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Population structure and reproductive biology of *Cichla vazzoleri* (Perciformes: Cichlidae): subsidies for fisheries management in the surroundings of REBIO Uatumã, Amazonas, Brazil

Cesar Augusto Chirosa Horie[1]*
https://orcid.org/0000-0002-8440-5819
* Contato principal

Claudia Pereira de Deus[2]
https://orcid.org/0000-0002-5537-7732

Cristhiana Paula Röpke[2]
https://orcid.org/0000-0002-3595-5443

Sidineia Aparecida Amadio[2]
https://orcid.org/0000-0001-5618-6770

[1] Instituto Chico Mendes de Conservação da Biodiversidade/ICMBio, Centro Nacional de Pesquisa e Conservação da Sociobiodiversidade Associada a Povos e Comunidades Tradicionais/CNPT. Base Avançada em Florianópolis/SC, Rua João Câncio Jacques, 1375, Costeira do Pirajubaé, Florianópolis/SC, Brasil. CEP: 88.047-011 <cesarchirosa@gmail.com>.

[2] Instituto Nacional de Pesquisas da Amazônia/INPA, Coordenação de Biodiversidade/CBIO, Brasil. <claudias@inpa.gov.br, krikaropke@gmail.com, amadio@inpa.gov.br>.

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Keywords: Parental care; size at first maturation; reproductive period; fishery management; peacock bass; hydroelectric plant.

ABSTRACT – *Cichla vazzoleri* (peacock bass) is a fish of great economic importance in the Balbina Reservoir (UHE Balbina, at Uatumã River, surroundings of REBIO Uatumã, state of Amazonas), due to both commercial and recreational fishing. The high fishing pressure over about 40 decades depleted the stock and decreased fish body size. In this paper we examined the effect of the REBIO Uatumã on sustaining fish stock, the population structure, and the reproductive biology of tucunaré based on monthly sampling over a year. The effect of the REBIO Uatumã was evaluated by comparing fish abundance and size inside and outside the protected area. The population structure in the reservoir was analyzed based on fish size distributions and sex ratio. Regarding reproductive biology, we determined the phases of gonadal development, mean size at first reproduction, fecundity, type of spawning, physiological indices, and reproductive period. The abundance and body size of *C. vazzoleri* were higher inside the protected area. The population structure demonstrated a prevalence of small to medium-sized individuals, with more males in the largest classes. The mean size at first sexual maturation was 267 mm of standard length for females, and all individuals larger than 310 mm were fully-matured adults. The species shows multiple spawning events, spawning throughout the year, mainly between October and January which is corroborated by most indices and the temporal distribution of ripe females. These results provide important information for the management of tucunaré stocks to avoid overexploitation of an important fishery resource.

Estrutura da população e biologia reprodutiva de *Cichla vazzoleri* (Perciformes: Cichlidae): subsídios para o ordenamento da pesca no entorno da REBIO Uatumã, Amazonas, Brasil

Palavras-chave: Cuidado parental; tamanho de primeira maturação; período reprodutivo; ordenamento pesqueiro; tucunaré; usina hidrelétrica.

RESUMO – *Cichla vazzoleri* é uma das espécies de tucunaré com grande importância econômica no reservatório de Balbina (UHE Balbina, no rio Uatumã, entorno da REBIO Uatumã, estado do Amazonas), pois é alvo da pesca comercial e recreativa. Devido à elevada pressão da pesca por quase 40 anos, o estoque e o tamanho desses peixes diminuiu. Neste artigo examinamos o efeito da REBIO Uatumã para a manutenção dessa população de peixes e seu estoque pesqueiro, a estrutura da população e a biologia reprodutiva dessa espécie, com base em amostragens mensais ao longo de um ano. O efeito da REBIO Uatumã foi avaliado por meio da comparação da abundância e do tamanho médio da espécie dentro e fora da área protegida. A estrutura populacional no reservatório foi analisada com base nas distribuições de tamanho dos peixes e suas proporções sexuais. Para a biologia reprodutiva foram determinadas as fases de desenvolvimento gonadal, tamanho médio na primeira reprodução, fecundidade, tipo de desova, índices fisiológicos e período reprodutivo. A abundância de *C. vazzoleri* e o tamanho médio dos peixes foi maior dentro da área protegida. A estrutura populacional demonstrou uma prevalência de indivíduos pequenos e médios. O tamanho médio na primeira maturação sexual foi de 267 mm de comprimento padrão para as fêmeas, e todos os indivíduos com mais de 310 mm de diâmetro são adultos totalmente maduros. A espécie apresenta múltiplos eventos de desova, reproduzindo-se ao longo do ano, com pico de atividade reprodutiva entre outubro e janeiro, corroborado pela maioria dos índices e distribuição temporal de fêmeas maduras. Os resultados trazem importantes informações que podem subsidiar a gestão do estoque de tucunaré para evitar a sobre-exploração desse relevante recurso pesqueiro.

Estructura Poblacional y Biología Reproductiva de *Cichla vazzoleri* (Perciformes: Cichlidae): Subsidios para el Manejo de Pesquerías en el Entorno de la REBIO Uatumã, Amazonas, Brasil.

Palabras claves: Cuidado parental; tamaño de la primera maduración; periodo reproductivo; manejo de pesqueiras; tucunaré; pavón; central hidroeléctrica.

RESUMEN – *Cichla vazzoleri* es una de las espécies de tucunare de gran importancia económica de la embalse de Balbina (UHE BALBINA, en el río Uatumá, en el entorno de la REBIO Uatumã, estado de Amazonas), donde la especie es utilizada en la pesca comercial y recreativa, contribuyendo la mayor parte de ingreso familiar local. En este artículo examinamos la estructura de la población y biología reproductiva de esta especie con base en muestras mensuales a lo largo del año. La estructura poblacional en lo embalse fue analizada con base a las distribuciones del tamaño de los peces y sus proporciones sexuales. Para la biología reproductiva fueron determinadas las fases de desarrollo gonadal, tamaño medio de la primera reproducción, fecundidad, tipo de desove, índice fisiológico y periodo reproductivo. La abundancia de *C. vazzoleri* y el tamaño medio de los peces fueron mayores dentro del área protegida. La estructura poblacional demostró una prevalencia de individuos pequeños y medios. El tamaño medio en la primera maduración sexual fue de 267 mm de longitud estándar para las hembras, y todos los individuos con más de 310 mm de diámetro son adultos totalmente maduros. La especie presenta varios eventos de desove, reproduciéndose a lo largo de todo el año, con pico de actividad reproductiva entre los meses de octubre y enero, corroborado por la mayoría de los índices y distribución temporal de hembras maduras. Los resultados traen informaciones importantes que pueden subsidiar el manejo de la población del tucunaré para evitar la sobre explotación de este importante recurso pesquero.

