



Smart Proteins and Functional Additives for Fishmeal Replacement in Aquaculture: Decision Frameworks, Species-Specific Limits, and Practical Pathways

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ABSTRACT

Aquaculture continues to rely heavily on fishmeal (FM) due to its superior digestibility, amino acid balance, and palatability; however, finite supply, climate sensitivity, and price volatility increasingly challenge its long-term sustainability. This review synthesizes evidence (2010–2025) on smart protein alternatives—plant proteins, insect meals, single-cell proteins, and animal by-products—and on functional feed additives that stabilize performance in low-FM diets. Rather than presenting a descriptive inventory, a decision-oriented framework was applied integrating growth, feed efficiency, gut health, immunity, cost, and life-cycle assessment (LCA) outcomes across species. Across multiple taxa, a 70–90% reduction of FM is feasible when limiting amino acids (lysine, methionine, taurine) are corrected and anti-nutritional factors are mitigated through processing. Omnivorous species (e.g., tilapia and carp) tolerate higher plant and by-product inclusion, whereas salmonids require low-fiber, low-ANF ingredients supported by taurine and methionine. Functional additives—including enzymes, probiotics, phytogenics, and emerging nanoparticle formulations—can further enhance gut integrity and immune performance, although nanoparticles require strict dose control and residue monitoring. We highlight practical inclusion ranges, common failure modes, and minimum experimental standards of ≥ 60 –75 days (≈ 8 –12 weeks, depending on the endpoint), alongside the need for seed quality reporting and farm-scale validation to translate laboratory findings into commercial practice. This review provides a structured, species-specific roadmap for reducing fishmeal dependence while maintaining performance, economic viability, and environmental sustainability in aquaculture.

INTRODUCTION

Aquaculture is expanding, enhancing food and nutrition security and supporting rural livelihoods (FAO, 2022, 2024; Garlock *et al.*, 2022). This sector has relied on

fishmeal (FM) for a long time, valued for its high protein (60–72%), superior amino acid balance, exceptional digestibility (>95%), and essential fatty acids (EPA, DHA) (Miles & Chapman, 2006; NRC, 2011; Swanson *et al.*, 2012; Salze & Davis, 2015).

However, full dependency on FM is under severe stress because the supply of forage fish is finite and climate-sensitive (Naylor, 2023; FAO, 2024; Majluf *et al.*, 2024; Wu, 2025). This causes market instability (Merino *et al.*, 2010; Wu *et al.*, 2025). Moreover, the high Fish In: Fish Out (FIFO) ratios in carnivorous species (Naylor *et al.*, 2023; Radhakrishnan *et al.*, 2024) drive the search for viable replacements and stabilizing additives (Wu *et al.*, 2025).

This review considers smart proteins such as blood meal and poultry by-products (circular economy) and insect meals/single-cell proteins (SCPs) that are scalable and nutrient-dense (Aspevik *et al.*, 2017; Veldkamp *et al.*, 2022). Functional additives such as probiotics, enzymes, and amino-acid top-ups (El-Saadony *et al.*, 2021; Hernández-Contreras *et al.*, 2023; Torres-Maravilla *et al.*, 2024) are used to improve gut health and mitigate ANFs (El-Saadony *et al.*, 2021; Lappi *et al.*, 2022).

Fishmeal substitution strategies have to be species-specific: omnivores (tilapia and carp) demonstrate high tolerance for plant, especially when enzymes are supplemented (Hussain *et al.*, 2024; Karolina & Justyna, 2025), whereas temperate species (salmonids) demand low-fiber, low-ANF ingredients supported by taurine and methionine (Henry *et al.*, 2019; Egerton *et al.*, 2020).

Finally, the translation of fish feed trial results from the laboratory to commercial farms is further hampered by inconsistent trial design and reporting (Mahmud *et al.*, 2023), and critical factors including seed quality, sex ratios, duration, and rearing system type are often overlooked in short-term trials (<8 weeks) (Mahmud *et al.*, 2023).

This review synthesizes current scientific evidence on smart proteins and functional additives, identifies key design limitations that hinder reproducibility, and proposes a forward-looking agenda that integrates circular economy principles (Aspevik *et al.*, 2017) with omics-based nutrition (Martin & Król, 2017) and rigorous farm-scale validation to support sustainable aquaculture (Mahmud *et al.*, 2023).

MATERIALS AND METHODS

Software, Visualization and Cost–LCA Normalization

All graphical illustrations were prepared using the statistical software R (Version 4.3.1) relying heavily on the ggplot2 package (Version 3.5.1) and dplyr (Version 1.1.4) for the Cost–LCA quadrant, the species–guild decision tree was created with DiagrammeR (Version 1.0.11). Both cost and environmental footprint data were normalized against fishmeal (FM = 1.0), supporting the visual representation in Fig. (3). These normalized values are compiled and summarized in Supplementary Table (S3).

Evidence Identification and Selection

Relevant literature was identified through a structured search of Web of Science, Scopus, ScienceDirect, and Google Scholar databases covering the period from January

1, 2010 to June 30, 2025. Search strings were comprehensive, such as “soybean meal”, “canola”, “black soldier fly”, “single-cell protein”, “microalgae”, “yeast”, “poultry by-product”, and “blood meal”, in combination with “growth”, “FCR”, “gut histology”, “immunity”, “fillet quality”, “residues”, “LCA”, and “cost”.

