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Research Article

Protein requirement for juveniles of *Leiarius marmoratus* (Siluriformes: Pimelodidae), with two dietary energy levels

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ABSTRACT. The yaque catfish, *Leiarius marmoratus*, is a native South American fish with characteristics that make it a promising species for aquaculture; however, its nutritional requirements at any developmental stage remain unknown. To determine the protein requirement for juveniles of *L. marmoratus* and evaluate the protein-sparing effect by increasing dietary energy, a feeding experiment was conducted with five levels of crude protein in the diet (22, 28, 34, 40, and 47%) and two energy levels (3,400 and 3,750 kcal metabolizable energy kg^{-1} diet). A total of 450 yaque fingerlings weighing 0.80 ± 0.1 g were used, randomly distributed in 30 tanks (15 fish $tank^{-1}$), fed to apparent satiation twice daily for 60 days. Zootechnical performance parameters were determined: weight gain (WG), feed conversion ratio (FCR), specific growth rate (SGR), protein efficiency ratio (PER), condition factor (K), and survival (S). Final weight, WG, K, and PER were influenced by protein level ($P < 0.05$), but not by energy level. Significance was detected in the protein-energy dietary interaction. Feed intake, FCR, and SGR were not significantly affected by energy level ($P > 0.05$) but were affected by protein level ($P < 0.05$). The protein-sparing effect was evident when the energy level increased from 3,400 to 3,750 kcal kg^{-1}. The protein requirement for juvenile yaque, determined by a second-order polynomial regression model, is between 38.1 and 42.0% crude protein, depending on the energy level present in the diet.

Keywords: *Leiarius marmoratus*; protein sparing; nutrition; feeding; aquaculture; catfish; tropical fish

INTRODUCTION

Leiarius marmoratus, commonly known as yaque, is a freshwater catfish belonging to the Pimelodidae family, native to South America. This species is widely distributed across the Amazon, Orinoco, and Essequibo river basins, inhabiting diverse aquatic environments throughout these major hydrological systems (Ramírez-Gil & Ajíaco-Martínez 2011). The yaque exhibits omnivorous feeding behavior, with notable adaptations that vary with the specific basin it inhabits, demonstrating remarkable ecological plasticity (Ramírez-Gil & Ajíaco-Martínez 2011). This behavioral flexibility translates into significant aquacultural advantages, as the species readily adapts to captive conditions and efficiently accepts formulated pelleted feeds (Matheus et al. 2021). Beyond its aquaculture potential, *L. marmoratus* holds considerable economic

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importance in both fisheries and commercial aquaculture. The species is highly valued gastronomically for its superior meat quality, characterized by light-colored flesh, mild flavor, and minimal intramuscular bones (Sánchez et al. 2009). Additionally, *L. marmoratus* plays a crucial role in hybrid production programs, serving as an extensively used parental species for the development of commercial fish hybrids (Paulino et al. 2020, Matheus et al. 2021). In the current context, where global aquaculture production reached a record high of 185.4 million tons in 2022, with 89% destined for human consumption (FAO 2024), diversification with native species is a key strategy for regional food security.

Modern aquaculture faces challenges related to protein efficiency and cost optimization. Protein constitutes the most expensive feed component (40-70% of total cost), making its efficient use critical for economic sustainability (Jayant et al. 2018). Determining species-specific protein requirements allows formulation of diets that maximize growth while minimizing costs and environmental nitrogen waste. Additionally, understanding protein-energy interactions enables optimization of feed formulations through the protein-sparing effect, in which adequate energy levels reduce protein catabolism for energy, allowing it to be used for growth (Gutiérrez-Espinosa et al. 2019, Souza de Castro-Silva et al. 2020).

Aquatic foods provide high-quality protein, accounting for 15% of animal protein and 6% of total protein worldwide, as well as essential nutrients such as omega-3 fatty acids, minerals, and vitamins (Boyd et al. 2022, FAO 2024). For species such as *L. marmoratus*, dietary protein not only determines growth performance but also influences the economic and environmental sustainability of cultivation. Determining specific nutritional requirements for native species such as *L. marmoratus* is fundamental to developing sustainable aquaculture in the Neotropical region (Souza de Castro-Silva et al. 2020). Protein requirements in Pimelodidae vary significantly among species (32-55% crude protein - CP), developmental stages, and environmental conditions, making species-specific research important (Teles et al. 2020).

Currently, feeding *L. marmoratus* in confined environments relies on commercial tilapia concentrates, with crude protein levels ranging from 24 to 36% (Mora-Sánchez et al. 2009), without consideration of their specific nutritional requirements. The protein-energy interaction represents another critical aspect in modern aquaculture nutrition. The optimal protein/energy ratio not only determines growth efficiency but also influences body composition, nutritional quality of the final product, and nitrogen excretion into the environment (Gutiérrez-Espinosa et al. 2019, Souza de Castro-Silva et al. 2020). The protein-sparing effect achieved through increased energy represents a strategy to optimize formulations, reduce costs, and minimize environmental impact.

In the context of the 2030 Agenda for Sustainable Development, aquaculture must simultaneously contribute to food security (SDG 2), the efficient use of resources (SDG 12), and the conservation of aquatic ecosystems (SDG 14) (Troell et al. 2023). For native species such as *L. marmoratus*, this implies developing technologies that maximize nutritional efficiency while preserving genetic diversity and promoting local economies.

Therefore, the objective of this study was to determine the protein requirement of juvenile *L. marmoratus* and to evaluate the protein-sparing effect of increasing the dietary energy level, thereby contributing to the development of sustainable technology packages for native species with aquaculture potential.

MATERIALS AND METHODS

All animal handling procedures were performed in accordance with the standards and regulations described by the Committee on Care and Use of Laboratory Animals established by the National Research Council (US) (1996). Authorization was also obtained from the Ethics Committee of the Universidad de los Llanos, and through Resolution Number 0001598 of July 24, 2019, issued by the National Aquaculture and Fisheries Authority (AUNAP, by its Spanish acronym), research permission was granted.