Introduction

Despite the great diversity of Amazonian fish species and the importance of fish to local economies, information about reproductive biology is still scarce for many commercially important fish. Information on population structure, reproductive biology and population dynamics have central importance to provide basic information for efficient implementation of management strategies of fishing resources[1]. Characteristics such as population size structure, mean lengths at first reproduction, reproductive period, type of spawning, fecundity, and gonadal indices are basic parameters necessary to guide decision-making and policy of resource use[2], although the lack of continuous monitoring is a limiting factor[3].

Cichla spp. (peacock bass) are the most harvested fish species in the Uatumã River basin, more specifically in the Balbina hydroelectric reservoir (Balbina HPP), located in the municipality of Presidente Figueiredo/AM, Brazil. The Balbina HPP was constructed in the second half of the 1980s by damming the Uatumã River. In addition to the strong modification of the natural *habitats*[4], the hydroelectric project caused significant transformations in the species composition, abundances, and biomasses of the regional ichthyofauna[5], as well as species ecology[6,7]. Following the *habitat* changes, the population of *Cichla* species increased to become the dominant species in the reservoir[4].

The success of this group in colonizing reservoirs has been described over different river basins after their introduction or natural occurrence[8,9,10,11]. Species of the genus *Cichla* inhabit preferentially calm, warm, and low turbidity waters[8]. All species are sedentary although movements can occur among environments[12,13], they are piscivores and have large body size[14]. In general, *Cichla* species show low fecundity, the oocytes are large and ellipsoidal, mating behavior involves the construction of spawning nests, and parental care[14,15]. In captivity conditions, they can reproduce over the year in waters with temperatures around 26 °C[16], however, in natural environments the length of the reproductive period seems to vary spatially and among species[11]. Males are larger than females and develop a nuchal protuberance in the reproductive period[15]. They are classified as species with equilibrium-type life-history strategy, according to the categories of reproductive strategies[17].

In the Balbina Reservoir, *Cichla vazzoleri (*Kullander and Ferreira, 2006)[18] is the most abundant species[19]. The habitat, formed with a large area of dead flooded forest, became a reproduction site for peacock bass by providing an enormous spawning substrate area. However, under continuous fishing pressure, summed to the tendency for the stabilization of ecosystem changes in the reservoir, and the reduction of primary production[20], the peacock bass population in Balbina reservoir has experienced a stock decrease and reduction in fish's body sizes[21]. Size reduction was first observed by local fishers in the 90's, about ten years after the building of the dam a higher frequency of individuals below 27 cm was present in fish landings compared to the 30-35 cm from years before, despite reductions in the numbers of fishers[21].

The reduction in the individual's body size should trigger negative feedback for population growth, as population-level fecundity is heavily dependent on larger fish in the population[22,23], mainly if such changes are more pronounced in females[24]. This effect can only be detected when the studied population structure and reproductive biology consider both males and females[2].

In 1990 the Federal protected area Uatumã Biological Reserve (REBIO Uatumã) was created with a total of 9,387 km^2 of the river basin[25]. Between 2007 and 2009 rules for *Cichla*`s fisheries management were applied[26], however, discontinued after that. During this period only fish larger than 30 cm could be fished and a fish closure season was defined between August and November. However, biological data to support such decisions were missing.

Here we investigate the effect of the protected area on *Cichla vazzoleri* conservation and fisheries sustainability by comparing the effect of the REBIO Uatumã in the abundance and population size structure in Balbina reservoir. A description of the reproductive biology of this species is also presented. We expected to find a higher abundance of fish and larger individuals in the protected side of the reservoir. Once much of the reproductive success of *Cichla vazzoleri* in Balbina Reservoir has been attributed to spawning habitat availability, we investigated the correlation between the reservoir water level and rainfall on reproductive activity. We expected higher reproductive activity during high water levels when spawning habitats would be more available. The information presented here provides basic information for the fisheries agreement and conservation of *Cichla vazzoleri* from 2014 until now.

Materials and Methods

Study area

The present study was undertaken at the Balbina Reservoir (01°50'56.7" S, 59°26'15.5" W), formed by the Uatumã River between 1987 and 1989 in Amazonas State, Brazil (Figure 1). The Balbina Reservoir is located in the municipality of Presidente Figueiredo, approximately 200 kilometers northeast of Manaus[21], with an average flooded area of 1.177 km^2[27]. The Federal protected area REBIO Uatumã was created in 1990 on the left bank side of the reservoir and helps to protect 9.387 km^2 of the river basin[25]. The protected area splits the Balbina Reservoir into two areas with different rules of use by local communities (Figure 1); fisheries are prohibited from the middle of the lake to the left bank and allowed from the middle of the lake to the right bank.

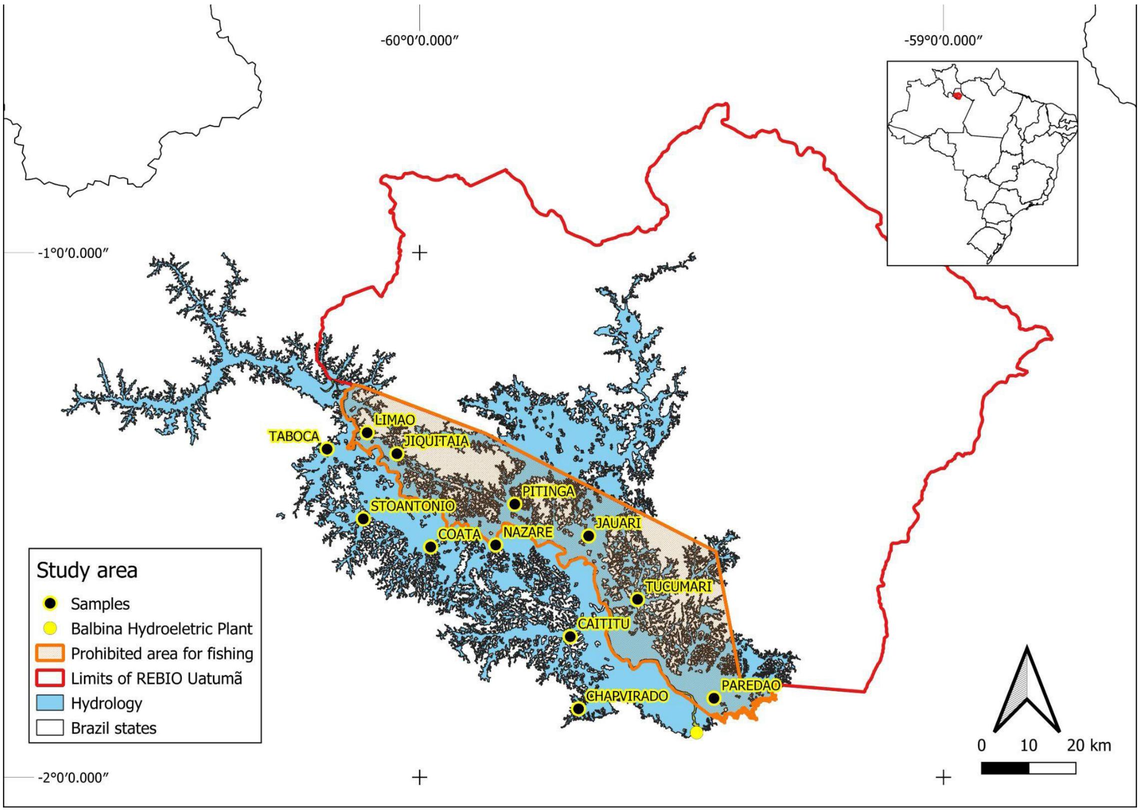

Figure 1 – Map of the sampling area showing the sampling sites for specimens of *Cichla vazzoleri* captured between October 2011 and September 2012.