Inclusion criteria consisted of peer-reviewed, controlled feeding trials. Trials were required to involve aquaculture relevant species and sufficient methodological detail. Studies such as conference summaries and non-peer-reviewed reports were not included. Review articles were read for context but were not used to judge the primary evidence or extract data.

Endpoint Definitions

Each trial was categorized for evidence synthesis so that consistent interpretation can be ensured across studies. Standard aquaculture metrics, initially final body weight and specific growth rate (SGR), were used to assess growth performance. Feed conversion ratio (FCR) was used as an integrative indicator of feed efficiency. Gut histology was evaluated using qualitative and quantitative assessments of intestinal tissue, with a specific focus on signs of intestinal integrity and inflammation. Both innate and adaptive immune parameters were used to define the immune response endpoint following experimental pathogen challenge. Life-cycle assessment (LCA) data were used to describe broader sustainability and economic effects, including greenhouse gas emissions, land use, and energy demand. Finally, cost was defined as the formulated diet cost relevant to commercial aquafeed use. These standardized definitions were applied uniformly to ensure objective, direct comparability across all alternative protein classes.

Evidence Counting and Confidence Scoring

Each eligible study was examined and counted based on the number and types of endpoints reported. A single study could contribute to multiple endpoints if related data were available, ensuring the record of each study’s contribution.

A structured rating system was used to judge the evidence. A score of 0 indicated the absence of primary studies for a given ingredient’s endpoint combination. Score 1 is given if the evidence only came from one single test, or unreliable short experiments. A moderate level of confidence (Score 2) was applied when two to four studies showed consistent results (including more than one farmed species). The highest confidence level (Score 3) was reserved for strong conclusions, to reach this score, researchers needed five or more studies covering several different species, and this level demanded validation from at least one long-term trial on an industry scale, or supported by LCA. This detailed approach, with scores translated visually (Fig. 1), allows for a clear distinction of well-established results from areas needing urgent research attention.

RESULTS

1. Overview of Fishmeal Context

1.1. Fishmeal: Role, Limitations, and the Case for Change

Traditionally fishmeal (FM) remains crucial due to its high digestibility (>95%), balanced amino acids (lysine/methionine), taurine, nucleotides, bioactive peptides, and LC-PUFAs (Miles & Chapman, 2006; Salze & Davis, 2015; Jamil *et al.*, 2023; Evrendilek, 2024). For salmonids, tilapia, catfish, carp, and shrimp, feed conversion ratio (FCR) is typically low and specific growth rate (SGR) is high when diets include FM (Egerton *et al.*, 2020; El-Saadony *et al.*, 2021; Hussain *et al.*, 2024). FM's continued importance is confirmed by the FAO (2024). Naylor *et al.* (2023) and Radhakrishnan *et al.* (2024) have stated that carnivores present more than 1 FIFO (Fish in: Fish out) rate.

Table 1. Comparative nutritional profiles of fishmeal, soybean meal, and black soldier fly (BSF) larvae meal in aquafeeds

Parameter	Fishmeal	Soybean Meal	BSF Larvae Meal
Crude Protein (%)	60–72 (Miles and Chapman, 2006)	44–50 (Davies and Jakeman, 2020)	40–60 (Sajid <i>et al.</i> , 2023; Rajeshbhai <i>et al.</i> , 2024)
Protein Digestibility (%)	>95 (Miles and Chapman, 2006)	80–88 (Davies and Jakeman, 2020)	85–92 (Rajeshbhai <i>et al.</i> , 2024)
Lysine (% of protein)	6.5–7.2 (NRC, 2011)	6.0–6.5 (Davies and Jakeman, 2020)	5.6–6.4 (Sajid <i>et al.</i> , 2023)
Methionine (% of protein)	2.2–2.8 (NRC, 2011)	1.3–1.5 (Davies and Jakeman, 2020)	1.7–2.2 (Sajid <i>et al.</i> , 2023)
Taurine Content	High (NRC, 2011; Salze and Davis, 2015)	Absent (Davies and Jakeman, 2020)	Moderate (Sajid <i>et al.</i> , 2023)
EPA/DHA (Omega-3)	High (NRC, 2011)	Negligible (Davies and Jakeman, 2020)	Low–moderate (Rajeshbhai <i>et al.</i> , 2024)
Anti-Nutritional Factors (ANFs)	None	Present (phytate, trypsin inhibitors) (Davies and Jakeman, 2020)	None; chitin may reduce digestibility (Rajeshbhai <i>et al.</i> , 2024)
Palatability	High (Miles and Chapman, 2006)	Moderate (Davies and Jakeman, 2020)	Moderate (Rajeshbhai <i>et al.</i> , 2024)

2024)

Table 2. Performance metrics for aquaculture species fed fishmeal-based diets

Species	Fishmeal Inclusion Level	FCR	SGR (%/day)	Reference
Atlantic salmon (<i>Salmo salar</i>)	35–45%	0.9–1.1	1.5–2.2	(Egerton <i>et al.</i> , 2020; Hong <i>et al.</i> , 2025)
Nile tilapia (<i>Oreochromis niloticus</i>)	20–30%	1.2–1.5	1.4–1.9	(Hussain <i>et al.</i> , 2024)
Pacific white shrimp (<i>Litopenaeus vannamei</i>)	25–30%	1.2–1.4	1.6–2.1	(Amaya <i>et al.</i> , 2007; El-Saadony <i>et al.</i> , 2021)
Catfish (<i>Pangasius</i> spp.)	20–30%	1.3–1.6	1.2–1.8	(Jamil <i>et al.</i> , 2023)

FCR = feed conversion ratio (feed intake/weight gain), SGR = specific growth rate, % per day.