Experimental units

A battery of 30 tanks, each with 21 L capacity, was used, which was supplied with water from a recirculation system composed of two biofilters in series, providing a continuous water flow of 0.1 L min^{-1} to each tank, to remove suspended particles and maintain constant physicochemical water parameters (temperature 27.3 ± 1.0°C, pH 7.1 ± 0.2, hardness 28 ppm, and ammonia concentration <0.02). To verify water quality, weekly monitoring was performed using an oximeter (EcoSense® DO200, YSI, Ohio, USA) and a pH meter (HI 98129, HANNA® instruments, USA) for ammonia, with a spectrophotometer (Hach®, Model DR2700). Water aeration was continuous in the filter system and in the tanks to maintain oxygen levels near saturation (7.0 ppm).

Biological material

Two thousand larvae of *L. marmoratus* were acquired from the fish farm (Villavicencio, Meta, Colombia), originating from the same broodstock pair and obtained by artificial reproduction. The larvae were maintained for a period of 36 days in a circular tank of 500 L capacity, with constant aeration; when they reached the size to begin the trial, 450 juveniles were selected, weighing 0.80 ± 0.09 g, which were fed a semi purified basal diet containing 30% CP and 3,000 kcal kg^{-1} of estimated metabolizable energy (ME kg^{-1}) (following the methodology of Meyer & Fracalossi 2004) for 15 days to adapt them to experimental conditions. Subsequently, they were randomly distributed in groups of 15 fish per tank in the experimental units. They were fed to apparent satiation with the experimental diets twice daily (9:00 and 17:00 h), seven days a week, and daily feed consumption per tank was recorded. At the beginning of the experimental phase and one day before each sampling, the animals were fasted for 24 h for individual weighing.

Experimental diets

Treatments consisted of 10 experimental diets, with different protein levels (22, 28, 34, 40, and 46%) and energy content (3,400 and 3,750 kcal ME kg^{-1} diet). These diets (Table 1) were prepared with the following semipurified ingredients: casein and gelatin as protein sources; dextrin as a carbohydrate source; vegetable and fish oils as lipid sources; Carboxymethylcellulose (CMC) as a binder; microcrystalline cellulose as an inert (non-digestible) component; and vitamin and mineral premixes. The diet preparation process was conducted according to Meyer & Fracalossi (2004).

Laboratory analysis

Moisture was determined using a food drying oven (Memmert) (AOAC Official Method 930.15). Diet samples were frozen, lyophilized (Lyophilizer, alpha 1-2LD plus), and pulverized in a micromill (Scienceware), after which proximate analyses were performed. Protein levels in diets were analyzed by the combustion method (AOAC Official Method 990.03), lipids according to the NTC 4969 method (ICONTEC, 2001), and ash by muffle incineration at 550°C for 6 h (AOAC Official Method 942.05). Energy was determined in a PARR calorimeter bomb (6200EA, USA), and crude fiber content was determined using intermediate filtration (ICONTEC 2002). The nitrogen-free extract value was obtained indirectly by subtracting the values for crude protein, lipids, ash, and fiber from 100%.

Zootechnical parameters

After a 24 h fasting period, all fish were anesthetized by immersion in a solution of tricaine methane sulfonate (MS-222, Sigma-Aldrich, USA) at 25 ppm until loss of equilibrium (approximately 3 min). Fish were then weighed and measured at the end of the experiment. Survival and biological indices were calculated using the following equations (Fracalossi et al. 2013):

$$\text{Survival}(\%) = \frac{\text{final number of fish}}{\text{initial number of fish}} \times 100$$

$$\text{Weight gain (WG; g)} = \text{final weight} - \text{initial weight}$$

$$\text{Feed intake (FI; g fish}^{-1}) = \frac{\text{total feed consumption (g)}}{\text{number of fish per tank}}$$

$$\text{Feed conversion ratio (FCR)} = \frac{\text{feed ingested (g)}}{\text{WG}}$$

$$\text{Specific growth rate (SGR; \% d}^{-1}) = \frac{\text{Ln (final weight)ht} - \text{Ln (initial weight}}{\text{number of days of bioassay}} \times 100$$

$$\text{Protein efficiency ratio (PER \%)} = \frac{\text{WG}}{\text{crude protein consumed per fish (g)}} \times 100$$

The condition factor, somatic indices, and intestinal coefficient were also estimated and calculated according to the following equations:

$$\text{Condition factor (K)} = \frac{\text{weight (g)}}{\text{length}^3\,\text{(cm)}} \times 100$$

$$\text{Hepatosomatic index (HSI)} = \frac{\text{liver weight (g)}}{\text{fish weight (g)}} \times 100$$

$$\text{Viscerosomatic index (VSI)} = \frac{\text{viscera weight (g)}}{\text{fish weight (g)}} \times 100$$

$$\text{Visceral fat index (VFI)} = \frac{\text{visceral fat weight (g)}}{\text{fish weight (g)}} \times 100$$

To determine somatic indices, at the beginning of the experiment, nine fish were taken from the total group, and six fish at the end of the trial from each tank, which were euthanized by overdose of tricaine methane sulfonate (MS-222, 100 ppm) until cessation of opercular movement for at least 10 min.

