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Evaluation of a Black Soldier Fly (*Hermetia illucens*) Larvae-Based Diet on the Growth Performance of the Nile Tilapia (*Oreochromis niloticus* l., Brazilian Strain) During Grow-Out Period in Côte d'Ivoire

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ABSTRACT

Tropical aquaculture is often constrained by the high cost of imported commercial feeds. This study evaluates a locally sourced alternative by investigating the potential of black soldier fly (Hermetia illucens) larvae meal as a sustainable protein ingredient in grow-out period for the Nile tilapia (Oreochromis niloticus L., Brazilian strain). A 120-day feeding trial was conducted at Nangui ABROGOUA University using fish with an average initial weight of 120g. Three diets were assessed: a commercial reference feed and two experimental formulations incorporating agroindustrial by-products. The DBSF diet included insect meal, whereas the DNBSF diet excluded it. All diets were isoproteic (29-30% crude protein), and fish were stocked at a density of 20 individuals/m³ under uniform rearing conditions. Tilapia fed the DBSF diet exhibited growth performance $(368.40 \pm 8 \text{ g})$ and feed conversion ratios (FCR = 1.56 ± 0.07) comparable to those fed the commercial diet $(379.20 \pm 5.7 \text{ g}; \text{ FCR} = 1.49 \pm 0.03)$. In contrast, the DNBSF diet resulted in significantly lower growth $(314.40 \pm 10.2 \text{ g})$ and feed efficiency (FCR = 1.98 ± 0.11). Peak body protein content (18%) was observed in fish receiving the reference diet. Economically, both experimental diets reduced feed costs per kilogram of weight gain by 64.69% with DBSF and 55.31% with DNBSF demonstrating their cost-effectiveness. Notably, the DBSF diet achieved the lowest production cost per kilogram of gain. These findings underscore the nutritional and economic viability of *H. illucens* larvae meal as a sustainable feed component, offering promising prospects for enhancing feed autonomy and reducing production costs in Ivorian aquaculture systems.

INTRODUCTION

Aquaculture is increasingly recognized as a strategic means of addressing the growing demand for animal protein in sub-Saharan Africa, particularly fish, driven by







rapid population growth and urbanization (FAO, 2022). However, its development is constrained by a heavy dependence on fishmeal, a high-quality yet costly and ecologically sensitive resource subject to global price fluctuations and sustainability concerns (Tacon & Metian, 2015; Naylor et al., 2021). Commercial feeds containing fishmeal remain largely inaccessible to small-scale producers, thereby exacerbating productivity disparities and impeding the expansion of inclusive aquaculture systems (Obiero et al., 2019; N'zue et al., 2022).

Attempts to substitute fishmeal with plant-based proteins have yielded mixed outcomes, owing to amino acid imbalances, antinutritional factors, and competition with human food and industrial uses, challenges that are particularly pronounced in tropical regions (NRC, 2011; Bamba et al., 2014; Munguti et al., 2021). These limitations highlight the urgent need for alternative protein sources that are locally available, nutritionally adequate, and economically feasible. Agricultural by-products such as oilseed cakes and cereal brans offer a promising foundation for practical feed formulations, especially when complemented by novel ingredients such as insect meal (Feng & Lee, 2014).

Among emerging alternatives, black soldier fly (*Hermetia illucens*) larvae meal has attracted considerable interest due to its capacity to convert organic waste into nutrient-rich biomass, abundant in essential amino acids and lipids (**Makkar** *et al.*, **2014**). Its local production requires minimal inputs, generates low environmental impact, and aligns with circular economy principles (**Henry** *et al.*, **2015**; **van Huis & Oonincx**, **2017**). Previous studies have demonstrated its beneficial effects on growth performance, feed conversion, and carcass quality in various aquaculture species, including tilapia (**Belghit** *et al.*, **2019**; **Shati** *et al.*, **2022**; **El-Sayed & El-Ghobashy**, **2023**). Nevertheless, research on insect-based diets remains limited in sub-Saharan Africa, where context-specific, affordable, and scalable feeding strategies are urgently required (**Obiero** *et al.*, **2022**).

This study seeks to address this gap by evaluating the nutritional and economic performance of two practical diets formulated from agricultural by-products; one enriched with *H. illucens* larvae meal (DBSF), and the other without (DNBSF), in comparison with a commercial reference diet. Using the Nile tilapia (*Oreochromis niloticus* L., Brazilian strain) reared under controlled conditions in Côte d'Ivoire, the trial assesses growth performance, feed efficiency, body composition, and cost-effectiveness. The overarching aim is to identify a locally sourced, sustainable alternative to imported feeds that can enhance profitability and resilience within tropical aquaculture systems.

MATERIALS AND METHODS

Experimental diets and preparation

Three diets were evaluated: a commercial imported reference feed (AR; KOUDIJS) and two locally formulated feeds derived from agricultural by-products. The experimental

diets, DBSF and DNBSF, were both isoproteic, containing 29% crude protein. The key distinction lay in the inclusion of black soldier fly (*Hermetia illucens*) larvae meal, constituting 10% of the DBSF formulation, while absent from DNBSF. This inclusion level was informed by the findings of **Barca** *et al.* (2023), who reported optimal growth and flesh quality in fish at comparable levels. Both experimental diets incorporated soybean meal, cottonseed meal, rice bran, and wheat bran. Palm and soybean oils served as lipid sources, while a vitamin–mineral premix (0.5%), salt, and shell powder were added to meet micronutrient requirements (Table 1).

The insect meal was produced locally under tropical conditions, following the method outlined by **Vodounnou** *et al.* (2024). Larvae were reared on organic substrates comprising food scraps, cereal brans, and surplus fruits and vegetables, under controlled environmental conditions of 27–30 °C and 65% relative humidity, as recommended by **Lowet** (2021). Harvesting occurred at the pre-pupal stage on day 15, identified by **Pornsuwan** *et al.* (2023) as optimal for protein and lipid yield. Post-harvest processing involved rinsing, euthanasia via immersion in hot water, drying at 65 °C for eight hours (**Suang** *et al.*, 2025), grinding through a 1mm sieve, and storage in airtight containers at ambient temperature.

