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Growth curve of selectively bred and non-selectively bred tambaqui (*Colossoma macropomum*)

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Abstract: The aim of this study was to evaluate the growth curve of selectively bred and non-selectively bred tambaqui (*Colossoma macropomum*). The experiment involved 388 fish (weight: 65.38 ± 20.00 g; age: 217 days), consisting of 252 fish from seven selectively bred families (18 fish per family) and 18 non-selectively bred fish (control group). Groups were placed in two 800-m² tanks. Biometric measurements were taken on nine occasions at 30-day intervals, for a period of 254 days. Weight and morphometric traits were evaluated. To describe the tambaqui growth behavior, we adopted the Gompertz nonlinear regression model. Greater growth ($p < 0.05$) was observed in selectively bred families compared with control group. Four families stood out with higher ($p < 0.05$) asymptotic values for weight (F1: 2448.7 g; F7: 2284.7 g; F5 2180.1 g; F4: 2080.5 g; and control: 1808.4 g) and other morphometric traits. None of the selectively bred families (except F5) had a higher growth rate and age at inflection point than the fish from control group. In conclusion, selectively bred and non-selectively bred fish present distinct growth curves, but some families have greatly superior growth.

Key words: Aquaculture, asymptotic value, fish of the Amazon basin, selective breeding of tropical fish, zootechnical performance.

INTRODUCTION

The tambaqui, *Colossoma macropomum* (Cuvier 1818), belongs to the Characiform order, Characidae family, and Myleinae sub-family, it is autochthonous of the Amazon basin, widely distributed in tropical parts of South America and Central Amazon (Araújo-Lima & Gomes 2013). This fish is considered the second largest scale fish of the Solimões River and Amazon River, which in the natural environment can reach up to 100 cm long and 30 kg (Nakatani et al. 2001).

According to the IBGE (Instituto Brasileiro de Geografia e Estatística), in 2017, the tambaqui was considered one of the most important species for the Brazilian economy, produced in 25 of the 26 Brazilian states, and representing the second largest production among aquatic organisms, with more than 88,000 t (IBGE 2019). This fish is economically important in many South American countries (Lopera-Barrero et al. 2011) mainly owing to its satisfactory performance, omnivorous feeding habit, highly appreciated meat, resistance to disease, and adaptability to low dissolved-oxygen levels in the water (Araújo-Lima & Gomes 2013).

The lack of breeding programs for native fish in Brazil has led many fish farmers to produce hybrid fish aiming to increase their yields. Noteworthy examples of such hybrids are the tambacu (female tambaqui × male pacu) and tambatinga (female tambaqui × male pirapitinga) (Lopera-Barrero et al. 2011). Although tambaqui was the most largely produced fish in Brazil in 2016 (13,992 ton - 27% of total fish production), hybrids also occupy a prominent third position in this ranking (44,948 ton - 8.9% of total fish production) (IBGE 2017). However, though hybrid fish may be higher yielding compared with their parents, this gain is restricted to a single generation, whereas the genetic gain obtained from selective breeding continues across the subsequent generations (Ponzoni et al. 2005).

Breeding programs for animal and plant breeding have been the basis of agricultural development in the world since the 1930s (Silva et al. 2018). Today, it is impossible to think of the production of poultry, pork, beef, soy, and corn, among other species, without breeding programs. For aquatic organisms with a focus on food production were published in the late 1960s to the early 1970s with salmon and trout (United States and Norway) (Hilsdorf et al. 2015, Silva et al. 2018). Research with some fish species has shown that genetic gains in growth rate can range from 8 to 12% per generation, in well-managed programs (Nguyen 2016), and these values may reach up to 15%. The lack of genetic selective breeding programs for fish may lead to the production of animals with productive potential lower than or equal to that of animals naturally present in the environment (Ponzoni et al. 2005).

At the end of 2008, a selective-breeding program for tambaqui was started in the northern state of Mato Grosso, Brazil — the first ever selective-breeding program with native fish in the country (Oliveira et al. 2012). The first generation of tambaqui bred for weight gain (G1) was obtained in January 2012, featuring a 14.8% higher growth rate than that of non-selectively bred fish and some families reaching an impressive 24.8% (Marcos et al. 2016). The aim of this study was to evaluate the growth curve of selectively bred and non-selectively bred tambaqui (*Colossoma macropomum*).

MATERIALS AND METHODS

Location and animals

Tambaqui families from the first generation of fish selectively bred for weight gain (G1) were obtained in January 2012 from the Central Unit for the Selective Breeding of Tambaqui Fish, located in Sorriso – MT, Brazil (12°51'56.40'' S; 55°50'03.30'' W). The progeny was generated after three years of formation of the base population, when the tambaqui reached sexual maturity. The seven tambaqui families assessed derived from the reproduction of seven males and seven females selected for their superior genetic potential for daily weight gain.

