Aquaculture Reports 48 (2026) 103511

Contents lists available at ScienceDirect

Aquaculture Reports

journal homepage: www.elsevier.com/locate/aqrep

Assessment of the energy and protein requirements for tambaqui (*Colossoma macropomum*, Cuvier 1818) using the factorial approach

Guilherme Wolff Bueno [a,d,*], Lincoln N. Oliveira [b], Cristielle N. Souto [b,c], Tavani R. Camargo [e], Danilo C. Proença [f], Igo G. Guimarães [b,c,**]

[a] São Paulo State University (UNESP), Aquaculture Center, Jaboticabal Campus, Jaboticabal, SP, Brazil
[b] Federal University of Goiás (UFG), Graduate Program in Animal Science (Zootecnia), Goiânia, GO, Brazil
[c] Federal University of Jataí (UFJ), Aquaculture Research Laboratory (LAPAQ), Jataí, GO, Brazil
[d] São Paulo State University (UNESP), Faculty of Agricultural Sciences of Vale do Ribeira (FCAVR), Registro, SP, Brazil
[e] Sample Innovation and Biotechnology in Animal Production, Brazil
[f] Biomonetize Company, Brazil

ARTICLE INFO

Keywords:
Aquaculture
Nutritional requirement
Metabolism
Factorial modeling
Growth rate
Feed intake

ABSTRACT

A factorial modeling approach was used to estimate digestible protein (DP) and digestible energy (DE) requirements of tambaqui (*Colossoma macropomum*) reared under pond culture conditions. The model integrates controlled laboratory experiments on maintenance requirements, nutrient digestibility, and protein and energy retention efficiencies with growth data from commercial pond farms spanning a wide range of body weights. Maintenance requirements were estimated as 0.2765 g DP $kg^{-0.75}$ day^{-1} and 10.84 kJ DE $kg^{-0.95}$ day^{-1} . Retention efficiencies for protein and energy were 30.82% and 33.47%, respectively, corresponding to deposition costs of 3.24 g DP g^{-1} protein gain and 3.34 kJ DE kJ^{-1} energy gain. The model predicts realistic feeding rates, feed intake (% body weight day^{-1}), and feed conversion ratios across growth stages, consistent with values reported for pond-cultured tambaqui under tropical conditions. Although the model tends to overestimate protein requirements at early growth stages, likely due to limitations in estimating protein retention efficiency, it provides coherent and biologically plausible indicators for nutritional management during grow-out. The proposed factorial framework is directly applicable to pond-based tambaqui production under typical tropical conditions and represents a robust decision-support tool for precision feeding and feed formulation, with potential for adaptation to other production systems when system-specific data are available.

1. Introduction

Global consumption of aquatic animal food continues to grow, reaching an estimated 20.7 kg per person in 2022, with forecasts projecting an increase to 21.3 kg by 2032. Aquaculture is expected to supply 60% of aquatic food for human consumption by then, reinforcing its expanding role in global food security. Currently, 83% of aquatic animal production for food comes from aquaculture, highlighting the dominance of freshwater species in the sector. With an average annual growth rate of 3% since 1961, surpassing that of all terrestrial meats combined, aquaculture has become one of the fastest-growing food production sectors worldwide, with significant potential to meet the protein needs of a growing population (Valenti et al., 2021; FAO, 2024).

In Brazil, freshwater fish farming produced 655.5 thousand tons in 2023, with tambaqui (*Colossoma macropomum*) being the primary native fish farmed, accounting for 17.3% of the total production (IBGE, 2023). Tambaqui naturally inhabits the Amazon and Orinoco River basins but is widely found throughout Latin American countries, where it holds a vital economic and social role as a protein source for low-income communities, especially in northern Brazil (Guimarães and Martins, 2015; Woynárovich & Van Anrooy, 2019). This species has favorable characteristics for commercial farming, such as high-quality meat that is well accepted, rapid growth, omnivorous diet, and adaptability to different farming systems (Amancio et al., 2019; Gomes and Silva, 2009; Lima et al., 2016; Woynárovich & Van Anrooy, 2019).

Despite the importance of tambaqui for Brazil and Latin American

* Corresponding author at: São Paulo State University (UNESP), Aquaculture Center, Jaboticabal Campus, Jaboticabal, SP, Brazil.
** Corresponding author at: Federal University of Goiás (UFG), Graduate Program in Animal Science (Zootecnia), Goiânia, GO, Brazil.
E-mail addresses: guilherme.wolff@unesp.br (G.W. Bueno), igoguimaraes@ufj.edu.br (I.G. Guimarães).

https://doi.org/10.1016/j.aqrep.2026.103511
Received 19 September 2025; Received in revised form 26 February 2026; Accepted 11 March 2026
Available online 14 March 2026

aquaculture, there is a lack of information and controversy regarding its nutritional requirements, especially during the intermediate and final stages of the production cycle. For example, a previous study on the protein and energy needs of tambaqui showed variations of up to 71% in published literature, with the most variation observed during the initial stage (1–50 g) and intermediate growth stage (100–250 g) (Guimarães and Martins, 2015). Currently, generic feeds for omnivorous fish are used, which do not allow the species' full growth potential to be expressed (Guimarães and Martins, 2015). Experimental evidence has shown that different levels of dietary phosphorus can support growth but may lead to trade-offs, such as reduced bone mineralization and immune response, highlighting the complexity of determining optimal requirements for tambaqui in the grow-out phase (Menezes et al., 2025). Moreover, generic feeds result in lower feed efficiency and greater environmental residue excretion, which can extend the production period and increase costs (Cho et al., 2006; Eroldogan et al., 2004; NRC, 2011). Additionally, the inclusion of cereal grains like sorghum, corn, and broken rice in tambaqui diets plays a key role in supplying digestible essential amino acids, contributing to the development of more cost-effective and environmentally sustainable feed formulations (Proença et al., 2025).

Given these challenges and the need for precise nutritional strategies, determining accurate protein and energy requirements becomes essential to guide feed formulation and improve production efficiency. This information serves as the foundation for formulating efficient diets from both productivity and economic perspectives (Teles et al., 2020). The energy and protein needs for fish are primarily assessed through dose-response experiments (Davis, 2015; Fernandes Júnior et al., 2016; Shearer, 2000). However, the factorial method has also been successfully used to determine protein and energy requirements for terrestrial animals and fish alike (Aguilar et al., 2021; Booth et al., 2010; Glencross, 2008; Van Tien et al., 2016). In this context, understanding ingredient composition and digestible amino acid contributions provides a crucial basis for applying bioenergetics and factorial models in aquaculture nutrition, which have proven to be practical and efficient tools for estimating and monitoring nutrient waste outputs, reducing feed waste, and improving environmental sustainability, particularly under neotropical farming conditions (Proença et al., 2025; Bueno et al., 2023).

The factorial method, although rarely used in fish nutrition, is traditionally employed to estimate the nutritional needs of other animal species (Aguilar et al., 2021; Lupatsch et al., 2001). This method assumes that the requirement for protein or energy equals the sum of the needs for maintenance and growth (Glencross, 2008). While the maintenance requirement mainly depends on body weight and temperature, making it proportional to metabolic weight, the growth requirement is determined by the amount of nutritional component ingested and retained (Aguilar et al., 2021; Amrkolaie et al., 2013).

Factorial models have been effectively used to estimate protein and energy requirements for fish, especially for marine carnivorous species like gilthead seabream *Sparus aurata*, European sea bass *Dicentrarchus labrax*, barramundi *Lates calcarifer*, yellowtail kingfish *Seriola lalandi*, beluga sturgeon *Huso huso*, and cobia *Rachycentron canadum* (Amrkolaie et al., 2013; Booth et al., 2010; Glencross, 2008; Lupatsch et al., 2003; Van Tien et al., 2016). This method has also been applied to freshwater omnivorous fish such as tilapia (*Oreochromis niloticus*) and pangasius (*Pangasianodon hypothalamus*) (Glencross et al., 2011; Van Trung et al., 2011). However, for tambaqui, the use of factorial models remains limited, and other important parameters like feeding rate are still not well understood.

The feeding rate, defined as the daily amount of feed needed to meet maintenance and growth requirements, is a key factor in determining appropriate feeding strategies (Biswas et al., 2006; Storebakken and Austreng, 1987). Inaccurate estimates of nutritional needs and feed intake can lead to decreased growth performance and inefficient nutrient use (NRC, 2011; Teles et al., 2020). Therefore, this study aimed to estimate the energy and protein needs for tambaqui using a factorial modeling approach, integrating data from commercial fish farms and laboratory trials. These estimates were then compared with existing literature to support better nutritional management strategies at different growth stages of the species.

2. Materials and methods

To establish the parameters needed for developing a factorial model estimating digestible protein and energy requirements for tambaqui (*Colossoma macropomum*), a series of five complementary experimental studies was conducted. These studies included: (i) determining energy and protein requirements for maintenance, (ii) assessing nutrient digestibility of a reference diet, (iii) estimating protein and energy utilization efficiencies, (iv) characterizing whole-body composition across different weight classes, and (v) evaluating growth rate in commercial pond conditions. All animal-related procedures were approved by the Ethics Committee on Animal Use of the Federal University of Goiás (CEUA/UFG; Protocol No. 114/15).

