrophytes.

The identification of the samples took place in the field, as well as preserving them in 10% formalin and later transferring to an alcohol solution. In the laboratory, biometrics, macroscopic determination of sex and definition of the state of gonadal development were undertaken, according to Nunes and Duponchelle (2009). Female gonads in the state of advanced maturation were removed and immersed in Gilson solution for oocyte dissociation. These were later counted and measured to estimate fertility and type of spawning.

The populational structure was described based on the frequency distribution (%) of the females and males in length classes (cm) (VIEIRA, 1980).

The average length of the first sexual maturation (L_{50}) was determined based on the adjustment of a sigmoid curve, representing the frequency distribution of sexually mature individuals, in a logistical function Y = 1/(1 + exp (- (tax)*(x - (L_{50})))), where: y = relative frequency of adult Imature) males and females in each length class; tax = change rate parameter between the non-reproductive and reproductive phases; x = average value of the standard length class (DUPONCHELLE; PANFILI, 1998).

In order to establish the breeding season, a temporal frequency distribution was used for the occurrence of animals considered sexually mature (with gonads in stages of maturation, mature, spawning or empty, and at rest). To confirm the reproductive period, a seasonal distribution of the average gonadossomatic relation (GSR) of the members of the studied population was conducted, determining the moment when it reaches its highest value, which is right before the spawning period. This parameter was calculated for each studied individual using the formula: GSR = (Wg/Wt)*100, where Wg is the gonad weight and Wt is the total weight of the individual (VAZZOLER, 1996). In order to detect possible significant differences in the seasonal distribution of the maturation stages, a variance analysis (ANOVA) was conducted.

The spawning type was characterized by the analysis of the frequency distribution of the diameters of the oocytes present in the mature gonads. This was achieved by measuring the oocytes in a subsample (10% of the total weight of the gonad), where all present oocytes were measured under a stereomicroscope using a micrometric ruler. In this analysis, six gonads in the stage mature were used.

In order to calculate fertility, the oocytes that were counted had a rate of 10% of the total weight of the studied ovaries and diameter equal to or greater than 1.20 mm (lot of vitellogenic oocytes). This was the modal diameter of the vitellogenic oocytes which were prepared for spawning. The degree of prematurity in the reproductive development of the species was obtained using the relationship between the size at first reproduction and the asymptotic size of the species. The following equation was used: D: $L_{50}/L\infty$, where L_{50} = average size at first maturation; $L\infty$ = average maximum length (asymptotic length) (VAZZOLER, 1996). In order to calculate $L\infty$ (asymptotic length), the empirical relation proposed by Pauly (1980) was applied, according to the equation: $L\infty$ = Mmax/0.95, where Mmax is the size of the largest sampled individual in the study.

RESULTS

For the 209 fish analysed in this study – 92 females and 117 males – the maximum total length found was 18.52 cm and 20 cm for females and males, respectively (Figure 3).

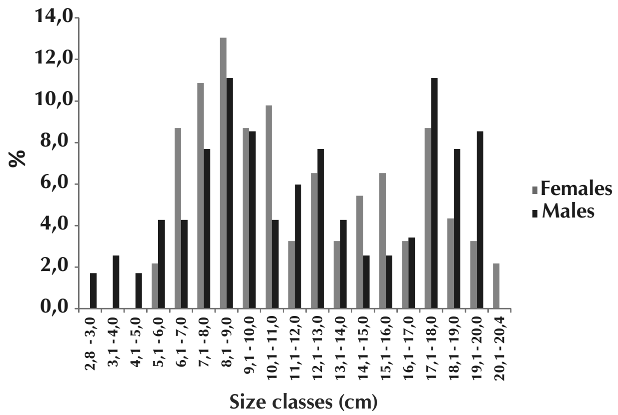

Figure 3 - Frequency of occurrence (%) for classes of standard lengths (cm) for females and males of *A. tetramerus*, sampled during the period of January to December 2012 in the Mamirauá Sustainable Development Reserve. N = 209.

For *A. tetramerus*, the average standard length at first sexual maturation was 6.49 cm for females and 8.35 cm for males (Figure 4). The fitting equations for the logistic curves were as follows: were as follows: for females 100*(1/(1+EXP(-1.9304*(x-(6.486220472))))), r^2=0.66 and for males 100*(1/(1+EXP(-2.1052*(x-(8.350751))))) r^2 = 0.82.

