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Digestible energy, protein, and energy–protein ratio requirements of *Pseudoplatystoma reticulatum*

Tarcila Souza de Castro Silva[1] | **Ricardo Basso Zanon**[2] | **Gerson Barreto Mourão**[2] | **José Eurico Possebon Cyrino**[2]

[1]Empresa Brasileira de Pesquisa Agropecuaria, Embrapa Agropecuária Oeste, Dourados, Brazil

[2]Department of Animal Science, University of São Paulo/ESALQ, Piracicaba, Brazil

Correspondence
Tarcila Souza de Castro Silva, Embrapa Agropecuária Oeste, BR 163, Km 253,6, P.O. Box # 449, 79804-970, Dourados, Mato Grosso do Sul, Brazil.
Email: tarcila.silva@embrapa.br

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Abstract

The use of novel aquaculture species depends on the determination of their nutritional requirements. This study aims at determining dietary protein, energy, and protein–energy ratio requirements of juvenile striped surubim, *Pseudoplatystoma reticulatum*, an economically important carnivorous South American catfish for capture fisheries and highly regarded for fish farming purposes. Juvenile striped surubim (53.6 ± 1.30 g, n = 525) were randomly stocked (n = 7) in 75 test cages (210 L) and hand fed for 60 days, two daily meals, with 25 diets formulated to contain five levels of digestible protein (DP) (320, 360, 400, 440, and 480 g/kg) and five levels of digestible energy (DE) (15.1, 15.6, 16.1, 16.6, and 17.2 MJ/kg) in a completely randomized design, 5 × 5 factorial scheme (n = 3). Dietary energy and protein level affected performance, feed efficiency, and metabolism while the whole-body composition was not affected by diets. Estimated dietary requirements for the best performance and best nutrient retention were 15.1 MJ/kg DE and 390 g/kg DP, therefore a 25.9 g/MJ of DP:DE ratio.

KEYWORDS

nutrient retention, *P/E* ratio, performance, striped surubim

1 | INTRODUCTION

Intensive fish farming relies on the use of balanced, species-specific aquafeeds. Therefore, determining nutritional and dietary requirements of novel aquaculture species is a basic need to develop this branch of the industry. Adequate protein and energy supplies are basic to proper biological functions and growth of fish, so determining protein and energy requirements is key for the farming of the species (Deng, Ju, Dominy, Murashige, & Wilson, 2011; Haidar, Bleeker, Heinsbroek, & Schrama, 2018; Sealey et al., 2013).

The striped surubim, *Pseudoplatystoma reticulatum*, a carnivorous, highly prized catfish from the Amazon and Prata Basin (Buitrago-Suárez & Burr, 2007), is a leading candidate for development of freshwater fish farming in South America (Kossowski, 1996; Valladão, Gallani, & Pilarski, 2018). All of *Pseudoplatystoma* sp. are very cannibalistic during early life history stages (Nuñez et al., 2008), but can be feed-trained and adapted to commercial, extruded dry feed, and intensively raised (Baras & Jobling, 2002; Valladão et al., 2018).

Protein is the most limiting nutrient of aquafeeds, especially for carnivorous fish, due to its high requirement and cost (Guy, Guy, Li, & Allen, 2018; Hassani, Mohseni, Hosseni, Sadati, & Pourkazemi, 2011; Sagada et al., 2017; Trushenski, Kasper, & Kohler, 2006). Fish use dietary protein not only as a plastic ingredient, but also as energy source. Dietary energy is not a nutrient "per se," but it is a rather important dietary component derived from the catabolism of dietary energy sources, chiefly lipids and carbohydrates, required for all body functions. Therefore, lipids and carbohydrates are included in aquafeeds in order to target a protein-sparing effect and, consequently, directing ingested protein to tissue deposition (Hillestad, Johnsen, & Åsgård, 2001; Mock et al., 2019; Ogino, Chiou, & Takeuchi, 1976). As a result, a balanced dietary energy–protein ratio elicits adequate dietary protein and energy intake, optimizing fish growth (Lee, Cho, & Kim, 2000) through all life stages (Twibell, Barron, & Gannam, 2016). However, it is important to consider that the nonprotein energy source thus appears as an effective regulator of muscle hyperplasia and hypertrophy (i.e., carbohydrate is less efficient than lipid) and low-dietary digestible protein (DP) to digestible energy (DE) ratio [DP:DE] may impair muscle growth (Alami-Durante et al., 2019). Additionally, the cost of ingredients (feedstuffs) with high nutritional value, such as lipids from marine sources (i.e., rich in omega-3 long-chain polyunsaturated fatty acids) has risen (Mock et al., 2019).

Several factors are involved in the determination of the dietary DP:DE ratio, making it difficult to compare results of dietary DP:DE between species, even those whose core of nutritional knowledge is already well established. For instance, there are still studies on dietary DP:DE requirements of tilapia under different criteria (i.e., performance, energy, and nitrogen balance parameters) in laboratory conditions (Haidar et al., 2018). In addition, studies have been carried out evaluating dietary protein–energy ratios in semi-intensive pond systems, in which natural food may influence growth of fish, altering the requirements of fish raised in different production systems (Kabir, Schrama, Verreth, Phillips, & Verdegem, 2019).

Interesting tools for the formulation and processing of cost-effective, environmentally-friendly aquafeeds are used by aquafeed plants. A common strategy has been used with the reduction in the dietary protein-to-lipid ratio, prompting more efficient protein utilization and reducing waste output and production cost (Mock et al., 2019; Rawles, Green, McEntire, Gaylord, & Barrows, 2018). Highly digestible feedstuffs bearing adequate protein, energy, and amino acid contents (Mo et al., 2019) as well as the use of the ideal protein concept (Rawles et al., 2018) also have been used for fish formulation.

Current research efforts still seek the best methodology for determining the dietary protein–energy ratio requirement of fish. Recent work by Haidar et al. (2018) report that procedures for the study of dietary DP:DE of tilapia not only use limited dietary DP:DE levels (ranging from a minimum of four to a maximum of nine levels) but also did not use an objective method of analysis (e.g., broken-line method) to estimate an optimum DP:DE ratio. However, these authors associate responses solely with the dietary DP:DE ratio, disregarding the effects of DP and DE levels as sources of variation, that is, analyzing as a factorial statistical model. Therefore, this study takes into consideration that response variables are influenced by several factors determining the protein, energy, and energy–protein ratio requirements of juvenile striped surubim, *P. reticulatum*, by examining the effects of energy and protein on performance, feed efficiency, and metabolism (Table 3 and Figure 1).