2.1. Study 1 – determination of energy and protein requirements for maintenance

Four weight classes (50, 100, 500, and 1.000 g), selected to represent key stages of the commercial production cycle of tambaqui (juvenile, intermediate, and grow-out phases), were purchased from commercial fish farms. Sample size and replication were defined based on previous fasting and metabolic loss studies in fish (Van Trung et al., 2011; Glencross et al., 2011), ensuring sufficient precision to estimate allometric relationships between body weight and nutrient losses. Fish were randomly assigned in triplicate groups (10 fish each) to 12 1000 L tanks connected to a recirculation system with mechanical and biological filtration, a water flow of 14.8 L min^{-1} per tank, constant aeration, and thermostatically controlled temperature (28 ± 0.5 ºC). Fish were individually weighed at the start and after 28 days of food deprivation to determine weight loss during the experiment. At the end of the trial, three fish per tank were euthanized by immersion in a lethal dose of clove oil, 200 mg L^{-1} (Fernandes et al., 2017), to assess body composition and measure dry matter, protein, lipid, and energy loss. Additionally, three fish of each weight class were weighed and euthanized at the beginning of the experiment to determine initial body composition. Protein and energy loss were calculated based on the geometric average of the initial and final weights. Subsequently, power regression analysis was used to obtain the exponents of metabolic weight for quantifying energy and protein loss.

2.2. Study 2 - digestibility of the reference diet

A reference diet (Table 1) was formulated and prepared to contain approximately 14.2 MJ kg^{-1} of digestible energy and 304.2 g kg^{-1} MS^{-1} of digestible protein. The nutritional levels were based on the analyzed proximate composition of feed samples used during the grow-out stage of tambaqui in commercial fish farms in Northern Brazil (Table 1). Chromic oxide (2.0 g kg^{-1}) was used as a digestibility marker to determine digestible nutrient values (Bremer Neto et al., 2005).

For diet preparation, the ingredients were ground finely (<1.0 mm), thoroughly mixed, and water was added to 25% of the dry mixture. The mixture was then extruded at 120 ºC using a simple screw laboratory extruder (Exteec®, Ribeirão Preto-SP) to produce 2 mm pellets. The pellets were dried in a forced air circulation oven at 65 ºC for 48 h and subsequently stored in a freezer at −18 ºC until use.

For the digestibility trial, 30 juvenile tambaqui (mean weight 369.9 ± 43.61 g) were randomly assigned to three 1000 L feeding tanks, connected to a recirculation system as described in item 2.1. Three cylindrical tanks with conical bottoms and a capacity of 200 L were used for feces collection. These tanks were equipped with aeration and a

Table 1
Formulation and chemical composition of the reference diet.

Ingredients	($g\ kg^{-1}$)
Corn	248.0
Poultry viscera meal	88.5
Wheat bran	160.0
Soybean meal	365.0
Meat and bone meal	100.0
Soybean oil	14.6
Dicalcium phosphate	6.7
Limestone	2.0
L-lysine	3.4
DL-methionine	1.0
Salt	6.0
Ascorbic acid[1]	0.6
Premix[2]	4.0
BHT[3]	0.2
Chemical composition	($g\ kg\ DM^{-1}$)
Dry matter	942.0
Gross energy ($kJ\ kg\ DM^{-1}$)	18.064,0
Crude protein	358.9
Lipids	76.1
Ashes	86.6
Crude fiber	52.5
Lys	17.4
Met	4.8

[1] L-ascorbyl-2-polyphosphate (50% of activity).
[2] Mineral and vitamin mix (IU or mg kg^{-1}): folic acid 600 mg, biotin 24 mg, choline chloride 54 g, niacin 12.000 mg, calcium pantothenate 6000 mg, vit. A 600000 IU, vit. B1 2400 mg, vit. B12 2400 mg, vit. B2 2400 mg, vit. B6 2400 mg, vit. C 24 g, vit. D3 100000 IU, vit. E 6000 mg, vit. K3 1200 mg, cobalt 1 mg, copper 300 mg, iron 5000 mg, iodine 10 mg, magnesium 2000 mg, selenium 10 mg, and zinc 3000 mg.
[3] Antioxidant: Butylated hydroxytoluene.

sedimentation device for feces collection (Guimarães et al., 2008).

Fish were fed twice daily (9 am and 5 pm) until apparent satiety throughout the trial. Feces collection began after seven days (adaptation period). Fish were transferred on alternate days to the feces collection tanks, where they stayed from 6:00 pm to 6:00 am, and feces were collected at 6-hour intervals (00:00 and 06:00) using Falcon tubes (50 mL) attached to the lower end of the conical bottom tanks. Falcon tubes were stored in an isothermal box with ice to reduce microbial activity and nutrient leaching. Feces samples were identified and frozen at −18 ºC immediately after collection. Subsequently, the feces were dried in a forced air circulation oven (55 ºC / 48 h) and finely ground for further analysis. Diets and feces were analyzed for Cr_2O_3 concentration (Bremer Neto et al., 2005), dry matter, crude protein, lipids, and gross energy content (AOAC, 2005). The apparent digestibility coefficient of the nutritional parameters was calculated according to the following equation (Cho, 1993):

$$ADC\ (n) = 100 - 100 \quad \times \left[\left(\frac{\%Cr2O3d}{\%Cr2O3f} \right) \times \left(\frac{\%\quad Nf}{\%\quad Nd} \right) \right]$$

In which, ADC (n) = apparent digestibility coefficient of the nutrient or nutritional parameter of the diet; Cr_2O_3 d = % of chromic oxide in the diet; Cr_2O_3 f = % of chromic oxide in the feces; N d = nutrient or nutritional parameter in the diet; N f = nutrient or nutritional parameter in feces.

2.3. Study 3 – energy and protein utilization efficiencies

Tambaquis (n = 150) from commercial fish farms were randomly assigned to 15 1000 L tanks connected to a recirculation system, as described in item 2.1. Groups of fish were weighed to ensure similar sizes across the groups. The water quality parameters stayed within the recommended levels for optimal tambaqui growth (Baldisserotto and Gomes, 2020) throughout the trial: temperature, 28.0 ± 1.0 ºC; pH, 6.9 ± 0.4; OD, 5.3 ± 1.2 mg L^{-1}; total ammonia, 0.5 ± 0.5; NH_3, 0.007 ± 0.007; NO_2, 0.25 ± 0.25.

After the adaptation period, the fish were weighed again (318.63 ± 38.73 g) and assigned to one of five different daily feeding rates (FR) in triplicate. The feeding rates were 0% (fasting), 0.75% BW, 1.5% BW, 2.25% BW, and 3.0% BW. The number of fish and replication per feeding level were defined to ensure adequate representation of intake–retention relationships across the tested feeding rates. The trial lasted 32 days. Fish were fed the reference diet described in item 2.2 twice daily (09:00 and 17:00), and any uneaten feed was collected 20 min after feeding, dried, and weighted, and this value was used to correct actual feed intake.

Weight was recorded weekly for each fish, at the start and end of the trial, to adjust feed levels and evaluate growth and feed efficiency. Three fish per tank were euthanized at the end to analyze body composition (dry matter, crude protein, lipid, and gross energy). Similarly, at the beginning of the trial, a sample of six fish was analyzed, and this data was used to calculate energy and protein utilization efficiencies.

The relationships between the intake and retention of digestible protein (DP) and digestible energy (DE) were expressed per unit of metabolic body weight, based on the coefficients of metabolic protein and energy obtained in study 1. The relationship among DP, DE, and body weight was described using quadratic polynomial regression. Linear models were also used, and the regression coefficient (a) of the equations ($y = ax + b$) was employed to determine the efficiency of protein and energy retention, with the reciprocal of a (shown as one over a) indicating the cost of protein and energy deposition for growth (Booth et al., 2010).

This experimental design allowed the evaluation of protein and energy utilization efficiency across a wide range of feeding levels, generating intake–retention relationships under controlled conditions. Expressing digestible protein and energy intake per unit of metabolic body weight ensured consistency with the allometric scaling of maintenance requirements determined in Study 1, allowing direct integration of both datasets within the factorial modeling framework.

Linear regression models were used to estimate retention efficiency under conditions where intake and retention were proportional, whereas quadratic models were applied to describe nonlinear responses across the full range of feeding rates. Retention efficiency was derived from the slope of the linear relationship between digestible intake and retained nutrient, with the reciprocal of the slope representing the cost of protein or energy deposition for growth, as commonly applied in factorial nutrition models.

2.4. Study 4 – variation in fish composition

Healthy tambaquis were collected from four different commercial fish farms in the municipality of Ariquemes (Rondônia – Brazil) to create 50 samples across five different weight classes (50, 100, 500, 1.000, and 1.500 g), selected to represent changes in whole-body composition across the main growth stages relevant to commercial tambaqui production. After collection and weighing, the animals were euthanized, and each sample, which consisted of a pool of three fish, was placed in an identified plastic bag and kept on ice during transport to the laboratory, where it was frozen at −18 ºC for further analysis. Each sample was initially ground, homogenized, and pre-dried in a forced air circulation oven at 65 ºC for approximately 72 h. Subsequently, the contents of dry matter, ash, crude protein, lipid, and crude energy were determined.