For induced reproduction, 5.50 mg carp pituitary extract/kg live weight was supplied on two occasions for females (10%; and 90% after 12 h) and 2.50 mg carp pituitary extract/kg live weight were provided in a single dose for males (Woynarovich & Horváth 1983). After gamete extrusion and fertilization, the eggs were incubated in the proportion of 1.00 g/L of water. After absorption of the vitelline sac, the post-larvae were placed in 500-L cages and fed a meal (36% crude protein) and zooplankton. Thirty-day-old fingerlings were placed in 3.00-m^3 hapas until they were 12.00-cm long (size required for inserting the microchip) and received the same meal as in the previous phase.

Fingerlings were later transported to the experimental units of the Experimental Farm of the Federal University of Mato Grosso, located in

Santo Antonio do Leverger - MT, Brazil (15° 51'56'' S; 56° 04'36'' W). A total of 388 young fish were used (average weight 65.38 ± 20.00 g and total length 15.00 ± 1.25 cm); 252 of them were retrieved from the seven families of the breeding program and 136 fish lacked any genetic selection, forming the control group. All fish were individually identified by a transponder implanted in the dorsal region. The trial began when the fish were 217 days old. This study was approved by the Ethics Committee on Animal Use (CEUA) of UFMT (approval nº. 23108.069114/2014-85) and process number 474767/2011.

Experimental units, diets, and water quality

The tambaqui genetic groups (selectively bred and control group) were placed into two 800-m² tanks. Each tank housed 126 selectively bred fish (18 fish per family; seven families in total) plus 68 fish from control group, totaling 252 selectively bred fish (36 fish per family) and 136 control fish. There was a partial replacement of water during the experiment (average 5%). Fish were fed (to satiety) twice daily (09:00 and 16:00 h) an extruded feed containing 32% protein.

Water quality was monitored weekly (in the morning). The following physico-chemical parameters were analyzed at the Laboratory of Fish Culture of the Experimental Farm: temperature, dissolved oxygen (YSI Pro 20, Yellow Springs Instruments), pH (Q400BC, Quimis®), total alkalinity (based on the methyl orange indicator solution), and non-ionized ammonia (Emerson et al. 1975). The water parameters were similar in both tanks, and the following mean values were recorded throughout the experiment: temperature: 30.3 ± 1.4 °C; dissolved oxygen: 5.1 ± 2.1 mg L^{-1}; pH: 6.9 ± 0.1; total alkalinity: 66.4 ± 27.4 mg L^{-1}; and non-ionized ammonia: 0.01 ± 0.01 mg L^{-1}.

Traits measured

The experiment started after a period of 15 days for the fish to acclimate to the earth tanks. The fish were deprived of feed for 12 h prior to the biometric measurements subsequently; they were anesthetized in an eugenol solution (50 mg L^{-1}) following the methodology described by Inoue et al. (2011). Biometric measurements were taken on nine occasions at 30-day intervals, for

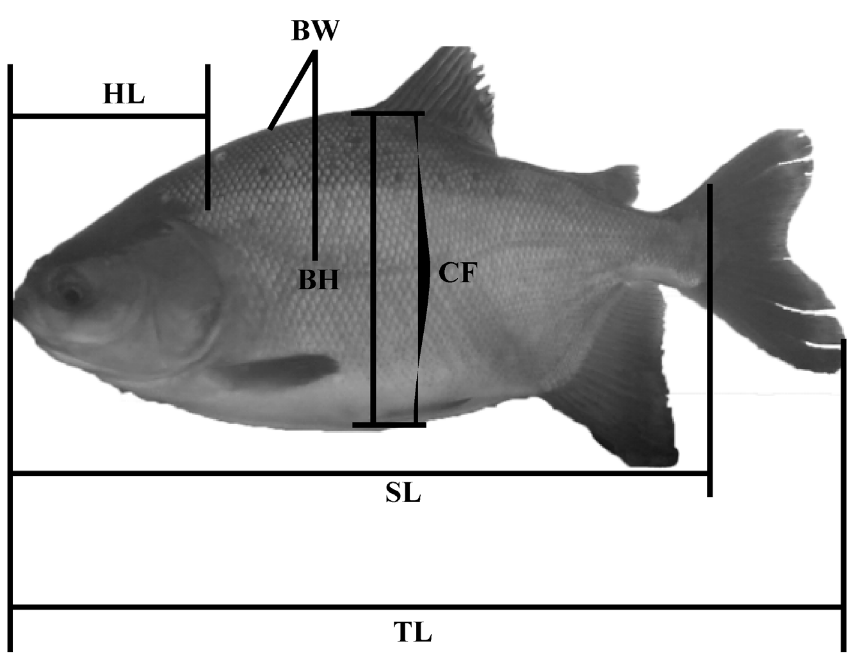

Figure 1. **Measured morphometric traits (cm) in tambaqui (*Colossoma macropomum*). Measurements: head length (HL), body height (BH), body width (BW), circumference (CF), standard length (SL), and total length (TL).**

