Ecosist. Recur. Agropec. 13(2): e4981, 2026
https://doi.org/10.19136/era.a13n2.4981

Centropomus undecimalis: Growth performance, hematological responses, and unitary feeding cost with graded soybean meal substitution

Centropomus undecimalis: Desempeño del crecimiento, respuestas hematológicas y costo unitario de alimentación con sustitución graduada de harina de soya

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Scientific article

Received: December 09, 2025
Accepted: July 24, 2026

ABSTRACT. This study evaluated the effects of replacing fishmeal (FM) with soybean meal (SM) in diets for juvenile common snook (*Centropomus undecimalis*) over a 120-day feeding trial. The relevance of this work lies in its contribution to sustainable aquaculture nutrition by partially substituting FM with SM, thereby reducing production costs and dependence on marine-derived inputs without compromising growth performance. Three diets containing 45% crude protein were formulated, in which FM was replaced at 0%, 35%, and 55% with SM. Each diet was administered to three groups of 16 fish, with an initial mean weight of 25.4 g and length of 15.5 cm. Growth parameters, digestive enzyme activity, and hematological variables were assessed. No significant differences were observed among treatments for growth, survival, or hematological parameters. However, the diet containing 55% SM reduced acidic protease activity, while the 35% SM diet significantly decreased feeding costs compared with the 0% and 55% SM diets. In conclusion, replacing 35% of FM with SM may be a promising alternative for juvenile snook culture, as it reduced feeding costs without negatively affecting growth, survival, or hematological parameters under the conditions evaluated.
Keywords: Digestive physiology, erythrocyte morphometry, plant-based feed, sustainable feeding, economic viability.

RESUMEN. Este estudio evaluó los efectos de sustituir harina de pescado (FM) por harina de soya (SM) en dietas para juveniles de robalo común (*Centropomus undecimalis*) durante 120 días. El presente estudio contribuye a la formulación de dietas acuícolas sostenibles, mediante la sustitución parcial de FM por SM, reduciendo costos y dependencia de insumos marinos sin detrimento de la eficiencia productiva. Se formularon tres dietas con 45% de proteína cruda y sustitución parcial de harina de FM por SM en un 0%, 35% y 55%. Cada dieta se administró por triplicado a grupos de 16 peces, con un peso promedio inicial de 25,4 g y una longitud de 15,5 cm. Se evaluaron indicadores de crecimiento, actividad de enzimas digestivas y parámetros hematológicos. Los resultados no mostraron diferencias significativas entre tratamientos para crecimiento, supervivencia y parámetros hematológicos, sin embargo, con la dieta con 55% SM se observó una reducción en la actividad de proteasa ácida, mientras que la dieta con 35% SM se obtuvo un costo significativamente menor del alimento en comparación con las dietas del 0% y 55% SM. En conclusión, reemplazar el 35% de FM por SM puede representar una alternativa prometedora para el cultivo de juveniles de róbalo, ya que reduce los costos de alimentación sin afectar negativamente el crecimiento, la supervivencia ni los parámetros hematológicos bajo las condiciones evaluadas.
Palabras clave: Fisiología digestiva, morfometría de eritrocitos, proteína de origen vegetal, alimentación sostenible, viabilidad económica.

How to cite: Gaitán-Ibarra S, Contreras-Sánchez WM, Blanco-Cervantes G, Cotes-Castro L, Villamizar-Villamizar N (2026) *Centropomus undecimalis*: Growth performance, hematological responses, and unitary feeding cost with graded soybean meal substitution. Ecosistemas y Recursos Agropecuarios 13(2): e4981. DOI: 10.19136/era.a13n2.4981.

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INTRODUCTION

The common snook (*Centropomus undecimalis*) is a highly valued species in Latin America due to its nutritional and gastronomic qualities and its high market value both nationally and internationally. Moreover, it is considered an emerging species for intensive aquaculture in the Americas (Rhody *et al*. 2014). *C. undecimalis* is euryhaline, capable of inhabiting marine, freshwater, and estuarine environments while maintaining stable blood osmolality across habitats. Species of the genus *Centropomus* are carnivorous and exhibit high energy requirements, which pose nutritional and management challenges for aquaculture (Alvarez-González *et al*. 2010). Consequently, research has focused on understanding the digestive and metabolic processes of *C. undecimalis* to develop nutritionally adequate, sustainable, and economically viable feeds that reduce dependence on fishmeal while meeting the species' physiological needs. However, despite its aquaculture potential, evidence is still limited on the physiological suitability of soybean meal as a partial fishmeal substitute in juvenile *C. undecimalis*, particularly across graded inclusion levels relevant for practical feed formulation (Alvarez-González *et al*. 2010).

Proteins are indispensable for fish growth, tissue formation, and maintenance; therefore, their inclusion in formulated diets is essential under culture conditions (Borges *et al*. 2010, Silvão and Nunes 2017). Nevertheless, excessive intake of animal-derived protein generates metabolic waste, such as nitrogenous compounds and uneaten feed residues, which can deteriorate water quality and compromise fish health (Li *et al*. 2012). Because feeds for carnivorous species typically contain high protein levels, they represent one of the major operational costs in aquaculture and exert pressure on wild fish populations used for fishmeal (FM) production. Incorporating plant-based protein sources has thus emerged as a sustainable alternative, reducing both the use of animal protein and nitrogen effluents (Ridwanudin and Sheen 2014, Hussain *et al*. 2024). This approach not only promotes environmental sustainability but also enhances economic efficiency. However, the inclusion of plant proteins can alter fish metabolism and nutrient utilization, making it necessary to evaluate their physiological and metabolic impacts (Hell and Hillebrand 2001, Krogdahl *et al*. 2003). Accordingly, the replacement levels evaluated in this study were selected to represent a control diet, an intermediate inclusion level close to previously reported acceptable substitution ranges, and a higher level intended to test the practical limits of soybean meal incorporation in this species.