1.2. Limitations and Sustainability

Despite being an ideal feed ingredient for fish, fishmeal (FM) has several limitations, including challenges in meeting increasing demand while maintaining stable prices (Merino *et al.*, 2010), higher energy use and greenhouse gas emissions in life cycle assessments (Veldkamp *et al.*, 2022; Wang *et al.*, 2022), concerns related to the sustainability of harvesting small pelagic species (Majluf *et al.*, 2024), and additional environmental burdens associated with processing energy requirements (Rajeshbhai *et al.*, 2024; Wu *et al.*, 2025). It is also important that traceability and eco-labels are considered (Borreagaard, 2025).

2. Smart Protein Solutions

Many potential alternatives of fishmeal are already in practice which can replace significant FM when AAs are corrected and ANFs mitigated (Egerton *et al.*, 2020; Mahmud *et al.*, 2023; Hussain *et al.*, 2024; Karolina & Justyna, 2025).

The aquaculture sector is shifting increasingly toward innovative, smart proteins due to the expense and environmental concerns associated with conventional protein (fishmeal). They can be categorized under four main classes such as plant, insect, SCP, and animal by-products. Processing (fermentation, enzymatic hydrolysis, defatting) this smart protein and additives support can broaden substitution of fish meal (Hussain *et al.*, 2024; Alves *et al.*, 2025) (Tables 1, 2).

2.1. Plant Proteins

Fishmeal is usually replaced in aquafeeds with plant proteins. This is mainly because they are more affordable and address the public concern (Gajardo *et al.*, 2017). Plant proteins (soy, canola/rapeseed, cottonseed, pea, duckweed) are cost-effective but limited by ANFs and AA shortfalls (Davies & Jakeman, 2020; Hussain *et al.*, 2024). Fermentation/enzymatic processing, combined with lysine/methionine/taurine fortification, improves digestibility and mitigates enteritis risk, particularly in salmonids (Henry *et al.*, 2019; Egerton *et al.*, 2020; Lappi *et al.*, 2022; Radhakrishnan *et al.*, 2024). Egerton *et al.* (2020) found that replacing some of the fishmeal with partly hydrolyzed fish protein hydrolysate (FPH) in a high plant protein (PHP) diet produced the same growth performance in fish as the original FM diet. However, other studies (Valente *et al.*, 2016) demonstrated that replacing FM with plant proteins had no adverse effect on animal growth, and one report (Kari, 2023) even showed an improvement.

2.2 Insect Meals

Insects such as black soldier fly larvae (BSFL), mealworms, and crickets provide 40–60% protein and beneficial lipids; however, their chitin content may support immune function while potentially reducing nutrient digestibility at high inclusion levels (Sajid *et al.*, 2023; Rajeshbhai *et al.*, 2024). Maintaining black soldier fly larvae (BSFL) inclusion at approximately 15–25%, supplemented with methionine and taurine, supports optimal growth performance (Veldkamp *et al.*, 2022; Oliveira *et al.*, 2023). (Table 3).

Table 3. Comprehensive comparison of eight type of insect meals

Type of Insect Meal	Key Nutritional Value Components (% in diet)	Effective Inclusion Level (% of FM Replacement)	Effect on Growth and Performance
1. Silkworm Pupa Meal (SPM) (<i>Bombyx mori</i>)	High Crude Protein (CP): 60.7% (Defatted: 81.7%); Lipids: 25.7%; Rich in lysine and threonine; Superior amino acid (AA) profile compared to soymeal (SM) (De Souza-Vilela <i>et al.</i> , 2019).	Up to 100% replacement was successful in common carp and Japanese sea bass (Ji <i>et al.</i> , 2015); Inclusion of <50% generally does not negatively affect performance.	Decent/Positive outcomes. High digestibility, sometimes better than fishmeal (FM). 100% replacement was possible without losing growth performance in common carp (Karthick Raja <i>et al.</i> , 2019). Inclusion of up to 30% successfully substituted FM in rainbow shark (Raja <i>et al.</i> , 2020).