a period of 254 days. All fish were evaluated for weight and the following morphometric measurements: total length, standard length, head length, body height, body width, and body circumference (Figure 1).

Statistical analysis

The experiment was conducted as a completely randomized design in which 2849 morphometric data of tambaqui belonging to selectively bred families (seven) plus a control groups were analyzed. To describe the tambaqui growth behavior, we adopted the nonlinear regression mathematical model proposed by Gompertz (Fialho 1999), as shown below:

$$y_i = A.e^{-e^{-B.(t-C)}}$$

Where:

Yi = weight (g) or size (cm) estimated at age *t*;

A = asymptotic weight (g) or size (cm) when *t* tends to plus infinite; i.e., this parameter can be interpreted as the weight or size when growth ceases;

B = relative growth at the inflection point (g day-1 per g of fish or cm day-1 per cm of fish);

C = age at the inflection point (days);

t = age (days); and

e = 2.718281828459.

The tambaqui growth curve parameters of both evaluated groups were estimated according to the Marquardt method modified using the NLIN procedure of SAS software. Eight Gompertz functions were tested and adjusted to compare the growth patterns of different traits between families and control group. The simplest model (M_8) revealed that the Gompertz function parameters were unique for both families, and the most complex model (M_1) showed that each family had a specific parameter. The other models indicated different numbers of constraints describing the growth curves between the tested families which showed one, two, or three parameters of the common model, as can be seen in Table I.

The adequacy of models was evaluated by the likelihood ratio test to check the equality of parameters in nonlinear models, adopting chi-square approximations (χ^2), as proposed by Regazzi & Silva (2010). Only the families with outstanding growth were used in the representation of the growth curves in the graphs, along with control group.

RESULTS

Model M_7 was the best-fitting for most families in all evaluated traits. Likewise, models M_3 and

Table I. Description of the tested models for the growth curve of tambaqui (*Colossoma macropomum*).

	Model Setting							
	M_1	**M_2**	**M_3**	**M_4**	**M_5**	**M_6**	**M_7**	**M_8**
Parameter	*Ai*	*A*	*Ai*	*Ai*	A	A	Ai	A
	Bi	Bi	B	Bi	B	Bi	B	B
	Ci	Ci	Ci	C	Ci	C	C	C

Parameters *A, B,* and *C* belong to the nonlinear mathematical model of Gompertz.
i = different parameters tested for selectively bred families and control (non-selectively bred).

M_4 were the best-fitting for most families for weight; M_1 for standard length; and M_1 and M_2 for head length. Families F1, F4, F5, and F7 showed the highest asymptotic values in comparison with control group for all analyzed traits; therefore, they were represented in the graph comparatively to control group (Table II; Figures 2 to 5).

Superior growth ($p < 0.05$) was observed in most of the selectively bred families (first generation of selection for weight gain - G1) compared with the non-selectively bred fish. Four families stood out (F1, F4, F5, and F7) for their higher ($p < 0.05$) asymptotic values (parameter A) in relation to control group, for all evaluated traits. One family (F2) showed higher ($p < 0.05$) asymptotic values for all evaluated traits, except head length, which was lower ($p < 0.05$), and two families (F3 and F6) had lower ($p < 0.05$) or equal asymptotic weights for all evaluated traits (Table II; Figures 2 to 5).

None of the selectively bred families had a higher relative growth rate (parameter B) than control group, for any of the evaluated traits. All families had similar growth rates to control for most of the evaluated traits, except F1 and F5, whose relative growth rate was lower ($p < 0.05$) for most of the evaluated traits. Only the relative growth rate for body width was similar between all families and control (Table II; Figures 2 to 5).

Age at the inflection point (parameter C) in the families was lower than ($p < 0.05$) or equal to those of control fish, except for family F5, which was older ($p < 0.05$) at the inflection point for the weight trait. In family F2, only standard length, and in family F3, only head length were associated with lower ($p < 0.05$) ages at the inflection point than control. However, this parameter was similar for all traits in family F4 and lower ($p < 0.05$) for all traits in family F5 compared with control. In the remaining families, three or more traits had a lower ($p < 0.05$) age at the inflection point than control. The lower age at the inflection point of some families for certain traits evinces an earlier accelerated growth (at the inflection point) (Table II; Figures 2 to 5).