2 | MATERIALS AND METHODS

2.1 | Culture conditions

Juvenile striped surubim (53.6 ± 1.30 g of weight; 20.1 ± 1.06 cm of total length; n = 525) were randomly stocked in 75 cages (210 L), housed in an indoor, closed recirculating system, equipped with plastic bead biofilter coupled to a sand filtering system (clarifier), 60 L/s turnover rate, with controlled aeration (dissolved oxygen 5.2 ± 0.73 mg/L in all cages), temperature (27.4 ± 0.77°C), photoperiod (12 hr light:12 hr dark), pH (7.6 ± 0.4), and unionized ammonia levels, which remained below detection thresholds for the duration of the trial. Temperature, pH, and dissolved oxygen were measured daily between feeding times with a multiparameter probe (Horiba, U-52, Kyoto, Japan) and ammonia was measured weekly, also throughout the duration of the experimental period, with a colorimetric test (Alfakit, Trindade, Florianópolis, SC, Brazil).

2.2 | Fish and experimental diets

Fish were conditioned to feed to apparent satiation in two daily meals (06 hr 30 min and 18 hr 30 min) for 60 days with diets formulated to contain five levels of digestible protein [DP] (320, 360, 400, 440, and 480 g/kg) and five levels of digestible energy [DE] (15.1, 15.6, 16.1, 16.6, and 17.2 MJ/kg) (Table 1). Values of digestible energy and protein of feedstuffs for striped surubim were derived from Silva et al. (2013), in which we used the methodology of feces collection by sedimentation. Feed ingredients were finely ground (0.8 mm), mixed (horizontal, double-helical mixer, 4 min per batch), and extruded (experimental extruder PQ-30 m; 2,5 mm dye; Inbramaq, Ribeirão Preto, SP, Brazil); processed diets were oven-dried (forced air flow; 45°C; 24 hr), stored in plastic bags, and kept refrigerated (5°C) until use.

2.3 | Collection calculation of data

At the beginning and at the end of the trial, fish were anesthetized (benzocaine; 100 mg/L) and individual fish weight (seven fish) from each replicate (cage) was recorded for the calculation of weight gain. At the end of the feeding period, two fish from each unit were sampled, euthanized by anesthetic overdose (1 g/L benzocaine), quickly frozen, ground, and stored for determination of whole-body composition. Two fish from each unit were sampled, euthanized by anesthetic overdose, exsanguinated, and laparatomized for measurement of visceral fat and whole liver. Sampled tissues were homogenized and frozen (−20°C) until analysis using standard Association of Official Analytical Chemists (2000) procedures and methods.

Blood samples (1 ml) were centrifuged (2000 *g*, 10 min) and serum was collected and frozen (−18°C) for later determination of blood protein (SP) and triglyceride (ST) by colorimetric assays using commercial kits by Bioclin® (K031—Belo Horizonte, MG, Brazil) and Laborlab® (1,770,290—Guarulhos, SP, Brazil), respectively. Performance and feed efficiency were evaluated based on the following variables (Deng et al., 2011; National Research Council, 2011): weight gain (g): WG = [(final body weight) – (initial body weight)]; feed consumption (g): FC; feed conversion rate: FCR = [(feed intake)/(weight gain)]; specific growth rate (% day^{-1}): SGR = {[ln (final body weight) – ln (initial body weight)] × 100}/feeding period (days); hepatosomatic index (%): HSI = [(liver weight/body weight) × 100]; liposomatic index (%): LSI = [(visceral fat weight/body weight) × 100]; viscerosomatic index (%):

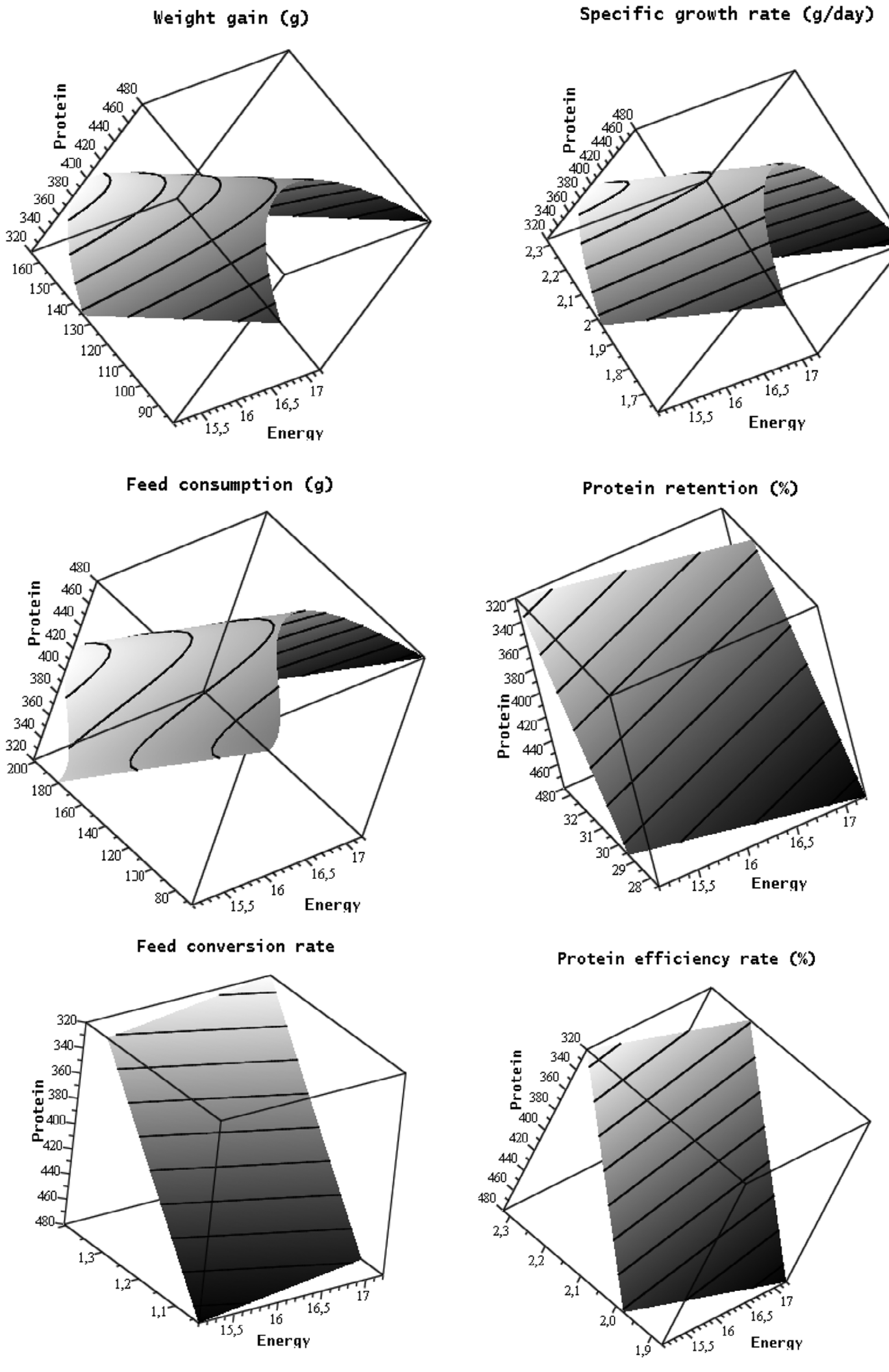

FIGURE 1 Analyzed variables in function of dietary digestible energy (MJ/kg) and protein (g/kg) for striped surubim—calculated by averaging three replicates with seven fish in each replicate. The fish were fed for 60 days with rations containing five levels of digestible protein (DP) (320, 360, 400, 440, and 480 g/kg) and five levels of digestible energy (DE) (15.1, 15.6, 16.1, 16.6, and 17.2 MJ/kg)