2. Black Soldier Fly Larvae Meal (BSFLM) (<i>Hermetia illucens</i>)	CP: 42.1% (Defatted: 56.9%); Lipids: 26.0%; High ash (>15%) and high calcium (7.56% of dry matter); Ca/P ratio is high (8.4). Most similar to FM in AA profile and protein digestibility (Alfiko et al., 2022).	Up to 50% (defatted) in Jian carp (Stadtlander et al., 2017); Max 40% (partially defatted) in rainbow trout (Cardinaletti et al., 2019); Up to 50% in African catfish (Adeoye et al., 2020); Up to 100% tested in Atlantic salmon. (Weththasinghe et al., 2021)	Maintains performance typically when partially replacing FM. 20% replacement showed no effect on growth in yellow catfish (Hu et al., 2017). 50% replacement improved growth and feed conversion ratio (FCR) in rainbow trout. However, substitution in turbot resulted in lower specific growth rate (SGR) (Li et al., 2017).
3. Housefly Maggot Meal (HMM) (<i>Musca domestica</i>)	CP: 50.4% (Defatted: 62.1%); Lipids: 18.9%; High phosphorus (1.6%) (Allegretti et al., 2017 ; De Souza-Vilela et al., 2019); Rich in Lysine and high in Tryptophan. High unsaturated fatty acids (60–70%) (Hawkey et al., 2021).	Cannot exceed 30% in catfish species without lowering growth performance (Saleh, 2020); Up to 75% of wet maggots used in diets for <i>Clarias gariepinus</i> juveniles (Emeka and Oscar, 2016); Up to 30% in Asian bass (no growth effect) (Lin and Mui, 2017).	Generally encouraging. Inclusion can boost growth and FCR. 34% substitution provided the best growth and survival rate in the Nile tilapia (<i>Oreochromis niloticus</i>) (Wang et al., 2017).
4. Yellow Mealworm Meal (YMM) (<i>Tenebrio molitor</i>)	CP: 52.8% (Defatted: 82.6%); Highest reported lipid content (36.1%) (van Huis, 2020); Lower in Lysine than FM. High unsaturated fatty acids (60–70%) (Makkar et al., 2014).	Up to 50% replacement possible in rainbow trout (Gasco et al., 2014); Up to 75% in yellow catfish juveniles (Ng et al., 2001); Up to 80% (defatted) tested in European sea bass (Basto et al., 2021).	Maintained growth when replacing up to 40% in African catfish. Inclusion of 18% improved immune response and bacterial resistance in yellow catfish. However, 50% substitution reduced growth in gilthead sea bream and European sea bass (Basto et al., 2021).
5. Lesser Mealworm Meal (LMM) (<i>Alphitobius diaperinus</i>)	CP: 57.3% (Defatted: 62.6%); Lipids: 8.5%; Ca/P ratio 1.18; Lower Lysine than FM (De Souza-Vilela et al., 2019).	Research data are scarce.	Research data is scarce. High chitin levels in adults may negatively affect growth (Khayrova et al., 2021).
6. House Cricket Meal (HCM) (<i>Acheta domestica</i>)	Highest CP: 63.3% (Defatted: 76.5%); Lipids: 17.3%; Ca/P ratio 1.28; Lower Lysine than FM. High unsaturated fatty acids (60–70%) (Hawkey et al., 2021).	Tested at 60% (mixed with rice bran) in hybrid tilapia; Tested at 25% in perch (Lee et al., 2017).	60% inclusion (with rice bran) yielded the best results in survival and growth rate in red hybrid tilapia. 25% replacement decreased fish growth and increased FCR in perch (Lee et al., 2017).

7. Banded Cricket Meal (BCM) (<i>Grylloides sigillatus</i>)	CP: 59.8% (Defatted: 69.0%); Lipids: 13.3%; Ca/P ratio 0.19; Lower Lysine than FM.	20% inclusion tested in rainbow trout (Józefiak <i>et al.</i>, 2019).	Full-fat meal at 20% inclusion showed no positive effects on survival or growth performance indicators in rainbow trout. More trials are required (Józefiak <i>et al.</i>, 2019).
8. Jamaican Field Cricket Meal (GAM) (<i>Gryllus assimilis</i>)	CP: 55.5%; Lipids: 11.8%; Lower Lysine than FM.	Tested in the Nile tilapia male fingerlings (Fontes <i>et al.</i>, 2019).	The tested meal may be used to feed Nile tilapia fingerlings (Fontes <i>et al.</i>, 2019).

3. Single-Cell Proteins (SCP)

SCP products are derived from microbial sources, including bacteria, yeast, and microalgae (**Jones *et al.*, 2020**), often providing 50–70% protein and LC-PUFAs (**Alves *et al.*, 2025**). They are generally optimized as a 5–15% functional supplement to effectively balance nutrients (**Pereira *et al.*, 2022**).

3.1 Yeast and Fungi

Desirable antioxidant properties of *Rhodotorula mucilaginosa* biomass and the EPA-producing capability of *Yarrowia lipolytica* are highly valued (**Tocher *et al.*, 2019**). In case of improving the physiology of fish, yeast SCP at 10% improved gut histology and FCR in low-FM catfish diets (**Wu *et al.*, 2025**).

3.2 Microalgae

Numerous studies have confirmed that microalgae are a successful replacement or additive for fishmeal and fish oil in aquafeeds, which generally leads to improved growth and quality across various aquaculture species (**Sirakov *et al.*, 2015**; **Sarkar *et al.*, 2018**). Species that are commercially important for their protein production include *Spirulina* (65%), *Dunaliella* (57%), and *Chlorella* (55%) (Table 4).

Table 4. Inclusion level of microalgae in feed in different species

Microalgae	Fish Species name	Inclusion level	Reference
Defatted <i>Desmodesmus</i> sp.	Salmon	10-20%	Kiron <i>et al.</i> (2016)
<i>Spirulina</i> algal meal	Rainbow trout	10%	Sirakov <i>et al.</i> (2012)
<i>Scenedesmus almeriensis</i>	Rainbow trout	40%	Thomas <i>et al.</i> (2018)

3.3 Bacteria

Bacterial SCP strains are an excellent source of nutrition. Its crude protein content is greater than 80 wt% and exhibit high values of essential amino acids. These strains also

produce vitamins, phospholipids, and other functional compounds and they can be cultivated using various feedstocks (Ritalia *et al.*, 2017).