2.5. Study 5 – determination of fish growth rate

This study was an observational field study conducted in commercial pond farms, aimed at characterizing growth performance across a wide range of body weights under practical production conditions. Diet composition was not experimentally controlled in this study, as the objective was not to estimate nutrient requirements, but rather to generate a realistic growth curve to support the factorial modeling framework.

Growth was assessed by collecting data from 27 commercial ponds across four fish farms in Ariquemes (Rondônia, Brazil), from December 2015 to December 2016. Fish weighing between 2.0 and 3031 g were used to generate the growth rate curve (g $fish^{-1}$ day^{-1}). The temperature was not included in the growth model due to insufficient data. As a result, the data in this study only apply to tambaqui raised at temperatures between 26 °C and 30 °C, which is the normal range in this region.

2.6. Chemical analysis

The chemical analysis of fish, diet, and feces samples followed the protocols established by AOAC (2005). Dry matter was determined by using a gravimetric method, where samples were oven-dried at 105 °C for 24 h. The energy content was measured with a calorimeter. Protein was assessed by measuring total nitrogen using the Kjeldahl method (% PB = N × 6.25). Lipids were extracted with ether as the solvent in a Soxhlet apparatus. The ash, or mineral matter, was measured by burning the sample in a muffle furnace at 550 °C for 6 h. The chromic oxide content in the diet and feces was determined by reading on a spectrophotometer at 550 nm after digesting the sample in nitric and perchloric acids (Bremer Neto et al., 2005).

2.7. Calculation and data analysis

Fish weights were transformed to the geometric mean of the initial and final weights before plotting on the figures. Linear and nonlinear models, including polynomial and power functions, were fitted to data collected from various studies using Microsoft Excel® and R© version 3.6.1.

Based on the environmental and management conditions under which the datasets were generated, the factorial model developed in this study is applicable to tambaqui cultured in pond-based systems under tropical conditions, within a temperature range of 26–30 °C, using feeding practices representative of commercial grow-out operations and experimental conditions commonly adopted in nutritional trials. The domain of applicability of the model is therefore restricted to this environmental and management context.

3. Results

3.1. Energy and protein loss during starvation

Protein and energy loss during 28 days of food deprivation increased with fish size (Figs. 1 and 2). The power regression model best fitted the data on protein and energy loss (Eqs. 1 and 2).

$$\text{Protein loss (g fish}^{-1}) = 0.0897\ (\text{body weight})^{0.7919}.\ R^2 = 0.8569 \quad (1)$$

$$\text{Energy loss (kJ fish}^{-1}) = 1.964\ (\text{body weight})^{0.9506}.\ (R^2 = 0.9564) \quad (2)$$

3.2. Digestibility of the diet

The apparent digestibility coefficients of dry matter, energy, protein, and lipids in the reference diet were 57.74 ± 1.39%, 69.54 ± 1.64%, 82.77 ± 1.59%, and 85.34 ± 0.79%, respectively. The values for protein, lipids, and digestible energy in the reference diet were 297.1 g kg^{-1}, 64.9 g kg^{-1}, and 12.56 MJ kg^{-1}, respectively.

3.3. Energy and protein retention

The relationship between the intake and retention of digestible protein (DP) and digestible energy (DE) was best described by a curvilinear model (Figs. 3 and 4, respectively) using quadratic equations (Eqs. 3 and 4). Linear regression was also used to determine the standard utilization coefficients (Eqs. 5 and 6), as previously reported by others (Glencross et al., 2011; Van Trung et al., 2011).

$$\text{Protein gain (g kg}^{-0.75}\text{ day}^{-1}) = -0.207\ (\text{DP intake})^2 + 0.8654\ (\text{DP intake}) - 0.2235\ (R^2 = 0.9669) \quad (3)$$

$$\text{Energy gain (KJ kg}^{-0.95}\text{ day}^{-1}) = -0.004\ (\text{DE intake})^2 + 0.7997\ (\text{DE intake}) - 12.328\ (R^2 = 0.9445) \quad (4)$$

$$\text{Protein gain (g kg}^{-0.75}\text{ day}^{-1}) = 0.3082\ (\text{DP intake}) - 0.0386\ (R^2 = 0.7578) \quad (5)$$

$$\text{Energy gain (kj kg}^{-0.95}\text{ day}^{-1}) = 0.3347\ (\text{DE intake}) - 5.6286\ (R^2 = 0.8122) \quad (6)$$

The maintenance protein (Eq. 7) and energy (Eq. 8) requirements for tambaqui were calculated based on the animals' metabolic weight and their intake of these components when retention equals zero (y = 0). Therefore, we used the quadratic models for protein and energy retention (Eqs. 3 and 4) and the exponents of metabolic weight for protein and energy loss (Eqs. 1 and 2).

$$\text{Maintenance protein requirement (g day}^{-1}) = 0.27\ \text{BW (kg)}^{0.79} \quad (7)$$

$$\text{Maintenance energy requirement (kJ day}^{-1}) = 10.84\ \text{BW (kg)}^{0.95} \quad (8)$$

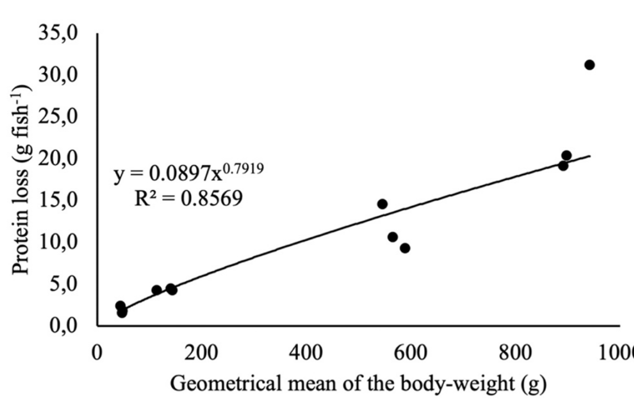

Fig. 1. Protein loss (g fish-1; body weight = geometric mean) in tambaquis fasted for 28 days at 28°C (each point represents a mean of 3 determination in a pooled sample of three fish per tank).

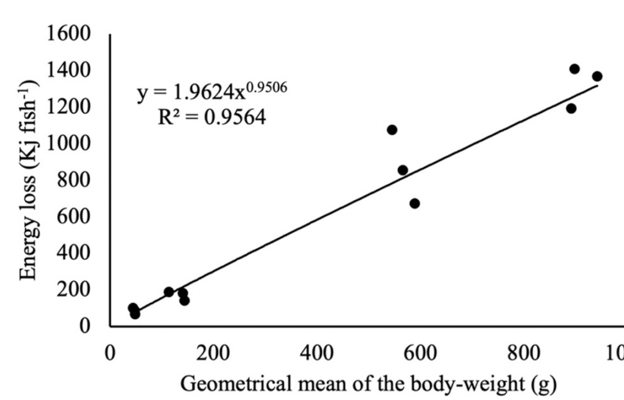

Fig. 2. Energy loss (KJ $fish^{-1}$; body weight = geometric mean) by tambaquis fasted for 28 days at 28 °C (each point represents a mean of 3 determination in a pooled sample of three fish per tank).

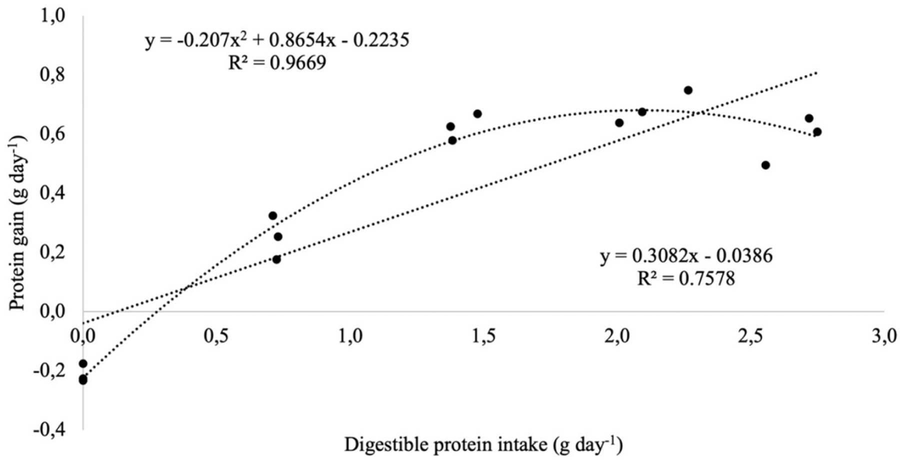

Fig. 3. Daily protein retention per metabolic weight (kg0.79) in tambaquis as a function of digestible protein intake (Dpi).

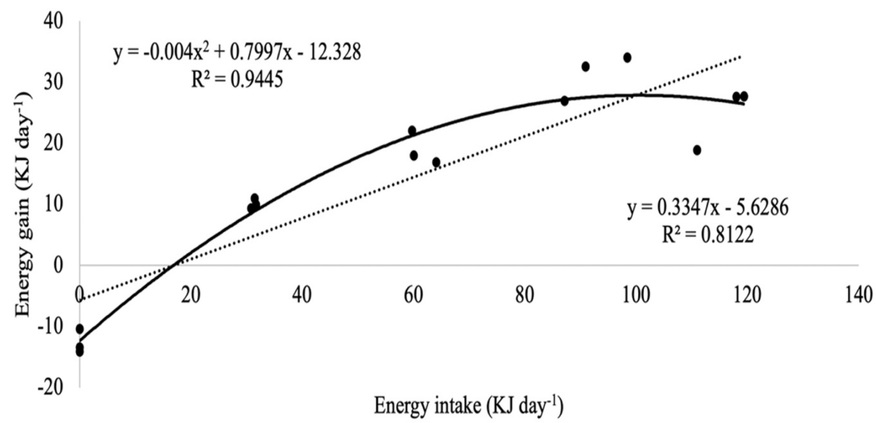

Fig. 4. Daily energy retention (KJ day^{-1}) per metabolic weight unit ($kg^{0.95}$) in tambaquis as function of digestible energy intake (DEi).

