



Current advances in alternative lipids for sustainable aquafeeds: Nutritional requirements, processing technologies, environmental sustainability, and future directions

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Abstract

Aquafeeds provide lipids for energy, EFAs, and fat-soluble vitamin absorption. Aquaculture demand is rising, while global fish oil (FO) production remains at 1 million metric tons. Most marine predators need EPA and DHA supplements, although freshwater animals can synthesize long-chain omega-3s from plant-derived C18 polyunsaturated fatty acids. FO has been the main lipid source in fish feed; however, limited marine-sourced sources and high demand and costs cause problems. We discuss alternate lipid sources in development, including vegetable oil, animal fat, microalgae oil, genetically engineered oilseed crops, insect oil, single-cell oil, and food sector byproducts. Lipid sources' nutritional quality and restrictions affect fish health and performance. Advanced technologies, including precision nutrition, lipid blending, encapsulation, and feed formulation, are examined. Some freshwater species can survive without FO, unlike marine fish that need EPA and DHA. Life-cycle assessment data show that insect oils and fish-processing byproduct oils have lower carbon, land-use, and water-use footprints than conventional FO and many crop-derived oils, emphasizing the importance of sustainability metrics in lipid selection. Multigenerational consequences, species-specific lipid demands, gut flora interactions, and consumer attitudes toward new feed components need more research.

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INTRODUCTION

Aquaculture has been the fastest-growing sector in food production, providing more than 50% of the total seafood for human consumption and becoming increasingly crucial for global food security (Dongyu, 2024). The growth of this sector has taken place at an average annual growth rate of 5.3%, whereas the wild capture fisheries have experienced little to no growth over the same period (Naylor et al., 2021). Although this expansion is important for meeting the growing demand for protein, it has increased pressure on marine-derived feed ingredients.

Conventionally, FO from the reduction of fisheries (such as anchovy, menhaden, capelin, and sandeel) has represented the benchmark lipid ingredient because of its well-balanced composition of n-3 LC-PUFAs (15–25% EPA and 8–15% DHA) (Turchini et al., 2009). Nevertheless, worldwide annual FO production capacity has saturated at about 1 million metric tons since the beginning of the 2000s, and its price has become highly volatile, increasing by more than 300% during the period from 2005 to 2020 (Dongyu, 2024). In this context, the use of such lipids is a significant constraint on

aquaculture sustainability, considering the expanding aquaculture industry for raising carnivorous marine finfish (such as salmon, sea bream, sea bass, tuna, cobia, and grouper).

This challenge is particularly pronounced in marine fish and certain crustaceans, which have limited abilities or even an inability to biosynthesize EPA/DHA starting from the C18 polyunsaturated fatty acids linoleic acid (LA, 18:2 n-6) and alpha-linolenic acid (ALA, 18:3 n-3) due to their deficient $\Delta 5$ and $\Delta 6$ fatty acid desaturase and elongase activities (Monroig et al., 2018). On the other hand, freshwater and diadromous fish (salmon, trout, carp, tilapia, and catfish) have operational elongation/desaturation mechanisms enabling them to transform the C18 PUFA into LC-PUFA (Glencross, 2009). Such an intrinsic biochemical difference results in various options for nutrition planning for these fish.

Hence, there has been an increasing amount of research conducted during the last two decades aiming at the development of effective approaches to substitute FO with alternative lipid sources for feed production, without negative effects on fish health, growth, reproduction, and final quality of the product consumed by humans (Sprague et al., 2016; Turchini et al., 2009; Tocher, 2003). Taking into account the formulation process, physiological effects, promising research trends, and particular knowledge gaps, the review provides a critical overview of the most important advancements in this field.

Statement of the Problem

The demand for fish oil (FO), a finite resource from the ocean that has been extensively utilized in fish feed formulations, has increased due to the swift growth of aquaculture. The use of FO raises concerns about environmental sustainability, limited supply, volatile pricing, and competition with human use of ocean resources. While many substitutes for FO have been discovered, there are still many unknowns about their nutritional value, influence on fish performance, sustainability, and human nutrition. Therefore, this review aimed to

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evaluate the suitability of alternative lipid sources as substitutes for FO in aquafeeds from nutritional, technological, physiological, and environmental perspectives.