DISCUSSION

The tambaqui selective-breeding program is recent, and the present is the first evaluation of the growth curve of different families from such program for this species. Our findings show great superiority of selectively bred fish (in most families) in comparison with their non-selectively bred counterpart. Although the selection-generation interval of tambaqui is long (sexual maturity around 3 years of age) compared with that of Nile tilapia (sexual maturity around 4-6 months of age), the current results show great potential for the development of the selective-breeding program for this species.

During the first stage of life, the growth curve is characterized by a slower development, followed by a period of self-acceleration until the maximum point of growth rate (around puberty) is reached, and then by a self-deceleration phase (Berg & Butterfield 1976, Weatherley & Gill 1987). This pattern was observed in the tambaqui (selectively bred and non-selectively bred) and this trend was confirmed by the adequacy test and revealed the existence of different parameters (A - asymptotic weight; B - relative growth curve; and C - age at the inflection point) between the selectively bred families and control group, indicating different growth behaviors.

The asymptotic value for weight obtained by most families is near that commonly adopted for the slaughter of tambaqui, which is approximately 2 kg, except for families F3 and F6 and control, whose respective weights were

Table II. Estimates of parameters of the best fitting models for weight, total length, standard length, head length, body height, body width, and body circumference of selectively bred families of tambaqui (*Colossoma macropomum*) and control group (non-selectively bred) after 254 days of culture length, head length, body height, body width, and body circumference of selectively bred families of tambaqui (*Colossoma macropomum*) and control group (non-selectively bred) after 254 days of culture.

		Families							
Trait	**Parameter**	**F1**	**F2**	**F3**	**F4**	**F5**	**F6**	**F7**	**Control**
Weight	A	2488.7*	2031.8*	1664.1*	2080.5*	2180.1*	1658.9*	2284.7*	1808.4
	B	0.0111*	0.0122*	0.013	0.0129	0.0111*	0.0133	0.0124	0.0125
	C	335.1	333.9	331.3	329.9	342.5*	325.2*	327.0*	333.9
	Model	M_4	M_4	M_7	M_7	M_1	M_3	M_3	-
Total length	A	48.8*	46.6*	44.2*	46.9*	48.6*	45.1	48.1*	45.8
	B	0.0109*	0.0114	0.0118	0.0120	0.0104*	0.0123	0.0114	0.0116
	C	230.5*	241.6	243.6	240.4	239.2*	239.0*	232.3*	243.4
	Model	M_1	M_7	M_7	M_7	M_1	M_5	M_3	-
Standard length	A	41.6*	39.8*	37.3*	39.9*	41.2*	37.8	41.3*	38.5
	B	0.0096*	0.0102*	0.0111	0.0109	0.0097*	0.0113	0.0102	0.0107
	C	233.9*	247.4*	250.0	246.2	245.3	242.2*	238.4*	248.4
	Model	M_1	M_1	M_7	M_7	M_4	M_5	M_3	-
Head length	A	12.0*	10.8*	11.2	11.6*	11.8*	11.2	12.1*	11.1
	B	0.0137	0.0151	0.0138*	0.0148	0.0131*	0.0138*	0.0134*	0.0150
	C	226.3*	238.2	233.9*	232.9	232.5*	233.9*	228.5*	237,2
	Model	M_3	M_7	M_2	M_7	M_1	M_2	M_1	-
Body height	A	23.6*	22.2*	19.5*	22.2*	22.1*	20.9	22.9*	20.9
	B	0.0086	0.0093	0.0106	0.0100	0.0088	0.0093	0.0095	0.0095
	C	252.6*	259.0	257.3	257.0	259.1	259.7	250.2*	261.0
	Model	M_3	M_7	M_7	M_7	M_7	M_8	M_3	-
Body width	A	8.0*	7.7*	7.1	7.6*	8.0*	6.6*	7.6*	7.1
	B	0.0098*	0.0099	0.0103	0.0109	0.0090*	0.0124	0.0114	0.0108
	C	256.6*	269.8	270.1	264.4	270.3	260.8	257.6*	265.5
	Model	M_1	M_7	M_8	M_7	M_4	M_7	M_3	-
Body circumference	A	45.0*	42.0*	39.2*	42.1*	42.8*	38.8*	43.4*	39.8
	B	0.0101*	0.0114	0.0115	0.0124	0.0098*	0.0119	0.0116	0.0114
	C	232.3*	240.9	244.7	241.5	240.8	240.0	232.7*	242.4
	Model	M_1	M_7	M_7	M_7	M_4	M_7	M_3	-