4. Animal By-Products

The robust amino acid profiles and ability to enhance palatability make animal by-products an ideal feed ingredient, though maintaining consistent quality control (QC) is a primary concern (Aspevik *et al.*, 2017). Their inclusion rate is typically used at 10-20% in salmonid diets (Henry *et al.*, 2019), and at 20-25% of replacement in fishmeal in species such as the butter catfish (Hossain *et al.*, 2025).

5. Processing Enhancements

The sustainable use of alternative ingredients depends mostly on balancing inclusion rates with species-specific sensitivities and mitigating ANFs. Salmonids are notably more sensitive, and require the use of low ANF ingredients, though for omnivorous species they successfully tolerate 30–40% plant material in mixed diets supplemented with enzymes. Thus, different alternatives are used cautiously, as SCPs at 5–10% for micronutrient balance, and 15-20% insects for bulk protein (Table 5, 6, 7 & Fig. 1).

Table 5. Concise ingredient blends: Omnivore vs. salmonid sensitivity

Alternative Ingredient	General Inclusion Rate & Key Requirements	Omnivore Guild (Tolerance)	Salmonid Guild (Sensitivity/Limit)
Plant Material	30–40% inclusion + phytase + Met/Lys required.	Works successfully at this high inclusion rate.	Requires low-ANF inputs due to higher sensitivity.
BSFL	15–20% inclusion + taurine required.	Outcomes are comparable to fishmeal (FM) controls.	Outcomes are assumed to approximate FM controls when taurine is supplemented.
Poultry By-product	10–20% inclusion.	Broadly acceptable inclusion.	Broadly acceptable inclusion.
SCP	5–10% inclusion.	Best utilized as functional complements.	Best utilized as functional complements.

Table 6. Comparative overview of smart protein sources in aquaculture

Protein source	Examples	Crude protein (%)	Key benefits	Limitations	Typical inclusion (%)
Plant-based proteins	Soybean, canola/rapeseed, duckweed	40–50	Cost-effective, widely available	ANFs; methionine & lysine deficits	20–40

Insect meal	BSF mealworm	larvae,	40–60	Immune benefits (chitin), good palatability	Scale/cost; chitin may reduce digestibility	10–30
Single-cell proteins (SCPs)	<i>Spirulina</i> , <i>Chlorella</i> , <i>Schizochytrium</i> , yeast		50–70	Dense nutrients; can use non-arable inputs	Cost, digestibility, scale-up	5–15
Animal by-products	Poultry by-product meal, blood meal		55–65	Waste valorization; strong amino-acid profile	Quality consistency; perception	10–25

Plant proteins	Moderate	Moderate	Low-Mod	Moderate	Low	NA	Moderate	High
Insect meals	Moderate	Moderate	Low-Mod	Low-Mod	Low	NA	Low-Mod	Low-Mod
SCP	Low-Mod	Low-Mod	Low	Low	Low	NA	Low-Mod	Low-Mod
Animal by-products	Moderate	Moderate	Low	Low	Low	NA	Moderate	High
	Growth	FCR	Gut histology	Immunity	Fillet quality	Tissue residues	LCA/Footprint	Cost

Fig. 1. Confidence in evidence across endpoints by ingredient class. Heatmap scoring confidence for growth, FCR, gut histology, immunity, fillet quality, residues, LCA, and cost (0 = none, 1 = low, 2 = moderate, 3 = high). Scores derive from primary studies identified in the 2010–2025 search; counts and representative citations are listed in Supplementary Table (S1).

Table 7. Strengths, weaknesses, necessary mitigations, and safe inclusion ranges for smart protein categories

Class	Key strengths	Key weaknesses (typical failure modes)	Mitigations required	Safe/typical inclusion bands*
Plant proteins (soy, canola, pea, duckweed)	Availability, cost; predictable specs	ANFs (phytate, trypsin inhibitors), fiber; Met/Lys deficits; enteritis risk (salmonids)	Fermentation/enzymatic hydrolysis; phytase/protease; Met/Lys top-ups; keep fiber low in salmonids	Omnivores: 30–50% with enzymes/AA; Salmonids: ≤15–25% low-ANF, with AA & histology monitoring
Insect meals (BSF, mealworm)	Good protein, lipids; chitin—potential immunomodulation; circularity	Chitin lowers digestibility at high inclusion; taurine shortfalls; scale/cost	Partial defatting; protease; taurine support in carnivores; blend with by-products	Omnivores: 10–30%; Salmonids: 10–20% with taurine
SCP (microalgae, yeasts, bacteria)	Dense nutrients; some LC-PUFA; non-arable inputs	Cell wall/nucleic acids; digestibility; cost/scale	Use as functional top-ups; pairing for AA/PUFA; processing to improve digestibility	Mixed diets: 5–15% typical
Animal by-products (poultry, blood)	Strong AA profile; palatability; waste valorization	Batch variability; perception/market access	QC specs (moisture, pathogens, AA profile); hydrolysis for palatability	10–25%; warm-water catfish: partial FM→blood meal feasible

6. Functional Feed Additives

Additives are valuable because they help bridge amino acid deficiencies, promote a stable microbiota, minimize stress responses, and bolster innate immunity. However, the ultimate success of any intervention is heavily influenced by the design quality of the trial (≥ 12 weeks is needed for additive evaluations (except larval phases)) (Table 8).