Digestive enzyme activity plays a central role in nutrient assimilation and metabolic responses in fish. Arriaga-Hernández *et al*. (2021) evaluated *Centropomus viridis* juveniles fed diets containing different levels of plant protein and reported optimal growth, protein efficiency, and feed conversion ratio (FCR) when 30% of FM was replaced with soybean meal (SM). Their findings also suggested that SM inclusion modulates protease and lipase activity, indicating possible metabolic adaptations to dietary composition. Similarly, the relationship between hematological parameters and growth performance is critical for determining the appropriate replacement levels of FM with SM and for assessing the physiological and health implications of such dietary changes (Santos *et al*. 2009). Arriaga-Hernández *et al.* (2021) reported that fish fed soybean-based diets maintained adequate immune responses, although a slight reduction in T lymphocyte activity was observed compared with fish fed FM-based diets. This reduction may indicate a diminished capacity of T

Ecosist. Recur. Agropec. 13(2): e4981, 2026
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lymphocytes to proliferate and mediate effective immune responses. In this context, Iqbal *et al*. (2022) and Abdo-de-la-Parra *et al*. (2023) demonstrated that hematocrit and hemoglobin concentrations can serve as reliable indicators of overall fish health and metabolic efficiency. Monitoring these parameters provides valuable insights into how dietary modifications influence oxygen transport and immune function both essential for growth and survival. However, hematological responses vary among species and environmental conditions, underscoring that aquaculture nutrition requires species-specific strategies rather than universal approaches.

Abdo-de-la-Parra *et al*. (2023) further emphasized the importance of assessing hematological parameters when testing different dietary protein and lipid levels in juvenile white snook (*C. viridis*). Despite their diagnostic value, these indicators are affected by multiple factors. Misra *et al*. (2006) and Kumar *et al*. (2005) highlighted that water quality, and environmental stress can significantly influence hematological profiles, complicating interpretation. Moreover, other dietary components such as carbohydrates and sesame seed inclusion have also been shown to affect hematological variables and growth performance (Hekmatpour *et al*. 2023, Mello *et al*. 2015). Therefore, while hematological parameters are essential for evaluating health status, they should be interpreted within a holistic framework that considers diet composition, water quality, and overall farm management.

For most marine fish species with aquaculture potential, the effects of replacing FM with SM remain poorly understood. A moderate substitution of fishmeal by soybean meal was expected to be physiologically acceptable for juvenile *C. undecimalis*, whereas higher substitution levels were expected to reduce dietary adequacy. Therefore, this study aimed to evaluate the effects of different levels of SM inclusion as a partial replacement for FM on growth, digestive enzyme activity, and hematological profile in *C. undecimalis* juveniles, thereby contributing to the understanding of the species' nutritional physiology and promoting its sustainable culture under captive conditions.

MATERIALS AND METHODS

Juvenile snook capture

One hundred forty-four juveniles of *C. undecimalis* (25.4 ± 1.93 g and 15.5 ± 0.86 cm of total length) were captured in the Ciénaga Grande de Santa Marta, Colombian Caribbean (10°43' to 11°00' North latitude and 74°16' to 74°38' West longitude). Fish were transported to the experimental farm of the University of Magdalena in Santa Marta at a density of four fish in a 30 L plastic bag, which contained water from the capture site (4 PSU, 28°C, 12 mg·L^{-1}), injected oxygen (24 mg·L^{-1}) and 7 µL·L^{-1} of eugenol as an anesthetic (Chaparro *et al*. 2006, Polonía-Rivera *et al*. 2017a).

Adaptation and maintenance

Once in the laboratory, fish were acclimated and maintained for three days at the same salinity as the capture site (4 PSU) in two 2 000 L tanks (0.72 m in height × 2.2 m in diameter) with filtered water and constant aeration. A modified prophylactic treatment by Bassleer (1997) was applied, consisting of adding an FMC solution (37% formaldehyde and 0.37 g methylene blue, with 0.02 vol/vol of water added to this new solution), mebendazole (0.37 mg/100 mL of water), and

e-ISSN: 2007-901X

Nifurpirinol (0.37 mg/100 mL of water). After this time, salinity gradually decreased at 1 PSU/hour until reaching zero salinity.

The fish started accepting food on the third day with live prey (*Oreochromis* spp. fingerlings) for one week, then gradually switched to Atlantic thread herring (*Opisthonema oglinum*) fresh pieces for 15 days, and finally, a mixture of fresh fish and 45% protein formulated feed at a 1:1 ratio until only balanced feed remained, a process that lasted approximately 20 days. Fish were fed to apparent satiety (5% of total biomass) in two daily feedings (09:00 and 17:00 h).

The water physicochemical parameters were kept within the optimal ranges reported for the cultivation of *Centropomus* spp. (Vidal-López *et al*. 2012) with a temperature of 28.7 ± 2.9 °C, pH of 7.2 ± 0.2, dissolved oxygen of 5.8 ± 0.9 mg·L^{-1}, and conductivity of 750.8 ± 26.3 µmho·cm^{-1}. Nitrite and ammonia were also measured, with values not exceeding 0.00 mg·L^{-1}.

Experimental design

Three diets with different levels of fish meal (FM) replacement by soybean meal (SM) were evaluated: D1 with 0% (control), D2 with 35%, and D3 with 55% SM. All diets contained 45% crude protein. Each treatment was performed in triplicate, and each 1 000 L plastic tank was considered an experimental unit. A total of 144 juvenile snook were randomly distributed among tanks (16 fish per tank; 48 fish per treatment). The experiment was conducted over 120 days. During this period, five biometric samplings were carried out to record production indicators and adjust feed supply. Oxygen, temperature, and pH were measured daily, while conductivity was recorded every 15 days using a multiparameter photometer (HANNA HI83300).

Diet formulation

Different proportions of fish meal, shrimp meal, soybean meal, fish oil, vitamin A, and a mineral premix were used to formulate the experimental diets (Table 1). The formulation was based on previous studies conducted by Álvarez-Lajonchère and Hernández-Molejón (2001) and Metochis *et al*. (2016). The ingredients used to prepare the experimental diets were ground using an electric mill (Javar M32Z), then sifted and homogenized with an industrial mixer (Javar 2500A). Pellets were produced using a 5 mm rotary die pelletizer and dried in an oven at 45 °C for 2 h (Gaitán-Ibarra *et al.* 2024). Proximate analysis of the formulated diets was performed using a Near InfraRed Spectrograph (NIRS™, DA1650), confirming that the obtained values were consistent with the theoretical formulation of each experimental diet (Table 2).