A: asymptotic weight (g) or size (cm), *B*: relative growth at the inflection point (g day-1 per g of fish or cm day-1 per cm of fish) and *C*: age at the inflection point (days) parameters belonging to the Gompertz model.
*Parameters followed by an asterisk indicates that the values obtained in the selectively bred families (F1, F2, F3, F4, F5, F6, and F7) differ ($p < 0.05$) statistically from control group (non-selectively bred).
Model = Best-fitting model according to χ^2 statistic ($p < 0.05$) - best-fitting model for each family compared with control group.

1664.1, 1658.9 g, and 1808.4 g. The final density of 0.24 fish/m^2 in the tanks provided adequate space for the growth of the fish, considering that this density corresponds to a final biomass of approximately 0.5 kg/m^2, deemed adequate for semi-intensive production systems (Ribeiro 2001). Moreover, the water parameters did not interfere with their growth, since the values recorded throughout the experiment were within the range considered appropriate for tropical-fish production (Boyd 1998).

The highest asymptotic value for weight was seen in family F1, which was heavier than control by 680.3 g (27.3%). In descending order, the highest asymptotic values were then obtained by families F7, F5, F4, and F2, which were 476.3, 371.7, 272.1, and 223.4 g heavier than control, respectively. These results show that, in only one generation, some families had performance superior to non-selectively bred fish. On the other hand, the asymptotic weights of families F6 and F3 were respectively 149.5 g and 144.3 g lower than those of control group.

In fish, selective breeding can provide a genetic gain of 15% per generation (Ponzoni et al. 2005). Three families (F1, F7, and F5) had an asymptotic weight 15% higher than that of control; two families (F4 and F2) had an asymptotic approximately 15% higher than that of control; and two families (F1 and F6) had a lower asymptotic weight than control. These findings demonstrate the great potential of tambaqui for selective breeding. If the tambaqui selective-breeding program maintains such gain, it will be possible to double the weight of the fish compared with non-bred fish in approximately seven generations.

The lower relative growth rate for the weight trait in families F1, F2, and F5 in relation to control group indicates that these families have a lower growth at the inflection point of the curve, which did not result in a higher asymptotic value for control group. Moreover, family F5 presented a higher age at the inflection point, indicating their delayed accelerated growth compared with control, whereas families F6 and F7 were younger at the inflection point, suggesting earlier accelerated growth in those fish. This clearly shows the existence of early and late

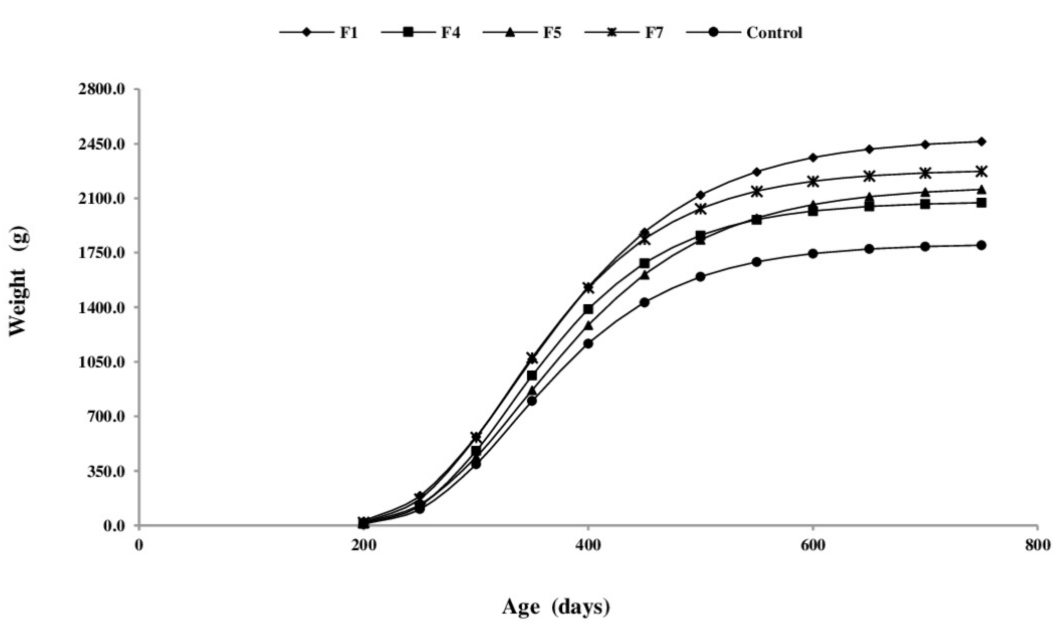

Figure 2. **Growth curves of weight (g) as a function of age in selectively bred families (F1, F4, F5 and F7) of tambaqui (*Colossoma macropomum*) and group non-selectively bred (control).**