Feed production was undertaken at a 300 kg scale using locally available equipment. Ingredients were milled individually and subsequently homogenized using a mechanical mixer (300 rpm, 2.2 kW). Oils were incorporated gradually to ensure uniform lipid distribution. The commercial imported diet (AR) was selected for its standardized formulation and widespread availability in Côte d'Ivoire, serving as a benchmark for nutritional adequacy and performance.

Proximate composition of all diets was analyzed at the Institute of Animal Husbandry and Genetics, Georg-August University of Göttingen, Germany. Analytical procedures adhered to the protocols of **Naumann and Bassler** (1976–1997), with laboratory methods detailed by **Rodehutscord** *et al.* (2004). Results are summarized in Table (2).

Table 1. Composition of the practical diets (g/100 g of feed as distributed) and characteristics of the ingredients used for the rearing of *Oreochromis niloticus*, Brazil strain, in tanks

Raw material	Diet DNBSF	Diet DBSF	Price	Protein (%) Lipids (%	Ash	Fiber	
	(%)	(%)	(FCFA/kg)		Lipius (70)	(%)	(%)
	Inclusion level of ingredients			Proximate chemical composition (as			
	in the diet (g /100 g of diet as fed			% of dry matter)			
Soybean meal	34.0	32.0	460	45.0	1.70	6.00	6.70
Cottonseed meal	23.0	15.0	340	40.0	20.0	5.90	12.9
Black soldier fly	0	10.0	200	42.1	26.0	26.6	7.00
larvae							
Rice bran (low-grade	18.0	18.0	65.0	12.0	14.1	5.20	5.30
flour)							
Wheat bran	20.0	20.0	150	15.0	3.90	5.60	10.4

Salt	1.50	1.50	200	_	_	_	_
Vegetable oils	1.50	1.50	1250	_	_	_	_
Vitamin and mineral	0.50	0.50	4000	_	_	_	_
premix *							
Shell powder	1.50	1.50	30.0	_	_	_	_

DNBSF: Local diet without Hermetia illucens meal; DBSF: Local diet enriched with Hermetia illucens meal; AR: Commercial reference feed (KOUDIDJS); * Premix composition: vitamin and mineral premix (IU or mg / kg of premix). Vitamin A: 4800 IU; Cholecalciferol (vitamin D): 2400 IU; Vitamin E: 4000 mg; Vitamin K: 800 mg; Vitamin B1: 400mg; Riboflavin: 1600 mg; Vitamin B6: 600 mg, Vitamin B12: 4 mg; Pantothenic acid: 4000 mg; Nicotinic acid: 8000mg; Folic acid: 400 mg; Biotin: 20 mg, Manganese: 22000 mg; Zinc: 22000 mg; Iron: 12000 mg; Copper: 4000 mg; Iodine: 400 mg; Selenium: 400mg; cobalt: 4.8 mg. ,Dashes (–): No data available.

Table 2. Proximate composition (% dry matter) and essential amino acid profile (% of protein) of experimental diets used for the tank culture of the Nile tilapia (*Oreochromis niloticus*, Brazilian strain)

Parameter	Diet DNBSF	Diet DBSF	Diet AR (reference)	Essential Amino Acid Requirements ¹
Dry matter (%)	82.6	83.1	89.7	
	Proxima	ate composition (%	5 DM)	
Crude protein	29.6	29.6	30.0	
Lipids	8.49	9.45	4.51	
Crude fiber	8.32	7.80	7.28	
Ash	5.45	7.52	6.99	
	Essential	amino acids (% of	protein)	
Arginine	7.79	7.32	6.34	4.20
Lysine	4.67	4.89	5.01	5.12
Methionine	1.51	1.58	2.26	2.68
Histidine	2.56	2.58	2.13	1.72
Phenylalanine	4.61	4.60	4.13	3.75
Tyrosine	3.19	3.59	3.59	3.75
Leucine	4.67	4.89	4.82	3.39
Isoleucine	4.00	3.65	3.40	3.11
Valine	4.64	4.99	3.43	2.80
Threonine	3.31	3.35	3.72	3.75
Arginine/Lysine ratio	1.67	1.50	1.26	0.82

DNBSF: Local diet without insect meal; DBSF: Local diet supplemented with Hermetia illucens larvae meal; AR: Commercial reference feed (KOUDIDJS); ¹ Essential amino acid requirements for Oreochromis niloticus according to NRC (2011).

Experimental design and research conditions

The study was conducted at the aquaculture station of Nangui Abrogoua University, located in Abidjan, Côte d'Ivoire ($5^{\circ}23'30''$ N, $4^{\circ}00'56''$ W). The experimental setup comprised nine concrete tanks ($2.80 \,\mathrm{m} \times 2.60 \,\mathrm{m} \times 0.80 \,\mathrm{m}$; Fig. 1), each with a working volume of $5\mathrm{m}^3$. Trials were carried out over two consecutive production cycles, each lasting 120 days. Water was continuously supplied from a borehole at a minimum flow rate of $2\mathrm{L}/\mathrm{min}$ per tank, ensuring stable physicochemical conditions and adequate oxygenation throughout the study.



Fig. 1. Experimental structures used for the trials

Experimental fish and procedures

Male Nile tilapia (*Oreochromis niloticus*, Brazilian strain), with an initial mean weight of 120g, underwent a 30-day acclimation period during which they were fed a commercial diet containing 30% crude protein. Following acclimation, fish were counted, batch-weighed, and randomly stocked at a density of 20 individuals/m³. Each dietary treatment was allocated to three replicate tanks. Fish were hand-fed three times daily (09:00, 11:00, and 15:00) at a feeding rate equivalent to 3% of body weight. Feed quantities were adjusted monthly based on average weights obtained by sampling 25% of the fish in each tank. Feeding was suspended on weighing days to prevent bias in intake and performance measurements.

At the end of each cycle, tanks were drained and fish were counted and batch-weighed to determine growth and survival. In addition, 30 fish per tank were randomly selected and individually weighed using a GENERIC electronic scale (accuracy: 1g) to calculate performance indicators, including final body weight (FBW), weight gain (WG), specific growth rate (SGR), feed conversion ratio (FCR), and survival rate. All results were expressed as means \pm standard deviation of the mean (SD).