Research questions

1. What are the alternative lipid sources that can effectively replace fish oil in aquafeeds?
2. How do alternative lipid sources influence fish health, performance, and product quality?
3. What technological advances have improved the utilization of alternative lipids in aquafeeds?
4. What future research directions are needed to achieve sustainable FO replacement in aquaculture?

MATERIALS AND METHODS

This study employed a narrative literature review methodology. Relevant peer-reviewed articles, review papers, book chapters, and other publications between 2000 and 2025 were obtained from databases such as Scopus, Web of Science, ScienceDirect, PubMed, and Google Scholar. The keywords that were used in the search include "aquafeed lipids," "fish oil replacement," "microalgae oil," "insect oil," "single cell oil," "omega-3 fatty acids," and "aquaculture nutrition." The literature was selected based on its relevance, scientific value, and contribution to the knowledge about lipid nutrition and new lipid sources in aquaculture.

Lipid nutrition in aquaculture species

Lipid classes and their physiological functions

Aquafeeds contain a variety of lipids with distinct roles. Up to 80–95% of all dietary lipids are neutral lipids, or triglycerides, which are the primary source of energy reserves. These are absorbed as free fatty acids and monoacylglycerols after being hydrolyzed by pancreatic lipase enzymes in the intestines. They are subsequently esterified and carried in chylomicrons. Phospholipids, also known

as polar lipids, are crucial parts of cellular membrane structures and serve as emulsifiers to make it easier for lipids to be absorbed and digested. These play a crucial role during the larval development phase when endogenous enzyme systems are underdeveloped. There is also evidence that shows marine larvae possess poor potential to produce phospholipids, which must be supplied through diet for proper development, avoiding deformities, and survival (Tocher et al., 2015; Cahu et al., 2009). Some common sources of phospholipids include soybean lecithin or marine-based ones.

Crustaceans like shrimps and crabs require sterols, particularly cholesterol, since they cannot convert sterols from acetates. The dietary requirement for sterols for molting, hormone synthesis of ecdysteroids, and structural integrity of cell membranes is vital (Tocher, 2003). On the other hand, fish need lesser amounts of cholesterol, though inclusion levels of between 0.5% and 1% are sufficient for improving stress tolerance and growth (Jobling, 2011).

The inclusion of wax esters is minimal since they are not prevalent in aqua feeds, although they occur naturally in zooplankton and copepods used during larval rearing stages. Wax esters take longer to digest when compared to triglycerides (Scott et al., 2002).

Essential Fatty Acid (EFA) Requirements: Species-Specific Variability

EFA's cannot be synthesized by fish and must be supplied through the diet. The exact EFA requirements depend on the fish species and their metabolic abilities. EFA needs of aquaculture species show wide variability depending on their mode of lipid utilization, natural habitat, and LC-PUFA biosynthesis capability using enzymes. Freshwater fishes have higher abilities to synthesize EPA and DHA from C18 fatty acids, while marine fishes need preformed EPA and DHA since they have poor desaturase and elongase capabilities (Table 1).

Table 1

Essential Fatty Acid Requirements, Metabolic Capability, and Recommended Lipid Sources for Major Aquaculture Species

Species group	Representative species	Essential fatty acid requirement	Biosynthetic capacity for EPA/DHA	Recommended lipid sources	Key references
Freshwater Fish	Carp (<i>Cyprinus carpio</i>), Tilapia (<i>Oreochromis niloticus</i>), Catfish (<i>Clarias gariepinus</i>)	LA (18:2n-6) and ALA (18:3n-3)	High capacity to convert C18 PUFAs to EPA and DHA	Soybean, rapeseed, and linseed oils	Glencross (2009); Monroig et al. (2018)
Diadromous Fish	Atlantic salmon (<i>Salmo salar</i>), rainbow trout (<i>Oncorhynchus mykiss</i>)	LA and ALA benefit from dietary EPA/DHA.	Moderate to high conversion capability	Vegetable oils supplemented with DHA-rich oils	Bell et al. (2003); Monroig et al. (2018)

Table 1

continues.