Experimental design and statistical analysis

The experimental design was a 2×5 factorial model with two energy levels and five protein levels in the diet (10 treatments). All data obtained were subjected to

Table 1. Composition of experimental diets (% dry matter). [a]Metabolizable energy, calculated from standard physiological values, where 1 g of protein and carbohydrates provides 4 kcal each and lipids 9 kcal (Lee & Putnam 1973). [b]Crude protein/metabolizable energy. [c]CMC, Carboxymethylcellulose. [d]Rovimix Tilapias® DSM Nutritional Products Colombia S.A: Vit A 750 KIU, Vit D_3 375 KIU, Vit E 10,833 mg, Vit K_3 1.666 mg, Vit B_1 1,833 mg, Vit B_2 2.916 mg, Vit B_6 1,833 mg, Vit B_{12} 3 mg, Vit C 41,666 mg, niacin 7,500 mg, pantothenic acid 8,333 mg, folic acid 833 mg, biotin 166 mg, copper 2,500 mg, iron 28,333 mg, manganese 2,500 mg, iodine 0.167 mg, zinc 21,666 mg, selenium 66.7 mg, magnesium 91,666 mg, inositol F.G. 58,333 mg, luctanox E 25 g. Stay-C, DSM Nutritional Products Colombia S.A. [e]Composition per 100 g of mixture: $Ca(H_2PO_4)$ 13.6 g; Ca lactate 34.85 g; $2MgSO_4\ 7H_2O$, 13.2 g; KH_2PO_4 24 g; NaCl 4.5 g; $AlCl_3$ 0.015 g, CMC 9.835 g. [f]Nitrogen-free extract: 100% - (crude protein% + fat% + ash% + fiber%) (Meyer & Fracalossi 2004). [g]Calculated value discounting the energy provided by cellulose (4,119 kcal kg^{-1}).

ME (kcal kg^{-1})[a]	Diets									
	3400 kcal kg^{-1}					3750 kcal kg^{-1}				
Protein (%)	22	28	34	40	46	22	28	34	40	46
P/E ratio (mg kcal^{-1})[b]	67	83	98	114	132	60	74	91	105	126
Ingredients										
Casein	19.9	25.8	31.8	37.7	43.7	19.9	25.8	31.8	37.7	43.7
Gelatin	3.7	4.8	5.9	7.0	8.1	3.7	4.8	5.9	7.0	8.1
Dextrin	37.0	31.0	25.6	20.0	15.0	47.0	41.0	35.6	30.0	24.0
CMC[c]	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
Cellulose	21.7	21.7	20.6	19.7	18.4	10.7	10.3	9.2	8.3	7.8
Corn oil	3.5	3.0	2.7	2.4	2.0	4.0	3.7	3.4	3.1	2.8
Fish oil	3.5	3.0	2.7	2.4	2.0	4.0	3.7	3.4	3.1	2.8
Premix[d]	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0
Macrominerals[e]	5.7	5.7	5.7	5.7	5.7	5.7	5.7	5.7	5.7	5.7
Proximate composition										
Dry matter (%)	94.1	92.7	90.3	90.1	92.3	94.8	93.3	96.6	95.9	96.9
Crude protein (%)	22.7	28.2	34.0	39.2	47.0	22.8	28.0	34.5	39.3	47.0
Crude fat (%)	7.0	5.1	5.0	4.6	3.7	7.1	6.7	5.2	5.4	4.3
Crude fiber (%)	18.4	15.4	13.7	13.7	9.2	7.8	7.1	5.5	6.3	6.1
Ash (%)	5.9	5.8	5.7	5.9	6.1	6.2	6.4	6.1	6.5	5.8
NFE [f]	46.0	45.5	41.6	36.6	34.0	56.1	51.8	48.7	42.5	36.8
Gross energy crude (kcal kg^{-1})[g]	3416	3473	3592	3703	3826	3905	4000	4115	4232	4332
ME (kcal kg^{-1})[a]	3378	3407	3474	3446	3573	3795	3795	3796	3758	3739

homoscedasticity tests using Levene's test and normality using the Shapiro-Wilk test, followed by an analysis of variance (ANOVA). Where significance was detected, multiple comparisons were applied using Tukey's test ($P < 0.05$). The model $Y = \mu + P_i + ME_j + (P\times ME)_{ij} + e_{ij}$ was used, in which Y represents the observed value; µ is the general mean of the characteristic; P*i* is the effect of protein where *i* = 22, 28, 34, 40, and 46%; ME corresponds to the effect of metabolizable energy level where *j* = 3,400 and 3,750 kcal kg^{-1}, $(P\times ME)_{ij}$ deviation due to the interaction between P and ME; e_i the error. Additionally, protein requirement was estimated by the second-order polynomial regression method following the methodology proposed by Zeitoun et al. (1976) using weight gain, in the model $Y = B0 + B1t + B2t^2 + e$, where Y represents the response, B0 the intercept, B1 and B2 regression coefficients, t treatment, and e the error. A significance level of 5% was adopted in all tests. Statistical analyses were performed using IBM SPSS (Statistical Package for the Social Sciences) Version 21 for Windows.

RESULTS

Water quality parameters during the experiment were maintained within acceptable ranges reported for the species (Lundberg & Littman 2003), and no phatological signs of parasites or disease were observed, as reflected in the survival rates.

Performance results are presented in Table 2. None of the treatments affected survival ($P > 0.05$). Final weight was significantly influenced by protein level ($P < 0.05$) but not by energy level, ranging from 9.99 ± 1.16 g (22% CP, 3,400 kcal kg^{-1}) to 19.85 ± 1.55 g (40% CP, 3,400 kcal kg^{-1}). However, a significant interaction between protein and dietary energy was detected ($P = 0.030$). WG, K, and PER followed the same trend as final weight. Performance results indicated that there was an effect ($P < 0.05$) on maximum fish growth when fed with 40 and 34% CP with 3,400 and 3,750 kcal kg^{-1}, respectively. At 3,400 kcal kg^{-1}, WG ranged from 9.19 ± 1.20 g (22% CP) to 18.95 ± 1.56 g (40% CP), while at 3,750 kcal kg^{-1}, it varied from 10.97 ± 1.55 g (22% CP) to 18.36 ± 0.56 g (34% CP).