The regional climate is tropical humid, with a rainy season between December and May providing 2000 mm of annual rainfall[25]. Reservoir levels are regulated by rainfall and the management of water flow to generate electrical energy, which provokes an annual unimodal water level pulse in the reservoir. The lake shows a thermal stratification during most of the year, with anoxic areas at greater depths, except in the rainy season[25]. The reservoir landscape is dotted by islands (hilltops), and most of the lake (except the former bed of the Uatumã River) is replete with innumerable standing dead trees, locally known as "*cacaia*"[21]. The reservoir is surrounded by dense ombrophilous forest, with some small, scattered human communities and the larger village of Balbina where the employees of the Balbina HPP generating station live. We established 12 sampling points along the banks of the reservoir, covering both, inside and outside the protected areas as well as in places of free use by fishers. The goal was to have samples as spread out as possible in both areas of the reservoir.

Data collection

Sampling was carried out monthly for 12 days, one day at each sampling site, between October 2011 and September 2012. In each site, standardized samplings were performed using live baits and long lines, totaling 3 hooks for 2 hours, between 7 am and 9 am. To better describe population structure, a cast net and a seine net (10 x 1.5 m) were used in shallow areas, close to the banks, generally containing submerged vegetation, sand, or stones to capture pre-adults and juveniles. These complementary samplings were not possible in every sampling site but equivalent effort was performed in the inside and outside REBIO Uatumã areas in the Balbina Reservoir.

Each specimen collected was identified, weighed (grams), measured to determine its standard length (mm), and sectioned ventrally to inspect the coelomic cavity to determine the gonadal reproductive phase and energy reserves (coelomic fat). The sex and the maturation levels of the gonads were classified according to the scale described by Brown-Peterson[28] with adjustments: immature, maturing, mature, and regenerating. The gonads were completely removed, weighed, and subsequently immersed in 5% formaldehyde for posterior confirmation of gonad development by histological sections[2]. Mature ovaries were held in Gilson solution[29] for oocyte dissociation to posterior estimates of fecundity and measuring the mature oocytes. Energetic reserves, based on the quantities of fat stored in the coelomic cavity, were estimated by visual inspection and classified following Santos[30], from 0 (0% fat) to 3 (100% fat).

All captured fish were sacrificed with a lethal dose (DL) of anesthetic solution of Eugenol (5 ml to 50 ml of 70% alcohol, diluted in 10 liters of water). Five testimony specimens were recorded in the INPA Fish Collection, under the numbers INPA 37652 (1 ex.) and INPA 37656 (4 ex.). All captures were carried out with ICMBio authorization (Sisbio 31139-1, 2, 3 2011/2013).

Data analyses

Numerical standardized abundance was recorded for each sampling point and the effect of the protected area (in and outside the REBIO Uatumã) was compared using the parametric *t* test, after verifying the assumptions of normality and homoscedasticity.

Based on the standardized capture, fish standard length was compared between areas (in and outside the REBIO Uatumã) using the Mann-Whitney test. The standard length structure was compared, using the Kolmogorov-Smirnov test[31]. The number of classes was determined by Sturges method[32], and differences among size classes were evaluated by G test from the absolute frequencies in each of the 14 length classes, for g.l.= 1, G values greater than 3.84 indicating significant differences from the expected proportion of 1:1[31].

Seven other population parameters were estimated based in the all individuals captured at the 12 sampling sites in the reservoir to allow a robust interpretation:

- The sex ratios were evaluated based on the quotient of the numbers of females and males encountered during the study period; the length classes were compared using the chi-square test (χ^2) to evaluate possible differences from 1:1 ratio, at a 5% level of significance.
- Length-weight relationships were estimated for the population (grouped by gender) using the power function $Wt = a * SL^b$[33], where Wt = total weight (grams), SL = Standard length (mm), a and *b* = the regression parameters used to characterize the length-weight relationship, using Past version 2.10 software, and employing a non-linear estimation using the Levenberg-Marquardt iteration method. The $L\infty$ value (the maximum asymptotic size or maximum theoretical size that a fish could attain) was obtained using FiSAT II version 1.2.2 software.
- The L_{50} was determined by each gender using a logistic function, proposed by King[34]: $P=1/(1+\exp[-r(L-L_m)])$, where (P) = the relative frequency of adults in a given length

class, (r) = the inclination of the curve, and (L_m) = length at first sexual maturation (L_{50}). The L_{100} was determined as the asymptote.

- Fecundity was considered as the total number of oocytes produced by a mature female per reproductive period, utilizing a gravimetric method[2]. The oocytes were measured in millimeters (greatest diameter) using an ocular micrometer mounted on a stereomicroscope (1x). The possible number of batches were estimated by the frequency of oocytes by class-size.
- Reproductive periods were determined by two methods: i) inspections of the graphic distributions of the relative temporal frequencies of females and males in all phases of gonad maturity[2], and ii) the categories within the Index of Reproductive Activity (IRA). The IRA was calculated for females only, per month, following Franco et al.[35], and classified as incipient ($0<IRA\leq5$), moderate ($5<IRA\leq10$), or intense ($IRA>10$)[36]. The months of reproductive peaks were considered those with the highest frequencies of mature specimens and IRA was classified as intense. The mean monthly values of IRA were correlated with the mean local precipitation and the mean levels of water in the reservoir through simple regressions.
- Physiological indices were estimated individually for males and females to complement information about the reproductive cycle of the species and were temporally compared using the Kruskal Wallis test after verifying the heteroscedasticity of the data. The Gonadosomatic Index (GSI) was calculated based on the expression $GSI=Gw/W_t x100$, where (GSI) = Gonadosomatic Index, (Gw) = gonad weight (g), and (Wt) = total weight of the fish (g)[2]. The fat index (FI) was analyzed based on mean monthly fat content[30]. The condition factor (K) was calculated according to the equation: W_t/SL^b; where (W_t) = total weight; (SL) = standard length, and (^{b}) = angular coefficient of the nonlinear ratio between weight and length.