Water quality management

Water from each dietary group was analyzed at weekly intervals in the morning (6.00 - 8.00 hours) and the afternoon (15.00 - 16.00 hours) for temperature (Celsius thermometer), dissolved oxygen (oxygen) and pH. Temperature (°C) was measured using a direct-reading thermometer; dissolved oxygen (mg/L) was assessed using a BIOBASE portable oximeter (model BOD-A1) equipped with an electrochemical probe; and pH was determined using a BIOBASE electronic pH meter (model PHB-4) fitted with a glass electrode and automatic temperature compensation.

Economic evaluation

For each dietary treatment, the feed cost per kilogram of diet and the cost per kilogram of weight gain were calculated based on prevailing local market prices for all ingredients at the time of the study. All costs are expressed in West African CFA francs (FCFA). In addition to ingredient costs, manufacturing expenses were estimated at 5000 FCFA per tonne and transportation at 20000 FCFA per tonne. These figures were incorporated into the total cost to reflect the actual economic conditions of local feed production.

Sampling procedures and chemical analyses

At the outset of the trial, twenty fish were randomly selected to determine baseline body composition. Following the 60-day feeding period, five fish from each tank (fifteen per treatment) were sampled, euthanized via thermal shock, homogenised, and stored at $70\,^{\circ}\text{C}$ for subsequent analysis. Feed ingredients and fish samples were analyzed in triplicate in accordance with **AOAC** (2003) protocols. Moisture content was determined by oven-drying samples at $105\,^{\circ}\text{C}$ until a constant weight was achieved. Crude protein was quantified using the Kjeldahl method (N × 6.25), a standard procedure in fish nutrition research (**Latimer**, 2016). Lipid content was extracted using petroleum ether in a Soxhlet apparatus. Ash was measured by incineration at $550\,^{\circ}\text{C}$ for 24 hours. Crude fiber was assessed via sequential acid and alkali digestion, following the method described by **Gul and Safdar** (2009).

Calculation of nutritional and economic indices

Zootechnical performances and economic viability of the experimental diets were assessed using established quantitative indicators. Weight gain (WG) was calculated as the difference between final and initial body weight, while daily weight gain (DWG) was derived by dividing WG by the duration of the trial (in days). Survival rate (%) was computed as the ratio of final to initial fish numbers, multiplied by 100.

Specific growth rate (SGR) was calculated using the formula: SGR (%/day) = 100 \times [(ln final weight – ln initial weight) / trial duration], as recommended by **Cho and Bureau (2001)** and **Cardei (2024)**.

Feed conversion ratio (FCR) was defined as the total dry feed intake divided by wet weight gain. Protein efficiency ratio (PER), following the method of **De Silva and Anderson** (1995) and validated in recent studies on insect-based diets (**Shati** *et al.*, 2022), was calculated as the ratio of weight gain to total protein consumed.

Economic efficiency was assessed by calculating the cost of producing one kilogram of weight gain using the formula: Cost/kg gain = diet cost (FCFA/kg) \times FCR, in accordance with Wilfart *et al.* (2023).

Cost reduction (%) relative to the control diet was expressed as: Cost reduction (%) = $100 \times [(\cos t/kg \text{ gain of control diet} - \cos t/kg \text{ gain of test diet}) / \cos t/kg \text{ gain of control diet}]$, as applied in previous studies by **Bamba** *et al.* (2014) and **Fregene** *et al.* (2020).

Statistical analysis

Statistical analyses were performed using IBM SPSS Statistics (version 20). The effects of dietary treatments on water quality and zootechnical parameters were examined. Prior to statistical testing, data distributions were assessed for normality using the Kolmogorov–Smirnov test.

Variables such as growth performance, body composition, and water physicochemical characteristics were analyzed to identify significant differences among treatments. Non-normally distributed data (e.g., physicochemical parameters) were evaluated using the Kruskal–Wallis non-parametric test. In contrast, normally distributed data (e.g., growth and body composition) were analyzed via two-way ANOVA, accounting for the effects of diet, tank, and their interaction. When significant differences were detected (P< 0.05), post hoc comparisons were conducted using Tukey's HSD test. All results are presented as mean values accompanied by their standard deviation (mean \pm SD).

RESULTS

Comparative analysis of DNBSF and DBSF diet formulations

Two practical diets were formulated using comparable base ingredients, as detailed in Table (1). The principal distinction between them lies in the DBSF formulation, which incorporated 10% black soldier fly (*Hermetia illucens*) larvae meal. This inclusion replaced a portion of conventional protein sources, specifically, 2% soybean meal and 8% cottonseed meal, resulting in a marked reduction in the average cost of protein inputs, from 460 FCFA/kg for soybean meal to 200 FCFA/kg for insect meal.

From a nutritional perspective, the addition of larvae meal improved the lipid profile of the DBSF diet, owing to the high fat content of the larvae (26%) compared with 1.70% in soybean meal and 20% in cottonseed meal. The ash content of the insect meal (26.6%) also exceeded that of traditional plant proteins, contributing to a higher mineral concentration. Fiber levels remained within a moderate range across both diets, with a slight reduction observed in DBSF due to the lower inclusion of cottonseed meal. All other components bran, salt, vegetable oils, vitamin–mineral premix, and shell powder were held constant across formulations to ensure uniform contributions of fiber, essential minerals, and micronutrients.

Comparative analysis of experimental diets

All three diets exhibited high dry matter content, with the reference diet (AR) achieving the highest value at 89.7% (Table 2). Crude protein levels were comparable across formulations: 29.6% in both DNBSF and DBSF, and 30% in AR, adequately meeting the nutritional requirements of the Nile tilapia *Oreochromis niloticus*. The DBSF diet contained the highest lipid concentration (9.45%), followed by DNBSF (8.49%) and

AR (4.51%). Fiber content was slightly lower in AR (7.28%) and DBSF (7.80%) than in DNBSF (8.32%). Ash content was the greatest in DBSF (7.52%), with AR and DNBSF recording 6.99% and 5.45%, respectively.