6.1. Probiotics and Prebiotics

Probiotics improve growth and immune function by enhancing digestibility and actively suppressing pathogens through the creation of compounds such as lysozyme, and organic acids (Eissa *et al.*, 2022). Their effects are often increased by combining prebiotics like inulin, MOS, and FOS (El-Saadony *et al.*, 2021; Soltani *et al.*, 2023; Preena *et al.*, 2025). Marine-adapted strains are now available (Torres-Maravilla *et al.*, 2024), though reliable data on their performance during stress remains limited.

6.2. Phytochemicals and Immunostimulants

Phytochemicals can be sourced from a wide range of plants such as leaves, stems, roots, seeds, fruits, and spices (Encarnaç o, 2016) and they offer antimicrobial and antioxidant benefits, while encapsulation of these components enhances stability and delivery (Hern andez-Contreras *et al.*, 2023). Encapsulated turmeric improved antioxidant status and feed conversion ratio under heat stress in tilapia (Radhakrishnan *et al.*, 2024).

Immunostimulants such as β -glucans, nucleotides, levamisole, and chitosan have been shown to enhance shrimp survival against *Vibrio* infections, even when the diet contains less fishmeal (Oliveira *et al.*, 2023).

6.3. Enzymes and AA Fortification

Commonly utilized enzymes in aquaculture diets include phytase, carbohydrase, protease, lipase, alpha-amylase, papain, and pepsin which can enhance nutrient availability and mitigate the negative effects of ANFs (Lappi *et al.*, 2022). Additionally, these supplements are used to correct limiting amino acid profiles in the feed. The effectiveness of these strategies is evidently found in improving salmon growth rates comparable to those fed fishmeal (FM) controls (Hong *et al.*, 2025).

6.4. Nanoparticles (Emerging)

Gold (Au), ferric oxide (Fe_2O_3), zinc oxide (ZnO), chitosan carriers, and nano-chromium (nano-Cr) have been reported to be effective at modifying the microbiota, enzyme activity, and immune signaling in aquaculture species but are currently confined to the research stage (Shahariar *et al.*, 2024). Their positive effects are generally observed at mid-range doses, though, caution is required under critical safety concerns; rigorous regulatory oversight and residue monitoring are essential to mitigate the significant risk of inducing oxidative stress through overdosing (Zhang, 2015; Shahariar *et al.*, 2024).

Table 8. Functional additives in aquafeeds and their biological functions

Additive type	Common sources/examples	Mode of action	Key benefits
Probiotics	<i>Bacillus</i> , <i>Lactobacillus</i> , <i>Saccharomyces</i>	Compete with pathogens; strengthen barrier; immunomodulation	Better gut health, nutrient uptake, disease resistance
Prebiotics	Inulin, MOS, FOS	Selectively fuel beneficial microbes	Stabilize microbiota; reduce dysbiosis; support probiotics
Phytochemicals	Garlic, ginger, neem, turmeric, oregano oil, capsaicin	Antimicrobial, antioxidant, anti-inflammatory; often encapsulated	Improved palatability, antioxidant status, stress resilience
Immunostimulants	β -glucans, nucleotides,	Activate innate immunity	Lower mortality during challenges; stronger

	levamisole, chitosan	(macrophages, lysozyme, complement)	baseline immunity
Digestive enzymes	Phytase, protease, amylase	Degrade ANFs; improve digestion and absorption	Higher feed efficiency; reduced waste loading
Amino acid fortifiers	Lysine, methionine, taurine	Correct limiting AAs in low-FM diets	Maintain growth and FCR; support metabolism
Nanoparticle additives (emerging)	AuNPs; Fe ₂ O ₃ -NPs; ZnO-NPs; chitosan nano-Cr	High surface area & bioavailability; microbiota/enzyme modulation; redox & immune signaling; carrier for co-actives	Species- & dose-dependent gains in growth/feed use, antioxidant/hematology, gut integrity & survival (early evidence) (Geffroy <i>et al.</i>, 2014; Zhang <i>et al.</i>, 2015; Thangapandiyani & Monika, 2020; Thangapandiyani <i>et al.</i>, 2020; Rakhi <i>et al.</i>, 2022; Ahmad <i>et al.</i>, 2023; Shahariar <i>et al.</i>, 2024)
Carotenoids	astaxanthin (red), tunaxanthin (yellow), canthaxanthin (orange red), beta-carotene (orange), and doradexanthins (yellow), zeaxanthin (red,) and echinone (red) (Lim <i>et al.</i>, 2018)	Precursors to vitamin A2	Boosted antioxidant status and gene expression (Rufchaei <i>et al.</i>, 2017). Enhance larval growth (Wang <i>et al.</i>, 2018)

7. Species-Specific Strategies

The successful strategy for reducing fishmeal reliance is heavily species-specific, with subtle differences between the flexibility of omnivores and the heightened sensitivities of carnivorous salmonids. Tropical species, including tilapia and shrimp, show strong tolerance for plant protein mixtures, often achieving up to 40–50% inclusion when ANFs are controlled and essential AAs are addressed. The use of blood and poultry by-products further increases the AA profile for these species, and important additives

like immunostimulants support survival, particularly in shrimp (Oliveira *et al.*, 2023; Hossain *et al.*, 2025). In contrast, temperate salmonids demand low-ANF, low-fiber inputs. Their diets necessitate strategic fortification with taurine and methionine, while utilizing substitutes like hydrolyzed by-products, microalgae, or taurine-supported black soldier fly larvae (Henry *et al.*, 2019; Egerton *et al.*, 2020; Hong *et al.*, 2025). The external validity of all research significantly depends on cross-cutting factors with mandatory standardization (Mahmud *et al.*, 2023) (Table 9).