Results

A total of 2362 fish were captured in the Balbina Reservoir, the abundance of *C. vazzolleri* was significantly higher inside the REBIO Uatumã when compared to the outside area (t = 3.351, df = 5.78, p-value = 0.01, mean inside = 248 individuals, mean outside = 145.66 individuals; Table 1). The mean size of the fish inside and outside the REBIO Uatumã in Balbina reservoir showed a significant difference, larger individuals occurred inside the protected area (U test = 428433.5, p-value <0.001, mean inside = 263.14 mm, mean outside = 232.44 mm; Table 1). The distribution by length classes was also different, the frequency of smaller fish was higher outside, while fish in the larger length classes were more frequent inside the REBIO Uatumã (KS = 0.2470; p <0.001, Table 2).

Table 1 – Numerical abundance (N) and mean values of fish sizes (SL in mm) of *C. vazzoleri* inside (In) and outside (Out) the REBIO Uatumã.

Sampling Site	REBIO Uatumã	N	Mean SL
Paredão	In	215	269,15
Tucumari	In	330	238,19
Jauari	In	286	261,9
Pitinga	In	302	247,87
Jiquitaia	In	221	286,58
Limão	In	134	313,4
Chapéu Virado	Out	123	248,8
Caititu	Out	174	199,77
Nazaré	Out	147	232,75
Coata	Out	137	239,95
Santo Antonio	Out	128	226,91
Taboca	Out	165	252,5

Table 2 – Numerical abundance (N) by size class (SL in mm) inside and outside the REBIO Uatumã in the Balbina Reservoir.

Size Class	Observed Abundance (N)		Total	Expected Abundance (N)	G test
	Outside	Inside			
21-60	3	1	4	2	1.046
61-100	16	4	20	10	7.709
101-140	17	2	19	9.5	13.552
141-180	80	17	97	48.5	44.430
181-220	219	238	457	228.5	0.790
221-260	310	505	815	407.5	47.112
261-300	157	430	587	293.5	131.992
301-340	46	211	257	128.5	114.771
341-380	12	49	61	30.5	24.073
381-420	10	20	30	15	3.397
421-460	3	7	10	5	1.645
461-500	1	4	5	2,5	1.927

From all specimens of *C. vazzoleri* sampled 1192 were females, 1145 males, and 25 juveniles (specimens under 100 mm of SL). The standard-length distribution of both sexes was considered significantly different (KS = 0.018; $p < 0.005$), although there was no significant difference between the mean standard length for each sex (Female = 250.08 ± 43.03; Male = 257.38 ± 56.72 mm)(Figure 2). The distributions per size classes showed that all individuals longer than 420 mm were males. The sex ratio per length class was not different for individuals measuring up to 360 mm; there was a predominance of males in the largest size classes, however, with significant differences in the classes 361-380 mm ($\chi^2 = 9.34$, $p < 0.01$), 401-420 mm ($\chi^2 = 6.39$, $p < 0.01$), and 421-440 mm ($\chi^2 = 4.00$, $p < 0.05$).

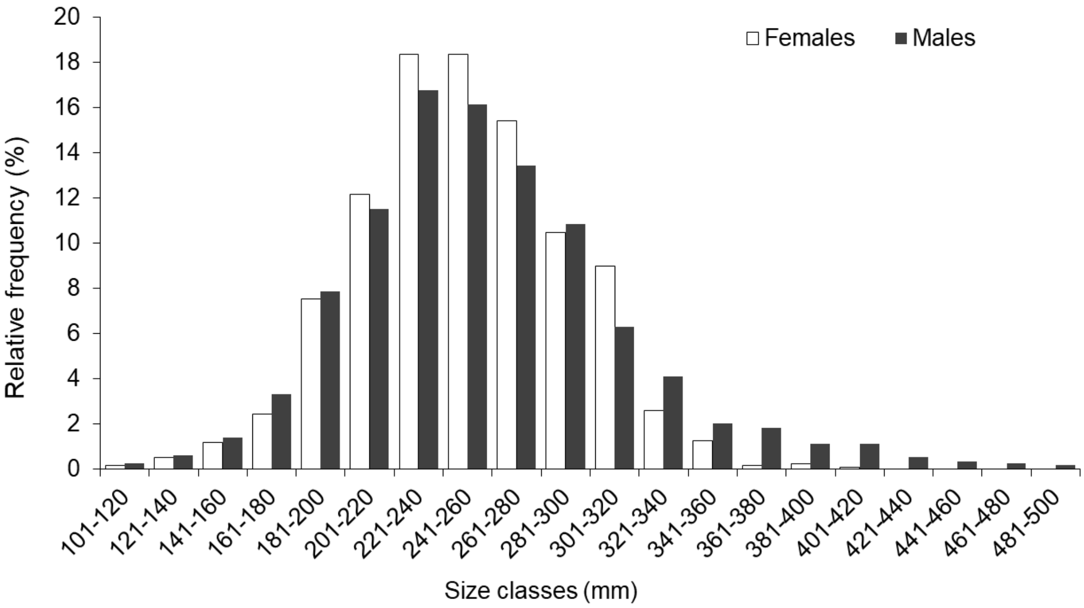

Figure 2 – Size distribution of male and female *Cichla vazzoleri* in the Balbina Reservoir, Amazonas, Brazil.

Length-weight relationships were determined for both sexes, and no significant differences were observed in the mean lengths and weights of males and females. The populational correlation coefficient (r) was 0.9958 and the relationship encountered followed the equation: $Wt = 0.000009 \times SL^{3.177}$ (Figure 3). The estimated L∞ for the *C. vazzoleri* population in the Balbina Reservoir was 514.5 mm of standard length.