FI, FCR, and SGR were not significantly affected by dietary energy level ($P > 0.05$) but were affected by protein level ($P < 0.05$), finding that the lowest feed intake and highest conversion rate were in the group of fish fed 22% CP. Specifically, fish fed 22% CP consumed 14.60 ± 1.19 g fish^{-1}, while those fed 40% CP consumed 19.90 ± 2.93 g fish^{-1}, representing a 36% increase in FI. The best FCR resulted in a protein level of 34% (1.04 ± 0.02 at 3,400 kcal kg^{-1} and 1.07 ± 0.05 at 3,750 kcal kg^{-1}), similar to groups fed diets of 28, 40, and 47% CP, respectively. However, it was significantly lower than the 22% recorded ($P < 0.05$). SGR ranged from 1.85 to 2.30, significantly higher for individuals fed 34% protein than for those fed 22%. The final length was affected by protein level ($P < 0.05$) but not by energy intake, which was lower in individuals fed 22% CP (10.62 ± 0.28 cm) and higher in those fed 40% CP (11.39 ± 0.37 cm), representing a 7.3% difference in body length.

Figure 1 presents the growth curves during the 60 days for each energy level. It was observed that at an energy level of 3,400 kcal kg^{-1}, fish fed 40% CP achieved the highest weight. The growth trajectories showed clear separation by day 20, with fish fed 40% CP reaching nearly double the weight of those fed 22% CP by the end of the trial. Regarding the energy level of 3,750 kcal kg^{-1}, the greatest weight gain was achieved with 34% CP. It was found that the growth of yaque at this evaluated stage can be explained by linear functions for each protein level.

The relationship between fish growth and dietary protein level was described by a second-order polynomial regression (Fig. 2), with Y = WG and X = % CP. Therefore, the optimal protein level for maximum WG was determined by deriving the function $WG = \beta 0 + \beta 1X + \beta 2(X)^2$ and setting it equal to zero. Thus, for the energy level of 3,400 kcal kg^{-1}, the equation was $Y = -0.0238x^2 + 1.9958x - 23.13$; therefore: $\delta WG/\delta CP = 1.9958 - (2 \times 0.0238) \times CP = 0$, solving for $CP = 1.9958/0.0476 = 42.0$, and for the energy level of 3,750 kcal kg^{-1}, $Y = -0.0276x^2 + 2.1017x - 23.114$, where Y = WG and X = % CP. Then: $\delta WG/\delta CP = 2.1017 - (2 \times 0.0276) \times CP = 0$, solving for $CP = 2.1017/0.0552 = 38.1$, which indicates a dietary protein requirement of 42.0 and 38.1% CP with 3,400 and 3,750 kcal kg^{-1} of energy content, respectively (Fig. 2). This represents a protein-sparing effect of 3.9 percentage points when dietary energy increased by 350 kcal kg^{-1}, demonstrating that higher energy availability reduces the dietary protein requirement for maximum growth.

Fish that received 47% dietary protein had the highest HSI value (3.44, with $P < 0.05$), while those fed 22% CP showed the lowest HSI value (2.17). The VSI did not vary significantly ($P > 0.05$) among dietary treatments. However, it was numerically higher in fish fed a diet of 47% CP and 3,400 kcal kg^{-1} (6.30 ± 0.45%) than in those fed a 22% CP diet (4.53 ± 0.35), though these differences were not statistically significant due to high within-group variation. VFI was influenced by protein levels ($P < 0.05$), but not by energy. Animals fed 22% CP showed a higher VFI (2.13 ± 0.47), whereas those receiving 40% CP had a lower VFI (0.56 ± 0.35). The ratio of intestine length to total length was unaffected by both protein and energy levels in the diet ($P > 0.05$), as shown in Table 3. This ratio remained consistent across all treatments, ranging from 0.87 ± 0.07 to 1.23 ± 0.07.

K was influenced by protein level ($P < 0.05$) with significant interaction between protein and dietary energy ($P = 0.008$). At 3,400 kcal kg^{-1}, K increased from 0.87 ± 0.09 (22% CP) to 1.44 ± 0.14 (47% CP), while at 3,750 kcal kg^{-1}, fish fed 34% CP exhibited the highest K value (1.50 ± 0.09), significantly exceeding those fed 22% CP (0.97 ± 0.19) or 28% CP (0.96 ± 0.09).

DISCUSSION

To determine nutritional requirements in fish, it is recommended to use experimental diets formulated with semipurified ingredients of well-defined chemical composition, thereby allowing complete control of the effect of the nutrient under evaluation (Fracalossi et al. 2013). Therefore, this research used a diet with a protein content ranging from 22 to 47%. To raise the protein content, the diet included less cellulose and dextrin and more casein and gelatin (see Table 1). The