Table 1. Formulation of experimental diets prepared with different levels of soybean meal (SM) as a substitute for fish meal.

Ingredients	SM replacement diet		
	D1 (0%)	D2 (35%)	D3 (55%)
Fish meal	44.878	31.295	22.606
Soybean meal	20.399	38.736	50.465
Shrimp meal	16.319	17.507	18.267
Cornmeal	15.335	10.384	7.217
Fish oil	0.767	0.520	0.361
Premixes	0.767	0.520	0.361
Carboxymethyl cellulose	1.534	1.039	0.722

Table 2. Proximate analysis and gross energy (dry matter basis) of experimental diets.

Diet	Protein	Humidity	Fat	Ash	Ross energy (kcal/100 g feed)	Energy to protein ratio
D1 (0% of SM)	45.96	12.85	5.59	13.38	370.69	7.03
D2 (35% of SM)	45.78	13.23	5.29	13.59	367.85	6.97
D3 (55% of SM)	45.94	14.11	5.60	15.15	362.08	6.77

Zootechnical Indicators

Growth performance, feed utilization, and body indexes. Weight and length of each fish were measured every 20 days to evaluate growth performance and adjust feeding rates accordingly. For this, fish were anaesthetized using eugenol at a rate of 7 $\mu L \cdot L^{-1}$ (Polonía-Rivera *et al*. 2017a). To determine the effect of FM replacements on growth and feed efficiency, production indicators were estimated, described by Abasubong *et al*. (2021) and De-Verdal *et al*. (2018) as follows:

Weight gain (WG): $WG = \frac{Final\ body\ weight\ (W_i) - Initial\ weight\ (W_i)}{Initial\ weight\ (W_i)} * 100$

Daily Growth Rate in terms of total length (DGRTL): $DGR_{TL} = \frac{Final\ total\ length - Initial\ total\ length}{number\ of\ rearing\ days}$

Weight gain or Absolute Growth Rate (AGR): $AGR = \frac{W_f - W_i}{t\ (days)}$

Relative Growth Rate (RGR): $RGR = \frac{W_f - W_i}{t(days)} * 100$

Specific Growth Rate (SGR): $SGR = \frac{\log W_f - \log W_i}{t(days)} * 100$

Protein Efficiency Rate (PER): $PER = \frac{W_f - W_i}{protein\ supplied}$

Food Efficiency Index (FER): $FER = \frac{W_f - W_i}{dry\ food\ consumed}$

Feed Conversion Ratio (FCR): $FCR = \frac{Food\ supplied}{W_f - W_i}$

Condition Factor (K): $K = 100\ \frac{W}{TL^3}$

Survival (S): $S = \frac{Final\ number\ of\ fish}{Initial\ number\ of\ fish}\ 100$

Enzymatic activity

Sample collection. At the end of the diet evaluation process, 18 specimens of *C. undecimalis* (6 fish per treatment) were sacrificed by immersion in cold water. The fish had an average weight of 40 ± 0.6 g and total length of 17.6 ± 0.3 cm (mean ± SD). Subsequently, the complete digestive tract of each individual was extracted, weighed, and placed in distilled water at 4°C; then, they were stored in saline solution at -80°C until processing (Arriaga-Hernández *et al*. 2021).

Preparation of Crude Enzyme extracts (CE). The digestive tracts were macerated in Tris HCl buffer, pH 7.5 at a ratio of 1:5 (weight: volume) and centrifuged at 12 000 xg for 10 min (4°C). The supernatant was used as the enzyme source (crude extract). The activity of acid proteases was determined according to Anson (1938) and modified by Walter (1984). Depending on the treatment, 0.1 mL of CE, 0.5 mL of pH 2 glycine buffer, and 0.5 mL of 1% haemoglobin were taken as substrate. The mixture was incubated at 37°C for 1 hour, and then 0.5 mL of cold 20% Trichloroacetic acid

(TCA) was added and kept at 4°C for 30 minutes to stop the reaction. Finally, samples were centrifuged at 10.000 xg for 10 min, and absorbance was measured at 280 nm in a spectrophotometer at 700 nm (Genesys 10 S UV VIS). The activity for essential proteases was determined according to the method of Kunitz (1946), with similar procedures as for acid proteases. A blank under similar conditions was prepared by adding TCA before starting incubation; all measurements were performed in triplicate. The total protein concentration was determined by the Lowry method (1951) using bovine serum albumin (BSA) as a standard (1mg·mL-1). Enzyme activity was calculated as U (U·mL^{-1}) as follows:

$$U\,mL-1 \;=\; Abs * Vf\,(mL)/(CE * VEC\,(mL) * t\,(min))$$

Where Abs: absorbance at 280 nm; Vf: total reaction volume; CE: extinction coefficient 0.005; VEC: volume of crude extract; t: time and mg of protein are the mg of soluble protein. Specific activity was calculated as follows: U (Unit * mg·prot-1) = (Total Activity)·(mg of soluble protein). Enzymatic activity was expressed as the amount of enzyme required to produce 1 micromole of tyrosine per minute at 37°C.

Haematological parameters

Before the enzymatic analysis, blood samples were collected from fish sedated with eugenol; Then, 1 mL of blood was drawn from the caudal vascular bundle using a heparinized syringe (0.6 × 25 mm gauge), transferred into Microtainer® tubes, and refrigerated. Haematocrit (Ht %), haemoglobin (Hb g/dL) and red blood cell count (RBC #cell·106/mL) were determined. Secondary parameters such as mean corpuscular volume (MCV fl), mean corpuscular haemoglobin (MCH pg) and mean corpuscular haemoglobin concentration (MCHC %) were determined according to Saravanan *et al*. (2011) and Atencio-García *et al.* (2007).