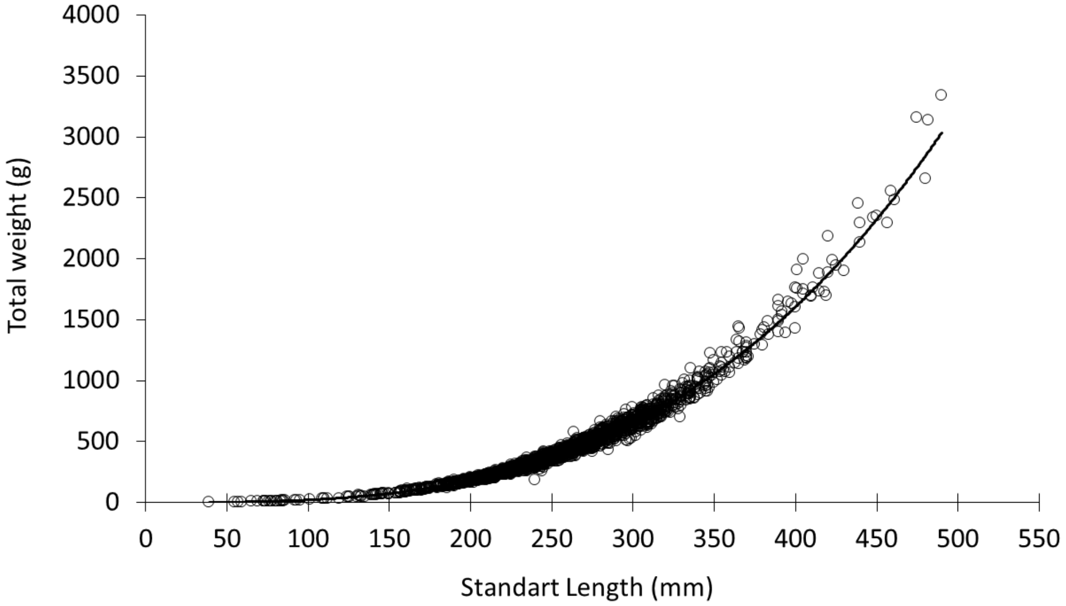

Figure 3 – Length/weight relationship of the *Cichla vazzoleri* population in the Balbina Reservoir, Amazonas, Brazil. Male and female data were pooled for this analysis. ($TW = -4.9554 \times SL^{3.1364}$; $R = 0.9958$; $R^2 = 0.9916$; $p < 0.0000$; n = 2.362)

Female individuals became sexually mature at lengths greater than males, (L_{50} F = 234.67 ± 0.47; L_{50} M = 216.69 ± 0.43) and they reached L_{100} at 290 and 310 mm respectively. The mean batch fecundity was 3548 ± 962 oocytes ($n = 56$; $245 \text{ mm} < F < 322 \text{ mm}$), with the highest fecundity (5679) being observed in a female with 316 mm and 7.62 g of gonad weight. The lowest fecundity was 1128 oocytes in a female with 261 mm and 3 g of gonad weight.

The oocytes have an ellipsoidal shape, with major axis diameters between 0.1 and 3 mm (mean 1.27 ± 0.69 mm). The analysis of the size distributions of vitellogenic oocytes demonstrated three size modes, with diameters between 0.1 and 0.8 mm, 0.9 and 1.4 mm, and 1.5 and 3 mm – indicating batch-spawning with indeterminate fecundity (Figure 4). There were, however, large individual variations in the numbers of oocyte batches, from two to five well-defined batches, with distinct oocyte size classes. Approximately 55.4% of the females had only two batches, 28.6% had three, 14.3% had four, and 1.8% had five.

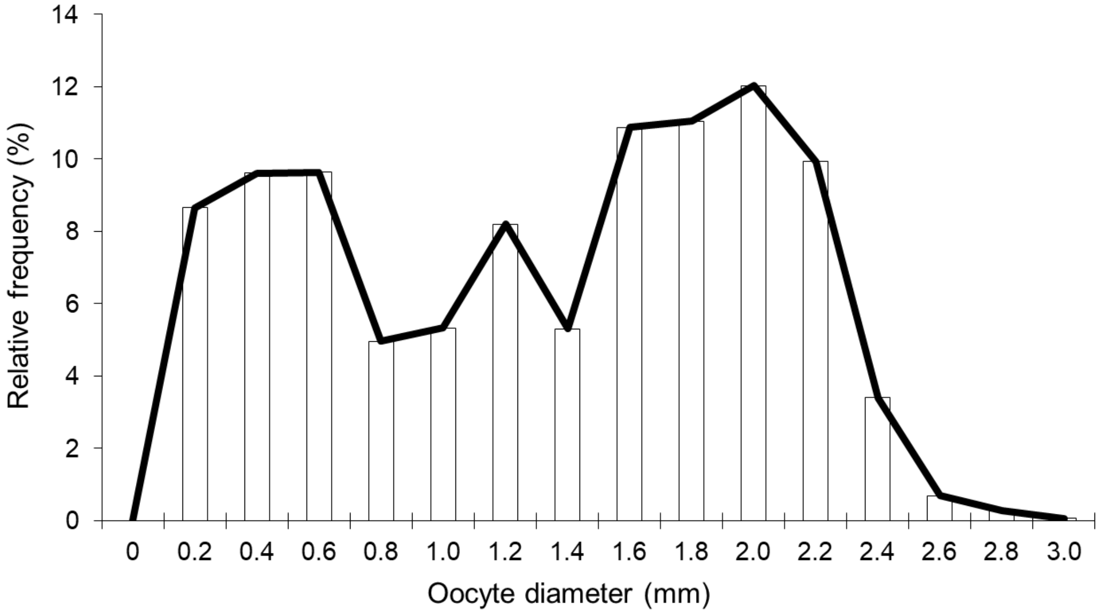

Figure 4 – Size frequency distribution of oocytes of ripe *Cichla vazzoleri* females in the Balbina Reservoir (n = 56), Amazonas, Brazil.

The graphic analysis of the temporal frequencies of males and females in different states of gonad maturity showed mature individuals during the entire study period, although with a higher frequency of mature females from September to January and a higher frequency of mature males between October and January. Immature as well as mature individuals were found at all times during the year for both sexes (Figure 5).