With regard to essential amino acids (EAAs), all diets exceeded baseline nutritional requirements, except for methionine and lysine, which remained below recommended thresholds. These amino acids are commonly deficient in plant-based and alternative protein sources, presenting limitations in the amino acid profiles of the tested diets. The DNBSF formulation exhibited the highest concentrations of arginine (7.79%) and isoleucine (4.00%), whereas DBSF showed elevated levels of lysine (4.89%), valine (4.99%), and threonine (3.35%). The AR diet was notable for its higher methionine (2.26%) and tyrosine (3.59%) content. The arginine-to-lysine ratio was highest in DNBSF (1.67), followed by DBSF (1.50) and AR (1.26), with all values exceeding the estimated requirement of 0.82.

A radar chart was used to compare the amino acid profiles (Fig. 2), specifically lysine, arginine, and the arginine/lysine ratio, of the three dietary formulations (DBSF, DNBSF, AR) against the nutritional requirements of *O. niloticus*. None of the diets met the recommended lysine level, with DBSF recording the lowest value and AR approaching the target, though still insufficient to fully support optimal growth and protein synthesis. In contrast, arginine concentrations exceeded the required threshold in all diets, with DNBSF and DBSF presenting notably high levels.

The arginine/lysine ratio was also above the recommended value of 0.82 in all formulations, with DBSF and DNBSF displaying the highest ratios. While this may partially compensate for the lysine deficiency, it does not fully rectify the amino acid imbalance.

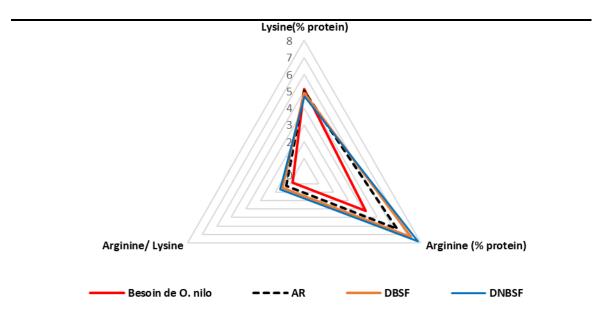


Fig. 2. Variation in the arginine/lysine ratio of experimental feeds (AR, DNBSF, DBSF) compared to the optimum for tilapia *O. niloticus*

Need for O. nilo: Essential amino acid requirements for Oreochromis niloticus; DNBSF: Local diet without insect meal; DBSF: Local diet supplemented with Hermetia illucens larvae meal; AR: Commercial reference feed (KOUDIDJS)

Water quality

Throughout the experimental period, key physicochemical parameters of the aquaculture environment were systematically assessed. Measurements of dissolved oxygen (ranging from 4.78 to 5.28 mg/L), temperature (27.9 to 28.2 °C), and pH (7.89 to 8.40) were subjected to statistical evaluation via the Kruskal-Wallis test, a non-parametric method appropriate for data lacking normal distribution. The analysis revealed no statistically significant difference across dietary treatments (P > 0.05), thereby affirming the uniformity of water quality conditions across all tanks.

Growth, feed utilization and economic indicators

The comparative evaluation of the DBSF, DNBSF, and reference (AR) diets revealed distinct outcomes in terms of growth performance, feed utilisation, and economic efficiency (Table 3). All experimental groups commenced the trial with comparable initial body weights (approximately 120g), and survival rates ranged from 88% to 91.8%, with no statistically significant differences (P > 0.05), confirming uniform baseline conditions and overall viability.

The fish grew from an initial average weight of 120g to a final mean body weight of 379.2 g during the experimental period of 120 days. Growth-related metrics demonstrated clear dietary effects. Final body weight (FBW), weight gain (WG), daily weight gain (DWG), and specific growth rate (SGR) were significantly higher in fish fed DBSF and

AR diets compared to those receiving DNBSF (P<0.05). The AR group achieved the highest FBW (379.2g), followed closely by DBSF (368.40 g), while DNBSF recorded the lowest (314.40 g). Similarly, SGR was greatest in the AR group (0.96%/day), marginally exceeding DBSF (0.93%/day), with DNBSF trailing (0.80%/day). These findings suggest that DBSF matches the biological efficiency of the reference diet, whereas DNBSF yields suboptimal growth outcomes.

Feed utilization parameters further substantiated these trends. Feed conversion ratio (FCR) and protein efficiency ratio (PER) were significantly improved in the DBSF and AR groups relative to DNBSF (P<0.05). DBSF recorded an FCR of 1.56 and a PER of 2.17, closely aligned with AR values (FCR = 1.49; PER = 2.24), while DNBSF exhibited less favorable results (FCR = 1.98; PER = 1.71).

From an economic perspective, both formulated diets offered substantial cost advantages over the reference diet. Feed costs were markedly lower for DBSF and DNBSF (343–344 F CFA/kg) compared to AR (1020 F CFA/kg). The cost per kilogram of weight gain was reduced to 537 F CFA/kg for DBSF and 679 F CFA/kg for DNBSF, in contrast to 1520 F CFA/kg for the reference diet. These reductions correspond to feed cost savings of 64.69% for DBSF and 55.31% for DNBSF. Despite its lower biological performance, DNBSF remains economically attractive. However, DBSF presents a more balanced profile, combining growth performance comparable to the reference diet with significantly reduced production costs.

Table 3. Growth performance, feed utilization efficiency, and economic effectiveness of juvenile *Oreochromis niloticus* (Brazil strain) reared on experimental diets over a 120-day period

Parameter	DNBSF	DBSF	Reference Diet
Initial Body Weight (IBW, g)	120±3.8a	120±2.5a	120±14.1a
Final Body Weight (FBW, g)	$314.40{\pm}10,2^a$	368.40 ± 8^{b}	379.20 ± 5.7^{b_c}
Weight Gain (WG, g)	194.40±10 ^a	248.40±8.3 ^b	259.20±5.6 ^{b°}
Daily Weight Gain (DWG, g/day)	1.62±0,1ª	$2.07\pm0.09^{\rm b}$	2,16±0.05b°
Specific Growth Rate (SGR, %/day)	0.80 ± 0.03^a	0.93 ± 0.03^{b}	$0.96\pm0.01^{\ b}$
Feed Conversion Ratio (FCR)	1.98 ± 0.11^{a}	1.56 ± 0.07^{b}	1.49 ± 0.03^{b}
Protein Efficiency Ratio (PER)	1.71±0.11a	2.17 ± 0.08^{b}	2.24 ± 0.05^{b}
Survival Rate (%)	88 ± 1.8^{a}	91.8 ± 1.3^{a}	89.3 ± 1.5^{a}
Feed Cost (F CFA/kg)	343	344	1020
Reduction in Feed Cost (%)	66.37	66.27	_
Feed Cost per kg Weight Gain (F			
CFA/kg)	679	537	1520
Reduction in Feed Cost per kg Weight			
Gain (%)	55.31	64.69	

Data are presented as mean \pm standard deviation (SD). Values in the same row with different superscripts (a, b, c) show significant differences at P < 0.05. SD refers to the standard deviation of the mean. P-values < 0.05 indicate statistically significant differences. DNBSF: Local diet without insect meal; DBSF: Local diet supplemented with Hermetia illucens larvae meal; AR: Commercial reference diet.