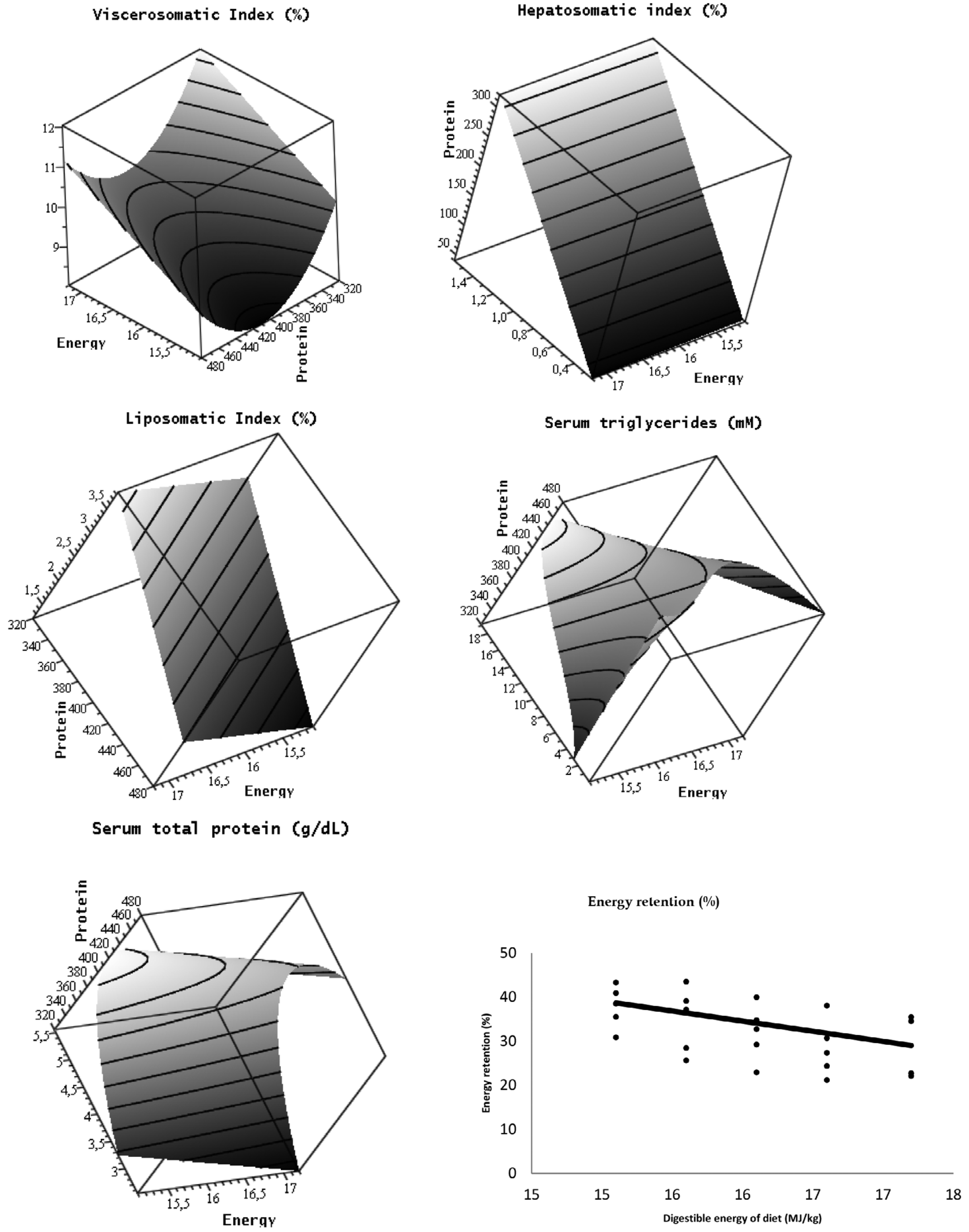

FIGURE 1 (Continued)

VSI = [(viscera weight/body weight) × 100]; protein efficiency rate (%): PER = [(weight gain/dietary protein intake) × 100]; energy retention (%): ERE = {[(final body energy × final body weight) − (initial body energy × initial body weight)/dietary energy intake] × 100}; protein retention (%): PRE = {[(final body protein × final body weight) − (initial body protein × initial body weight)/dietary protein intake] × 100.

TABLE 1 Dietary formulation and calculated composition of diets fed to juvenile *Pseudoplatystoma reticulatum* for 60 days (as-fed basis)