Table 9. Comparative feeding strategies for tropical versus temperate aquaculture species under fishmeal reduction

Category	Tropical species (<i>L. rohita</i> , <i>P. hypophthalmus</i> , <i>O. niloticus</i> , <i>L. vannamei</i>)	Temperate species (<i>S. salar</i> , <i>O. mykiss</i> , <i>C. lavaretus</i>)
Digestive traits	Better carbohydrate use; moderate tolerance to ANFs	High protein & lipid needs; low tolerance to fiber/ANFs
Common challenges	Gut dysbiosis under heat/salinity stress; growth dips in FM-free trials	Enteritis, reduced digestibility, skeletal issues if FM replaced excessively
Preferred protein sources	Soybean/duckweed/canola; blood meal, poultry by-products	Hydrolyzed poultry meal; BSF meal; microalgae (e.g., <i>Schizochytrium</i>)
Additive strategy	Probiotics + prebiotics; phytase/protease; phytogenics; immunostimulants	Taurine & methionine; phytase (if plants used); FOS/yeast fractions; probiotics
Typical inclusion (alternatives)	Up to 40–50% plant (with enzymes/AA fortification); animal by-products as needed	Up to 25–30% mixed alternatives (BSF, poultry, microalgae) with AA supplementation
Evidence anchors	Warm-water catfish were sustained on partial FM → blood meal inclusion (Aspevik <i>et al.</i> , 2017; Hossain <i>et al.</i> , 2025)	Salmonids: FM-reduced diets were sustained with insect/microalgae + AA support (Henry <i>et al.</i> , 2019; Egerton <i>et al.</i> , 2020; Hong <i>et al.</i> , 2025)

Notes: ANFs = anti-nutritional factors; FOS = fructo-oligosaccharides; “typical inclusion” indicates commonly reported practical ranges—final levels vary depending on species, life stage, processing, amino-acid balance, and palatability.

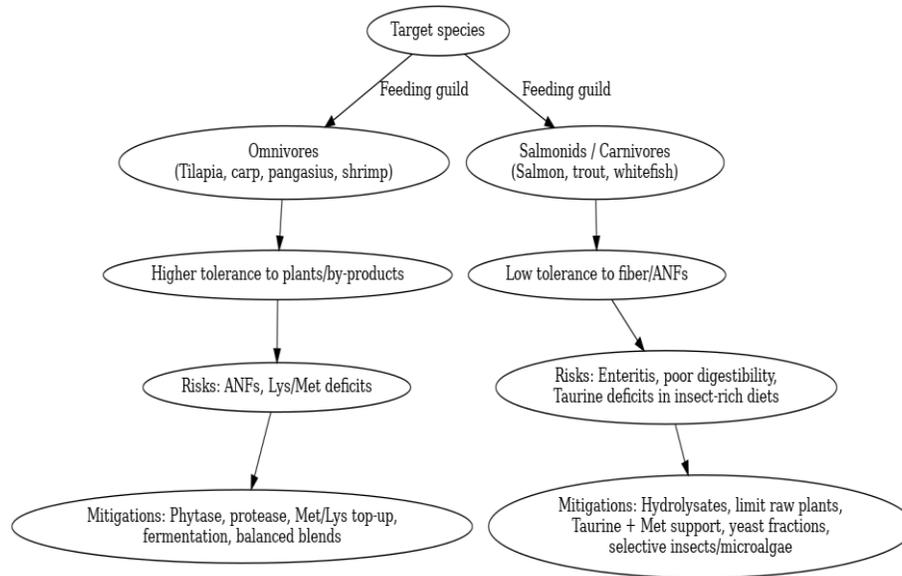


Fig. 2. Decision tree for ingredient blending and mitigations. Flowchart for omnivores vs salmonids showing inclusion bands (plants, insects, SCP, by-products), mitigation packs (enzymes/processing/AA support; microbiome supports), and monitoring flags (FCR drift, histology, off-flavour). Detailed branching rules are in the Supplementary Table (S2)

DISCUSSION

1. Challenges and Practical Levers

Among several impediments, the main ones are involved in managing ANFs in plant and insect chitin, and this regularly requires enzymatic processing and correcting amino acid imbalances (Davies & Jakeman, 2020; Lappi *et al.*, 2022). Based on this, species specificity indicates that salmonids must accept low-ANF diets fortified with taurine/methionine (Henry *et al.*, 2019; Egerton *et al.*, 2020). Again, the practical acceptability is restricted by unstable market and the initial costs of new proteins (Merino *et al.*, 2010). For ensuring real-world translation, trials must meet standards of ≥ 60 –75 days duration, farm validation, and rigorous safety oversight for emerging nanoparticles (Mahmud *et al.*, 2023; Shahariar *et al.*, 2024) (Table 10).