Erythrocyte morphometry. Blood samples were taken from the same Microtainer tube and were spread onto slides. The spreads were air dried, fixed with methanol for 30 minutes, stained with Giemsa for 15 minutes and rinsed with distilled water. For the morphometric evaluation of erythrocyte parameters, images were captured using the same optical equipment at a magnification of 100X (Leica DM500, Leica ICC50W). Erythrocytes isolated with well defined borders were selected in each image and processed using ImageJ software (Schneider *et al*. 2012). Forty cells of each sample were measured for four parameters: erythrocyte length (EL), erythrocyte width (EW), nucleus length (NL), and nucleus width (NW). From these, secondary data were derived: erythrocyte size (ES = (EL/2) x (EW/2) x π), nucleus size (NS = (NL/2) x (NW/2) x π), form factor or circularity index (CI = EL/EW), relation nucleus size/erythrocyte size (NS/ES), relation nucleus size/cytoplasm size (NS/CS) and deformation index (DI = (EL-EW)/(EL+EW)) (Najiah *et al*. 2008).

Cost benefit analysis

A comparative economic analysis between the control diet versus the experimental diets was performed by calculating the unitary feeding cost (UFC), according to Iqbal *et al*. (2022) and Nunes *et al*. (2023). The economic evaluation and the costs associated with snook farming developed by Polonía *et al*. (2017b) were also considered. Market prices of each ingredient first calculated the cost of formulation of each diet, and the UFC was calculated using the following equation:

$$UFC \;=\; Feed\ cost\ (per\ kilogram)\ x\ FCR$$

Statistical analysis

Regarding performance indicators, the normality (Shapiro Wilk) and homoscedasticity (Levene) tests were applied to all data sets obtained. In cases where assumptions were met, a repeated measures analysis of variance with a between subject factor was used, meaning a three level condition (replacement of FM by SM: 0, 35, and 55%). Additionally, the assumption of sphericity was examined, and variations in the differences of all possible pairs of intragroup conditions were found to be equal (Mauchly's sphericity test >0.05). If this assumption was not met, the Greenhouse Geisser correction (>0.75) was used; otherwise, the Huynh Feldt correction was applied. Between subject differences were assessed using the Tukey test, while post hoc comparisons for repeated measures were conducted using the Bonferroni test. The comparison of marginal means was conducted to determine the performance of the variables during the five biometrics carried out during the trial. When normality and homoscedasticity assumptions were not met, the non parametric Friedman test was utilized, and within group differences were established using the Wilcoxon signed rank test. On the other hand, for haematological aspects, all data were analysed using the non parametric Kruskal Wallis test, as they did not meet the assumptions of residual normality (Shapiro Wilk $p < 0.05$) and variance homogeneity (Levene $p < 0.05$). Likewise, median comparisons were made using the Mann Whitney U test.

RESULTS

Performance in growth variables

At the end of the experiment, 100% survival rate was recorded in all treatments. Although the performance indicators WG, AGR, RGR, SGR, PER, FER, and FCR met the assumptions of normality and homoscedasticity, no statistically significant differences were observed between treatments ($p > 0.05$), due to variability in the data rather than the absence of treatment effects. No significant differences were found in size increment or condition factor (K) among treatments (Table 3).

Temporal variation in growth related indicators across the five biometric samplings is shown in Figure 1. Regarding Daily Growth Rate (DGR) in terms of total length (0.035 ± 0.005 cm·day^{-1}) and Condition Factor (K) (0.684 ± 0.017), although no differences were observed between treatments in both size increment and condition factor, significant differences were evident among samplings with p values of 0.007 and 0.003, respectively. To establish differences between each pair of samplings, the Wilcoxon test indicated differences between the first biometric measurement and the others.

Enzymatic activity

Acidic protease activity was highest in the 0 and 35% SM groups (106.8 ± 3.8 and 112.1 ± 6.5 U·mL^{-1}, respectively) and lower in the 55% SM treatment (86.8 ± 5.1 U·mL^{-1}) ($p = 0.00019$). Regarding basic protease, a slight increase was observed in the 55% SM group (21.2 ± 4.2 U·mL^{-1}), although this difference concerning the other treatments was not statistically significant ($p = 0.682$; Figure 2).

Table 3. Zootechnical performance variables for common snook (*Centropomus undecimalis*) during experimental trial with diets at 0, 35 and 55% replacement of fish meal with soybean meal. Data is expressed as mean ± SD.

Variables	Unit	Replacement percentage		
		0%	35%	55%
DGRTL	cm/day	0.035 ± 0.002	0.035 ± 0.005	0.032 ± 0.003
WG	%	12.242 ± 0.394	11.400 ± 1.999	11.196 ± 2.328
AGR	g/day	0.206 ± 0.027	0.173 ± 0.022	0.208 ± 0.074
RGR	%	20.666 ± 2.736	17.333 ± 2.187	20.767 ± 7.476
SGR	%	0.609 ± 0.017	0.534 ± 0.085	0.532 ± 0.152
PER	-	0.432 ± 0.034	0.591 ± 0.095	0.409 ± 0.097
FER	-	0.246 ± 0.019	0.336 ± 0.054	0.228 ± 0.054
FCR	-	10.919 ± 0.760	6.438 ± 0.439	6.561 ± 1.816
K	-	0.695 ± 0.020	0.663 ± 0.024	0.693 ± 0.021
Survival	%	100	100	100

DGRTL: Daily Growth Rate in Total Length; WG: Weight Gain; AGR: Absolute Growth Rate; RGR: Relative Growth Rate; SGR: Specific Growth Rate; PER: Protein Efficiency Ratio; FER: Feed Efficiency Ratio; FCR: Feed Conversion Ratio; K: Condition Factor. Values are presented as mean ± standard deviation (SD).

Hematological parameters

No significant differences were detected among treatments for the evaluated hematological parameters (Kruskal–Wallis, $p > 0.05$). Descriptively, hematocrit, hemoglobin, and red blood cell count tended to show higher mean values in fish fed the 35% SM diet, whereas mean corpuscular hemoglobin (MCH) and mean corpuscular hemoglobin concentration (MCHC) showed higher mean values in the 0% SM treatment. In contrast, the lowest mean values for most parameters were observed in fish fed the 55% SM diet (Table 4).