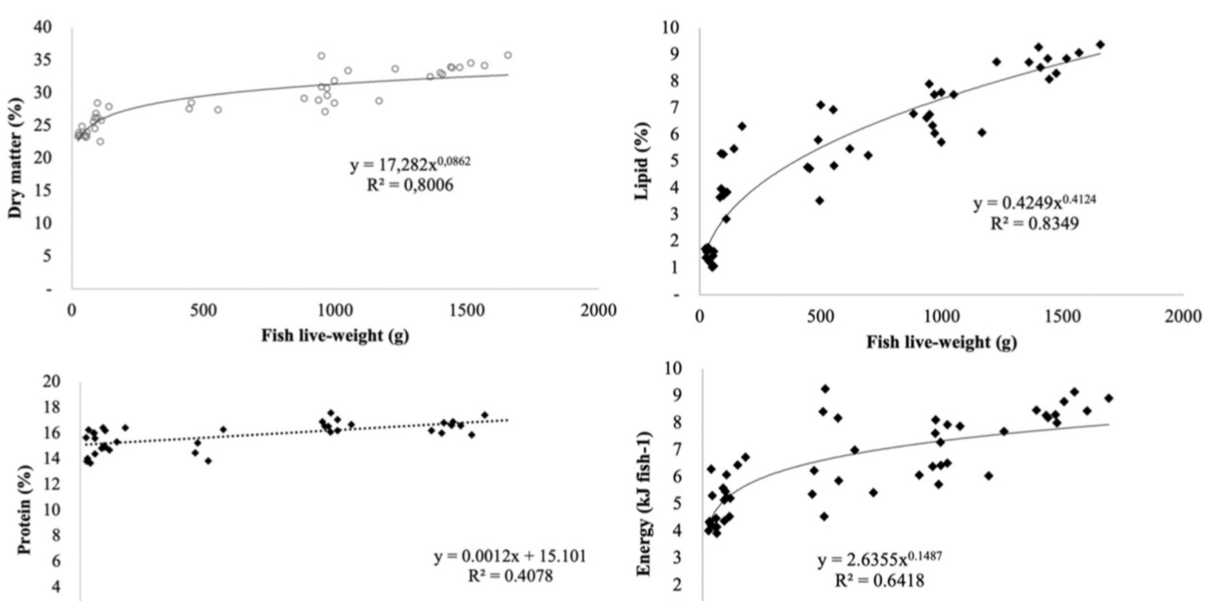

Fig. 5. Variation in the whole-body dry matter (%), lipid (%), protein (%) and energy (Kj) content of tambaqui raised in earthen ponds with increasing body weight.

3.4. Nutritional composition of the whole body

The whole-body composition of tambaqui varied significantly across different weight ranges (Fig. 5). An increase in fat accumulation and energy density was seen with higher live body weight, while the body protein content remained relatively stable across various fish weights (Eqs. 9–12).

$$\text{Dry matter content (\%)} = 17.282\ (\text{body weight})^{0.0862}\ R^2 = 0.8006) \quad (9)$$

$$\text{Lipid content (\%)} = 0.4249\ (\text{body weight})^{0.4124}\ (R^2 = 0.8349) \quad (10)$$

$$\text{Protein content (\%)} = 0.0012\ (\text{body weight}) + 15.101\ (R^2 = 0.4078) \quad (11)$$

$$\text{Energy content (kJ g}^{-1}\text{ fish}^{-1}) = 2.6355\ (\text{body weight})^{0.1487}\ (R^2 = 0.6418) \quad (12)$$

3.5. Growth rate of tambaqui raised in ponds

Growth data from 27 lots, each containing between 600 and 40.000 tambaquis raised in ponds at temperatures from 26 ºC to 30 ºC and stocking densities of 0.3–0.5 fish per m^2, were used to estimate the growth rate of this population across size classes ranging from 2.0 to 3.031 g (Fig. 6, Eq. 13).

$$\text{DWG (g day}^{-1}) = 0.3007\ (\text{body weight})^{0.4495}\ (R^2 = 0.8516) \quad (13)$$

3.6. Estimation of protein and energy requirements for tambaqui

Using the equations derived from the models in studies 1–5, the protein and energy requirements for tambaquis of different weight classes were estimated (Table 2). The calculations were based on the predicted growth equation, the energetic cost of that weight gain, the efficiencies of that energy gain, and the maintenance energy requirement. Total DE requirement was calculated based on the maintenance DE requirement and the DE requirement for growth. The digestible energy content of the reference diet formulated in this study was considered for diet specification. The protein requirement was calculated similarly to the energy requirement.

4. Discussion

The present study established comprehensive estimates of digestible protein (DP) and digestible energy (DE) requirements for tambaqui across a wide weight range, integrating data from starvation trials, digestibility assays, whole-body composition analysis, on-farm growth observations, and factorial modeling. Protein and energy losses during fasting increased with body size, and the reference diet showed high digestibility of protein (82.77%) and lipids (85.34%). Whole-body analysis revealed stable protein content but progressive fat accumulation and higher energy density with increasing weight. Growth data from commercial ponds enabled the derivation of predictive equations for daily weight gain, which, combined with nutrient retention efficiencies, allowed estimation of maintenance and growth requirements. Overall, the results indicate that tambaqui's nutrient demands vary substantially with size, highlighting the need for stage-specific feed formulation to improve nutrient utilization, reduce waste output, and enhance production efficiency.

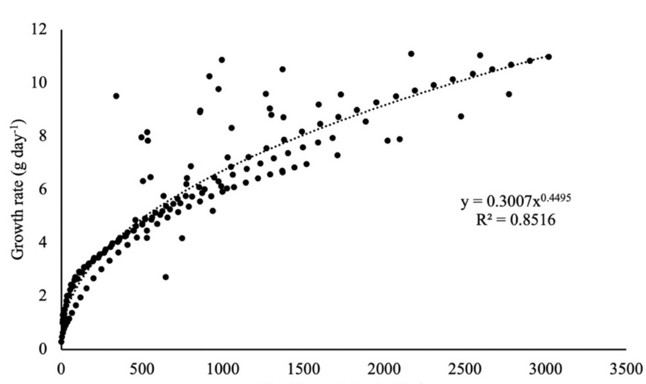

Fig. 6. Growth rate (DWG; g $fish^{-1}$ day^{-1}) of tambaquis commercially raised in ponds in the municipality of Ariquemes-RO as a function of body weight (g).

The growth curve derived from commercial pond data indicated that tambaqui daily weight gain increased with body size, reaching an average of 6.5 g day^{-1} for fish between 2.0 and 3031 g and maximum gain of 10.4 g day^{-1}. These values are higher than those reported by Arbeláez-Rojas et al. (2002) and Fernandes et al. (2010), who observed an average of 4.5 g day^{-1} for fish between 90.4 and 1477 g under similar temperature conditions but at higher stocking densities (0.6–1.0 fish m^{-2}). Applying the factorial model from the present study to the weight ranges evaluated in those works resulted in predicted gains of 2.3 and 8.0 g day^{-1}. The lower performance in previous studies is likely related to the higher densities used, which exceeded the average of 0.4 fish m^{-2} in the farms that provided the data for the present model, as well as possible feed management issues, as suggested by the high feed conversion ratio (2.93) reported by Fernandes et al. (2010). In contrast, Sousa et al. (2016) found a high growth rate of 8.9 g day^{-1} for fish weighing between 225.3 g and 983.4 g in ponds at 29.46 ± 1.34 ºC at a density of 0.4 fish m^{-2}. For the same weight range, our model estimated 6.7 g day^{-1}. However, the higher growth rate in Sousa et al. (2016) was associated with a relatively poor FCR of 2.31, likely due to the constant feed rate of 3% used. This is above the average FCR of 1.47 recorded in the farms from the present study. Similar efficiency was reported by Melo et al. (2001), with an FCR of 1.50 over three years of production from 0.3 to 3100 g at 28.3–28.9 °C and 0.33 fish m^{-2}.