Proximate composition of experimental fish

The proximate composition of the Nile tilapia *Oreochromis niloticus* (Brazil strain) carcasses varied significantly across dietary treatments, as detailed in Table (4). In terms of moisture content, values ranged from 73.8 to 75.8% among the experimental diets, whereas the initial carcass displayed a significantly higher level at 77% (P < 0.05). Despite this, no significant differences were found between DNBSF, DBSF and AR diets. Conversely, crude protein content increased significantly following the feeding trial (P < 0.05). The reference diet (AR) produced the highest concentration at 18%, followed by DBSF at 17.1% and DNBSF at 15.9%. These results suggest enhanced protein assimilation across all treatments compared to the initial carcass value of 15%, with DBSF notably outperforming DNBSF. Regarding lipid content, a significant downward trend was observed (P < 0.05). The AR group recorded the lowest value (6.3%), followed by DNBSF (7%) and DBSF (7.7%), while the initial carcass contained 6.8%. This pattern implies that dietary formulation influenced lipid deposition, with DBSF contributing to a higher fat accumulation. Finally, ash content increased significantly across treatments (P < 0.05). The AR diet yielded the highest mineral concentration (1.7%), followed by DBSF (1.4%) and DNBSF (1.3%), all surpassing the initial carcass value of 1.2%.

Table 4. Carcass composition of juvenile *Oreochromis niloticus* (Brazil strain) reared on experimental diets

Parameter	DNBSF	DBSF	AR (Reference Diet)	Initial Carcass
Moisture (%)	$75,8\pm0.35^{a}$	$73,8\pm0.14^{a}$	74 ± 0.6^{a}	77 ± 0.8^{b}
Crude protein (%)	$15,9 \pm 1.03^{a}$	$17,1\pm 1.02^{b}$	18± 1°	15 ± 1.03^{d}
Total lipids (%)	$7\pm0.6^{\rm a}$	$7,7 \pm 0.8^{b}$	$6.3 \pm 0.6^{\circ}$	$6.8 \pm .08^{d}$
Total ash (%)	$1,3\pm0.15^{a}$	$1,4\pm0.3^{a}$	$1,7 \pm 0.3^{b}$	$1,2\pm0.14^{a}$

Data are presented as mean \pm standard deviation (SD). Values in the same row with different superscripts (a , b , c , d) show significant differences at P < 0.05. SD refers to the standard deviation of the mean. P-values < 0.05 indicate statistically significant differences. DNBSF: Local diet without insect meal; DBSF: Local diet supplemented with Hermetia illucens larvae meal; AR: Commercial reference diet

DISCUSSION

The present investigation was conducted under environmentally stable conditions, with physicochemical parameters, namely dissolved oxygen (4.78– 5.28mg/ L), temperature (27.9– 28.2°C) and pH (7.89- 8.40), remaining within optimal thresholds for the cultivation of the Nile tilapia *Oreochromis niloticus* in tropical settings, as delineated by **Boyd** *et al.* (2022). The absence of statistically significant variation among treatments (P > 0.05) affirms the environmental uniformity, thereby permitting attribution of observed biological responses solely to dietary interventions. This methodological

consistency lends credence to subsequent zootechnical, nutritional and economic interpretations.

From a nutritional perspective, all experimental diets, DNBSF, DBSF and AR were formulated to contain crude protein levels approximating 30%, in accordance with NRC (2011) guidelines. Nonetheless, their essential amino acid compositions diverged considerably. The DNBSF diet exhibited elevated arginine (7.79%) and isoleucine (4.00%) concentrations; DBSF was enriched in lysine (4.89%), valine (4.99%) and threonine (3.35%); whereas AR was distinguished by higher methionine (2.26%) and tyrosine (3.59%) levels. These compositional differences are of functional relevance, given their roles in protein biosynthesis, somatic growth and energy metabolism (Feng et al., 2020; Schader et al., 2023).

The limited mortality observed in the present study (88-91.8%) was predominantly recorded following handling procedures. This suggests that the deaths may be attributed to the stress induced by manipulation, rather than the experimental treatments themselves. Handling stress is a well-documented factor influencing fish mortality, particularly in aquaculture settings (Barton, 2002). Survival rates did not differ significantly between treatments (P > 0.05), suggesting that none of the diets had a harmful impact on fish viability. However, growth performance metrics, including weight gain (WG), final body weight (FBW), daily weight gain (DWG), and specific growth rate (SGR), were significantly superior in fish fed DBSF and AR diets compared to those receiving DNBSF (P<0.05). This disparity may be partially attributed to an unfavourable arginine/methionine ratio in DNBSF, which could compromise amino acid bioavailability and provoke competitive inhibition at intestinal transport sites (Li et al., 2009; Zhou et al., 2012), thereby impairing metabolic efficiency. The DBSF diet, incorporating 10% Hermetia illucens larvae meal, demonstrated enhanced amino acid balance, partially mitigating methionine deficiency and promoting superior growth outcomes. This is corroborated by feed efficiency indices: feed conversion ratio (FCR) and protein efficiency ratio (PER) were significantly improved in DBSF (FCR = 1.56 ± 0.07 ; $PER = 2.17 \pm 0.08$) and AR (FCR = 1.49 ± 0.03; $PER = 2.24 \pm 0.05$) relative to DNBSF (p < 0.05). The insect-derived lipids in DBSF likely contributed to increased dietary energy density and enhanced feed conversion efficiency (Makkar et al., 2014; Vallod & Le Reste, 2023). Furthermore, the reduction in dietary fibre (from 8.32% to 7.80%) may have facilitated improved nutrient absorption and gastrointestinal transit (Kaeffer, 2020), while the elevated ash content (7.52%) supported mineral accretion, particularly in skeletal tissues. Taken together, the inclusion of Hermetia illucens larvae meal in DBSF confers nutritional and functional benefits comparable to the AR reference diet, whilst embracing principles of circular economy. This formulation strategy harmonizes zootechnical efficacy with ecological sustainability and economic pragmatism. Comparable findings were reported in a previous study employing inclusion levels, albeit with equivalent fishmeal replacement rates (Fronte et al., 2021). importantly, the

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incorporation of insect-derived protein into aquafeeds has demonstrated potential to enhance fish growth performance and feed efficiency, offering a sustainable alternative to conventional fishmeal. Recent research by **Hasan** *et al.* (2023) confirms their nutritional value, noting high protein levels and balanced amino acids that support healthy development in fish.