Reproductive females and males of the species could be found throughout the year. However, both sexes exhibited strongest reproductive activity during the rising water period. For the females and males of *A. tetramerus*, the highest GSR value was obtained during the rising water period, confirming this period as the peak for reproductive activity for this species, that is, its reproductive season (Figure 5) The ANOVA showed significant differences in the seasonal distribution of the gonadossomatic relation for both sexes during the rising water period in comparison with the other seasons. This indicates that the species has a season for maximum (peak) sexual activity during this period.

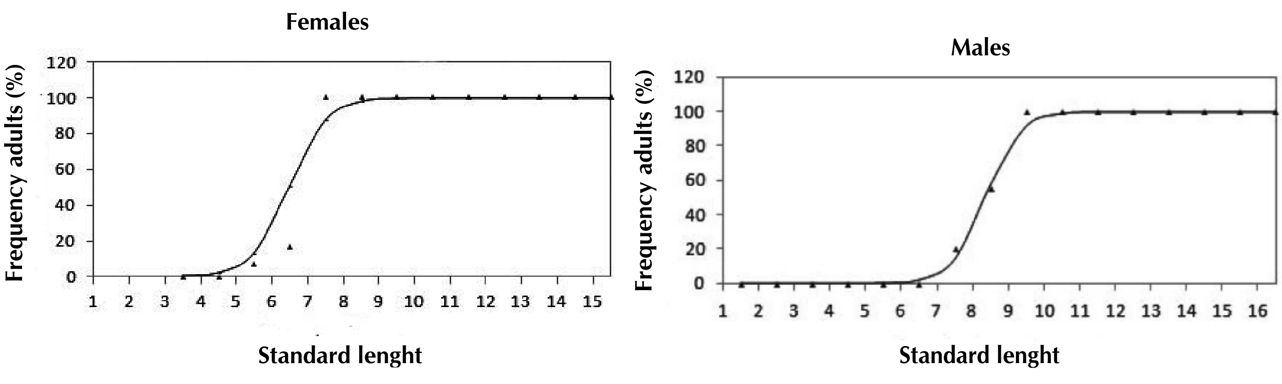

Figure 4 - Average length at first sexual maturation (L_{50}) for females and males of *A. tetramerus* in the Mamirauá Sustainable Development Reserve.

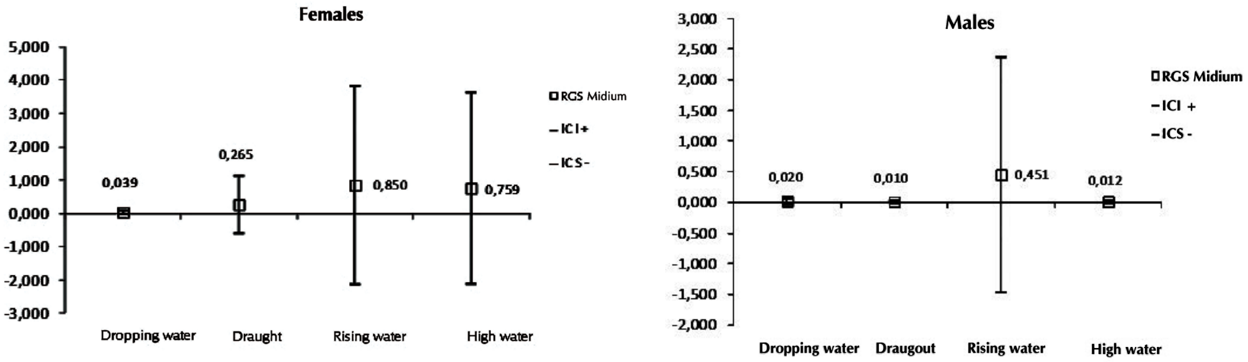

Figure 5 – Average gonadossomatic relation (GSR) of females and males for each season and their confidence interval values.

The average fertility of *A. tetramerus* in the MDSR was 1,477, with a minimum of 580 oocytes and a maximum of 2,480 oocytes (N = 6). The diametric distribution of oocytes proved to be multimodal, showing synchronous development in more than two groups (Figure 6).

The rate of premature sexual development for *A. tetramerus* had values of 0.36 and 0.49 for females and males, respectively.