Dry matter, lipid, and energy content of tambaqui increased with growth, a pattern consistent with previous reports in other fish species and higher vertebrates, which tend to deposit more fat and reduce moisture percentage as development progresses, leading to higher energy density (Shearer, 1994; Lupatsch et al., 1998). In the present study, the whole-body lipid content increased from 21.3 g kg^{-1} to 86.7 g kg^{-1}, and the energy density from 4.52 to 8.42 kJ g^{-1} in tambaquis from 50 to 1500 g, respectively. Substantial increases in lipid and energy content have also been reported for other omnivorous fish. For instance, tilapias from 19 to 963 g had an increase in lipid and energy content from 25.6 to 52.0 g kg^{-1} and from 4.17 to 5.93 kJ g^{-1}, respectively (Van Trung et al., 2011), while pangasius from 10 to 1000 g had an increase from 97.5 to 148.6 g kg^{-1} and 6.5–10.0 kJ g^{-1} in whole-body content of lipids and energy, respectively (Glencross et al., 2011). In contrast to the variations in lipid and energy content, whole-body protein content in tambaqui averaged 163.4 g kg^{-1}. It remained relatively constant with growth, a trend commonly observed in fish, and with slight variation even among species. Previous studies reported similar whole-body protein concentration in tambaquis (160.0 g kg^{-1}) and other phylogenetically related species (pacu) (142.0–161.0 g kg^{-1}) for weights ranging from 19 g to 963 g (Van der Meer et al.,1996; Bicudo et al., 2010). Comparable stability in protein content has also been observed in other omnivorous fish, such as tilapia (158.6 g kg^{-1}) and pangasius (162.4 g kg^{-1}), across a wide range of weight classes (from 10 to 1000 g) (Van Trung et al., 2011; Glencross et al., 2011).

In this study, the metabolic losses of protein and energy in tambaqui of different weight classes, subjected to 28 days of food deprivation at 28 ± 0.5 °C, were described by allometric equations, with exponents of 0.79 for protein metabolism and 0.95 for energy metabolism (Eqs. 1 and 2). These results indicate that protein metabolism scales with body weight at a lower rate than energy metabolism. The factorial models are

Table 2
Protein and energy requirements for tambaqui at different growth stages raised in ponds at 26–30°C.

Body weight (g)	10	50	100	500	1000	1500	2000	2500	3000
DWG (g $fish^{-1}$ day^{-1})[A]	0.85	1.75	2.38	4.91	6.71	8.05	9.16	10.13	10.99
Energy									
Metabolic BW ($kg^{0.95}$)	0.013	0.058	0.112	0.518	1.000	1.470	1.932	2.388	2.840
$DE_{maintenance}$ (kJ $fish^{-1}$ day^{-1})[B]	0.14	0.63	1.22	5.61	10.84	15.93	20.94	25.89	30.78
Body energy (kJ g^{-1} $fish^{-1}$)[C]	3.71	4.72	5.23	6.64	7.36	7.82	8.16	8.44	8.67
Energy gain (KJ $fish^{-1}$ day^{-1})[D]	3.14	8.23	12.46	32.62	49.39	62.94	74.76	85.44	95.28
DE_{growth} (kJ $fish^{-1}$ day^{-1})[E]	9.24	24.20	36.64	95.95	145.25	185.12	219.88	251.28	280.24
DE_{total} (kJ $fish^{-1}$ day^{-1})[F]	9.38	24.83	37.85	101.56	156.09	201.05	240.83	277.17	311.02
% DE used for maintenance	1.46%	2.54%	3.21%	5.52%	6.94%	7.93%	8.70%	9.34%	9.90%
Protein									
Metabolic protein BW ($kg^{0.75}$)	0.032	0.106	0.178	0.595	1.000	1.355	1.682	1.988	2.280
$DP_{maintenance}$ (g $fish^{-1}$ day^{-1})[G]	0.009	0.029	0.049	0.164	0.277	0.375	0.465	0.550	0.630
Protein gain (g $fish^{-1}$ day^{-1})[H]	0.13	0.26	0.36	0.74	1.01	1.22	1.38	1.53	1.66
DP_{growth} (g $fish^{-1}$ day^{-1})[I]	0.41	0.85	1.16	2.39	3.27	3.92	4.46	4.93	5.35
DP_{total} (g $fish^{-1}$ day^{-1})[J]	0.421	0.879	1.210	2.557	3.544	4.296	4.927	5.483	5.985
% DP used for maintenance	2.08%	3.33%	4.06%	6.43%	7.80%	8.72%	9.44%	10.03%	10.53%
Diet specifications									
DP: DE ratio (g MJ^{-1})[K]	44.90	35.41	31.96	25.18	22.71	21.37	20.46	19.78	19.24
Dietary DE level (MJ kg^{-1})	12.56	12.56	12.56	12.56	12.56	12.56	12.56	12.56	12.56
Dietary DP level (g kg^{-1})	564.06	444.81	401.52	316.31	285.23	268.40	257.01	248.49	241.71
Feed intake (g $fish^{-1}$ day^{-1})	0.75	1.98	3.01	8.08	12.43	16.01	19.17	22.06	24.76
Feed intake (% BW)	7.47	3.95	3.01	1.62	1.24	1.07	0.96	0.88	0.83
FCR by weight range	0.88	1.13	1.26	1.65	1.85	1.99	2.09	2.18	2.25
FCR over the whole weight range	0.99	1.10	1.18	1.55	1.70	1.80	1.87	1.93	1.99

[A] DWG (g day^{-1}) = 0.3007 (body weight)$^{0.4495}$; Eq. (1).
[B] Maintenance digestible energy requirement (kJ day^{-1} $fish^{-1}$) = 10.84 (body weight)$^{0.95}$; Eq. (13).
[C] Body energy content (kJ g^{-1} $fish^{-1}$) = 2.6355 (body weight)$^{0.1487}$; Eq. (5).
[D] Energy gain (kJ $fish^{-1}$ day^{-1}) = Body energy content (kJ g^{-1} $fish^{-1}$) × DWG (g day^{-1}).
[E] DE requirement for growth (kJ $fish^{-1}$ day^{-1}) = Energy retention (kJ $fish^{-1}$ day^{-1}) ÷ 0.34. 0.34 is the partial efficiency of the energy retention coefficient derived from Eq. (11)
[F] Total digestible energy requirement (kJ $fish^{-1}$ day^{-1}) = DE maintenance + DE growth.
[G] Digestible protein requirement for maintenance (g $fish^{-1}$ day^{-1}) = 0.2765 × (body weight)$^{0.75}$; Eq. (12).
[H] Protein gain (g $fish^{-1}$ day^{-1}) = DWG (g $fish^{-1}$ day^{-1}) × Body protein (%). Because the body protein % was fairly stable across fish live weights, we considered 15.1% of live weight for all calculations.
[I] DP requirement for growth (g $fish^{-1}$ day^{-1}) = Protein gain (g $fish^{-1}$ day^{-1}) ÷ 0.31. 0.31 is the partial efficiency of the energy retention coefficient derived from Eq. (10).
[J] Total digestible protein requirement (g $fish^{-1}$ day^{-1}) = DP maintenance + DP growth.
[K] DP: DE ratio (g MJ^{-1}) = DP total (g $fish^{-1}$ day^{-1}) ÷ DE total (MJ $fish^{-1}$ day^{-1}).

based on the premise that the energy and protein requirements of an animal are the sum of the requirements for maintenance and growth. The maintenance requirement depends on the weight of the fish and the temperature of the water, being proportional to the metabolic weight (Lupatsch et al., 2001). At a constant temperature, the metabolic weight can be determined by the exponent (b) of the allometric equation a × PC (kg) ^{b}, which describes changes in protein and energy metabolism according to body weight (Lupatsch and Kissil, 2005).

The exponent obtained for the metabolic protein weight of tambaqui (0.79) was close to that reported for tilapia (0.85, Van Trung et al., 2011) and pangasius (0.83, Glencross et al., 2011). In contrast, the energy metabolism of tambaqui was slightly higher than that generally observed in other species, which have exponents close to 0.8: *Sparus aurata* – 0.83 (Lupatsch et al., 1998), *Dicentrarchus labrax* – 0.79 (Lupatsch et al., 2001), *Epinephelus aeneus* – 0.80 (Lupatsch and Kissil, 2005), *Seriola lalandi* – 0.86 (Booth et al., 2010), *Oreochromis niloticus* – 0.85 (Van Trung et al., 2011), *Pangasianodon hypothalamus* – 0.84 (Glencross et al., 2011), *Rachycentron canadum* – 0.82 (Van Tien et al., 2016). Although the 0.8 exponent is generally accepted as a standard to explain energy metabolism in fish (Lupatsch et al., 2003), there might be variations between 0.6 and 1.0 (Withers, 1992). Exponent values below 1.0 indicate a decline in metabolic rate with animal growth, resulting in maintenance energy requirements per unit of body weight in larger fish. In this study, the exponent estimated for tambaqui indicates that, as in other species, maintenance energy expenditure decreases with growth, but at a slower rate than commonly observed in fish.

As important as understanding the maintenance costs for energy and protein is evaluating how efficiently these nutrients are utilized for growth. In the present study, the efficiency was determined based on the regression analysis of protein or energy retention as a function of ingestion of protein or digestible energy, standardized by the metabolic protein ($BW^{0.79}$) or energy ($BW^{0.95}$) of animals. Although some studies claim that this response is linear, in the present study, the protein and energy retention responses by tambaqui were better expressed by polynomial quadratic models (Eqs. 3 and 4) (Lupatsch et al., 1998, 2001, 2003; Lupatsch and Kissil, 2005; Van Tien et al., 2016). Polynomial quadratic regression models have also been consistently adopted in the validation of the factorial method for studying protein and energy metabolism for several fish species: *Lates calcarifer* (Glencross, 2008); *Seriola lalandi* (Booth et al., 2010); *Huso huso* (Amrkolaie et al., 2013), *Oreochromis niloticus* (Van Trung et al., 2011) and *Pangasianodon hypothalamus* (Glencross et al., 2011).