Hemoglobin showed higher mean values in the 35% SM replacement (15.30 $g \cdot Dl^{-1}$), whereas the lowest mean value was observed in the 55% SM treatment (11.72 $g \cdot dL^{-1}$). The red blood cell count (RBC) varied from 1.82 to 2.34, with a mean of 2.15 x 106 $cells \cdot mL^{-1}$; the most significant increase was seen with 35% SM replacement, and the lowest corresponded to 0% replacement. Mean corpuscular volume (MCV) fluctuated from 213.93 fl to a minimum of 117.11 fl in the 0% SM replacement, with a mean of 196.22 fl in the 35% SM diet. MCH ranged from a maximum of 77.6 pg to a minimum of 42.8 pg, with a mean of 36.54 pg in the 0% SM replacement, whereas MCHC ranged from a maximum of 36.54% to a minimum of 36.28%, with a mean of 36.43% in the 0% SM replacement.

Erythrocyte morphometry

Erythrocytes of *C. undecimalis* showed an oval morphology, with erythrocyte length ranging from 7.87 to 9.79 μm and erythrocyte width ranging from 4.51 to 6.29 μm. Significant differences among treatments were detected for erythrocyte length (EL), nucleus length (NL), nucleus size (NS), circularity index (CI), nucleus-to-cytoplasm ratio (NS/CS), and deformation index (DI), whereas the remaining morphometric variables did not differ significantly (Table 5).

Ecosist. Recur. Agropec. 13(2): e4981, 2026
https://doi.org/10.19136/era.a13n2.4981

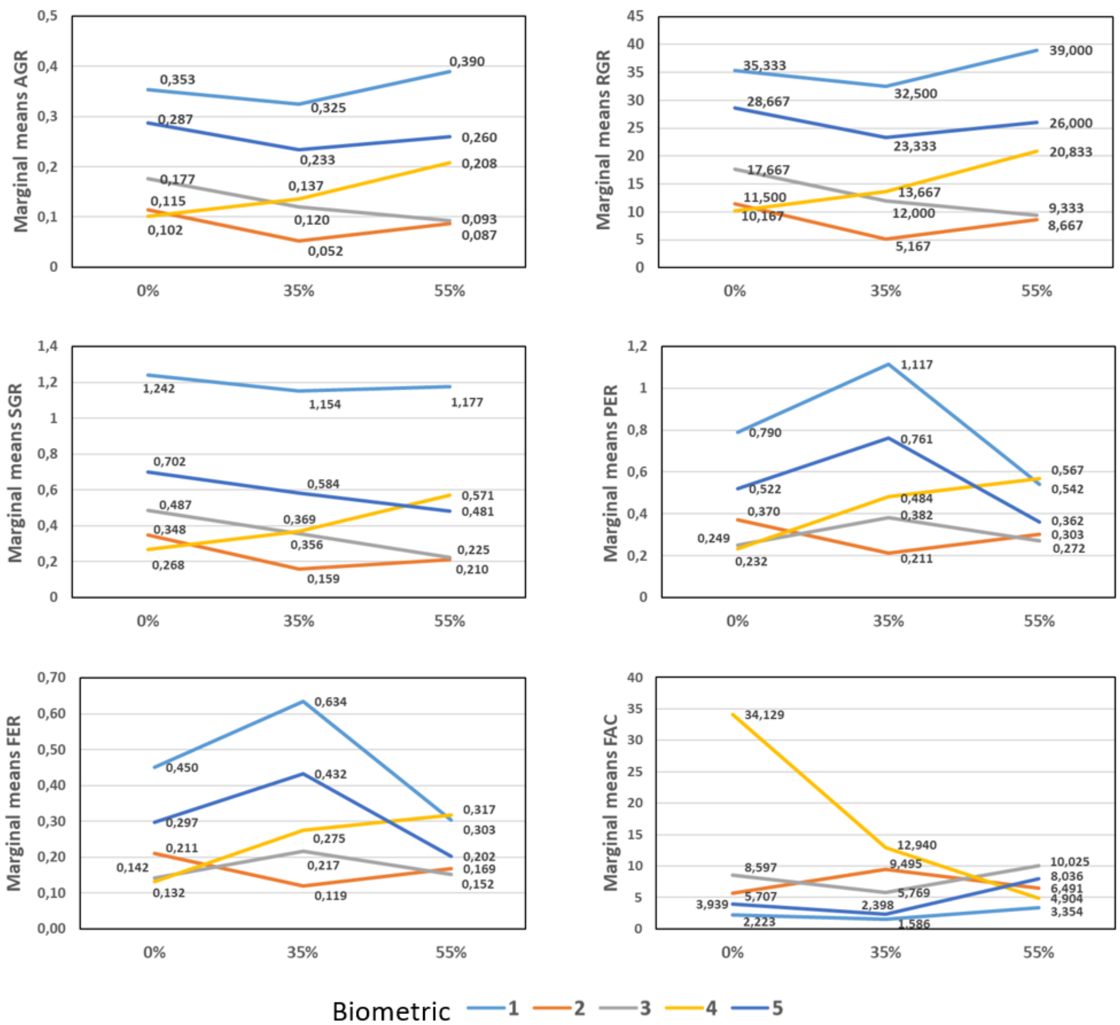

Figure 1. Marginal means of the performance variables obtained during the five samplings throughout the experiment.