Table 10. Main challenges in replacing fishmeal and practical ways to address them

Challenge	Underlying cause	Practical levers	Example citations
ANFs & digestibility (plant, insect)	Phytate/tannins/trypsin inhibitors; chitin elevates the indigestible fraction	Fermentation/enzymatic hydrolysis; heat/pressure; phytase/protease; partial defatting; AA fortification	(Davies and Jakeman, 2020; Lappi <i>et al.</i> , 2022; Sajid <i>et al.</i> , 2023; Rajeshbhai <i>et al.</i> , 2024)
AA limitations	Methionine/lysine/taurine shortfalls depress growth	Targeted AA top-ups; blend complementary proteins; use hydrolysates for palatability	(Egerton <i>et al.</i> , 2020; Lappi <i>et al.</i> , 2022)
Species sensitivity	Salmonids poorly tolerate fiber/ANFs; omnivores more flexible	Keep fiber low for salmonids; FOS/yeast fractions; gradual ramp; monitor FCR/SGR	(Henry <i>et al.</i> , 2019; Egerton <i>et al.</i> , 2020; Hernández-Contreras <i>et al.</i> , 2023; Hong <i>et al.</i> , 2025)
Cost & scale	Early-stage insect/SCP supply; FM price volatility	Regional protein baskets; valorize blood meal/poultry by-products; process upgrades; co-product logistics	(Merino <i>et al.</i> , 2010; Aspevik <i>et al.</i> , 2017; Auzins <i>et al.</i> , 2024; Hossain <i>et al.</i> , 2025)
Regulatory/market	Uneven approvals; traceability demands	Follow FAO codes; third-party certification; transparent sourcing & LCA claims	(FAO, 2010; Borregaard, 2025)
Evidence gaps	Few long, multi-endpoint trials; limited mechanistic markers	Longer trials; omics endpoints; stress-testing; include cost & LCA	(Martin and Król, 2017; Ghamkhar and Hicks, 2020; Mahmud <i>et al.</i> , 2023;

Lagoumintzis
and Patrinos,
2023;)

Emerging tech risk Nanoparticle dose/residue/ecology not standardized Conservative dosing; residue monitoring; environmental risk plans (Shahariar *et al.*, 2024)

Notes: AA = amino acids; ANFs = anti-nutritional factors; FCR = feed conversion ratio; SGR = specific growth rate; LCA = life-cycle assessment; FOS = fructo-oligosaccharides.

2. Future Directions (2026–2030)

To optimize future blends, priority should be given to precision nutrition, and integrating 'omics' markers with performance data (Martin & Król, 2017). It has been reported that scaling up circular feeds, such as waste-fed insects, requires better field-scale quality control and logistics (Radhakrishnan *et al.*, 2024). All of these indicate a need for rigorous trial standards of ≥ 60 days and immediate establishment of global governance for novel nanoparticle additives (Mahmud *et al.*, 2023; Shahariar *et al.*, 2024). It is also predicted that by 2030, blended proteins could commonly achieve $\geq 75\%$ FM replacement at a competitive price (Mahmud *et al.*, 2023), with region-specific LCA and cost models remaining limited (Fig. 3).

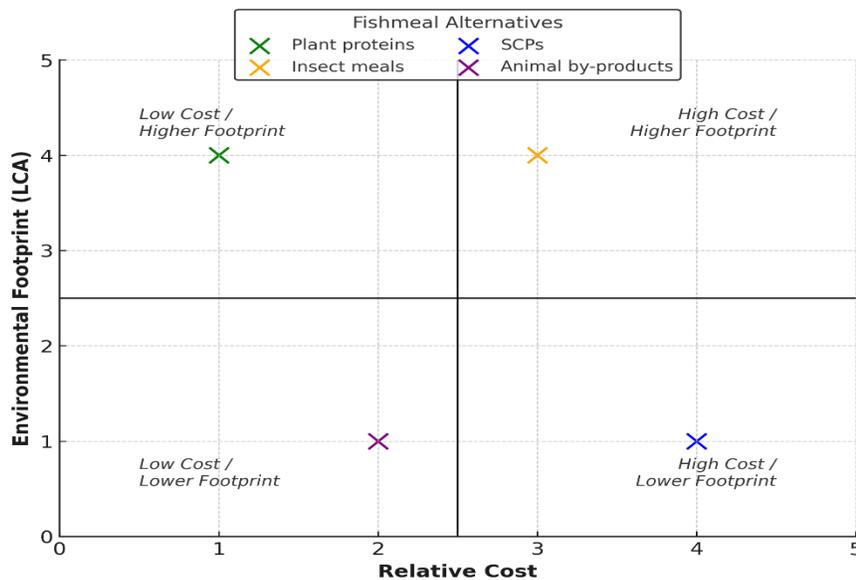


Fig. 3. Cost–LCA quadrant for major fishmeal alternatives. X-axis: relative cost index (ingredient cost per kg digestible protein, FM = 1.0). Y-axis: relative environmental footprint index (composite LCA normalized to FM = 1.0). Dotted lines mark FM baselines ($x = 1.0$, $y = 1.0$). Point placements and sources are in Supplementary Table (S3)

CONCLUSION

The sustainable reduction of fishmeal (FM) is crucial, driven by mounting ecological and economic pressures. Future resilience will depend on integrating omics-guided formulation, precision feeding, and robust circular sourcing, while ensuring that emerging materials such as nanoparticles are subject to strict safety oversight, including dose and residue monitoring within regional quality control frameworks. Ultimately, laboratory successes must be translated into practice through standardized farm trials, particularly those spanning 60–75 days .

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