Digestible energy (MJ/kg)	15.1					15.6					16.1					16.6					17.2				
Digestible protein (g/kg)	**320**	**360**	**400**	**440**	**480**	**320**	**360**	**400**	**440**	**480**	**320**	**360**	**400**	**440**	**480**	**320**	**360**	**400**	**440**	**480**	**320**	**360**	**400**	**440**	**480**
Treatment	1	2	3	4	5	6	7	8	9	10	11	12	13	13	14	15	16	17	18	19	21	22	23	24	25
Poultry by-product meal (584 g/kg CP; 19.9 MJ/kg GE)	15.0	43.7	42.9	42.4	42.8	37.1	43.8	42.9	42.4	43.6	44.5	43.7	42.9	42.7	44.4	36.4	43.7	42.8	43.5	45.3	18.3	43.7	42.8	44.3	26.8
Fish meal (634 g/kg CP; 18.4 MJ/kg GE)	11.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Meat and bone meal (449 g/kg CP; 15.3 MJ/kg GE)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—	9.39	—	—	—	—
Soybean meal (462 g/kg CP; 17.3 MJ/kg GE)	32.5	16.4	29.3	36.8	32.7	15.0	18.3	29.8	37.0	23.1	4.7	19.1	30.2	34.2	12.8	19.3	19.5	31.6	23.9	2.5	36.2	20.0	33.0	13.6	—
Gelatin (937 g/kg CP; 19.6 MJ/kg GE)	—	—	—	3.1	10.2	—	—	—	3.1	15.2	—	—	—	4.5	20.4	—	—	—	9.8	25.7	—	—	—	15.0	40.5
Corn ground (78 g/kg CP; 16.5 MJ/kg GE)	23.4	19.9	20.2	0.5	0.4	17.9	23.2	18.1	—	—	16.4	22.5	15.7	—	—	24.1	20.3	8.4	0.0	0.0	13.9	18.2	1.2	—	—
Fish oil (39.0 MJ/kg GE)	11.2	8.5	4.9	—	—	13.5	9.8	6.6	2.1	3.3	15.5	11.4	8.3	4.6	6.8	16.0	13.2	9.0	8.1	10.3	16.0	14.9	9.8	11.5	16.0
Starch (15.2 MJ/kg GE)	—	—	—	14.7	11.1	—	—	0.1	13.0	11.4	—	—	0.3	11.4	11.4	—	—	5.4	11.4	11.4	3.7	—	10.5	11.4	11.4
Wheat bran (156 g/kg CP; 16.7 MJ/kg GE)	1.5	8.8	—	—	—	12.8	1.8	—	—	—	16.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cellulose (16.5 MJ/kg GE)	—	0.2	0.1	—	0.3	—	0.6	—	—	1.0	0.3	0.8	0.1	0.2	1.7	0.8	0.8	—	0.9	0.0	0.0	0.8	0.3	1.6	2.8
Calcitic calcarium	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.8	—	—	—	—	—	—	—	—	—
Dicalcium phosphate	2.0	—	—	—	—	1.18	—	—	—	—	—	—	—	—	—	—	—	0.2	—	2.4	—	—	—	—	—
Mineral and vitaminic premix[a], salt[b], and antioxidant[c]	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52	2.52

TABLE 1 (Continued)

Digestible energy (MJ/kg)	15.1					15.6					16.1					16.6					17.2				
Digestible protein (g/kg)	**320**	**360**	**400**	**440**	**480**	**320**	**360**	**400**	**440**	**480**	**320**	**360**	**400**	**440**	**480**	**320**	**360**	**400**	**440**	**480**	**320**	**360**	**400**	**440**	**480**
Calculated chemical composition[d]																									
Starch (g/kg)	150	150	126	132	100	150	150	113	114	100.	150	140	100	100	100	150	127	100	100	100	119	113	100	100	100
Calcium (g/kg)	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
Digestible energy (MJ/kg)	15.1	15.1	15.1	15.1	15.1	15.6	15.6	15.6	15.6	15.6	16.1	16.1	16.1	16.1	16.1	16.6	16.6	16.6	16.6	16.6	17.2	17.2	17.2	17.2	17.2
Crude fiber (g/kg)	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30
Available phosphorus (g/kg)	12.9	12.1	11.8	11.7	11.7	12.6	11.9	11.8	11.7	11.7	12.3	11.9	11.8	11.7	11.8	10.0	11.9	11.8	11.7	11.8	11.1	11.9	11.7	11.8	11.8
Lipid (g/kg)	149	146	107	52	52	188	158	124	72	85	216	173	139	97	120	210	189	144	132	154	198	205	149	166	189
Digestible protein (g/kg)	320	360	400	440	480	32	360	400	440	480	32	360	400	440	480	32	360	400	440	480	32	360	400	440	480

Note: The ingredients were from Mogiana Alimentos S. A. (Brazil), except cellulose that was from Rhoster Company (Brazil).

Abbreviations: CP, crude protein; GE, gross energy.

[a]Premix composition (/kg): folic acid 250 mg; pantothenic acid 500 mg; biotin 125 mg; cobalt 25 mg; copper 2000 mg; choline 25,000 mg; iron 13,820 mg; iodine 100 mg; manganese 3,750 mg; niacin 5,000 mg; selenium 75 mg; zinc 17,500 mg; vitamin A 1000,000 UI; vitamin B_1 1,250 mg; vitamin B_{12} 3,750 mg; vitamin B_2 2,500 mg; vitamin B_6 1875 mg; vitamin C 42,000 mg; vitamin D_3 500,000 UI; vitamin E 20,000 UI; vitamin K_3 500 mg.

[b]Salt 0.5 g/kg.

[c]Antioxidant 0.02 g/kg.

[d]Chemical composition of the ingredients utilized was previously analyzed by our research Group (i.e., Silva, Moro, Bomfim, Dairiki, & Cyrino, 2013).

2.4 | Statistical analysis and presentation of data

The trial was set up in a completely randomized design, 5 × 5 factorial scheme (digestible energy × digestible protein), seven fish per replicate (n = 3). A two-way analysis of variance (ANOVA; α = .05) was used to detect differences between the 25 treatments. Because all studied variables presented heterogeneity of variance (common in biological responses), similar variances (variances up to four times greater or lesser among themselves were considered similar) were grouped and considered in regression mixed models; thus for the analysis of each variable, four (carcass moisture and lipids), five (WG; ERE; LSI; carcass crude protein), six (SGR; FC; PRE; VSI; SPT; carcass gross energy), seven (HSI; ST), eight (PER), and nine (FCR; carcass ash) groups of variances were included in the models. Significant effects of treatments (energy and protein) were submitted to polynomial analysis using the PROC MIXED procedure of the statistical package SAS, Version 9.1.3 (SAS Institute Inc., Cary, NC). An array of models for each variable studied was determined (Littel, 2002; Littel, Milliken, Stroup, Wolfinger, & Schabenberger, 2006), considering regression from first- to third-degree order for each parameter (energy and protein) and their possible interactions. The best model for each variable was determined using the lowest values of Akaike Information Criterion (AIC), corrected version AICc, and Bayesian information criterion (BIC); procedures followed the statistical package guide. The graphs (Figure 1) and the optimization of the equations—maximum and minimum points—were made using the Maple Program (Version 13, Waterloo, Ontario, Canada: Waterloo Maple Software). The response surface for each variable was analyzed considering the root mean of standard error (MSE), R^2, and coefficient of variation.

The averages and *SDs* of the analyzed variables were grouped by the digestible energy and protein levels (five of each) to facilitate the presentation of results in the tables.

3 | RESULTS

3.1 | Growth and survival

Dietary protein and energy levels affected juvenile striped surubim growth performance (Table 2). Dietary protein linearly affected WG and SGR, and a cubic effect was detected for FC; dietary energy levels linearly affected all growth variables. The greater WG, SGR, and FC estimated was for fish-fed diets containing the lowest DE level (15.1 MJ/kg) for all variables and 389, 389, and 391 g/kg of DP, respectively (Table 3 and Figure 1). Survival exceeded 92% in all treatments, and the cause of the deaths was behavioral, that is, it did not result from effects of the treatments.