Biochemical analyses of fish carcasses further substantiated the dietary impact on body composition. Moisture levels remained consistent across treatments (P > 0.05), suggesting uniform tissue hydration (Yeo et al., 2024). In contrast, crude protein content increased significantly post-intervention (P < 0.05), reaching 18% in AR, 17.1% in DBSF and 15.9% in DNBSF compared to an initial baseline of 15.0%. The present study confirms that dietary formulation significantly influences the proximate composition of Nile tilapia *Oreochromis niloticus*, consistent with prior findings on tilapia nutritional sensitivity (El-Sayed, 2006; Makkar et al., 2014). In contrast, crude protein levels rose markedly post-feeding, with DBSF-fed fish approaching the reference diet's efficacy. The enhancement may be attributed to the high-quality amino acid profile of Hermetia illucens larvae, which has been shown to support efficient protein deposition in fish (Henry et al., 2015; Belghit et al., 2018). Although the reference diet remains superior, the DBSF formulation approaches its efficacy, reinforcing the potential of insect meal as a sustainable protein source. Total lipid content showed a clear decreasing trend (P < 0.05), with the lowest level recorded in the AR group (6.3%), followed by DNBSF (7%) and DBSF (7.7%). Interestingly, the initial carcass contained 6.8% lipids, suggesting that dietary composition influenced lipid metabolism. The relatively higher lipid content in DBSF-fed fish may be linked to the presence of insect-derived fats, which contribute to dietary energy, without adversely affecting growth performance (Gasco et al., 2020). Ash content increased across all treatments, indicating enhanced mineral deposition (Chapman, 2003; FiBL, 2023). DBSF outperformed DNBSF, suggesting improved mineral bioavailability, potentially attributable to insect meal components such as chitin (Borrelli et al., 2017). Although the reference diet remains superior, DBSF demonstrated promising nutritional adequacy and supports its potential as a sustainable alternative in aquafeed development (van Huis et al., 2013; Józefiak et al., 2016).

From an economic standpoint, both DNBSF and DBSF diets demonstrated substantial cost advantages over the AR formulation. Feed costs were reduced by approximately 66%, primarily through the utilisation of locally sourced, low-cost ingredients such as rice bran, cottonseed cake, and agricultural by-products. Unlike AR, the formulated diets capitalize on regional availability, thereby minimizing logistical and procurement expenditures. The DBSF diet, in particular, benefits from the integration of *Hermetia illucens* larvae reared on organic waste, enhancing its cost-effectiveness and sustainability. The cost per kilogram of weight gain was reduced by 55.31% for DNBSF and 64.69% for DBSF, underscoring their economic efficiency.

These findings resonate with the work of Barragán-Fonseca et al. (2017), who underscored the potential of *Hermetia illucens* in circular agro-food systems, particularly for biowaste valorization. They also corroborate the conclusions of Adissin et al. (2021), who advocated for the adoption of alternative feed formulations in tropical aquaculture, emphasising their affordability and contextual relevance. By incorporating functional ingredients derived from circular economy principles, DBSF and DNBSF diets offer a sustainable and economically viable solution aligned with food security imperatives in sub-Saharan Africa. Although practical diet DBSF and AR (reference) differ in compositional attributes, they converge in terms of zootechnical and nutritional performance. Despite certain technical limitations, practical diet DNBSF remains a costeffective alternative. The strategic incorporation of *Hermetia illucens* larvae meal into locally formulated diets represents a promising avenue for sustainable aquaculture development, reducing ecological impact and enhancing resilience in resourceconstrained tropical regions. These outcomes are consistent with FAO (2024) recommendations and affirm the potential of DBSF as a nutritionally robust, economically sound and ecologically responsible feed solution for West African aquaculture systems.

CONCLUSION

This study demonstrates that *Hermetia illucens* larvae meal improves growth and feed efficiency in the Nile tilapia while lowering production costs. The insect-based diet, crafted from local agro-industrial by-products, offers a sustainable alternative to commercial feeds. Carcass analysis showed enhanced protein retention and balanced lipid metabolism. To advance aquaculture sustainability, future efforts should focus on refining native plant proteins. Optimizing their nutritional value will support cost-effective, eco-efficient production across sub-Saharan Africa.

REFERENCES

- Adissin, A. J.; Houessou, A. M. and Gnonlonfin, G. J. B. (2021). Utilisation de la farine d'insectes dans l'alimentation des poissons en Afrique de l'Ouest : potentiel et perspectives. *Revue Africaine d'Aquaculture*, 13(2); 45–58.
- **AOAC** (2003). Official Methods of Analysis of the Association of Official Analytical Chemists (17th ed.). AOAC International.
- Bamba, Y.; Ouattara, N.; Soro, Y.; Ouattara, A.; Yao, K. and Gourène, G. (2014). Evaluation of production efficiency of Nile tilapia (*Oreochromis niloticus* L.) fed diets containing crop residues in combination with cocoa bean shell and coconut oil cake in Côte d'Ivoire. *Livestock Research for Rural Development*, 26(10), Article #172. https://www.lrrd.org/lrrd26/10/bamb26189.htm