Using these models and considering the retention as zero, the maintenance requirements for tambaqui were calculated to be 0.2765 g $kg^{0.79}$ day^{-1} for protein and 10.84 KJ $kg^{0.95}$ day^{-1} for energy. These values are lower than those observed for other omnivorous fish species, such as tilapia, 0.45 g $kg^{0.854}$ day^{-1} and 25.9 KJ $kg^{0.849}$ day^{-1} (Van Trung et al., 2011), and the pangasius, 0.47 g $kg^{0.834}$ day^{-1} and 39.7 KJ $kg^{0.844}$ day^{-1} (Glencross et al., 2011). This lower maintenance cost for energy and protein in tambaqui represents a nutritional and economic advantage for farming, as a greater proportion of dietary nutrients can be directed towards growth rather than maintenance. Nevertheless, due to the absence of similar studies with this species, further research is required to validate these findings.

After establishing the maintenance requirements for protein and energy, the next step was to determine the efficiency and cost associated with nutrient deposition for growth. Linear models were also adjusted for protein (Eq. 5) and energy (Eq. 6) retentions. The regression coefficients (0.3082 for protein and 0.3347 for energy) represent, respectively, the efficiency of protein and energy retention, while their reciprocal values indicate the cost of body deposition of protein (3.24) and energy (3.34). In practical terms, for each 1 g of retained body protein, it is necessary to consume 3.24 g of digestible protein. For each one kJ of deposited body energy, the consumption of 3.34 kJ of digestible energy is required. Based on these values, the protein and energy requirements for growth were calculated by multiplying the estimated daily retention of each component derived from daily weight gain and body composition by the respective cost of deposition.

The efficiency of protein (30.82%) and energy (33.47%) retention by tambaqui observed in this study was lower than that observed in factorial models developed for tilapia (51.7% and 44.0%) and pangasius (45.5% and 55.3%) (Van Trung et al., 2011; Glencross et al., 2011). However, dose-response studies with tambaqui in the early stages showed protein retention efficiency similar to that observed in this study. Sousa Lima et al. (2016) observed protein retention efficiencies between 29.5% and 47.6% in tambaqui fry fed diets containing different levels of crude protein between 0.35 g and 15.11 g. Sandre et al. (2017) reported protein retention efficiencies ranging from 28.3% to 35.9% in tambaquis with body weight between 10 g and 250 g fed different levels of carbohydrates and lipids and similar DP levels (23.6%).

The digestible protein requirement predicted by the factorial model ranged from 564.06 to 241.71 g kg^{-1} for tambaqui with body weights between 10 and 3000 g. In comparison, dose-response studies using tambaquis between 0.2 g and 280 g body weight reported crude protein requirements ranging from 250 to 481 g kg^{-1} (Amancio et al., 2019; Buzollo et al., 2019; De Almeida et al., 2011; Hernandez et al., 1995; Merola and Cantelmo, 1987; Oishi et al., 2010; Sousa Lima et al., 2016; Santos et al., 2010; Santos et al., 2013; Van der Meer et al., 1995; Vidal et al., 1998). Despite the wide range of reported values, 75% of these studies recommended between 300 and 328 g kg-1 of crude protein for tambaquis in the early stages (up to 280 g of body weight). While the dose–response method is restricted to the weight range studied, the factorial method enables prediction across a broader range of weights, which is an advantage for production planning. This distinction is relevant because young fish have higher protein requirements due to elevated nutrient retention and tissue accretion rates during rapid growth (Conwey, 1994). Additionally, the immature digestive system of early-stage fish reduces their ability to efficiently digest carbohydrates and lipids, making protein the primary energy source in these phases (Guimarães and Martins, 2015).

Guimarães and Martins (2015), in their review on tambaqui protein nutrition, recommended stage-specific dietary crude protein levels: 440–480 g kg^{-1} for fish between 1 and 50 g; 320–350 g kg^{-1} for those between 50 and 150 g; and 280 g kg^{-1} for fish over 150 g. Applying the factorial model developed in the present study and considering the protein digestibility of the reference diet (82.77%), the estimated crude protein requirements for tambaqui were 479 g kg^{-1} for fish of 50 g, 411.1 g kg^{-1} for fish of 150 g, and between 351 and 302 g kg^{-1} for fish between 500 and 3000 g. When compared to the values in the review and other dose–response studies, these estimates suggest that the factorial model may overestimate the protein requirements, particularly in the early growth stages. This interpretation is further supported by the protein-to-energy (P/E) ratios obtained in the present study, which ranged from 44.9 g MJ^{-1} (10 g fish) to 19.24 g MJ^{-1} (3000 g fish), values generally higher than those in previous reports (Table 2).

This apparent overestimation at early growth stages likely reflects a combination of methodological constraints inherent to the factorial approach and intrinsic physiological characteristics of juvenile tambaqui. From a methodological perspective, protein retention efficiency is derived from intake–retention relationships that tend to stabilize at higher feeding levels and body weights, which may limit their accuracy when extrapolated to small fish with rapid growth rates and high metabolic turnover. From a biological standpoint, early growth stages in fish are characterized by ongoing development of the digestive system, including the acquisition of enzymatic capacity and absorptive efficiency. Ontogenetic increases in digestive enzyme activities and absorptive functions have been documented, with juveniles exhibiting lower digestive capacity compared to larger fish, which can constrain nutrient utilization efficiency at small body sizes (Kolkovski, 2001; Zambonino Infante and Cahu, 2007). In addition, limited utilization of non-protein energy sources during early growth stages may increase amino acid oxidation and reduce apparent protein retention efficiency (Kaushik and Seiliez, 2010), contributing to higher protein requirement estimates generated by factorial models.

Dose–response trials with juvenile tambaqui have reported lower DP/DE ratios for optimal performance. Camargo et al. (1998) observed best results in 30–180 g fish at 17.4–19.1 g CP MJ^{-1} ME, while Filho et al. (2018) found similar levels (17.1–19.9 g CP MJ^{-1} ME) in 71–110 g juveniles. Higher ratios of 22.8 g CP MJ^{-1} DE and 25.4–27.8 g CP MJ^{-1} CE were recommended by Santos et al. (2013) and Van der Meer et al., (1995) for tambaquis of 50–120 g and 5–125 g, respectively. Thus, although the factorial model developed here may yield higher protein requirement estimates, it provides realistic and coherent performance indicators for feed intake (%BW day^{-1}) and feed conversion ratio (FCR). Estimated feed intake ranged from 7.5% to 0.83% BW day^{-1} , and FCR from 0.88 to 2.25, for tambaquis weighing 10–3000 g. These values are consistent with those observed in pond-cultured fish at 26–30 °C and stocking densities of 0.3–0.5 fish m^{-2} (Melo et al., 2001), reinforcing the practical applicability of the factorial approach for commercial production.

Despite this practical consistency, the applicability of the proposed factorial model is inherently linked to the environmental and management conditions under which it was developed. The model was established under pond culture conditions, with water temperatures ranging from 26 to 30 °C and feeding practices representative of commercial tambaqui grow-out operations. Its direct applicability is therefore restricted to production systems operating under similar conditions. In alternative systems, such as higher-density ponds, cage culture, or recirculating aquaculture systems, changes in fish activity, maintenance energy expenditure, feed intake patterns, and nutrient utilization efficiency are expected. Consequently, model parameters related to maintenance requirements and retention efficiencies may differ, requiring system-specific calibration before direct application. In addition, it is important to acknowledge that the factorial modeling approach adopted in this study is based on specific statistical assumptions and scaling relationships. Alternative statistical frameworks or modeling strategies could potentially yield different numerical estimates of protein and energy requirements. However, the overall biological trends and allometric relationships identified here are expected to remain consistent, as they are grounded in established metabolic and physiological principles. Further validation studies are therefore warranted to assess the performance of the proposed estimates under practical farming conditions and to strengthen the applicability of the approach. Nevertheless, the factorial framework presented here remains biologically robust, providing a solid conceptual basis for adaptation to other production systems when appropriate system-specific data are available.

5. Conclusions

The factorial modeling approach provides a solid framework for assessing dietary protein and energy utilization in tambaqui, offering indicators that support more precise and sustainable feeding strategies. Although the model developed here tends to overestimate protein needs during early growth stages, likely due to limitations in estimating protein retention efficiency, its predictions for feed intake and feed conversion match values commonly observed in pond culture at 26–30 °C and 0.3–0.5 fish m^{-2}. This consistency emphasizes its potential as a decision-support tool for nutritional management in similar farming conditions. Future improvements, particularly in measuring nutrient retention efficiencies, could enhance its accuracy and broaden its application across different production systems and environmental scenarios.