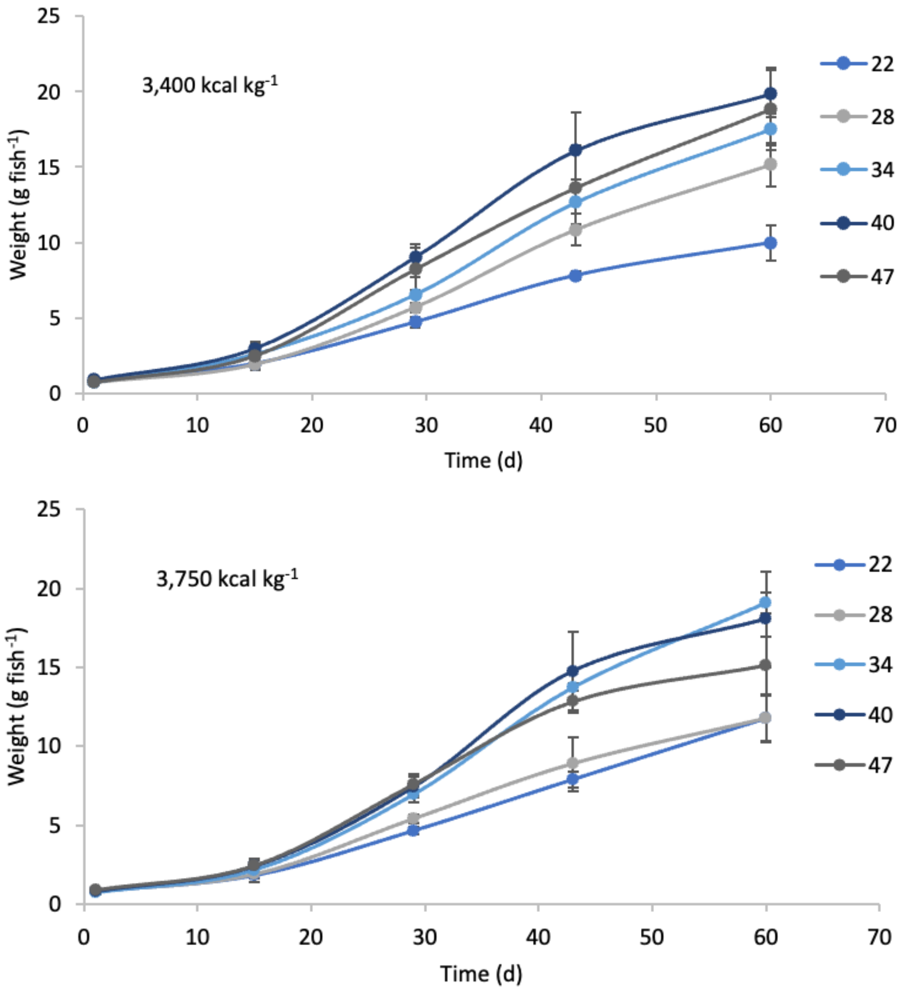

Figure 1. Growth curve of juvenile *Leiarius marmoratus* fed different protein levels and energy levels of 3,400 and 3,750 kcal kg^{-1}.

composition of each diet was corroborated by laboratory bromatological analysis. Various reports on nutritional requirements indicate that study fish, when fed balanced diets with semipurified ingredients, do not reject or reduce consumption (Velasco-Garzón & Gutiérrez-Espinosa 2020), which is corroborated in yaque, as the animals adapted to, accepted, and consumed the feed adequately.

WG and SGR allow evaluation of protein deposition in tissues (Jayant et al. 2018). In this experiment, initial body weight was similar among treatments; however, final body weight and WG of fish fed a diet containing 22% CP and 3,400 kcal kg^{-1} of energy were significantly lower. The more adequate the diet for growth, the less feed is needed to produce a unit of WG (Hepher 1993). When fed at higher protein concentrations (34 and 40%), feed conversion was better (between 1.04 and 1.10); however, there was no effect when the diet's energy level was increased while maintaining the same protein content. It can be inferred that diets with lower protein concentration do not meet the species' requirement, resulting in poor performance and greater visceral fat accumulation (Table 3). A comparable situation was reported by Cornélio et al. (2014) in *Pseudoplatystoma reticulatum*, who found that animals fed a 30% CP diet showed lower performance, and by Jayant et al. (2018) in *Pangasianodon hypophthalmus*, where fish fed a 20% CP diet had the lowest WG. Likewise, excess dietary protein reduces fish growth, that is, performance, probably due to the high cost of extra protein catabolism (Thanh et al. 2018), which was evident in this research, where fish receiving the diet containing 47% CP showed reduced WG, and energy level was also influenced, with weight being significantly lower for fish receiving feed with 47% CP and 3,750 kcal kg^{-1} of energy (Table 2).

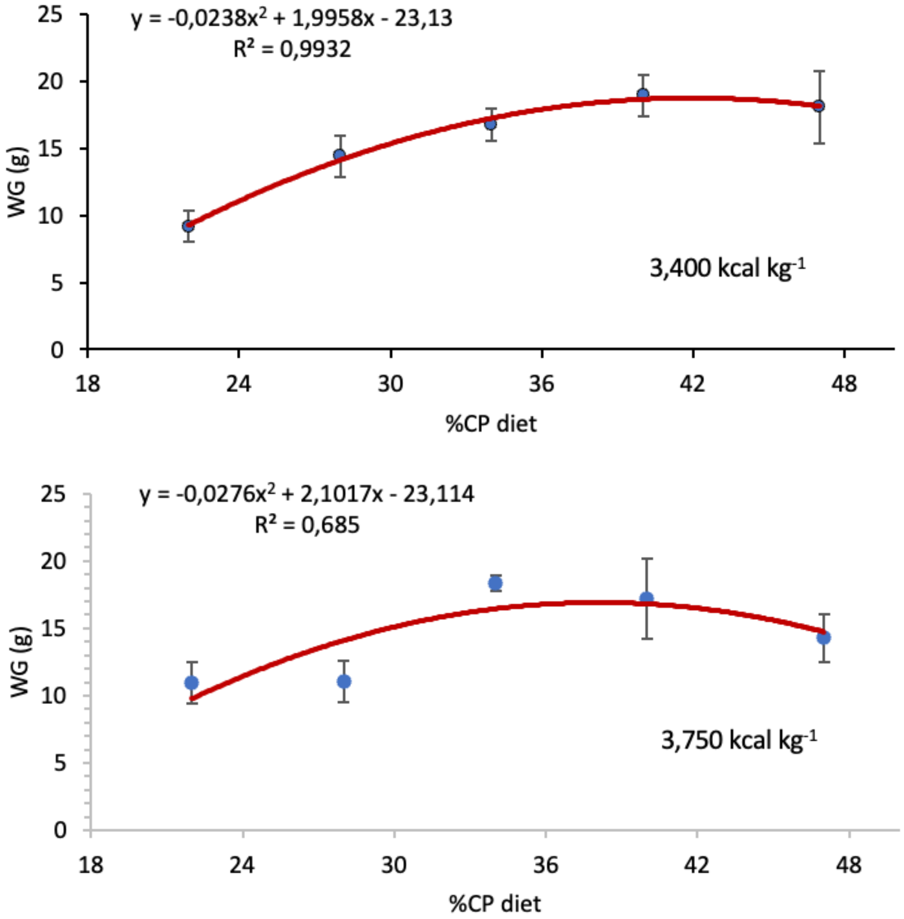

Figure 2. Estimation of protein requirement of juvenile *Leiarius marmoratus* with 3,400 and 3,750 kcal kg^{-1} in the diet.