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- Barca, A.; Abramo, F.; Nazerian, S.; Coppola, F.; Sangiacomo, C.; Bibbiani, C.; Licitra, R.; Susini, F.; Verri, T. and Fronte, B. (2023). *Hermetia illucens* for replacing fishmeal in aquafeeds: Effects on fish growth performance, intestinal morphology, and gene expression in the zebrafish (*Danio rerio*) model. *Fishes*, 8(3), 127. https://doi.org/10.3390/fishes8030127
- **Barragán-Fonseca, K. B., Dicke, M. and van Loon, J. J. A.** (2017). Nutritional value of the black soldier fly (*Hermetia illucens* L.) and its suitability as animal feed A review. *Journal of Insects as Food and Feed*, 3(2): 105–120. https://doi.org/10.3920/JIFF2016.0055
- **Barton, B. A.** (2002). Stress in Fishes: A Diversity of Responses with Particular Reference to Changes in Circulating Corticosteroids. *Integrative and Comparative Biology*, 42(3): 517–525, https://doi.org/10.1093/icb/42.3.517
- Belghit, I.; Liland, N. S.; Gjesdal, P.; Biancarosa, I.; Menchetti, E.; Li, Y. and Lock, E. J. (2018). Insect-based diets for Atlantic salmon (*Salmo salar*): Effects on growth performance, nutrient digestibility and intestinal morphology. *Aquaculture Nutrition*, 24(2): 101–112
- Belghit, I.; Liland, N. S.; Gjesdal, P. Biancarosa, I.; Menchetti, E.; Li, Y. and Lock, E. J. (2019). Black soldier fly larvae meal can replace fish meal in diets of seawater phase Atlantic salmon (*Salmo salar*). *Aquaculture*, 511: 734270. https://doi.org/10.1016/j.aquaculture.2019.734270
- Borrelli, L.; Coretti, L.; Dipineto, L.; Bovera, F.; Menna, F.; Chiariotti, L.; Nizza, A.; Lembo, F. and Fioretti, A. (2017). Insect-based diet modulates gut microbiota composition and SCFAs production in laying hens. *Scientific Reports*, 7, Article 16269
- **Boyd, C. E.; Tucker, C. S. and Hargreaves, J. A.** (2022). Aquaculture Water Quality Management in Tropical Systems (2nd ed.). Springer
- **Cardei, M.** (2024). Aquaculture performance metrics: Advances in growth modelling and feed efficiency. *Aquaculture Science Review*, 42(1): 15–29
- **Chapman, F. A.** (2003). Aquaculture Nutrition: Fish Feed Formulation. University of Florida, Institute of Food and Agricultural Sciences
- **Cho, C. Y. and Bureau, D. P.** (2001). A review of diet formulation strategies and feeding systems to reduce excretory and feed wastes in aquaculture. *Aquaculture Research*, 32(S1): 349–360. https://doi.org/10.1046/j.1355-557x.2001.00031.x
- **De Silva, S. S. and Anderson, T. A.** (1995). Fish Nutrition in Aquaculture. Chapman and Hall
- **El-Sayed, A. F. M.** (2006). Tilapia culture. CABI Publishing. https://doi.org/10.1079/9780851990149.0000

- **El-Sayed, A-F. M. and El-Ghobashy, H.** (2023). Performance of Nile tilapia (*Oreochromis niloticus*) fed diets containing black soldier fly larvae meal. *Aquaculture Research*, 54(2): 1234–1242. https://doi.org/10.1111/are.16045
- **FAO** (2022). The State of World Fisheries and Aquaculture 2022. Food and Agriculture Organization of the United Nations. https://doi.org/10.4060/cc0461en
- **FAO** (2024). The State of World Fisheries and Aquaculture 2024: Blue Transformation. Food and Agriculture Organization of the United Nations. https://doi.org/10.4060/cd0683en
- **Feng, Y. and Lee, H. G.** (2014). Agricultural by-products as alternative feed ingredients for aquaculture. *Journal of Applied Aquaculture*, 26(3): 213–229. https://doi.org/10.1080/10454438.2014.930009
- **Feng, Y.; Chen, X. and Lee, H. G.** (2020). Amino acid profiles and digestibility of alternative protein sources for aquafeeds. *Aquaculture Reports*, 17, 100345. https://doi.org/10.1016/j.aqrep.2020.100345
- **FiBL** (2023). Organic Aquaculture: Nutritional Standards and Mineral Requirements. Research Institute of Organic Agriculture. https://www.fibl.org
- **Fregene, B. T.; Adeyemi, A. A. and Olayemi, F. F.** (2020). Economic evaluation of insect-based diets in tilapia farming. *African Journal of Aquatic Science*, 45(3): 267–275
- Fronte, B.; Zarantoniello, M.; Randazzo, B.; Truzzi, C.; Giorgini, E.; Maricchiolo, G. and Antonucci, M. (2021). Insect meal inclusion in aquafeeds: A review of the effects on fish growth, health and environmental sustainability. *Reviews in Aquaculture*, 13(4), 1935–1956. https://doi.org/10.1111/raq.12558
- Gasco, L.; Biasato, I.; Dabbou, S.; Trocino, A. and Gai, F. (2020). Insect fats in animal nutrition: Nutritional value and functional properties. *Animals*, 10(11), Article 1920
- **Gul, S. and Safdar, M. N.** (2009). Proximate composition and mineral analysis of selected vegetables grown in Pakistan. *Pakistan Journal of Nutrition*, 8(5): 555–560. https://doi.org/10.3923/pjn.2009.555.560
- **Hasan, I.; Rimoldi, S.; Saroglia, G. and Terova, G.** (2023). Sustainable fish feeds with insects and probiotics positively affect freshwater and marine fish gut microbiota. *Animals*, 13(10), 1633. https://doi.org/10.3390/ani13101633
- **Henry, M.; Gasco, L.; Piccolo, G. and Fountoulaki, E.** (2015). Review on the use of insects in the diet of farmed fish: Past and future. *Animal Feed Science and Technology*, 203: 1–22. https://doi.org/10.1016/j.anifeedsci.2015.03.001
- Józefiak, D.; Nogales-Merida, S.; Rawski, M.; Kierończyk, B. and Mazurkiewicz, J. (2016). Insects: A natural nutrient source for poultry A review. *Annals of Animal Science*, 16(2): 297–313