Marine Fish	Gilthead seabream (<i>Sparus aurata</i>), European seabass (<i>Dicentrarchus labrax</i>), Atlantic cod (<i>Gadus morhua</i>)	Require preformed EPA and DHA.	Limited endogenous synthesis due to low $\Delta 5/\Delta 6$ desaturase activity	Fish oil (FO), microalgal oils, GM oilseed oils	Riche et al. (2023); Trushenski et al. (2019); Santigosa et al. (2021); Izquierdo et al. (2015)
High-Value Marine Carnivores	Cobia (<i>Rachycentron canadum</i>), grouper (<i>Epinephelus</i> spp.), tuna (<i>Thunnus</i> spp.)	High dietary requirement for EPA and DHA ($\approx 2\text{--}3\%$)	Very limited LC-PUFA biosynthesis	DHA-rich FO and algal oil blends	Trushenski et al. (2019); Monroig et al. (2022)
Marine Fish Larvae	Seabream larvae, Seabass larvae, Turbot larvae	High DHA requirement (1.5–3%) for neural and visual development	Minimal biosynthetic capability	DHA-enriched live feeds and microalgal oils	Koven et al. (2009); Cahu et al. (2009)
Crustaceans	Shrimp (<i>Penaeus</i> spp.), Crabs	EPA and DHA, 2–4% dietary phospholipids, and 0.5–1% cholesterol for optimal growth, molting, reproduction, and survival	Limited fatty acid synthesis	FO, phospholipids, cholesterol-rich ingredients	Glencross & Smith (2001); Tocher (2015)

Fish species inhabiting both freshwater and marine environments (carp, tilapia, catfish, rainbow trout, and Atlantic salmon) usually require consuming C18 PUFAs in their diets: linoleic acid (LA) – 18:2n-6 and/or α -linolenic acid (ALA) – 18:3n-3. As summarized in Table 1, freshwater and diadromous species generally possess greater desaturase and elongase activity than marine species, resulting in greater flexibility in fish-oil replacement strategies (Monroig et al., 2018). However, the degree of synthesis of these enzymes

differs. For example, rainbow trout synthesizes up to 10–15% of EPA from ALA and up to 5–8% of DHA from ALA.

Marine fish (gilthead sea bream, European sea bass, Atlantic cod, turbot, cobia, grouper, and yellowtail) have reduced or inactive $\Delta 5$ and $\Delta 6$ desaturase enzymes, mainly in the liver and intestine, where long-chain polyunsaturated fatty acids (LC-PUFAs) are synthesized in fish (Monroig et al., 2018). As a result, marine fish need to be provided with EPA and DHA in their feed rations.

The required range of EFA is between 0.5 and 1.5% EPA and DHA for sea bream and 2–3% for more specialized species such as cobia and tuna (Trushenski et al., 2019; Jobling, 2011). Marine fish larvae need even greater EFAs (1.5–3% DHA only) because of accelerated nervous and visual system development (Bell & Sargent, 2003).

There is another category of organisms—shrimp and crustaceans—which have special demands on lipids. Along with phospholipids (2–4%) and cholesterol (0.5–1%), penaeid shrimps require EPA and DHA as sources of omega-3 LC-PUFA for normal growth, survival, and reproduction. However, some crustacean species can synthesize DHA from EPA (Glencross & Smith, 2001).

Quantitative lipid requirements

Different species have different lipid requirements in their diet, depending on the species' biological status and husbandry method. Marine carnivores usually need 15-25% lipid in their diet, whereas omnivores in freshwater do well on 6-12% lipid content (Jobling, 2011). In high-energy diets containing 30-40% lipid, rapid growth and a good feed conversion ratio (less than 1.0) are achieved in the grow-out period for Atlantic salmon, utilizing the protein-sparing effect of lipids (Torstensen et al., 2005). However, an excess of dietary Lipid may lead to hepatic steatosis (fatty liver), decreased feed consumption, and poor immune response in lipid-insensitive species.

Current advances in alternative lipid sources for aquafeeds

Terrestrial Vegetable Oils

Of all the FO replacer options, vegetable oils have received the greatest amount of attention because of their worldwide availability, reasonable price, and consistent supply. Among vegetable oils, the main sources are soybeans, rapeseed, palm, sunflower, linseed, and olive oils.