DISCUSSION

Understanding the reproductive biology of the species, and in particular the size at first sexual maturation, is fundamental for achieving good stock management by correctly identifying the minimum size for capture and the mesh size of fishing nets (HILBORN; WALTERS, 1992; QUEIROZ; CRAMPTON, 1999; BATISTA et al., 2004; FABRÉ; BARTHEM, 2005). Even if these regulations are widely ignored by users and not enforced by the authorities (BATISTA et al., 2004). A study conducted by Sánchez-Botero; Araújo-Lima (2001) mentions that *A. tetramerus* living in várzea lakes in the Central Amazon are 11 cm long at first reproduction (L_{50}), thus being larger

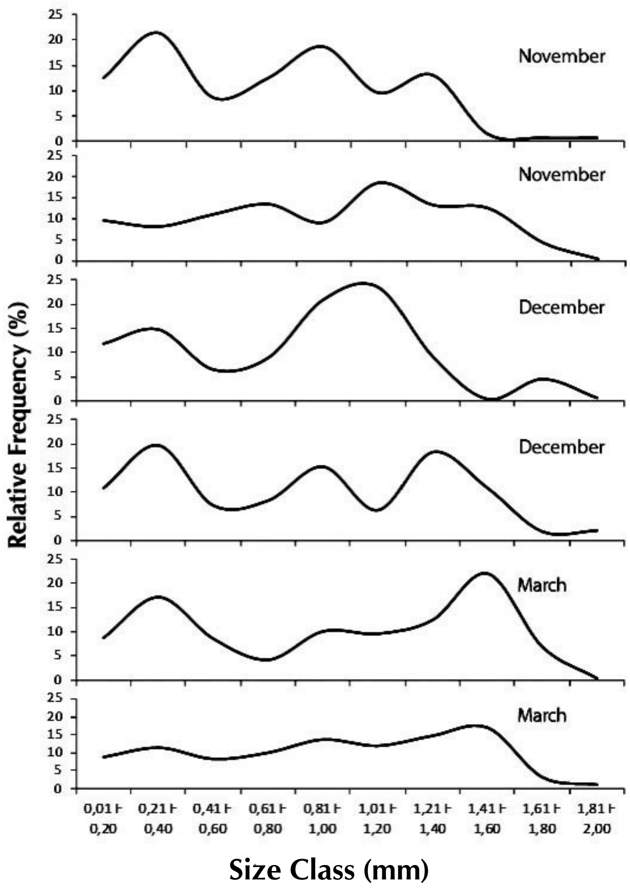

Figure 6 - Diametric frequency of the oocytes of six mature females of *A. tetramerus* in different phases of the hydrological cycle (months of November, December and March).

than estimated in the present in this study. The *A. tetramerus* analysed here showed a tendency of precocious sexual maturation. In other words, in the Médio Solimões region, the várzea area of Mamirauá, the animals reach sexual maturity before they are 50% of their asymptotic size. It is presumed that a species that reaches sexual maturation prematurely benefits from an efficient mechanism to increase its genetic representation in the next generation as it has a proportionally longer period of reproductive activity throughout its expected lifespan (VAZZOLER, 1996). There are many biotic and abiotic factors that can be involved in the reduction of maturation size, such as an increase in food availability, increase in fishing pressures and predation as mortality agents, and genetic determination of the species (VAZZOLER, 1996; LOWE-MCCONNELL, 1999; BARBIERE et al., 2004). Premature sexual maturation could be a strategy developed to reduce the effect of a high predation rate on the population, which can reduce recruitment since the animals could be removed from the population before having the opportunity to reproduce (QUEIROZ; CRAMPTOM, 1999). In the region of this study, the species is not regularly captured.

The reproduction of *A. tetramerus* took place throughout the year, showing a peak of reproductive activity during the rising water period. This period in Mamirauá included the months of December through April. This reproductive seasonality is common among tropical species, indicating an adaptation to this type of environment such that they can benefit from various food resources offered during this period. This is likely the reason why many Amazon fish species show alignment between the end of gonad maturation and the beginning of the rising water season (VAZZOLER, 1996; LOWE-MCCONNELL, 1999).

Cichlids, such as *Heros efasciatus, Acarichthys heckeli* and *Mesonauta insignis* that inhabit blackwater environments, also in the Médio Solimões region, and *A. ocellatus,* which comes from both whitewater and blackwater environments in the western region of the Amazon, equally showed peaks of reproductive activity in the rising water periods, (FAVERO et al., 2010 a,b) (SANTOS et al., 2006). The rising water season has environmental conditions that are more favourable to the survival of offspring, such as an increase in food availability with the arrival of allochthonous material in the aquatic environment, more space to escape from predators, and in some circumstances, greater availability of oxygen dissolved in the waters (CRAMPTON, 1999; LOWE-MCCONNELL, 1999).