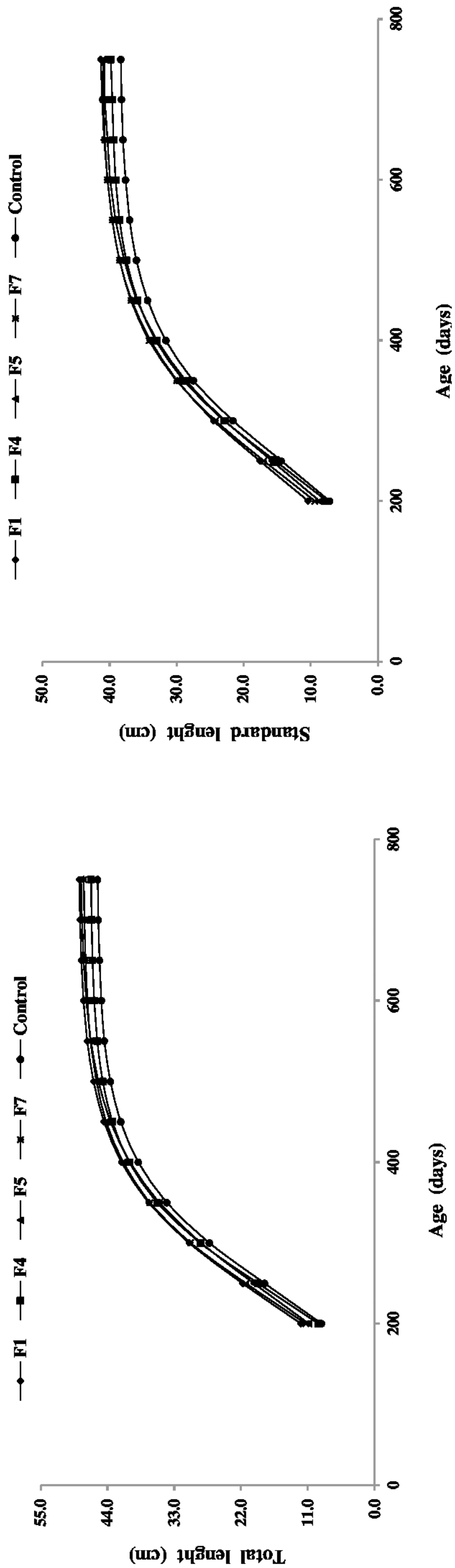

Figure 3. Growth curves of total length (cm) and standard length (cm) as a function of age in selectively bred families (F1, F4, F5 and F7) of tambaqui (*Colossoma macropomum*) and group non-selectively bred (control).

families with respect to the relative growth rate at the inflection point of the curve.

All families presented higher asymptotic values than control for total and standard lengths, except families F3 (lower growth) and F6 (similar growth), where as family F1 stood out for those traits (highest asymptotic value). The lower relative growth rate for total and standard lengths of families F1, F2 (only for standard length), and F5 in relation to control indicates that these families have a lower growth rate at the inflection point. Furthermore, the lower age at the inflection point of families F1, F2 (only for standard length), F5 (only for total length), F6, and F7 as compared with control indicates that these families are earlier for accelerated growth at the inflection point. These results show the lower growth rate and age at the inflection point in some families compared with control did not necessarily translate to a lower asymptotic value, in those families.

Interestingly, the age at the inflection point was much lower for total length (between 230.5 and 243.6 days) and standard length (between 233.9 to 250.0 days) in than for weight (between 325.2 and 342.5 days) in all families and control group, indicating an earlier accelerated growth for those traits in comparison with weight. The same response was observed for the other morphometric traits. Therefore, tambaqui is earlier in morphometric growth than in weight gain.

The higher asymptotic value for head length shown by families F1, F4, F5, and F7 compared with control is a consequence of their higher growth for the morphometric traits (mainly total and standard lengths). Mello et al. (2015) observed slow growth for this characteristic, with similar growth curves between the studied tambaquis (males and females – generation G0), thus indicating a constant exponential growth. This relationship was not seen in family

F2, which despite showing a higher asymptotic value for total and standard lengths compared with control, had a smaller head. This result denotes that this family can be exploited aiming at the production of fish with a higher carcass yield, since a large head size is not desirable as it can reduce the carcass yield (Vandeputte et al. 2017).