3.2 | Feed efficiency

Feed efficiency of striped surubim is reflected on FCR, PER, PRE, and ERE values (Table 4). Both dietary energy and protein linearly affected FCR, PER, and PRE, but only DE levels affected ERE. Increasing dietary DP improved FCR of striped surubim. The best estimated FCR was obtained by juvenile striped surubim fed diets containing the highest DP level (480 g/kg) and the lowest DE level (15.1 MJ/kg DE). This DE level also resulted in the best estimated value of ERE, PER, and PRE; and the dietary protein levels of the last two were the lowest levels tested (320 g/kg) (Table 3 and Figure 1).

3.3 | Whole-body composition and tissue indices

Varying dietary protein and energy levels did not affect the whole-body composition of striped surubim (Table 5). However, dietary energy and protein levels altered fish metabolic rate, that is, visceral indexes. Dietary energy and

TABLE 2 Average of performance data of juvenile striped surubim, *Pseudoplatystoma reticulatum* fed for 60 days with diets containing different levels of digestible protein and energy

Variables		IW[a]	FW[a]	WG[a]	SGR[a]	FC[a]	Survival
		g	g	g	% day $^{-1}$	g	%
Digestible energy (MJ/kg)	15.1	53.5 ± 0.64	187.1 ± 19.54	133.6 ± 19.11	2.07 ± 0.17	172.4 ± 2.78	98.1 ± 3.30
	15.6	53.6 ± 1.26	191.3 ± 21.60	137.6 ± 20.74	2.09 ± 0.17	181.7 ± 2.35	92.4 ± 6.60
	16.1	53.3 ± 1.49	171.7 ± 15.01	118.3 ± 14.27	1.92 ± 0.14	166.0 ± 2.02	93.3 ± 9.90
	16.6	53.9 ± 1.01	169.8 ± 17.50	115.9 ± 16.79	1.83 ± 0.15	175.5 ± 4.05	92.4 ± 9.46
	17.2	53.3 ± 1.05	176.3 ± 14.96	123.0 ± 14.11	1.97 ± 0.16	157.9 ± 7.44	97.6 ± 4.12
Digestible protein (g/kg)	320	53.9 ± 0.78	166.3 ± 19.70	112.4 ± 19.31	1.86 ± 0.20	188.6 ± 5.36	93.3 ± 9.31
	360	53.4 ± 1.15	192.9 ± 14.92	139.5 ± 14.38	2.13 ± 0.12	185.3 ± 1.63	95.2 ± 6.60
	400	53.6 ± 1.09	198.4 ± 22.09	144.8 ± 21.33	2.17 ± 0.16	203.9 ± 2.76	92.4 ± 9.46
	440	53.8 ± 0.96	186.5 ± 18.73	132.7 ± 18.40	2.04 ± 0.17	155.7 ± 1.49	97.1 ± 4.95
	480	53.3 ± 1.43	138.9 ± 15.62	85.6 ± 14.25	1.52 ± 0.17	132.3 ± 8.35	92.4 ± 6.60

Abbreviations: FC, feed consumption; FW, final weight; IW, initial weight; SGR, specific growth rate; WG, weight gain.
[a]Variable that presented significant effect of treatments (energy and protein) by the two-way analysis of variance (ANOVA; α = .05) and that was submitted to a posterior polynomial analysis, considering a 5 × 5 factorial scheme. The values briefly presented were obtained by calculating the mean of the seven fish in each experimental unit, then the average of the three replicates, and finally the average and *SD* of the digestible energy and protein levels (five of each).

protein linearly affected HSI and also linearly affected visceral lipid accumulation of striped surubim. Consequently, dietary energy and protein levels affected VSI of striped surubim (quadratic effect of protein and linear of energy). The best HSI, LSI, and VSI responses were registered for fish-fed diets containing 17.2 MJ/kg DE and 320 g/kg DP, 15.1 MJ/kg DE and 480 g/kg DP, and 15.1 MJ/kg DE and 412 g/kg DP, respectively (Tables 3, 6 and Figure 1).

3.4 | Blood analysis

Serum triglyceride contents were linearly affected by increasing dietary energy levels and cubically affected by dietary protein levels. The lowest estimated ST was registered for fish fed 17.2 MJ/kg of DE and 480 g/kg of DP diet, while the highest level was registered for fish fed 15.1 MJ/kg of DE and 449 g/kg of DP in the diet. Furthermore, dietary contents of 419 g/kg of DP (quadratic effect) and 15.1 MJ/kg DE (linear effect) resulted in higher serum total protein levels (5.57 g/dl) (Tables 3, 6 and Figure 1).

Combined analysis of models of each variable allowed showed that 15.1 MJ/kg DE and 390 g/kg DP, that is, a 25.9 g/MJ of DP:DE, yield the best growth performance and feed efficiency of striped surubim (Table 3 and Figure 1). When metabolic indicators are also considered, fish health is also favored by diets containing these same DE and DP levels; once fish meet their nutritional requirements, they are healthier and more resistant to disease.

4 | DISCUSSION

4.1 | Responses to dietary *P:E*

Juvenile striped surubim growth was affected by dietary protein and energy levels. Fish growth is influenced by many factors such as species, age, and environmental conditions (Cho, 1992; Farhat & Khan, 2011; Sealey

TABLE 3 Analyzed variables: minimum and maximum estimated values (per fish) and their corresponding protein and energy levels with the equation and determination coefficient for striped surubim, *Pseudoplatystoma reticulatum*