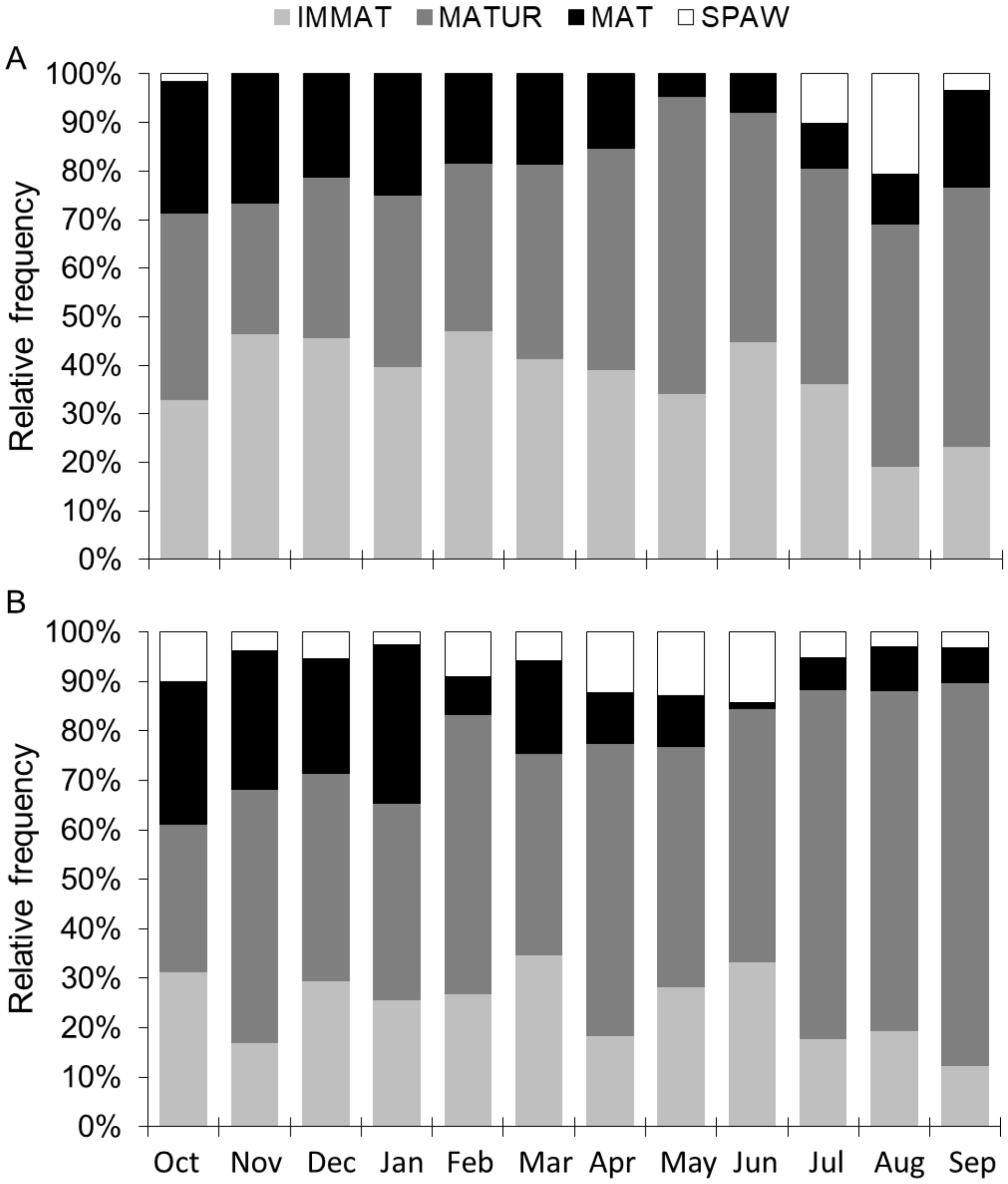

Figure 5 – A: female; B: male. Monthly percentages of IMAT – immature, MATUR – maturing, MAT – mature, SPAW – regenerating specimens of *Cichla vazzoleri* collected in the Balbina Reservoir, Amazonas, Brazil.

The IRA was most intense between October and January, being moderate in February, March, and September and incipient between April and August (N of observed females: 1192; N of ripe females: 228). The IRA had significant correlation with both rainfall ($R^2 = 0.019$; $F_{(1.10)} = 0.197$; $p < 0.005$) and reservoir water levels ($R^2 = 0.247$; $F_{(1.10)} = 3.284$; $p < 0.001$), with IRA being most intense (October-January) when both precipitation and reservoir water levels were low (Figure 6).

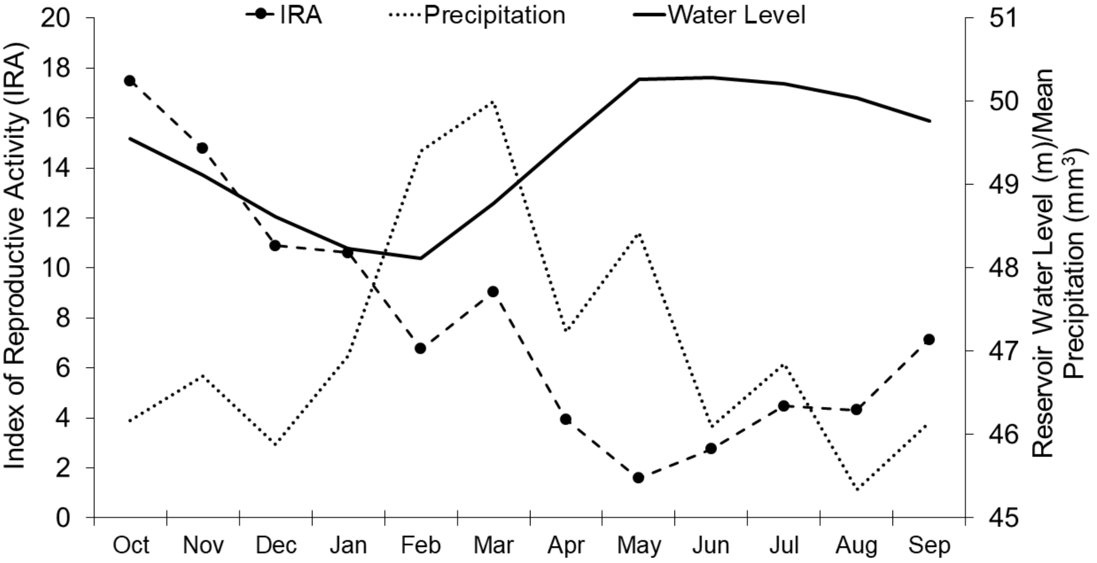

Figure 6 – Monthly values of the index of reproductive activity (IRA), regional precipitation, and the water levels of the Balbina Reservoir, Amazonas, Brazil. The second axis represents both the water level and precipitation.

The reproductive peak from October to January was corroborated by the high values observed for all of the physiological indices, which were significantly different during the different months. The GSI (KW: H (df = 11, N = 2362) = 31.23; $p < 0.001$) demonstrated significant but lowest variation during the year compared to the FI (KW:H (df = 11, N = 2362) = 214.53; $p < 0.001$) and K (KW:H (df = 11, N = 2362) = 55.66; $p < 0.001$) with significant and higher increases in October and November compared to the other months (Figures 7A, B and C).