The lower relative growth rate for head length in families F3, F5, F6, and F7 did not result in a lower asymptotic value for this trait in relation to control. These data show that although those families had a lower relative growth rate, their growth continued for a longer period, leading to a higher asymptotic value for head length (except in F3 and F6). The lower age at the inflection point in families F1, F3, F5, F6, and F7 compared with control indicate that these families are earlier than control in accelerated growth for head length.

A noteworthy finding was that the relative growth rate for head length was higher in selectively bred and control families than for the other traits, and that age at the inflection point was lower than the other traits in both groups of families. These findings suggest a high growth rate at the inflection point and an early accelerated growth of head length in comparison with the other traits.

The higher asymptotic value for body height in families F1, F2, F4, F5, and F7 compared with control group indicates that these families have a greater growth for this trait than non-selectively bred fish. Although the relative growth rate was similar between the families and control, the lower age at the inflection point in families F1 and F7 indicates an early accelerated growth thereof compared with control, which resulted in the higher asymptotic values obtained by those families compared with the others.

The higher asymptotic value for body length and body circumference in all families (except

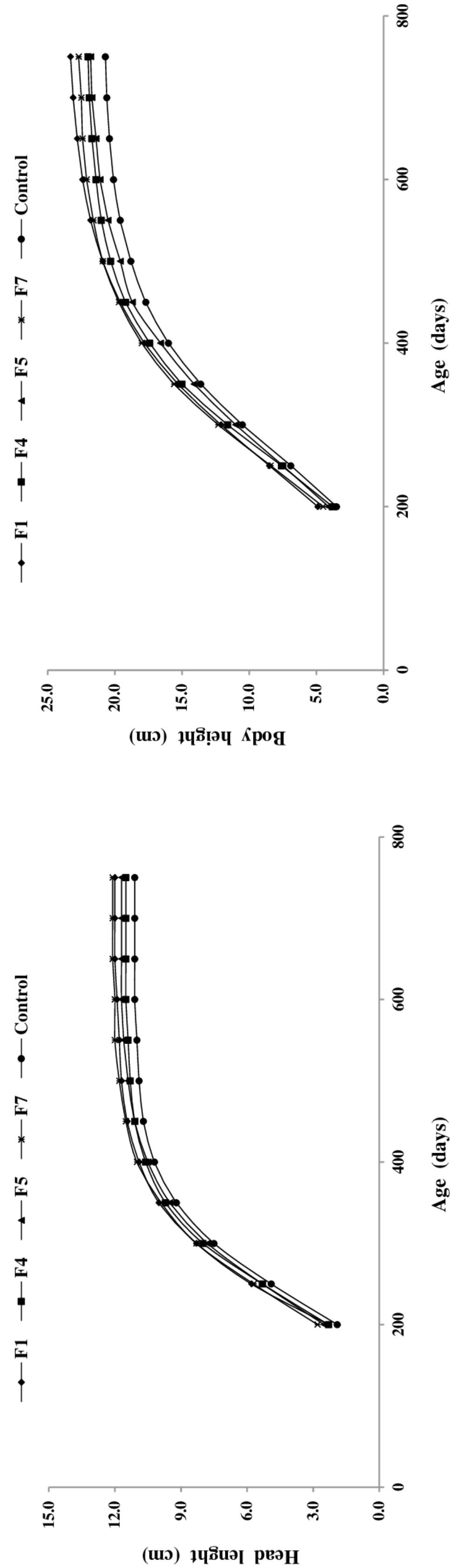

Figure 4. Growth curves of head length (cm) and body height (cm) as a function of age in selectively bred families (F1, F4, F5 and F7) of tambaqui (*Colossoma macropomum*) and group non-selectively bred (control).