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- **Kaeffer, B.** (2020). Rôle des fibres alimentaires dans la digestion et la santé intestinale des poissons. *Nutrition & Aquaculture*, 8(1): 12–19
- **Latimer, G.W. (Ed.).** (2016). Official Methods of Analysis of AOAC International (20th ed.). AOAC International
- **Li, P.; Mai, K.; Trushenski, J. and Wu, G.** (2009). New developments in fish amino acid nutrition: Towards functional and environmentally oriented aquafeeds. *Amino Acids*, 37(1): 43–53. https://doi.org/10.1007/s00726-008-0151-1
- **Lowet, F.** (2021). Optimisation du maintien des conditions abiotiques dans les élevages d'*Hermetia illucens* par un système de brassage et de suivi automatisé. Master thesis, Gembloux Agro-Bio Tech, Université de Liège. https://matheo.uliege.be/handle/2268.2/11069
- Makkar, H. P. S.; Tran, G.; Heuzé, V. and Ankers, P. (2014). State-of-the-art on use of insects as animal feed. *Animal Feed Science and Technology*, 197: 1–33. https://doi.org/10.1016/j.anifeedsci.2014.07.008
- **Munguti, J. M.; Musa, S. and Ogello, E. O.** (2021). Challenges and opportunities in the use of plant-based ingredients in aquafeeds for African aquaculture. *Aquaculture Reports*, 19, 100611. https://doi.org/10.1016/j.aqrep.2021.100611
- **N'zue, K. A.; Kouadio, A. M. and Yao, K. A.** (2022). Accessibilité économique des aliments piscicoles en Côte d'Ivoire : état des lieux et perspectives. *Revue Africaine d'Aquaculture*, 12(1): 15–27
- **Naumann, C. and Bassler, R.** (1976–1997). VDLUFA-Methodenbuch: Die chemische Untersuchung von Futtermitteln (Vol. III, with supplements 1983, 1988, 1993). Darmstadt: VDLUFA-Verlag
- Naylor, R. L.; Hardy, R. W.; Bureau, D. P., Chiu, A.; Elliott, M.; Farrell, A. P. and Nichols, P. D. (2021). A 20-year retrospective review of global aquaculture. *Nature*, 591(7851): 551–563. https://doi.org/10.1038/s41586-021-03308-6
- **NRC** (**National Research Council**). (2011). Nutrient Requirements of Fish and Shrimp. *National Academies Press*. https://doi.org/10.17226/13039
- **Obiero, K.; Munguti, J. and Charo-Karisa, H.** (2019). Aquaculture development in Africa: The role of policy and institutional frameworks. *Journal of Applied Aquaculture*, 31(2): 122–144. https://doi.org/10.1080/10454438.2018.1491354
- **Obiero, K.; Munguti, J. and Wainaina, M.** (2022). Sustainable aquaculture in sub-Saharan Africa: Challenges and opportunities. *Aquaculture Reports*, 22, 100956. https://doi.org/10.1016/j.aqrep.2022.100956
- **Pornsuwan, K.; Chotivanich, T. and Sangsawang, W.** (2023). Optimal harvest timing of *Hermetia illucens* larvae for nutrient yield. *Journal of Insect Science*, 23(1): 45–53. https://doi.org/10.1093/jisesa/iead012

- **Rodehutscord, M.; Kapocius, M.; Timmler, R. and Dieckmann, A.** (2004). Linear regression approach to study amino acid digestibility in broiler chickens. *British Poultry Science*, 45(1): 85–92. https://doi.org/10.1080/00071660410001668905
- **Schader, C.; Müller, A. and Stolze, M.** (2023). Optimising amino acid balance in aquafeeds for sustainable growth. *Aquaculture Nutrition*, 29(1): 88–102
- **Shati, A. A.; El-Morshedy, M. and El-Sayed, A.-F.M.** (2022). Black soldier fly larvae meal as a sustainable protein source for Nile tilapia. *Aquaculture Nutrition*, 28(4), 1023–1032. https://doi.org/10.1111/anu.13245
- **Suang, T.; Khamhaeng, S. and Phongphisut, S**. (2025). Post-harvest processing of *Hermetia illucens* larvae: Effects on nutrient retention. *Insect Technology and Feed Science*, 3(2): 88–96. https://doi.org/10.1016/j.itfs.2025.03.004
- **Tacon, A. G. J. and Metian, M.** (2015). Feed matters: Satisfying the feed demand of aquaculture. *Reviews in Fisheries Science & Aquaculture*, 23(1): 1–10. https://doi.org/10.1080/23308249.2014.987209
- **Vallod, D. and Le Reste, M.** (2023). Lipides fonctionnels issus d'insectes pour l'alimentation piscicole : efficacité et durabilité. *Revue Française d'Aquaculture Durable*, 11(1): 34-47
- van Huis, A. and Oonincx, D.G.A.B. (2017). The environmental sustainability of insects as food and feed: A review. *Agriculture*, 7(5), 91. https://doi.org/10.3390/agriculture7050091
- van Huis, A.; Van Itterbeeck, J.; Klunder, H.; Mertens, E.; Halloran, A.; Muir, G. and Vantomme, P. (2013). Edible insects: Future prospects for food and feed security. FAO Forestry Paper 171. Rome: Food and Agriculture Organization of the United Nations. https://www.fao.org/4/i3253e/i3253e.pdf
- Vodounnou, J. V.; Iko, R.; Sintondji, W.; Tossavi, E.; Kpogue, D. and Micha, J.-C. (2024). Rearing of black soldier fly (*Hermetia illucens*) larvae as a tool for managing agricultural byproducts. *Discover Agriculture*, 2, 91. https://doi.org/10.1007/s44279-024-00109-z
- Wilfart, A.; Espagnol, S. and Aubin, J. (2023). Economic and environmental assessment of alternative aquafeeds in tropical systems. *Journal of Cleaner Production*, 412, 137289. https://doi.org/10.1016/j.jclepro.2023.137289
- **Yeo, D.; Tan, B. and Ng, W.** (2024). Effects of dietary protein on moisture retention and muscle quality in tilapia. *Aquaculture Research*, 55(1):112–120
- **Zhou, X.; Feng, L. and Jiang, W.** (2012). Interaction of dietary methionine and arginine on growth and amino acid transport in tilapia. *Fish Physiology and Biochemistry*, 38(3): 785–794.