Variables	Maximum value	*E* MJ/kg	*P* g/kg	Minimum value	*E* MJ/kg	*P* g/kg	R^2	Equation
Weight gain (g)	168	15.1	389	73	17.2	480	0.50	$WG = -1.014 \times 10^{+3} - 1.423 \times 10^{+1}E + 5.042P - 6.476 \times 10^{-3}P^2 + 7.659IW$
Specific growth rate (g/day)	2.40	15.1	389	1.46	17.2	480	0.45	$SGR = -1.198 \times 10^{+1} - 7.424 \times 10^{-2}E + 5.378 \times 10^{-2}P - 6.876 \times 10^{-3}P^2 + 9.089 \times 10^{-2}IW$
Feed consumption (g)	201	15.1	391	69	17.2	480	0.68	$FC = 5.065 \times 10^{+3} - 1.663x10^{+1}E - 4.436 \times 10^{+1}P + 1.207 \times 10^{-1}P^2 - 1.083 \times 10^{-4}P^3 + 3.005IW$
Feed conversion rate	1.41	17.2	320	1.02	15.1	480	0.16	$FCR = 2.426 + 2.783x10^{-2}E - 1.940x10^{-3}P - 1.629x10^{-2}IW$
Protein efficiency rate (%)	2.32	15.1	320	1.86	17.2	480	0.44	$PER = 2.929 - 0.05.154 \times 10^{-2} E - 2.120 \times 10^{-3}P + 1.566 \times 10^{-2}IW$
Protein retention (%)	33.59	15.1	320	25.30	17.2	480	0.25	$PR = -7.973 - 9.047 \times 10^{-1}E - 2.511 \times 10^{-2}P + 1.168IW$
Energy retention (%)	39.73	15.1	–	25.66	17.2	320	0.20	$ER = 5.020 \times 10^{+1} - 4.594E + 1.071IW$
Viscerosomatic index (%)	12.25	17.2	320	7.77	15.1	412	0.54	$VI = 2.362 \times 10^{+1} + 9.598 \times 10^{-1}E - 1.959x10^{-1}P + 2.377 \times 10^{-4}P^2 + 1.896 \times 10^{-1}IW$
Hepatosomatic index (%)	2.39	15.1	480	1.48	17.2	320	0.12	$HI = -1.467 - 8.271x10^{-3}E + 4.792 \times 10^{-3}P + 3.042 \times 10^{-2}IW$
Liposomatic index (%)	3.98	17.2	320	1.07	15.1	480	0.52	$LI = -6.109 + 4.4045 \times 10^{-1}E - 1.073 \times 10^{-2}P + 1.07610^{-1}IW$
Serum triglycerides (mM)	17.16	15.1	449	0.23	17.2	480	0.21	$ST = 1.093 \times 10^{+2} + 3.241 \times 10^{+1}E - 3.617P + 1.339 \times 10^{-2}P^2 - 1.181 \times 10^{-5}P^3 - 8.369 \times 10^{-2}EP - 3.805 \times 10^{-1}IW$
Serum total protein (g/dl)	5.57	15.1	419	2.63	17.2	320	0.12	$SP = -3.801 \times 10^{+1} - 3.345x10^{-1}E + 1.979 \times 10^{-1}P - 2.362 \times 10^{-4}P^2 + 1.330 \times 10^{-1}IW$

Note: *E* is the dietary energy level; *P* is the dietary protein level; EP is the dietary energy to protein ratio; IW is the initial weight; R^2 is the determination coefficient. Estimates were calculated by averaging three replicates with seven fish in each replicate. The fish were fed for 60 days with rations containing five levels of digestible protein (DP) (320, 360, 400, 440, and 480 g/kg) and five levels of digestible energy [DE] (15.1, 15.6, 16.1, 16.6, and 17.2 MJ/kg), in a 5 × 5 factorial scheme.

TABLE 4 Average of feed efficiency data of juvenile striped surubim, *Pseudoplatystoma reticulatum* fed for 60 days with diets containing different levels of digestible protein and energy

Variables		FCR[a]	PER[a] (%)	PRE[a] (%)	ERE[a] (%)
Digestible energy (MJ/kg)	15.1	1.29 ± 0.15	2.10 ± 0.12	32.89 ± 2.64	37.74 ± 4.93
	15.6	1.32 ± 0.11	2.17 ± 0.29	32.89 ± 4.95	34.74 ± 10.05
	16.1	1.40 ± 0.14	2.02 ± 0.22	29.68 ± 3.39	31.80 ± 8.11
	16.6	1.52 ± 0.24	1.99 ± 0.18	30.66 ± 3.54	28.43 ± 8.28
	17.2	1.28 ± 0.53	2.04 ± 0.14	30.54 ± 3.52	30.72 ± 7.39
Digestible protein (g/kg)	320	1.68 ± 0.28	2.24 ± 0.19	34.51 ± 4.06	27.04 ± 9.71
	360	1.33 ± 0.11	2.26 ± 0.21	34.08 ± 4.10	32.14 ± 6.70
	400	1.41 ± 0.13	1.96 ± 0.23	29.34 ± 4.55	35.25 ± 7.37
	440	1.17 ± 0.08	2.02 ± 0.17	31.21 ± 3.08	33.88 ± 8.20
	480	1.55 ± 0.59	1.74 ± 0.23	26.22 ± 3.31	34.22 ± 6.49

Abbreviations: ERE, energy retention; FCR, feed conversion rate; PER, protein efficiency rate; PRE, protein retention.
[a]Variable that presented significant effect of treatments (energy and protein) by the two-way analysis of variance (ANOVA; α = .05) and that was submitted to a posterior polynomial analysis, considering a 5 × 5 factorial scheme The values briefly presented were obtained by calculating the mean of the seven fish in each experimental unit, then the average and *SD* of the three replicates, and finally the average of the digestible energy and protein levels (five of each).

TABLE 5 Whole body composition (wet weight basis) of juvenile striped surubim, *Pseudoplatystoma reticulatum* fed for 60 days with diets containing different levels of digestible protein and energy

Variables		Moisture (g/kg)	Crude protein (g/kg)	Lipids (g/kg)	Ash (g/kg)	Gross energy (MJ/kg)
Digestible energy (MJ/kg)	15.1	719 ± 13.5	156 ± 5.4	76 ± 10.0	29 ± 2.1	7.1 ± 0.56
	15.6	727 ± 27.6	152 ± 9.5	73 ± 22.7	30 ± 4.5	6.7 ± 1.00
	16.1	727 ± 28.8	150 ± 7.2	77 ± 30.1	30 ± 3.4	6.8 ± 1.16
	16.6	730 ± 27.2	154 ± 7.2	69 ± 25.2	31 ± 7.1	6.6 ± 1.23
	17.2	725 ± 23.8	151 ± 6.2	75 ± 22.5	31 ± 4.7	6.8 ± 0.96
Digestible protein (g/kg)	320	730 ± 27.6	155 ± 8.1	68 ± 27.5	30 ± 4.5	6.5 ± 1.07
	360	729 ± 18.0	152 ± 6.7	72 ± 16.5	29 ± 4.7	6.7 ± 0.76
	400	713 ± 29.1	151 ± 6.7	85 ± 27.3	30 ± 4.6	7.4 ± 1.25
	440	730 ± 22.2	155 ± 9.8	69 ± 18.4	31 ± 4.5	6.6 ± 0.88
	480	722 ± 21.3	153 ± 4.2	77 ± 18.6	29 ± 2.7	7.0 ± 0.79

Notes: The values briefly presented were obtained by calculating the mean of the two fish in each experimental unit, then the average and *SD* of the three replicates, and finally the average of the digestible energy and protein levels (five of each).

et al., 2013), a reasonable explanation for the relatively lower WG (407%) and SGR (1.5% day^{-1}) recorded for the juvenile striped surubim in comparison with that recorded for fingerling speckled surubim *Pseudoplatystoma coruscans* (WG = 937–1,089%; SGR = 3.7–4%/day) by Martino, Cyrino, Portz, and Trugo (2002b).