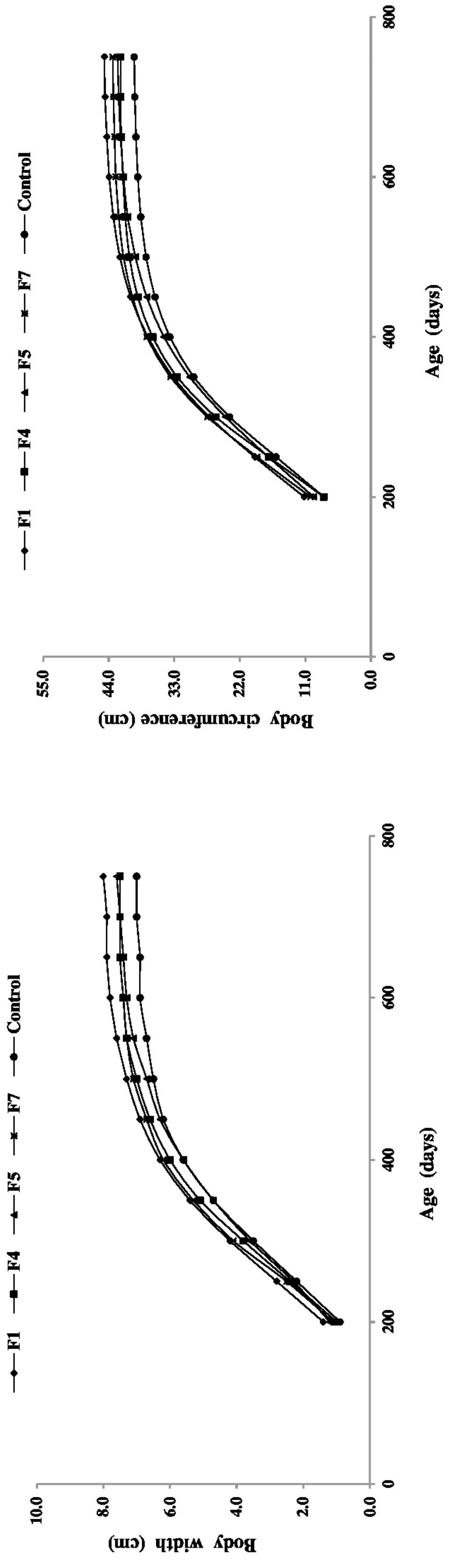

Figure 5. Growth curves of body width (cm) and body circumference (cm) as a function of age in selectively bred families (F1, F4, F5 and F7) of tambaqui (*Colossoma macropomum*) and group non-selectively bred (control).

F3 and F6) in relation to control may indicate a higher carcass yield in the former fish. In this regard, this trait could also be used in a future selection aimed at increased carcass yields. Additionally, the lower relative growth rate of families F1 and F5 suggests that body length and body circumference in those families had a lower relative growth at the inflection point of the curve in comparison with control. The lower age at the inflection point for families F1 and F7 indicates that they had an earlier accelerated growth, which contributed to the higher asymptotic value of families F1 and F7 for body length and F1 and F5 for body circumference.

All across the globe, expressive results have been observed in aquatic organisms from genetic gain promoted by selective breeding, as seen for Nile tilapia (Ridha 2006, Ponzoni et al. 2011, Thodesen et al. 2011), carp (Nguyen 2016), rainbow trout, Atlantic salmon, and channel catfish (McAndrew & Napier 2010). However, the selective breeding of aquatic organisms is rather recent in Brazil. Although the selective-breeding program for Nile tilapia (an exotic species) is already well-established in Brazil, with satisfactory genetic gains obtained in each selection generation (Oliveira et al. 2012, Reis Neto et al. 2014, Porto et al. 2015, Oliveira et al. 2016), tambaqui is the first aquatic organism in a selective-breeding program with native species in this country. The present results demonstrate great growth in most of the selectively bred families in comparison with the non-selectively bred fish.

Therefore, selectively bred and non-selectively bred fish have different growth curves and the asymptotic value for weight and morphometric traits is higher in selectively bred families in comparison with non-bred fish; for this attribute, family F1 stood out with a 27.3% higher asymptotic value than control. None of the selectively bred families has a higher relative growth rate for weight or morphometric traits than non-selectively bred fish. Selectively bred families (except F5) have a lower age at the inflection point (earliness in accelerated growth) for weight and morphometric traits in relation to non-selectively bred fish.

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Each author presented relevant contribution to elaboration of the present manuscript as fallows: Rebeca Marcos conducted and carried out practical activities throughout the experiment, prepared the figures and tables and wrote the article. Main responsible for the final text. Carlos de Oliveira conducted the statistic and data analysis. Ruy Filho (co-advisor), conducted the interpretation of the statistical analysis, discussion of the results and reviewed drafts of the paper. Janessa Abreu conducted the orientation of the activities and monitored all the experimental stages in Cuiabá (MT). Caio de Barros conducted practical activities of biometrics, management and slaughter of fish. Darci Fornari and Nelson Lopera-Barrero were responsible for the production of the genetically improved tambaqui families and contributed with some financial support. Ricardo Ribeiro and Danilo Júnior contributed to the studies in the formation of the tambaqui genetic improvement program and to the final review of the article. Jayme Povh conducted the orientation of the activities, monitored all the experimental, sampling design, methodology and discussion of the results. Assisted in the writing of the final manuscript. All authors revised the manuscript and approved the final version.