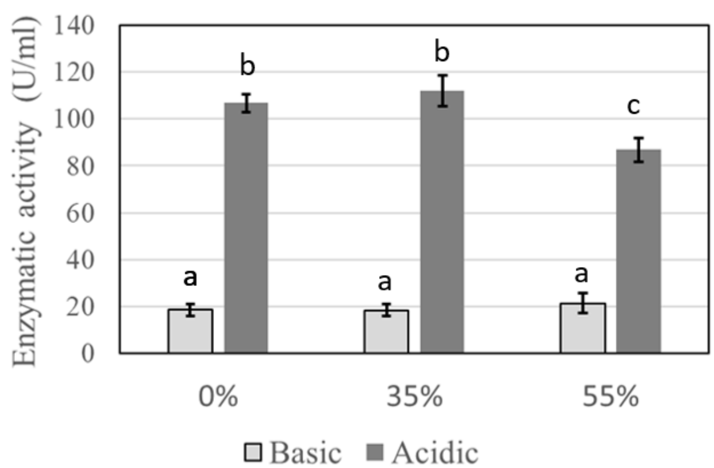

Figure 2. Enzymatic activity values observed in *Centropomus undecimalis* juveniles for acidic and basic proteases in diets with 0%, 35% and 55% SM replacement. The letters indicate statistical differences.

e-ISSN: 2007-901X

Table 4. Hematological parameters in *Centropomus undecimalis* with diets replacing fishmeal with soybean meal at 0, 35, and 55%. Ht: Hematocrit, Hb: Hemoglobin, RBC: Red blood cell count, MVC: Mean corpuscular volume, MCH: Mean corpuscular hemoglobin, MCHC: Mean corpuscular hemoglobin concentration.

Replacement percentage	Descriptive statistics	Ht (%)	Hb ($g \cdot dl^{-1}$)	RBC ($x106cel \cdot ml^{-1}$)	MCV (fl)	MCH (pg)	MCHC (%)
0	Min	26.00	9.50	1.82	117.11	42.8	36.28
	Max	43.00	15.60	2.22	213.93	77.6	36.54
	Mean	35.00	12.73	1.97	178.35	36.54	31.65
	SD	6.84	2.46	0.13	38.61	13.94	0.11
35	Min	40.00	14.60	1.980	170.94	62.4	36.36
	Max	44.00	16.00	2.340	212.12	77.3	36.50
	Mean	42.00	15.30	2.153	196.22	36.51	28.93
	SD	2.00	0.70	0.180	22.13	7.97	0.07
55	Min	25.00	9.10	2.020	121.36	44.2	36.36
	Max	39.00	14.20	2.310	179.72	64.4	36.47
	Mean	32.20	11.72	2.140	150.19	36.41	28.21
	SD	5.87	2.14	0.130	23.93	8.68	0.04

Table 5. Morphometric parameters of erythrocytes (mean ± SD) in *Centropomus undecimalis* fed diets replacing fishmeal with soybean meal at 0, 35, and 55%. Letters indicate statistical difference.

Morphometric parameters	Unit	Replacement percentage		
		0%	35%	55%
Erythrocyte length (EL)	(µm)	9.13 ± 0.24^{a}	8.44 ± 0.33^{b}	9.1 ± 0.72^{a}
Erythrocyte width (EW)	(µm)	5.14 ± 0.20	5.54 ± 0.49	5.47 ± 0.64
Nucleus length (NL)	(µm)	3.3 ± 0.10^{a}	2.91 ± 0.23^{b}	2.94 ± 0.29^{b}
Nucleus width (NW)	(µm)	2.17 ± 0.07	2.06 ± 0.10	2.16 ± 0.22
Erythrocyte size (ES)	(µm2)	36.83 ± 2.30	36.67 ± 3.47	39.37 ± 7.43
Nucleus size (NS)	(µm2)	5.63 ± 0.27^{a}	4.71 ± 0.56^{b}	5.04 ± 0.98^{a}
Cytoplasm size (CS)	(µm2)	31.2 ± 2.26	31.96 ± 3.44	34.32 ± 6.55
Circularity index (CI)	-	1.8 ± 0.04^{a}	1.55 ± 0.17^{b}	1.69 ± 0.09^{b}
Nucleus-cytoplasm ratio (NS/CS)	-	0.18 ± 0.01^{a}	0.15 ± 0.02^{b}	0.15 ± 0.01^{b}
Deformation index (DI)	-	0.15 ± 0.01^{a}	0.21 ± 0.05^{b}	0.25 ± 0.02^{c}

When treatments were compared, significant differences ($p < 0.05$) in EL, NL, and NS/CS were consistently observed between the control group (0% replacement) and the two soybean meal diets (35% and 55% SM). Differences in NS were detected only between the control and the 35% SM treatment ($p < 0.0001$), while DI differed among all treatments. The remaining variables did not show significant differences (Table 5).

UFC comparative analysis

The replacement of FM with SM reduced diet cost as the replacement percentage increased. The unitary feeding cost (UFC) differed significantly between the control diet and the 35% and 55% SM diets ($p < 0.05$). Among the evaluated diets, the 35% SM treatment showed the lowest UFC value.

Because only three replacement levels were evaluated, the polynomial trend should be interpreted cautiously and considered only as an exploratory reference: Y = 0.0323X2 - 2.7302X + 143.86; R2 = 0.989; p value = 0.000 (Figure 3).

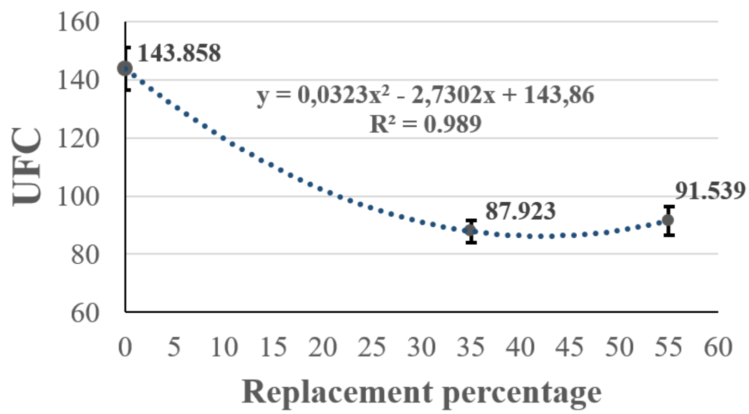

Figure 3. A second order polynomial function that graphs the unit feeding cost (UFC) and the different replacement percentages of FM by SM, used for feeding juvenile snook (*Centropomus undecimalis*) for 120 days. Points indicate the meaning of three replicates ± the standard error of the mean (SEM).