Dietary protein requirements of striped surubim (390 g/kg) neared the requirements of several carnivorous fish, such as the sunshine bass (408 g/kg), Malaysian catfish, *Mystus nemurus* (420 g/kg), and the bagrid catfish, *Horabagrus brachysoma* (391 g/kg) (Brown, Nematipour, & Gatlin III, 1992; Giri, Sahoo, Paul, Mohanty, & Sahu, 2011; Ng, Soon, & Hashim, 2001), but far exceeded dietary protein requirement of the benthopelagic, bighead carp *Aristichthys nobilis* (301 g/kg) (Santiago & Reyes, 1991), and the omnivore, channel catfish, *Ictalurus punctatus* (240 g/kg) (Robinson & Li, 1997). As a matter of fact, feeding habits of fish influence morphological and physiological characteristics of the digestive tract, so different species do require, use, and metabolize nutrients differently.

TABLE 6 Average of visceral indexes and blood data of juvenile striped surubim, *Pseudoplatystoma reticulatum* fed for 60 days with diets containing different levels of digestible protein and energy

Variables		IVS[a] (%)	IHS[a] (%)	ILS[a] (%)	TGL[a] (mM)	PT[a] (g/dl)
Digestible energy (MJ/kg)	15.1	9.06 ± 1.43	1.98 ± 0.23	1.91 ± 0.64	791 ± 258.0	3.39 ± 4.97
	15.6	9.73 ± 0.86	1.94 ± 0.25	2.30 ± 0.50	691 ± 204.9	3.35 ± 4.99
	16.1	9.46 ± 0.64	1.93 ± 0.23	3.00 ± 0.43	600 ± 161.3	2.46 ± 3.87
	16.6	9.91 ± 0.48	1.96 ± 0.31	2.72 ± 0.38	653 ± 202.8	3.23 ± 4.57
	17.2	9.49 ± 0.84	1.84 ± 0.24	2.00 ± 0.57	737 ± 88.9	2.63 ± 4.63
Digestible protein (g/kg)	320	11.87 ± 1.72	1.92 ± 0.51	3.87 ± 0.78	581 ± 178.8	3.89 ± 3.89
	360	9.55 ± 0.50	1.59 ± 0.11	3.01 ± 0.45	632 ± 124.0	4.39 ± 4.39
	400	8.65 ± 0.86	2.00 ± 0.29	1.91 ± 0.37	892 ± 275.1	6.17 ± 6.17
	440	9.34 ± 0.54	2.30 ± 0.22	2.28 ± 0.60	825 ± 168.3	4.91 ± 4.91
	480	8.91 ± 0.94	1.90 ± 0.20	1.31 ± 0.45	556 ± 180.4	3.61 ± 3.61

Abbreviations: IHS, hepatosomatic index; ILS, liposomatic index; IVS, viscerosomatic index; PT, serum protein; TGL, serum triglycerides.

[a]Variable that presented significant effect of treatments (energy and protein) by the two-way analysis of variance (ANOVA; α = .05) and that was submitted to a posterior polynomial analysis, considering a 5 × 5 factorial scheme. The values briefly presented were obtained by calculating the mean of the seven fish in each experimental unit, then the average of the three replicates, and finally the average and *SD* of the digestible energy and protein levels (five of each).

The ideal DP:DE ratio for striped surubim (25.9 g/MJ) was lower than values estimated for Persian sturgeon, *Acipenser persicus* (22 g/MJ) (Mohseni, Pourkazemi, Hosseni, Hassani, & Bai, 2013) and African catfish, *Clarias gariepinus* (20.5 g/MJ) (Ali & Jauncey, 2005). Smaller values were found for Atlantic salmon (19 g/MJ) (Einen & Roem, 1997), rohu, *Labeo rohita* (18.4 g/MJ) (Satpathy, Mukherjee, & Ray, 2003) and Nile tilapia, *Oreochromis niloticus* (16.6 g/MJ) (Haidar et al., 2018).

The comparison and discussion of data reported in different articles dwelling on a number of species is further complicated by the method of analysis and data presentation, that is, units of measurement. Some authors consider digestible protein and energy values while others consider crude protein and gross energy values; some authors estimate energy and protein values on a dry matter basis and others on an as-fed basis. Einen and Roem (1997); Haidar et al. (2018); Mohseni et al. (2013) have already highlighted these concerns and the difficulties therein derived regarding comparative discussion of data on fish nutrition requirements, especially dietary protein and energy.

Dietary protein and energy requirements of striped surubim near that of juvenile speckled surubim (400 g/kg CP and 15.8 MJ/kg GE) were reported by Zanardi, Boquembuzo, and Koberstein (2008). However, values reported refer not only to dietary digestible protein and energy requirements, but also to dietary crude protein and energy requirements. Cornélio et al. (2014) worked also with gross energy in addition to isoenergetics diets (19.25 MJ/kg) to determine nutritional requirements of crude protein, corresponding to 448 g/kg, for juvenile striped surubim (16 g). It is thus safe to infer that dietary, digestible energy, and protein requirements for optimal performance and feed efficiency and, therefore, minimized waste outputs for juvenile striped surubim (53.6 g) are 15.06 MJ/kg of DE, 390 g/kg of DP, and 25.9 g/MJ of DP:DE. Considering the importance of meeting amino acid requirements, further studies are needed to improve the striped surubim's nutritional requirements.

Fish fed diets with higher DE (17.2 MJ/kg) and DP (480 g/kg) endured weight loss, possibly resulting from nutritional imbalance, similar to that registered for the grouper *Epinephelus malabaricus* fed isocaloric diets (15.1 MJ/kg of gross energy) containing low levels of crude protein (0 and 8%) (Shiau & Lan, 1996). The weight loss of fish from this treatment may also have resulted from poor feed consumption, consequence of poor palatability (gelatin under extrusion results in very hard pellets) of the diet, which had generous quantities of gelatin (Glencross, Booth, & Allan, 2007). Moreover, the varying contents of protein sources can influence not only palatability but also diet nutrient contents and profile, prompting feeding groups to perform differently (Shiau & Lan, 1996). In this context, the large quantity of gelatin may also have influenced the reduced growth of surubim since despite its high protein content it has a moderate content of lysine (3.55%), when compared to other feedstuffs, such as fishmeal (4.5–5.2%). Finally, reduced feed consumption of fish fed diets containing higher dietary energy and protein levels may be a consequence of the aggregate dietary energy contents, since fish not only use ingested protein as an energy source but also eat first to meet nutritional energy requirements (Haidar et al., 2018; Lee et al., 2000; Lee & Putnam, 1973).