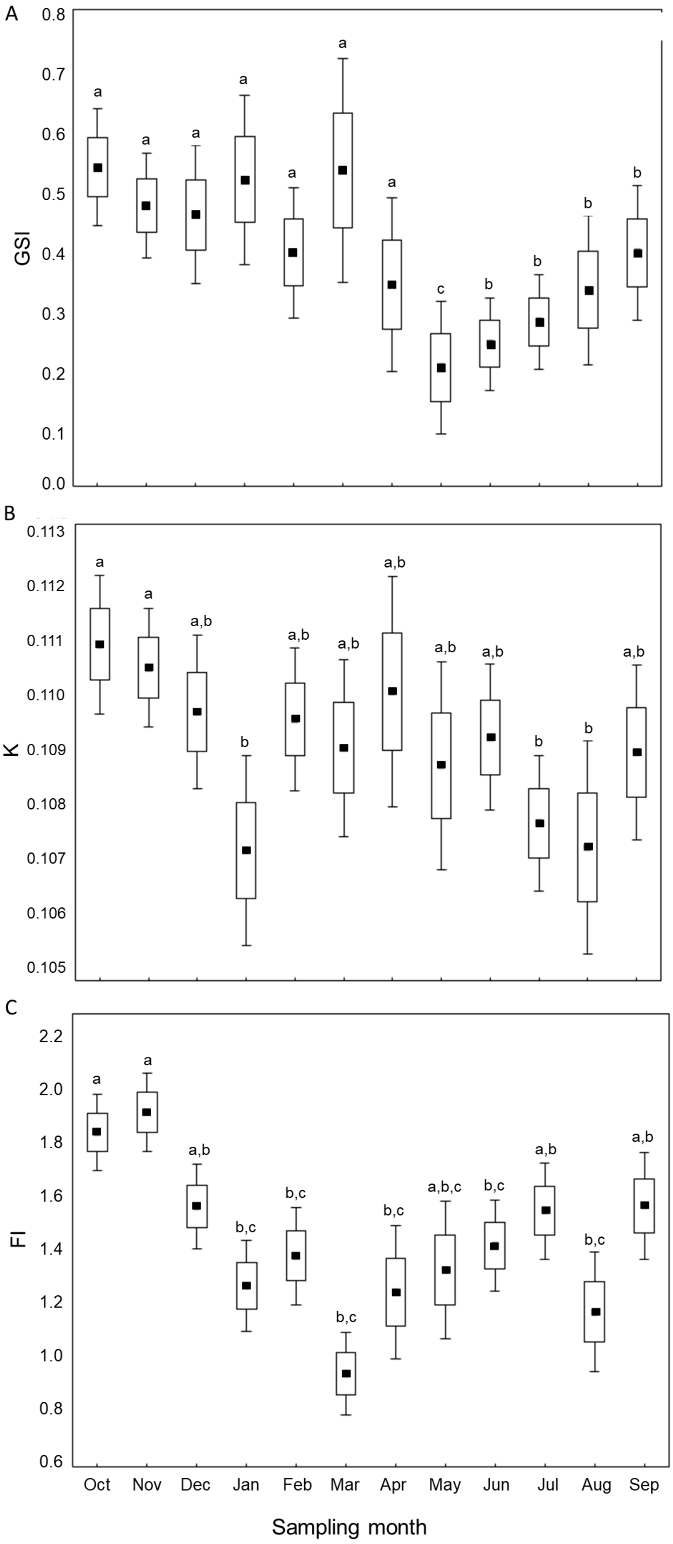

Figure 7 – Monthly variation of: **A:** gonadossomatic index (GSI); **B:** body condition (K); and **C:** fat index (FI). All three indexes showed significant differences between months. Black Squares represent the means, and whiskers the standard error. Different letters on top of the bars means significant differences.

Discussion

We found higher fish abundance inside the REBIO Uatumã, notably for larger individuals, those from the size of first reproduction (L_{50}) to the size of L_{100} when they are all likely to be adults. The mean body size was also higher inside the protected area. Altogether, these results suggest that overfishing outside the protected areas and fisheries at Balbina Reservoir may have been at least partially sustained by the ecological spillover of larger fish from the protected area. Which occurs when individuals from protected areas move to adjacent areas of non-protected sustaining recruitment or population structure[37]. Based on data for marine protected areas Claudet et al.[38] found that the spillover effect seems to occur especially for sedentary large-sized species. *Cichla* species are considered sedentary, despite records of movements ranging from a few meters to a few kilometers which usually increase as fish grow[12,13]. The movement of larger *Cichla vazzoleri* over the reservoir may contribute to keeping larger individuals in the population outside protected areas.

One of the concepts of the analytical models used to evaluate fishing stocks is that there should be neither too few nor too many large fish under a sustainable use of fish stocks, which would indicate over- or under-utilization of those resources respectively [39]. Few individuals near L_{100} and $L\infty$ body size were found and despite the present study not directly analyzing the age structure of the population, the observed low frequency of larger specimens indicated that there were few old fish in the population. Particularly for outside protected areas this results suggested that the input of young in the population have been kept by females in first reproduction with a short reproductive life. Santos and Oliveira Jr.[21] noted that average tucunaré sizes (mainly *Cichla monoculus*) became reduced from 30-35 cm in the 1980s, to 24-27 cm in the 1990s in the Balbina Reservoir. The average size found in the present study for *C. vazzoleri* was near 21-25 cm (both sexes), which suggests a progressive reduction in the body size of the population. Additionally, Santos and Oliveira Jr.[21] noted that *Cichla* sp. (corresponding to *C. vazzoleri* in the current classification) can reach up to approximately 75 cm in standard length, however, in this study the largest size was 49 cm. The combined information showed that the population of *C. vazzoleri* is overfished in the Balbina Reservoir. The minimum size of fishing fixed at 30 cm[26] may have contributed to truncate the population structure and the observed reduction in average size. The regulation of maximum size of fishing at 55 cm proposed in 2014[40] may have little effect on increasing the frequency of larger individuals given the rareness of this class size.

Our results show that the *C. vazzoleri* population in the Balbina Reservoir has a sex ratio biased towards males in the largest classes, although males were smaller than females at the time of first sexual maturation (216 mm vs 235 mm respectively). Slight male predominance was also observed in populations of *Cichla monoculus* in the Bolivian Amazon[10]. In places where peacock bass species were introduced, populations of different species showed proportions close to 1:1, with temporal variations[10]. These variations are common in fish, according to the life cycle, which may have differences between growth and mortality for both sexes[2].

The population structure with males being larger than females appears to be common for species of the Cichlidae family, as well as for other species showing exclusive paternal or biparental care[41]. Larger males have also been observed among the Cichlidae family in Lake Tanganyika in Africa[42], in Lake Jiloá in Nicaragua[43], as well as in reservoirs in the northeast and southeast regions of Brazil and also in the Bolivian Amazon[10]. Growth studies of *C. orinocensis* in Venezuela, undertaken by Taphorn and Barbarino[44], suggested that both sexes grow equally in the first year of life, but males soon thereafter increased their growth rates. A similar growth pattern was observed for *C. ocellaris* in Panama[41]. Suzuki and Agostinho[45] suggested that this type of growth may be adaptive for species that demonstrate biparental territorial defense and/or offspring protection.

Size at sexual maturation (L_{50}) can differ considerably among different species of the genus *Cichla,* and populations of the same species inhabiting different regions. For instance, Gomiero and Braga[46], registered L_{50} sizes of 20 cm of total length, for *C. ocellaris* at Volta Grande Reservoir in São Paulo- Brazil, but 21.5 cm for *C. monoculus*. In contrast, at Santarém-Brazil, the L_{50} of *C. monoculus* was 29 cm[16]. Those great variations in life-history characteristics appear to be related to the adaptive importance of rapid responses to changes in environmental conditions, resulting in species that can quickly respond to the damming of a river and/or anthropic pressures, such as those related to fishing activities[47][48][16]. Regarding the history of intense fisheries pressure over reproductive class sizes, it is likely that the L_{50} sizes have decreased over time. However, the closeness and connectivity of both areas at Balbina Reservoir would also blur the fisheries effect. A comparison of the L_{50} inside and outside the protected area would be desirable although it was not possible due to data limitation.