DISCUSSION

The results of the present study indicate that replacing fish meal with 35% or 55% soybean meal did not significantly affect growth performance or survival in juvenile *C. undecimalis*. Although no statistical differences were observed among treatments, the 35% SM diet showed numerically lower FCR and higher PER and FER values. These results are consistent with those reported by Arriaga-Hernández *et al.* (2021) for *C. viridis*, in which a 30% replacement of fish meal by soybean meal supported acceptable productive performance. Likewise, Arenas *et al.* (2022) reported no significant growth differences in *C. undecimalis* fed diets with high digestible carbohydrate levels. However, the weight gain recorded in the present study was lower than that reported by Silvão and Nunes (2017) for the same species, suggesting that factors other than protein substitution level may also have influenced productive performance under the conditions evaluated.

The relatively high FCR values observed in this study may be partly explained by the elevated maintenance costs of this euryhaline species under culture conditions, particularly those associated with osmoregulatory adjustment. In juvenile *C. undecimalis*, salinity has been shown to alter energy partitioning, as fish reared at 0, 25, and 35 ppt invest more energy in feed processing than those maintained at 12 ppt, indicating that part of the dietary energy may be diverted from growth to homeostatic regulation (Gracia-López *et al.* 2006). Recent evidence also shows that salinity modulates growth and osmoregulatory function in juvenile common snook, which may help explain the modest weight gain and low feed conversion efficiency recorded across treatments (De-Mello *et al*. 2024).

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Although no significant differences were detected in growth performance, previous studies in carnivorous fish suggest that higher soybean meal inclusion levels may affect nutrient utilization and digestive physiology, potentially due to imbalances in essential amino acids and the presence of antinutritional factors in soybean meal, such as protease inhibitors, oligosaccharides, phytoestrogens, phytates, saponins, and lectins (Krogdahl *et al*. 2003, Hernández *et al.* 2007, Rahmah *et al*. 2016, Krishnan and Jez 2018, Murashita *et al*. 2018).

Other soy products, such as fermented soy PepSoy (52% crude protein) in *C. undecimalis*, have resulted in weight gain and SGR that surpassed those feds with soybean meal. However, the 5% FM level differences were not statistically significant for any parameter (Rombenso *et al*. 2013). The favorable results of PepSoy are likely due to the fermentation, extrusion, purification, and defatting of soybeans, which allow better assimilation (Hancock *et al*. 1989, Jones *et al*. 1989, Burnham *et al*. 2010, Bakke-McKellep *et al*. 2007). However, these processes do not eliminate anti nutritional factors (ANFs) and biological limitations (Gatlin *et al*. 2007). In *Lateolabrax japonicus*, diets with fish meal (FM) and different soybean meal (SM) inclusion levels were tested (FM, SM50% and SM75% diets). No significant differences were found in final body weight, weight gain (WG) and specific growth rate (SGR) between those fed with FM and SM50. However, FM replacement to 75% of SM led to significant differences, such as lower feed efficiency (FE) and protein efficiency ratio (PER). Moreover, fish fed with an SM75 diet exhibited lower apparent digestibility coefficients (Zhang *et al*. 2018). As suggested by previous studies, SM in the diet of carnivorous fish is recommended to be incorporated at low levels, considering potential intestinal impacts, such as inflammation and reduced intestinal folds, affecting both mucosa and epithelial absorption function (Baeverfjord and Krogdahl 1996, Bakke-McKellep *et al*. 2007, Merrifield *et al*. 2011).

Due to their anatomy and metabolism, fish of the genus *Centropomus* are considered strict carnivores with a segmented digestive tube and differential enzymatic activity: higher acidic proteases in the stomach and basic proteases in the intestine. Indeed, digestive enzymes in fish exhibit an adaptive layout and activity relative to the dietary nutrient content (Lundstedt *et al*. 2004). The physiological responses of fish to FM replacement with SM are species specific (Zhou *et al*. 2018). However, a particular trend is observed among carnivorous fish, which suggests that SM use may decrease digestive enzyme production (Murashita *et al*. 2018, Li *et al*. 2012), affecting digestibility, nutrient utilization, and fish health (Lazzari *et al*. 2010, Zhang *et al*. 2018). As observed in this study, acid protease activity was higher than basic protease, which is consistent with the findings reported by Arriaga-Hernández *et al*. (2021) in *C. viridis*, Jesús-Ramírez *et al*. (2017) in *C. parallelus* and Concha-Frías *et al*. (2018) in *C. undecimalis*.

In the present study, the observed acidic protease activity in fish fed with the SM diets may have been due to the poor effect of soy carbohydrates on cholecystokinin production (Murashita *et al*. 2008), which is secreted by the intestinal mucosa and stimulates gallbladder contraction; it also may have affected the production and release of pancreatic digestive enzymes, which are crucial in the secretion of proteolytic enzymes in vertebrates (Pearson and Brownlee 2005). The decrease in protease enzymatic activity with increasing SM content found in this research has also been observed in various carnivorous species such as *Lateolabrax maculatus* (Wang *et al*. 2021), *Lateolabrax japonicus* (Li *et al*. 2015, Zhang *et al*. 2018), *Pagrus major* (Murashita *et al*. 2018), *Lates calcarifer* (Ma *et*

e-ISSN: 2007-901X

al. 2019), *Totoaba macdonaldi* (Trejo-Escamilla *et al*. 2017), and in other species regardless of their feeding habits (Yu *et al*. 2012, Li *et al*. 2015, Liu *et al*. 2017, Liu *et al*. 2020).

Regarding hematological parameters in fish, it has been suggested that several factors, such as species, size, age, physiological status, environmental conditions, protein source, and the quality and quantity of food, have a significant influence (Witeska *et al*. 2023). The blood composition of teleost fish comprises approximately 20-40% of blood cells and 80-60% of plasma (Ranzani-Paiva and Tavares-Dias 2024). For *C. undecimalis*, the hematological parameter values evaluated in this study fell within these suggested ranges (Esmaeili 2021, Fazio 2019, Witeska *et al*. 2023). However, Hematocrit (Ht), Hemoglobin (Hb), Mean Corpuscular Volume (MCV), and Mean Corpuscular Hemoglobin Concentration (MCHC) were higher than those reported by Mello *et al*. (2015) for the same species and by Santos *et al.* (2009) for *C. parallelus*. Nevertheless, Ht and Hb levels, as reported by Abdo-de-la-Parra *et al*. (2023), were found to be higher than those obtained in this study when diets with 40% protein (comprised of 42.72% FM) and 10% lipids were used in *C. viridis*. This difference may be associated with the higher protein and lipid levels tested in that study, which could have favored a greater erythropoietic response and oxygen transport capacity, thereby contributing to higher Ht and Hb values.