On the other hand, several authors mention that PER decreases with increasing dietary protein levels (Haidar et al. 2018, Souza de Castro-Silva et al. 2020), which is related to the use of excess protein to provide energy for growth (Salhi et al. 2004). In this study, as dietary protein level increased, PER values increased, but only up to a certain level; when fish were fed a diet of 47% CP, PER decreased significantly, a different result from that reported in *Rhamdia quelen* (Salhi et al. 2004), where PER was not significantly affected by dietary protein level. As an indicator of nutritional status, SGR is a good reference for protein quality (Martínez-Palacios et al. 2007). The maximum SGR observed in *L. marmoratus* in the present work (2.32%) was higher than the rate found by Mora-Sánchez et al. (2009) of 1.80%; this difference can be attributed to experimental conditions, initial fish sizes, and diet composition, since they used a commercial extruded feed not specific to the species. For other Pimelodidae, such as *R. quelen*, various authors have reported SGRs ranging from 1.5 to 5.8%, indicating that higher dietary protein levels negatively affect growth (Meyer & Fracalossi 2004, Salhi et al. 2004). In *P. reticulatum*, the SGR ranged from 2.16 to 3.07% d^{-1} and increased with protein level up to a certain point; at the highest protein level (55%), it began to decrease (Cornélio et al. 2014). A similar behavior was observed in *P. hypophthalmus* (Jayant et al. 2018) and, in the present study, in *L. marmoratus*, corroborating the finding that excess protein leads to decreased growth. This effect has also been noted in *Mystus nemurus*, where growth increased with dietary protein levels between 20 and 40%, while at 47 and 53% CP, growth was reduced (Ng et al. 2001). In a hybrid of *Pseudoplatystoma fasciatum* × *Leiarius marmoratus*, they found SGR ranging from 2.51 to 4.51% d^{-1} when fed diets with different protein/lipid ratios; animals fed the diet with higher protein and lower lipid content showed significantly higher SGR (Campeche et al. 2018). For *Clarias gariepinus*, an SGR in the range of 1.70 and 1.94% d^{-1} is reported

Table 2. Zootechnical parameters of juvenile *L. marmoratus* fed diets containing different protein and energy levels. Mean values of three replicates. Mean values followed by different letters in the same column show a significant difference ($P < 0.05$): A, B, and C compare the energy level of 3,400 kcal kg^{-1} in the diet; a, b, and c compare the energy level of 3,750 kcal kg^{-1} in the diet; x, y compare means with each protein level. K: condition factor, FCR: feed conversion ratio, SGR: specific growth rate, PER: protein efficiency ratio. *Mean values of six replicates, comparing without differentiation of energy content in the diet. Mean values followed by different letters in the same column differ significantly ($P < 0.05$). n.s.: no significant.

Treatment	Final weight (g fish^{-1})	Final length (cm fish^{-1})	K	Total consumption (g fish^{-1})	Weight gain (g fish^{-1})	FCR	SGR	PER
22:3400	9.99 ± 1.16^{Cx}	10.53 ± 0.35	0.87 ± 0.09B^{x}	15.10 ± 0.75	9.19 ± 1.20^{Bx}	1.66 ± 0.15	1.81 ± 0.12	2.84 ± 0.27^{Ax}
28:3400	15.16 ± 1.47^{Bx}	11.10 ± 0.57	1.13 ± 0.23^{ABx}	18.04 ± 0.54	14.42 ± 1.55^{Ax}	1.26 ± 0.12	2.17 ± 0.14	3.05 ± 0.27^{Ax}
34:3400	17.51 ± 1.07^{ABx}	10.88 ± 0.36	1.37 ± 0.13^{Ax}	17.43 ± 1.04	16.77 ± 1.20^{Ax}	1.04 ± 0.02	2.28 ± 0.19	3.13 ± 0.07^{Ax}
40:3400	19.85 ± 1.55^{Ax}	11.53 ± 0.39	1.28 ± 0.04^{Ax}	20.88 ± 1.02	18.95 ± 1.56^{Ax}	1.11 ± 0.11	2.21 ± 0.07	2.58 ± 0.25^{ABx}
47:3400	18.85 ± 2.75^{ABx}	10.93 ± 0.45	1.44 ± 0.14^{Ax}	19.61 ± 1.56	18.08 ± 2.69^{Ax}	1.09 ± 0.08	2.29 ± 0.06	2.12 ± 0.16^{Bx}
22:3750	11.77 ± 1.46^{bx}	10.70 ± 0.24	0.97 ± 0.19^{bx}	14.09 ± 1.48	10.97 ± 1.55^{bx}	1.30 ± 0.24	1.89 ± 0.17	3.63 ± 0.63^{ax}
28:3750	11.74 ± 1.48^{bx}	10.71 ± 0.39	0.96 ± 0.09^{bx}	13.13 ± 2.31	11.08 ± 1.55^{bx}	1.18 ± 0.11	1.93 ± 0.15	3.25 ± 0.29^{abx}
34:3750	19.10 ± 0,67^{ax}	10.83 ± 0.22	1.50 ± 0.09^{ax}	19.64 ± 1.11	18.36 ± 0.56^{ax}	1.07 ± 0.05	2.32 ± 0.09	2.81 ± 0.12^{abcy}
40:3750	18.02 ± 3.03^{ax}	11.25 ± 0.37	1.23 ± 0.08^{abx}	18.93 ± 4.19	17.19 ± 3.02^{ax}	1.10 ± 0.07	2.18 ± 0.10	2.41 ± 0.16^{bcx}
47:3750	15.14 ± 1.82^{aby}	11.41 ± 0.32	1.01 ± 0.10^{by}	17.35 ± 2.28	14.27 ± 1.78^{aby}	1.23 ± 0.26	2.04 ± 0.07	1.85 ± 0.37^{cx}
22*		10.62 ± 0.28^{b}		14.60 ± 1.19^{c}		1.48 ± 0.26^{b}	1.85 ± 0.14^{c}	
28*		10.91 ± 0.49^{ab}		15.59 ± 3.08^{bc}		1.22 ± 0.10^{a}	2.05 ± 0.19^{bc}	
34*		10.86 ± 0.27^{ab}		18.54 ± 1.55^{ab}		1.06 ± 0.35^{a}	2.30 ± 0.14^{a}	
40*		11.39 ± 0.37^{a}		19.90 ± 2.93^{a}		1.10 ± 0.85^{a}	2.19 ± 0.08^{ab}	
47*		11.17 ± 0.44^{ab}		18.48 ± 2.14^{ab}		1.16 ± 0.19^{a}	2.17 ± 0.15^{ab}	
Analysis of variance (P-value)								
Protein	<0.0001	0.020	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Energy	n.s.	n.s	n.s.	n.s	n.s.	n.s.	n.s.	n.s
Protein×Energy	0.030	n.s	0.008	n.s	0.032	n.s.	n.s.	0.024