CRediT authorship contribution statement

Igo G. Guimarães: Writing – original draft, Supervision, Project administration, Conceptualization. **Danilo C. Proença:** Writing – review & editing, Visualization, Methodology. **Tavani R. Camargo:** Writing – review & editing, Visualization, Methodology. **Cristielle N. Souto:** Writing – original draft, Methodology, Investigation. **Lincoln N. Oliveira:** Writing – original draft, Validation, Formal analysis, Data curation. **Guilherme Wolff Bueno:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The authors thank T. M. Faria for technical assistance in the sampling and for helping with experimental feed preparation. The second author was granted a scholarship from Fundação de Amparo à Pesquisa do Estado de Goiás (FAPEG). Igo G. Guimarães was funded through a research fellowship from CNPq/Brazil (Produtividade em Pesquisa PQ, No. 305344/2015–3) and this study was partially funded using this resource. We want to extend our appreciation to the São Paulo Research Foundation (FAPESP) [grant no. 2022/02756-4] and Secretariat of Science, Technology and Innovation of Sao Paulo (SCTI/SPAI) [grant 008.00000373/2025-21] for their support.

Data availability

The dataset generated and analyzed during this study is publicly available in Mendeley Data (DOI: 10.17632/kxnmmd42yx.1).

References

Aguilar, F.A.A., Mourão, G.B., Cyrino, J.E.P., 2021. Digestible energy and protein requirements for maintenance and growth of pacu (Piaractus mesopotamicus): a factorial approach-based model. Sci. Agric. 78 (6). https://doi.org/10.1590/1678-992X-2020-0026.

Amancio, A.L.L., Silva Neto, M.R., Jordão Filho, J., Fonseca, S.B., Silva, J.H.V., 2019. Dietary protein requirements for tambaqui *Colossoma macropomum* (Cuvier, 1818) juvenile. Rev. Ciência Agron. ômica 50 (2), 259–266. https://doi.org/10.5935/1806-6690.20190030.

Amrkolaie, A.K., Yansari, A.T., Khalesi, M.K., 2013. Calculation of protein and energy requirements in beluga sturgeon (*Huso huso*) using a factorial approach. J. Anim. Physiol. Anim. Nutr. 97, 485–494. https://doi.org/10.1111/j.1439-0396.2012.01289.x.

AOAC International, 2005. Official methods of analysis of AOAC International, 18th ed.). AOAC International, Gaithersburg, MD, USA. https://doi.org/10.1002/0471740039.vec0284.

Arbeláez-Rojas, G.A., Fracalossi, D.M., Fim, J.D.I., 2002. Composição corporal de tambaqui, *Colossoma macropomum*, e matrinxã, *Brycon cephalus*, em sistemas de cultivo intensivo, em igarapé, e semi-intensivo, em viveiros. Rev. Bras. De. Zootec. 31 (3), 1059–1069. https://doi.org/10.1590/S1516-35982002000500001.

Baldisserotto, B., Gomes, L.D.C., 2020. Espécies. Nativas para piscicultura no Brasil, 3rd ed.). Editora UFSM.

Bicudo, A.J.A., Sado, R.Y., Cyrino, J.E.P., 2010. Growth performance and body composition of pacu *Piaractus mesopotamicus* (Holmberg 1887) in response to dietary protein and energy levels. Aquac. Nutr. 16 (2), 213–222. https://doi.org/10.1111/j.1365-2095.2009.00653.x.

Biswas, G., Jena, J.K., Singh, S.K., Patmajhi, P., Muduli, H.K., 2006. Effect of feeding frequency on growth, survival and feed utilization in mrigal, Cirrhinus mrigala, and rohu, Labeo rohita, during nursery rearing. Aquaculture 254 (1–4), 211–218. https://doi.org/10.1016/j.aquaculture.2005.08.001.

Booth, M.A., Allan, G.L., Pirozzi, I., 2010. Estimation of digestible protein and energy requirements of yellowtail kingfish Seriola lalandi using a factorial approach. Aquaculture 307, 247–259. https://doi.org/10.1016/j.aquaculture.2010.07.019.

Bremer Neto, H., Graner, C.A.F., Pezzato, L.E., Padovani, C.R., 2005. The spectrophotometric method on the routine of 1,5-diphenylcarbazide was adjusted on chromium determination in feces, after its utilization as a biological marker as chromium (III) oxide. Ciência Rural 35 (3), 691–697. https://doi.org/10.1590/S0103-84782005000300033.

Bueno, G.W., Bernal, F.E.M., Roubach, R., Skipper-Horton, J.O., Sampaio, F.G., Fialho, N. S., Bureau, D.P., 2023. Modeling of waste outputs in the aquatic environment from a commercial cage farm under neotropical climate conditions. Aquac. Environ. Interact. 15, 133–144. https://doi.org/10.3354/aei00457.

Buzollo, H., Sandre, L.C.G.D., Neira, L.M., Nascimento, T.M.T.D., Jomori, R.K., Carneiro, D.J., 2019. Digestible protein requirements and muscle growth in juvenile tambaqui (Colossoma macropomum). Aquac. Nutr. 25 (2), 1–11. https://doi.org/10.1111/anu.12888.

Camargo, A.C.S., Vidal Junior, M.V., Donzele, J.L., Santos, L.C., 1998. Níveis de energia metabolizável para tambaqui (Colossoma macropomum) dos 30 aos 180 gramas de peso vivo. Rev. Bras. De. Zootec. 27 (3), 409–415 (sem DOI).

Cho, C.Y., 1993. Digestibility of feedstuffs as a major factor in aquaculture waste management. In: Kaushik, S.J., Luquet, P. (Eds.), Fish Nutrition in Practice (Les Colloques No. 61. INRA, Paris, pp. 365–374.

Cho, S.H., Lee, S.M., Park, B.H., Lee, S.M., 2006. Effect of feeding ratio on growth and body composition of juvenile olive flounder Paralichthys olivaceus fed extruded pellets during the summer season. Aquaculture 251, 78–84. https://doi.org/10.1016/j.aquaculture.2005.05.041.

Conwey, C.B., 1994. Amino acids requirements of fish. A critical appraisal of present values. Aquaculture 124, 1–11. https://doi.org/10.1016/0044-8486(94)90349-2.

Davis, D.A., 2015. Feed and feeding practices in aquaculture. Elsevier, Cambridge, UK, p. 403. https://doi.org/10.1016/C2019-0-03580-7.

De Almeida, L.C., Lundstedt, L.M., Moraes, G., 2011. Growth and metabolic responses of tambaqui (Colossoma macropomum) fed levels of protein and lipid. Aquac. Nutr. 17, 253–262. https://doi.org/10.1111/j.1365-2095.2010.00759.x.

Eroldogan, O.T., Kumlu, M., Aktas, M., 2004. Optimum feeding rates for European sea bass Dicentrarchus labrax L. reared in seawater and freshwater. Aquaculture 231, 501–515. https://doi.org/10.1016/j.aquaculture.2003.10.020.

FAO, 2024. Blue Transformation in Action. Rome, Italy. The State of World Fisheries and Aquaculture 2024. FAO. https://doi.org/10.4060/cd0683en.

Fernandes, I.M., Bastos, Y.F., Barreto, D.S., Lourenço, L.S., Penha, J.M., 2017. The efficacy of clove oil as an anesthetic and in euthanasia procedure for small-sized tropical fishes. Braz. J. Biol. 77 (3), 444–450. https://doi.org/10.1590/1519-6984.15015.

Fernandes, T.R.C., Doria, C.R.C., Menezes, J.T.B., 2010. Características de carcaça e parâmetros de desempenho do tambaqui (Colossoma macropomum, Cuvier, 1818) em diferentes tempos de cultivo e alimentado com rações comerciais. Bol. do Inst. De. Pesca 36 (1), 45–52 (sem DOI).

Fernandes Júnior, A.C., Carvalho, P.L.P.F., Pezzato, L.E., Koch, J.F.A., Teixeira, C.P., Cintra, F.T., Damasceno, F.M., Amorin, R.L., Padovani, C.R., Barros, M.M., 2016. The effect of digestible protein to digestible energy ratio and choline supplementation on growth, hematological parameters, liver steatosis and size-sorting stress response in Nile tilapia under field condition. Aquaculture 456, 83–93. https://doi.org/10.1016/j.aquaculture.2016.02.001.

Filho, E.C.T.N., Mattos, B.O., Santos, A.A., Barreto, K.A., Albinati, R.C.B., Vidal, L.V.O., Sánchez-Vázquez, F.J., Fortes-Silva, R., 2018. Geometric approach to evaluate the energy/protein balance in tambaqui (*Colossoma macropomum*): can fish ensure nutritional intake targets by postingestion signals? Aquac. Nutr. 24 (2), 741–748. https://doi.org/10.1111/anu.12602.

Glencross, B.D., 2008. A factorial growth and feed utilization model for barramundi, Lates calcarifer, based on Australian production conditions. Aquac. Nutr. 14, 360–373. https://doi.org/10.1111/j.1365-2095.2007.00543.x.

Glencross, B., Hien, T.T.T., Phuong, N.T., Cam Tu, T.L., 2011. A factorial approach to defining the energy and protein requirements of Tra catfish, Pangasianodon hypothalamus. Aquac. Nutr. 17 (2), 396–405. https://doi.org/10.1111/j.1365-2095.2010.00774.x.

Gomes, L.C., Silva, C.R., 2009. Impact of pond management on tambaqui, Colossoma macropomum (Cuvier), production during growth-out phase. Aquac. Res. 40, 825–832. https://doi.org/10.1111/j.1365-2109.2009.02170.x.

Guimarães, I.G., Martins, G.P., 2015. Nutritional requirement of two Amazonian aquacultured fish species, Colossoma macropomum (Cuvier, 1816) and Piaractus brachypomus (Cuvier, 1818): A mini review. J. Appl. Ichthyol. 31 (4), 57–66. https://doi.org/10.1111/jai.12976.