Concurrent lower dietary protein and higher dietary energy levels reduced growth performance of striped surubim. It has been reported that excess dietary energy hampers fish growth, protein retention, and feed efficiency (Daniels & Robinson, 1986). However, nitrogen loss can be reduced to some extent with increasing dietary energy, and to some extent, increased dietary protein levels can improve growth and feed efficiency (McGoogan & Gatlin III, 2000).

Results on FCR for striped surubim were similar to those recorded for speckled surubim by Martino et al. (2002b); Martino, Trugo, Cyrino, and Portz (2003, 2005), varying on 0.7 to 1.1. PER and ERE are typically expected to decrease with increasing dietary protein levels (De Silva, Gunasekera, Collins, & Ingram, 2002; Haidar et al., 2018; Sá, Pousão-Ferreira, & Oliva-Teles, 2006). Estimated value of PER is similar to those recorded for juvenile speckled surubim (Martino et al., 2002b; Martino et al., 2003). In such a context, the concurrent and detailed, broad range assessment of recorded DE and DP requirements seems adequate and necessary, for it may set a basis for the definition of detailed nutrient flow models of nutritional requirements and energy use of fish (Bureau, Hua, & Azevedo, 2008; Hernandez-Llamas, 2009).

The best value of PRE is less than those reported for speckled surubim—40 to 48% (Martino et al., 2003; Martino et al., 2005). The best value of ERE was higher than that reported for speckled surubim (34–36%) by Martino, Trugo, Cyrino, and Portz (2005). The best values of PRE and ERE were registered for fish fed the lowest dietary energy level, that is, diets containing 150 and 100 g/kg dietary lipid, respectively. Martino, Cyrino, Portz, and Trugo (2002a) registered improved growth performance of fingerling speckled surubim when dietary lipid contents were increased from 60 to 180 g/kg, consequently increasing dietary gross energy from 18.6 to 21.5 MJ/kg. However, Martino et al. (2005) did not register improved feed efficiency by juvenile speckled surubim when dietary lipid levels were further increased from 190 to 270 g/kg. Comparing the results herein reported with those reported by Martino et al. (2003, 2005) elicits inferring that striped surubim has lower dietary energy (and lipids) requirement than speckled surubim.

4.2 | Other physiological responses

Dietary protein and lipid levels did not affect carcass composition of striped surubim, like Malaysian mahseer, *Tor tambroides* (Ng, Abdullah, & De Silva, 2008), and white sea bream, *Diplodus sargus* (Sá et al., 2006); similar results were recorded for speckled surubim fed with different carbohydrate and lipid levels by Martino et al. (2005). Nevertheless, some authors reported the effects of diet on the composition of fish (Giri et al., 2011; Haidar et al., 2018; Mohseni et al., 2013), particularly with respect to carcass energy and moisture content (Martino, Cyrino, Portz, & Trugo, 2002a). Differences between reported results can be explained by the fact that, in addition to diet, whole-body composition of fish can be affected by many exogenous (water temperature and salinity and feeding strategy) and endogenous (age, sex, species, size, life stage) factors (Shearer, 1994).

Increased dietary energy levels as a result of dietary lipid, carbohydrate, and protein excess often result in accumulation of fat and increased hepatic (HSI) and visceral (LSI and VSI) mass and size (Sealey et al., 2013). HSI of striped juvenile surubim was similar to those reported by Daniels and Robinson (1986) for juvenile red drum, *Sciaenops ocellatus*, and Lee, Jeon, and Lee (2002) for juvenile rock fish, *Sebastes schlegelii*. Visceral lipid accumulation of striped surubim was similar to that registered for sunshine bass by Keembiyehetty and Wilson (1998) and speckled surubim by Martino et al. (2002a) and Martino et al. (2005). As expected, dietary energy and protein levels affected VI of striped surubim, as also reported by Lee and Putnam (1973) for the rainbow trout, *Oncorhynchus mykiss* Martino et al. (2002b) for the small fingerling speckled surubim (2.75 g), and Valente et al. (2011) for the Senegalese sole, *Solea senegalensis*. However, Martino et al. (2005) did not report the effects of dietary carbohydrate and lipid levels on HSI and VSI for large fingerling speckled surubim (5.1 g). Results validate considerations of Lee et al. (2002) who stated that the first sign of dietary nutrient imbalance is altered metabolic indicators, which do not necessarily and immediately hamper fish growth or health.

The lowest estimated value of HSI (1.5%) was similar to that reported by Bicudo, Borghesi, Dairiki, Sado, and Cyrino (2012) for striped surubim (1.4 to 2.6%), but higher than that registered for speckled surubim (0.9%) by Martino et al. (2005). The dietary energy levels did not markedly influence HSI, that is, HSI of fish fed diets containing 15.1 MJ/kg DE was close to that of fish fed 17.2 MJ/kg DE. The range in the HSI response, 1.6–2.4%, detected only in the graphical analysis, may be correlated to the range in the dietary protein levels (320–480 g/kg). The best value estimated for LSI (1.1%) was within the range reported for larger striped surubim (0.6–1.6%) by Bicudo et al. (2012). Considering the influence of visceral fat in the visceral mass, the lowest and, therefore, better estimated VSI was 7.77, which is superior to the values reported for the speckled surubim (5.1 to 5.8%) by Martino et al. (2005) and striped surubim (4.5 to 5.0%) by Bicudo et al. (2012).

Serum triglycerides and total protein are reliable indicators of fish health and performance; that is, serum protein is related with the lysozyme activity, important in animal defense systems (Misra, Das, Mukherjee, & Pattnaik, 2006). Comparable values (5.80–16.65 g/dl) of SP were reported by Bicudo et al. (2012) for juvenile striped surubim. Feeding Senegalese sole high-lipid diets resulted in increased ST levels (Valente et al., 2011). The lowest estimated ST was registered for fish fed the highest levels of DE and DP. However, juvenile striped surubim fed diets containing 15.1 MJ/kg of DE and 320 g/kg of DP also had blood ST levels close to the estimated minimum, a clear demonstration of the importance of careful analysis of the cubic effect of the treatment. To conclude, dietary energy and protein level affected performance, feed efficiency, and metabolism. Estimated dietary requirements for the best performance and best nutrient retention were 15.1 MJ/kg DE and 390 g/kg DP, therefore a 25.9 g/MJ of DP:DE ratio.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

ORCID

Tarcila Souza de Castro Silva https://orcid.org/0000-0003-4591-6736
Ricardo Basso Zanon https://orcid.org/0000-0002-3143-0463
Gerson Barreto Mourão https://orcid.org/0000-0002-0990-4108
José Eurico Possebon Cyrino https://orcid.org/0000-0002-8942-0102

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