The decrease in hematological parameters with increasing SM percentage in diets found in the present study has also been observed in other species fed with other vegetable alternatives, such as 25% of fava bean meal in sturgeon (*Huso huso*), 33.3% and 60% soybean meal replacement in *Lutjanus guttatus* with, or in *Heteropneustes fossilis* with 50% soybean meal generating non-significant decreases in Ht, Hb, RBC, MCH, MCHC, and MCV (Howlader *et al*. 2023, Hosseini and Khajepour 2013, González-Rodríguez and Castillo-Vargasmachuca 2012). Conversely, in tilapia Oreochromis niloticus, adding different levels of maltose in the diet did not significantly affect mentioned hematological parameters (Ighwela *et al*. 2012). Although no significant differences were found in the evaluated hematological parameters in this study, it can be suggested that snook can be fed up to 55% SM replacement without causing severe physiological effects; however, this replacement value could place *C. undecimalis* near the limit of physiological impact, as shown by Howlader *et al*. (2023), who found no significant differences with 50% replacement but did with 75% SM in *H. fossilis*.

In summary, this species appears to possess and immunological plasticity in response to alternative diets (35% SM). Unlike species such as *H. fossilis* or *Lutjanus guttatus*, *C. undecimalis* has shown the ability to maintain hematological homeostasis even when fed partially unbalanced diets. This suggests an efficient adaptation to dietary variation, possibly linked to its opportunistic ecology and its capacity to feed on a wide range of prey in natural estuarine and marine environments (Álvarez-Lajonchère and Tsuzuki 2008). On fact, the high values of Hb and Ht in fish fed with 35% SM replacement suggest a substantial improvement in oxygen transport and fish metabolism, aligning with better performance in growth parameters in this treatment. These values are consistent with other trials, Hb ranges between 19.9 and 2.6 g·dL^{-1} (Esmaeili 2021, Hosseini and Khajepour 2013). However, this does not imply any blood anomaly such as anemia, since Haematocrit (Ht) remained >20% (Southamani *et al*. 2015).

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Although soybean meal has good digestibility and an acceptable amino acid profile (Arriaga-Hernández *et al*. 2021) its antinutritional components can be detrimental to carnivorous fish if used in high quantities (Kumar *et al*. 2005). This could be related to the decrease in hematological indicators recorded at the 55% replacement diet. This may occur due to tannins, phytic acid, and saponins, which become allies in anaerobic metabolism, generating blood lactate and reducing pH (Hemre *et al*. 1991).

The oval morphology observed in *C. undecimalis* erythrocytes is consistent with the general hematological pattern described for teleost fishes (Bento *et al*. 2018, Najiah *et al.* 2008, Fang *et al.* 2014). In the present study, significant differences among treatments were detected in erythrocyte length (EL), nucleus length (NL), nucleus size (NS), circularity index (CI), nucleus-to-cytoplasm ratio (NS/CS), and deformation index (DI), whereas the remaining morphometric variables did not change significantly. Because erythrocyte morphometry may vary in response to environmental conditions, diet composition, and physiological status (Srivastava and Choudhary 2010, Rahman and Baek 2019), these results suggest that soybean meal inclusion influenced some aspects of erythrocyte shape. However, given that no marked alterations were detected in the overall hematological profile, these morphometric changes should be interpreted as subtle structural variation rather than clear evidence of hematological impairment under the evaluated conditions (Fazio 2019, Witeska *et al*. 2023).

As the replacement of fishmeal (FM) with soybean meal (SM) increased, the diet cost decreased. The unitary feeding cost (UFC) differed significantly between the control diet and the diets with 35% and 55% SM inclusion ($p < 0.05$). The 35% SM diet also showed the lowest feed conversion ratio (FCR). However, it is important to note that the study did not include intermediate replacement levels between 0% and 35%, which could potentially have resulted in an even lower UFC. This analytical limitation underscores the need for further research to examine the economic and productive impacts of incremental FM replacement levels in aquafeeds.

In conclusion, based on the results obtained in the present study, soybean meal (SM) appears to be a viable alternative to fish meal (FM) in the diets of common snook (*Centropomus undecimalis*), particularly at a 35% replacement level. This level of inclusion-maintained growth performance and resulted in a lower feed conversion ratio (FCR) compared to the other treatments, indicating improved feed utilization. Moreover, the group fed with 35% SM exhibited trends toward higher hematocrit and hemoglobin values, suggesting a favorable physiological response. However, increasing SM levels beyond this point may be associated with changes in blood parameters, which could reflect physiological adjustments potentially linked to dietary composition. Overall, these findings support the inclusion of plant-based proteins in aquaculture diets, highlighting the importance of precise formulation to promote fish health and production efficiency.

CONCLUSION

Overall, the results suggest that partial replacement of fish meal by soybean meal, particularly at 35%, may be feasible under the conditions evaluated, although further studies are required to confirm its physiological and productive implications across a broader range of inclusion levels.

ACKNOWLEDGMENTS

We thank the entire technical and scientific team of the Aquaculture Hangar project from the Biodiversity and Applied Ecology Research Group - GIBEA at the Universidad del Magdalena. SG-I thanks the "programa de becas de excelencia doctoral del bicentenario I (MinCiencias)" for funding its doctoral studies in Marine Sciences. Funding for this research was provided by the Sistema General de Regalías (SGR), under the Project: "Implementación de sistemas productivos en la piscicultura marina del róbalo para el fomento de su producción en el departamento del Magdalena" under collection permit No. 2433 dated October 13, 2022, from the Autoridad Nacional de Acuicultura y Pesca – AUNAP.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest related to this manuscript.

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