(Ahmad 2008), and for *Hemibagrus wyckioides* from 1.48 to 2.98% d^{-1} (Deng et al. 2011). According to results obtained in *L. marmoratus*, the species adapted well to the experimental diets and therefore utilized them effectively.

In *L. marmoratus*, the feeding rate in this trial ranged from 3.3 to 4.7% per day, with higher rates for fish receiving the 22% CP diet regardless of energy level. This rate was higher than that reported in the same species by Mora-Sánchez et al. (2009) and in species such as *R. quelen* (Meyer & Fracalossi 2004), *Ictalurus punctatus* (Gaylord & Gatlin III 2001), and in *M. nemurus* (Ng et al. 2001), which was in the order of 2.5% d^{-1}.

K was influenced by protein level ($P < 0.05$), but not by energy level. However, a significant interaction between protein and dietary energy was detected: animals fed a diet containing 3,400 kcal kg^{-1} and 47% protein had significantly higher K than those receiving a diet with 22% CP. At an energy level of 3,750 kcal kg^{-1}, K was significantly higher in fish fed a diet containing 34% CP than in those fed diets containing 22 or 28% CP. K recorded in *L. marmoratus* ranged from 0.87 to 1.50, values similar to those reported in *Pseudoplatystoma fasciatum* fed diets containing between 45.3 and 46.6% CP (Bicudo et al. 2012); and higher than those found in a hybrid of *Pseudoplatystoma reticulatum* × *Leiarius marmoratus* (0.67-0.76) that received diets containing between 36 and 49% CP (Almeida 2015), and in *Pimelodus grosskopfii* (0.57-0.61) (Zapata 2017).

A direct relationship was found between protein level and HSI (Table 3), a result that may be a consequence of glycogen deposition in the liver, similar to that reported by Jayant et al. (2018) in *P. hypophthalmus*; in *R. quelen* (Melo et al. 2016), they found that increasing protein level and reducing carbohydrates and lipids in the diet attenuated glycolytic activity and induced hepatic gluconeogenesis, this as a strategy to provide metabolic energy from amino acids. VSI of *L. marmoratus* were not significantly affected by dietary treatments, similar to results in species such as *P. hypophthalmus* (Jayant et al. 2018) and a hybrid of *Pseudoplatystoma fasciatum* × *Leiarius marmoratus* (Campeche et al. 2018).

The intestinal coefficient (IC) was not affected by dietary protein or energy levels and ranged from 0.87 to 1.23 (Table 3). However, there is great divergence in what is reported for this species at larger sizes; for example, Acosta-Santos et al. (2011) classifies it as omnivorous with carnivorous tendency, based on specimens from the Amazon basin, while for specimens captured in the Orinoco basin, Ramírez-Gil & Ajiaco-Martínez (2011) report it as strictly omnivorous, also basing their conclusion on the value obtained from the intestinal length/standard length ratio which was 1.6. Considering the enzymatic analysis results from wild *L. marmoratus* adults, Gutiérrez-Espinosa & Zapata (2019) affirm that, at this stage, the species can be identified as more omnivorous than carnivorous, as greater enzymatic activity is observed during the intestinal digestion phase. Matheus et al. (2021) reported that the intestine of *L. marmoratus* is short but has longitudinal folds that increase the contact surface, with more pronounced folds in the anterior region of the intestine, highlighting its role in digestion and absorption, characteristics consistent with the intestinal coefficient found in the present study.

The crude protein requirement in the diet for the growth of juvenile *L. marmoratus* (weight between 0.80 and 20 g) was estimated at 38.1 and 42.0, with energy contents of 3,750 and 3,400 kcal kg^{-1}, respectively, using the polynomial regression model (Zeitoun et al. 1976). These requirements are similar to those reported for other catfish species such as juveniles of *P. hypophthalmus* (37.1%) (Jayant et al. 2018), *R. quelen* (37-37.3%) (Meyer & Fracalossi 2004, Salhi et al. 2004), *P. hypophthalmus* (37.1%), *Clarias batrachus* (40.25%) (Jindal 2011); but lower than *Mystus nemurus* (44%) (Ng et al. 2001), *Clarias macrocephalus* (46.1%) (Thanh et al. 2018), *P. reticulatum* (49.3%) (Cornélio et al. 2014), *Hemibagrus wyckioides* (44.1%) (Deng et al. 2011), and higher than *I. punctatus* (25-36%) (Wilson & Moreau 1996).