Guimarães, I.G., Pezzato, L.E., Barros, M.M., Tachibana, L., 2008. Nutrient digestibility of cereal grain products and by-products in extruded diets for Nile tilapia. J. World Aquac. Soc. 39, 781–789. https://doi.org/10.1111/j.1749-7345.2008.00214.x.

Hernandez, M., Takeuchi, T., Watanabe, T., 1995. Effect of dietary energy sources on the utilization of protein by Colossoma macropomum fingerlings. Fish. Sci. 61 (3), 507–511. https://doi.org/10.2331/fishsci.61.507.

2023. IBGE (Instituto Brasileiro de Geografia e Estatística). (2023). Produção Pecuária Municipal.

Kaushik, S.J., Seiliez, I., 2010. Protein and amino acid nutrition and metabolism in fish: current knowledge and future needs. Aquac. Res. 41, 322–332. https://doi.org/10.1111/j.1365-2109.2009.02174.x.

Kolkovski, S., 2001. Digestive enzymes in fish larvae and juveniles—implications and applications to formulated diets. Aquaculture 200, 181–201. https://doi.org/10.1016/S0044-8486(01)00700-1.

Lima, C.S., Bomfim, M.A.D., Siqueira, J.C., Ribeiro, F.B., Lanna, E.A.T., 2016. Crude protein levels in the diets of tambaqui, Colossoma macropomum (Cuvier, 1818), fingerlings. Rev. Caatinga 29 (1), 183–190. https://doi.org/10.1590/1983-21252016v29n121rc.

Lupatsch, I., Kissil, G.W., 2005. Feed formulations based on energy and protein demands in white grouper (Epinephelus aeneus). Aquaculture 248, 83–95. https://doi.org/10.1016/j.aquaculture.2005.03.004.

Lupatsch, I., Kissil, G.W., Sklan, D., 2001. Optimization of feeding regimes for European sea bass Dicentrarchus labrax: a factorial approach. Aquaculture 202, 289–302. https://doi.org/10.1016/S0044-8486(01)00779-7.

Lupatsch, I., Kissil, G.W., Sklan, D., 2003. Comparison of energy and protein efficiency among three fish species Sparus aurata, Dicentrarchus labrax and Epinephelus aeneus: energy expenditure for protein and lipid deposition. Aquaculture 225, 175–189. https://doi.org/10.1016/S0044-8486(03)00288-6.

Lupatsch, I., Kissil, G.W., Sklan, D., Pfeffer, E., 1998. Energy and protein requirements for maintenance and growth in gilthead seabream (Sparus aurata L.). Aquac. Nutr. 4, 165–173. https://doi.org/10.1046/j.1365-2095.1998.00065.x.

Melo, L.A.S., Izel, A.C.U., Rodrigues, F.M., 2001. Criação de tambaqui (Colossoma macropomum) em viveiros de argila/barragens no Estado do Amazonas. Embrapa Amazônia Ocidental, Manaus.

Menezes, L.L.C., Machado, V.M., Souto, C.N., Proença, D.C., Bueno, G.W., Guimarães, I. G., 2025. Dietary phosphorus requirement for tambaqui, Colossoma macropomum, in the grow-out phase. J. Anim. Physiol. Anim. Nutr. https://doi.org/10.1111/jpn.70005.

Merola, N., Cantelmo, O.A., 1987. Growth, feed conversion and mortality of cage-reared tambaqui, Colossoma macropomum, fed various dietary feeding regimes and protein levels. Aquaculture 66 (3–4), 223–233. https://doi.org/10.1016/0044-8486(87)90108-6.

National Research Council (NRC), 2011. Nutrient requirements of fish and shrimp. The National Academy Press, Washington, USA. https://doi.org/10.17226/13039.

Oishi, C.A., Nwanna, L.C., Pereira Filho, M., 2010. Optimum dietary protein requirement for Amazonian tambaqui, Colossoma macropomum Cuvier, 1818, fed fish meal free diets. Acta Amaz. 40 (4), 757–762. https://doi.org/10.1590/S0044-59672010000400017.

Proença, D.C., Sena, M.F., Araújo, J.G., Bueno, G.W., Guimarães, I.G., 2025. Contribution of amino acids in cereal grain products to precision feed formulation for tambaqui (Colossoma macropomum) using a digestibility approach. J. Anim. Physiol. Anim. Nutr. https://doi.org/10.1111/jpn.70000.

Sandre, L.C.G., Buzollo, H., Nascimento, T.M.T., Neira, L.M., Jomori, R.K., Carneiro, D.J., 2017. Productive performance and digestibility in the initial growth phase of tambaqui (Colossoma macropomum) fed diets with different carbohydrate and lipid levels. Aquac. Rep. 6, 28–34. https://doi.org/10.1016/j.aqrep.2017.02.003.

Santos, M.Q.C., Lima, M.A.C., Santos, L., Pereira-Filho, M., Ono, E.A., Affonso, E.G., 2013. Feeding strategies and energy to protein ratio on tambaqui performance and physiology. Pesqui. Agropecu. ária Bras. 48 (8), 955–961. https://doi.org/10.1590/S0100-204X2013000800021.

Santos, L., Pereira Filho, M., Sobreira, C., Ituassu, D., Fonseca, F.D., 2010. Exigência proteica de juvenis de tambaqui (Colossoma macropomum) após privação alimentar. Acta Amaz. 40, 597–604. https://doi.org/10.1590/S0044-59672010000300021.

Shearer, K.D., 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. Aquaculture 119, 63–88. https://doi.org/10.1016/0044-8486(94)90444-8.

Shearer, K., 2000. Experimental design, statistical analysis and modelling of dietary nutrient requirement studies for fish: a critical review. Aquac. Nutr. 6 (2), 91–102. https://doi.org/10.1046/j.1365-2095.2000.00134.x.

Sousa, R.G.C., Prado, G.F., Pyñeiro, J.I.G., Bezerra Neto, E.B., 2016. Avaliação do ganho de peso do tambaqui cultivado com diferentes taxas de proteínas na alimentação. Biota Amazônia 6 (1), 40–45. https://doi.org/10.18561/2179-5746/biotaamazonia.v6n1p40-45.

Storebakken, T., Austreng, E., 1987. Ration level for salmonids: I. Growth, survival, body composition, and feed conversion in Atlantic salmon fry and fingerlings. Aquaculture 60 (3–4), 189–206. https://doi.org/10.1016/0044-8486(87)90287-0.

Teles, A.O., Couto, A., Enes, P., Peres, H., 2020. Dietary protein requirements of fish–a meta-analysis. Rev. Aquac. 12 (3), 1445–1477. https://doi.org/10.1111/raq.12391.

Valenti, W.C., Barros, H.P., Moraes-Valenti, P., Bueno, G.W., Cavalli, R.O., 2021. Aquaculture in Brazil: past, present and future. Aquac. Rep. 19, 100611. https://doi.org/10.1016/j.aqrep.2021.100611.

Van der Meer, M.B., Huisman, E.A., Verdegem, M.C.J., 1996. Feed consumption, growth and protein utilization of Colossoma macropomum (Cuvier) at different dietary fish meal/soya meal ratios. Aquac. Res. 27, 531–538. https://doi.org/10.1111/j.1365-2109.1996.tb01283.x.

Van der Meer, M.B., Machiels, M.A.M., Verdegem, M.C.J., 1995. The effect of dietary protein level on growth, protein utilization and body composition of Colossoma macropomum (Cuvier). Aquac. Res. 26, 901–909. https://doi.org/10.1111/j.1365-2109.1995.tb00885.x.

Van Tien, T., Chinh, D.T.M., Huong, T.T.M., Phuong, T.H., Irvin, S., Glencross, B., 2016. Development of a nutritional model to define the energy and protein requirements of cobia, Rachycentron canadum. Aquaculture 463, 193–200. https://doi.org/10.1016/j.aquaculture.2016.05.037.

Van Trung, D., Diu, N.T., Hao, N.T., Glencross, B., 2011. Development of a nutritional model to define the energy and protein requirements of tilapia, Oreochromis niloticus. Aquaculture 320 (1), 69–75. https://doi.org/10.1016/j.aquaculture.2011.07.029.

Vidal Jr, M.V., Donzele, J.L., Camargo, A.C.S., Andrade, D.R., Santos, L.C., 1998. Níveis de proteína bruta para tambaqui (Colossoma macropomum), na fase de 30 a 250 gramas. 1. Desempenho dos tambaquis. Rev. Bras. De. Zootec. 27, 421–426.

Withers, P.C., 1992. Comparative Animal Physiology. Brooks/Cole Publishing Company, Belmont, CA, p. 949.

Woynárovich, A., Van Anrooy, R., 2019. Field guide to the culture of tambaqui (Colossoma macropomum, Cuvier, 1816). FAO Fisheries and Aquaculture Technical Paper No. 624. FAO, Rome, Italy, p. 132.

Zambonino Infante, J.L., Cahu, C.L., 2007. Dietary modulation of some digestive enzymes and metabolic processes in developing marine fish: applications to diet formulation. Aquaculture 268, 98–105. https://doi.org/10.1016/j.aquaculture.2007.04.032.