Like most Cichlidae species, the batch-spawning reproduction and fecundity of *Cichla vazzoleri* can be classified as indeterminate following Murua and Saborido-Rey[49]. The variability in the numbers of batches among individuals, with the large predominance of two batches, may be linked to the presence of an annual period of major reproductive activity during which females lay most mature egg batches (mainly between October and January, which corresponds to the dry season and beginning of the rainy season). Spawning is the most metabolically demanding activity in the lives of fish, whether occurring as a single spawning event or over multiple spawning seasons[50]. Due to energetic demands, many individuals tend to produce only a few batches and spawn only during the most environmentally favorable period[48]. Any eventual loss of offspring would be rapidly replaced by a new batch of maturing oocytes. A similar pattern was observed by Rossoni et al.[51] for *Symphysodon aequifasciatus* ("acará disco") in the lower Purus River, and by Chellappa et al.[52] for *C. monoculus* in reservoirs in the Brazilian semiarid region.

Cichla species have demonstrated particularly accentuated and extended parental care, watching over eggs, larvae, and juveniles[41][53]. Zaret[41] observed that *C. ocellaris* pairs equally share caring for their nests and juveniles; the same behavior was observed with *C. vazzoleri* in the present study. In the Balbina Reservoir, mating pairs remain near standing dead trees to protect their nests and are visible near the water surface while shepherding the juveniles.

That set of reproductive tactics has high energy demands. The conditions of the individuals of *C. vazzoleri*, as indicated by their body conditions and body cavity fat, appeared to progressively increase between May and December, following the increase of IRA. Such a seasonal pattern seems to be a response to the seasonality of the environment. The lower water level of the reservoir between December and April is probably the period of high predation and when *C. vazzoleri* can store energy for the subsequent allocation to gonadal development and parental care. Seasonal pattern or energy storage and allocation was reported by Arrington et al.[54] for *C. temensis* in the Cinaruco River. Energetic costs and behavioral adaptations associated with reproduction (such as gonad maturation, nest building, spawning, and offspring care) probably account for the decline of FI and K observed in *C. vazzoleri* from October to March. Vazzoler[2] noted that flooding events could serve as environment triggers for spawning, as they amplify the available aquatic landscape and provide more abundant food and shelter resources.

Environmental events have likewise been suggested as synchronizing agents for reproduction in various species of the genus *Cichla*. Winemiller[23] discussed the synchronization of spawning with pulses of river flooding, as seen in the Cinaruco River, with gonadal maturation during the period of rece-ding waters (from December to May) and nidification and spawning of *Cichla* sp. at the end of the dry season. In the midcourse of the Negro River, near the municipality of Barcelos, Amazonas, individuals of *C. temensis* showed a high gonadosomatic index between November and April (rising and flood water levels), suggesting that spawning occurs during that period of the flood pulse[55]. Similarly, the spawning of other tucunaré species has been reported to occur during the end of the dry period and beginning of the rainy season: *C. ocellaris* in Panama[41]; *C. orinocencis* in Lake Guri, Venezuela[22]; *C. monoculus* in the region around Santarém-Brazil[16]; *C.* cf. *ocellaris* and *C. monoculus* in the Volta Grande Reservoir in southeastern Brazil[46].

Here, the peak of reproductive activity of *C. vazzoleri* occurred during the period that includes progressive reductions in the water level of the Balbina Reservoir and shortly before the beginning of the rainy season. This pattern of reproductive synchronization with dry conditions is similar to that observed downstream from the Volta Grande dam for *C.* cf. *ocellaris* and *C.* cf. *monoculus*[56]. The water level in the Balbina Reservoir, however, had greater predictive power in terms of IRA than rainfall, suggesting that reproduction is synchronized with regional-level water accumulations rather than the immediate effect of local rainfall. The observed reproductive period was significantly different from that regarded as the closure season before 2014 (August - November), and the adjustments in closure season after 2014 to November - May may have contributed to local fish recruitment and the following size classes[26,40].

Other environmental factors acting as triggers and synchronizing agents for the initiation of the reproductive period of peacock bass may be likewise related to reservoir water levels. Franco et al.[35] suggested that the hydrobiological stability of reservoirs with long water residence is a factor that can favor the reproduction of species that build nests, such as peacock bass. Taphorn and Barbarino[44] reported the synchronization of the reproductive period of *C. orinocensis* with the time of the greatest annual zooplankton production (a pattern also observed among marine fish species in temperate regions, e.g., Ware[57], with reproductive success being related to the synchronization of egg and larval production with food resource availability[58]. Rabelo and Araujo-Lima[59] observed that only two fish species (*Hemigrammus levis* and *Hemiodopsi goeldii*) constituted the main prey of *C. monoculus* in the Balbina Reservoir, accounting for 90% of the stomach contents analyzed. Investigations on the life histories of such prey fish (such as *Hemigrammus levis* and *Geophagus* spp. – which are commonly used as bait and have been observed in the stomach contents of *C. vazzoleri*), could aid in better understanding the complex reproductive strategy of peacock bass.

Conclusion

The results presented here guided the Balbina fishing agreement, leading to the publication that regulates fishing in the unprotected area of the reservoir[40] which may help to sustain the stock of *Cichla vazzoleri* for local fisheries. The results presented here bring important observations on the ecology and management to improve regulations and track population response to regulations.

The ongoing overfishing of *C. vazzoleri*, is indicated by the current fish's small lengths, early maturation, and lower abundance and frequency of large individuals. The minimum size of fishing set in 30 cm in 2007 (still applied) may have contributed to keeping stock of *C. vazzoleri* in Balbina reservoir despite the average size of fish being lower than reported in the 90s. The REBIO Uatumã likely contributed to the large sizes observed outside the protected area as well as to the sustainability of the fisheries. The maximum size of capture of 55 cm, set in 2014, may have little effect on the recovery of the larger class size of *C. vazzoleri* once the frequency of individuals and mainly females at or upper this class is rare. A lower limit of the maximum size of capture would be desirable for body size recovery and to prevent overfishing growth. Initiatives to increase the frequency of fish with larger body sizes would also keep the market value of the commercialized fish[60].

We found that breeding occurs between October and January, which was used to update the closure season previously set between August and November[26][40]. The set of fisheries quota[40] together with the match between closure season and reproductive period may avoid the fishing of fish under parenting and increase the abundance of fish, initially in the first class sizes and at the long term the abundance of fish in larger class size.

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