The protein requirements determined in the present study (38.1-42.0% CP) for juvenile *L. marmoratus* are supported by the morphoanatomical characteristics of the digestive tract described by Matheus et al. (2021). These authors reported that *L. marmoratus* exhibits digestive tract characteristics typical of carnivorous fish, including a short, distensible esophagus with longitudinal folds, a highly distensible saccular stomach with well-developed gastric glands composed of oxynticopeptic cells, and a short intestine with longitudinal folds. The presence of oxynticopeptic cells with numerous mitochondria in the cardiac and fundic regions of the stomach, along with an apical tubulovesicular system for the secretion of hydrochloric acid and pepsinogen (Matheus et al. 2021), supports the species' capacity to process high-protein diets. Although some authors classify *L. marmoratus* as omnivorous, the anatomical characteristics described by Matheus et al. (2021) align with the high protein

Table 3. Body indices calculated in juvenile *Leiarius marmoratus*. HIS: hepatosomatic index, VSI: viscerosomatic index, VFI: visceral fat index, IC: intestinal coefficient, IL: intestine length, TL: total length. *Mean values of six replicates, comparing without differentiation of energy content in the diet. Mean values followed by different letters in the same column differ significantly ($P < 0.05$). n.s.: no significant.

Treatment	HSI	VSI	VFI	IC IL/TL
22:3400	2.08 ± 0.35	4.53 ± 0.35	1.81 ± 0.31	0.94 ± 0.17
28:3400	2.78 ± 0.37	5.08 ± 0.57	1.47 ± 0.40	1.16 ± 0.43
34:3400	2.61 ± 1.23	5.45 ± 0.36	0.58 ± 0.09	1.14 ± 0.30
40:3400	3.38 ± 1.31	5.85 ± 0.39	0.74 ± 0.45	1.11 ± 0.13
47:3400	3.31 ± 1.63	6.30 ± 0.45	0.27 ± 0.13	1.23 ± 0.07
22:3750	2.26 ± 0.60	4.71 ± 0.36	2.45 ± 0.38	0.92 ± 0.06
28:3750	2.53 ± 0.49	5.03 ± 1.23	1.29 ± 0.10	0.99 ± 0.18
34:3750	2.88 ± 0.25	4.01 ± 2.11	2.25 ± 2.14	0.87 ± 0.07
40:3750	2.81 ± 0.10	4.93 ± 0.25	0.38 ± 0.03	1.19 ± 0.12
47:3750	3.56 ± 0.09	4.88 ± 0.48	0.92 ± 0.34	1.04 ± 0.11
22*	2.17 ± 0.43^{a}		2.13 ± 0.47^{b}	
28*	2.66 ± 0.39^{ab}		1.38 ± 0.28^{ab}	
34*	2.75 ± 0.61^{abc}		1.42 ± 1.64^{ab}	
40*	3.10 ± 0.34^{bc}		0.56 ± 0.35^{a}	
47*	3.44 ± 0.19^{c}		0.59 ± 0.42^{a}	
Analysis of variance (*P*-value)				
Protein	<0.01	n.s	<0.01	n.s
Energy	n.s.	n.s	n.s.	n.s
Protein/Energy	n.s.	n.s	n.s.	n.s

requirements observed in the present study, suggesting that the species maintains morphological adaptations for the efficient utilization of animal protein.

The protein requirements determined in the present study (38.1-42.0% CP) may be related to the digestive enzyme profile and morphoanatomical characteristics of *L. marmoratus*. Previous studies by Gutiérrez-Espinosa & Zapata (2019) demonstrated that adult *L. marmoratus* exhibits greater enzymatic activity during the intestinal digestion phase, suggesting omnivorous tendencies despite its carnivorous morphology. The relatively high protein requirement observed in juveniles could reflect ontogenetic differences in digestive capacity, with younger fish requiring higher protein concentrations to compensate for lower enzymatic efficiency. Future research evaluating the correlations among dietary protein levels, digestive enzyme activities (proteases, lipases, amylases), and apparent digestibility coefficients would provide valuable insights into the metabolic basis of these nutritional requirements. It could help optimize feed formulations for different developmental stages.

In *L. marmoratus,* total feed consumption was not affected by dietary energy content but increased proportionally to the dietary protein level up to 40%; above 47%, it decreased. An increase in FI due to increased dietary protein concentration was also observed by Meyer & Fracalossi (2004) in *R. quelen*. A possible explanation for the lack of reduction in FI with increased dietary energy was that the variation range used in this experiment (350 kcal kg^{-1}) was not sufficient to reduce feed consumption as expressed by Meyer & Fracalossi (2004), coupled with the fact that carbohydrates are less effective than lipids in reducing FI (Jantrarotai et al. 1998).

Based on WG results, the crude protein requirement in the diet for maximum growth of juvenile *L. marmoratus* was estimated at 38.1 and 42.0% with crude protein and energy contents of 3,750 and 3,400 kcal kg^{-1}, respectively, at a temperature of 27.3 ± 1.0°C. The protein-sparing effect was evident when dietary energy level increased from 3,400 to 3,750 kcal kg^{-1}.

Credit author contribution

M.C. Gutiérrez-Espinosa: study conception, experimental design, experiment execution, data collection and analysis, statistical analysis, interpretation of results, original manuscript writing and subsequent revisions; V. Hurtado-Nery: study design, supervision of experimental work, analysis and interpretation of results and critical review of the manuscript; C. Hernández: study design, interpretation of results and critical review of the scientific content of the manuscript. All authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no potential conflict of interest in this manuscript.

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