There does not seem to be a clear trend in literature with respect to Neotropical cichlid fertility, but existing studies almost always indicate low fertility because they are compared with other groups of fish with higher fertility rates, such as characids (SATO et al., 2003). However, when comparing fertility with other species in this same family of a similar size, we can consider the numbers found to represent a relatively high fertility for *A. tetramerus*. The average fertility of the species was close to, and slightly higher, than that of other species of the same family with similar body sizes and inhabiting Amazonian environments, such as *Pterophyllum scalare,* with a variation of 300 to 1000 sticky eggs (SOARES et al., 2008; COY; CÓRDOBA, 2000) and Red discus, *Symphysodon discus*, with an average of 536 to 1490 oocytes (CÂMARA, 2004; ROSSONI et al., 2010). Fertility is related to various factors, such as the size of the individuals, environmental conditions, and reproductive behaviour of the species (ARAÚJO, 2009). *A. tetramerus* exhibits parental care behaviour (KEENLEYSIDE, 1979; HURTADO-GONZALES et al., 2010; REIS; KULLANDER; FERRARIS JR, 2003). Fertility seems to be a parameter that is inversely proportional to the degree of parental care (LAGLER et al., 1977). As this study indicates, this species has significant reproductive investment, allocating considerable energy to the production of oocytes, such as its high fertility and protection of its offspring.

The synchronous development of oocytes in more than two groups suggests multiple or partial spawning for this species. A species' spawning type is related to its type of oocyte development and to its frequency of release of mature oocytes in a single reproductive period or season (VAZZOLER, 2006; ARAÚJO, 2009). Many of these spawnings are related to ecological factors (LOWE-MCCONNELL, 1999). Partial spawning is a common strategy for Neotropical cichlids, such as the cases of *Astronotus ocellatus* (SILVA et al., 1993), *Pterophylum scalare* (YAMAMOTO et al., 1999), and *Chaetobranchus flavescens* (SANTOS et al., 2004). This reproductive strategy allows for an increase in the number of oocytes eliminated during a single reproductive period, thus increasing the probability of survival of at least some offspring (NIKOLSKY, 1963).

The precocity in the reproduction suggests a tendency of early maturation for *A. tetramerus,* both for the females and for the males. Species with values lower than 0.5 are considered to be of early maturation, such as is the case with this species, while those with values 0.5 this figure are considered to be species of late maturation.

In the same habitat, we can find species of fish with different types of life histories. They can respond to environmental variations in different ways (WINEMILLER, 1989; WINEMILLER, 2005). The species that form the Cichlidae family are generally considered K-strategists. This life strategy involves the production of a smaller number of offspring individuals, but which are capable of surviving adverse conditions imposed by the environment.

The species that exhibit the reproductive characteristics associated with this strategy normally have sophisticated lifecycle mechanisms, such as high degrees of territoriality, mating and offspring care (VAZZOLER, 1996). In this study, the majority of discussed attributes indicate that this species uses an equilibrium reproductive strategy, at least in várzea environments where this study was conducted. However, it should be noted that one of the studied attributes is more typical of fish with an opportunistic strategy, premature sexual maturation. Bringing together attributes of different reproductive strategies and life histories can occur as a guarantee for reproductive success in a dynamic and unpredictable environment, such as the Amazon várzeas. Whitewater environments probably have higher predation pressure, which can result in additional costs to the survival of the species, such as shortened lifespan and increased growth rate, among others (QUEIROZ, 2007; LOWE-MCCONNELL, 1999). This seems to be the case documented in this study.

CONCLUSION

The majority of the reproductive attributes of the species *Aequidens tetramerus* are related to the equilibrium strategy (K), such as prolonged reproductive period, partial spawning, as well as the previously reported parental care. However, there are at least two attributes related to the opportunistic strategy (r), such as premature maturation and high fertility. More studies are needed to standardise the survey of the reproductive attributes of this family. These might improve the understanding of life history patterns and possible ecological and evolutionary relationships of these species, such as the different types of environments where they live, as well as contribute significantly to the sustainable use and conservation of these species.

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