Soybean oil is the most common vegetable oil in the world. It has a very high LA content (approximately 50-55%) and moderate amounts of

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ALA (6-8%). The replacement of 40-60% of FO with soybean oil in salmonids and 60-80% in tilapia and catfish has been successful without any adverse effects on growth performance (Trushenski et al., 2006). Complete replacement causes a reduction in EPA and DHA in tissues and changes in immunity (Montero et al., 2015).

Rapeseed (canola) oil stands out among vegetable oils due to its ideal n-6 to n-3 ratio (2:1) and high ALA content (8-10%). It is a suitable single-source dietary fat for the complete production period for Atlantic salmon with no effect on growth and survival, although Torstensen et al. (2005) reported that complete replacement of fish oil with a vegetable-oil blend in which rapeseed oil was a major component reduced fillet EPA and DHA concentrations by approximately 50% relative to fish-oil-fed controls. Rapeseed oil in an equal mixture with FO is sufficient to keep the fillet's DHA at an acceptable level for human consumption (Sprague et al., 2016).

Palm oil is the most widely produced vegetable oil and is very economical. It consists mainly of saturated fats (45-50% palmitic acid, C16:0), mono-unsaturated fats (40-45% oleic acid, C18:1), and a low amount of polyunsaturated fats (10-12%). The digestibility is excellent in warm-water fish (tilapia, catfish, and *pangasius*) but rather low in cold-water salmonids, limiting its use to 20-40%. The unsustainability of palm oil cultivation has made some retailers reluctant to use it.

The oil extracted from linseeds/flaxseeds has been found to be extremely high in ALA content (50-60%), while its n-6 content is very low. Linseed oil has been studied in relation to its ability to increase the synthesis of LC-PUFA within freshwater fish. However, a high content of ALA may result in the competitive inhibition of LA metabolism and eicosanoid synthesis, which negatively affects immune functions (Bell & Tocher, 2009).

Vegetable oil effectiveness summary: all types of fish tolerate their partial inclusion into fish diets in amounts of 40-70%. They can fully substitute FO when rearing freshwater and Diadromous fish, if

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supplemented with enough ALA, yet marine fish need to be fed DHA from other sources.

Animal Fats and Rendered Oils

Fats derived from terrestrial livestock and poultry processing are widely available, cheap byproducts. Poultry fat (comprising about 25-30% saturated, 45-50% mono-unsaturated, and 20-25% PUFA) has been successfully incorporated into the diets of rainbow trout and Atlantic salmon in proportions ranging from 30-50% total dietary Lipid (Bureau et al., 2008). Highly saturated (containing up to 45-55% saturated fatty acids), beef tallow and lard exhibit reduced digestibility in cold water (Ng, 2003). Hydrolyzed feather oil represents a novel oil but requires purification to remove indigestible protein components.

Rendered fish byproduct oils (fish-processing trimmings, viscera, and frames) constitute a partial circle approach. They contain a fatty acid composition resembling that of FO from whole fish, though having increased oxidative potential. Malcorps et al. (2019) estimate that 30% of FO could be substituted for byproduct oil in the feeds, thereby decreasing FIFO significantly. Problems associated with animal fats: Accumulation of persistent organic pollutants (POPs), dioxins, and PCBs in animal fats, as well as regulatory maximum inclusion levels, must be considered when feeding animals. Moreover, trans fatty acids formed during the rendering process can negatively impact fish health (Bureau et al., 2008).

Microalgae and thraustochytrid oils

The heterotrophic cultivation of microalgae and thraustochytrids (marine protists), which inherently synthesize large amounts of DHA and, depending on species, small amounts of EPA, is considered the closest analog of FOs. The most widely commercialized are Schizochytrium species that synthesize 35-50% DHA and negligible amounts of EPA (Miller et al., 2006). *Cryptothecodinium cohnii* synthesizes DHA (>40%) without the synthesis of any additional PUFA. *Nannochloropsis* and *Phaeodactylum* are characterized by a high content

Sci. Technol. Arts Res. J., July –Sep, 2026, 15(3), R1-R17 of EPA (20-30%) but low DHA production. Several research studies demonstrate that algal oils are able to replace FOs entirely in feeding regimes of Atlantic salmon, gilthead sea bream, and rainbow trout while not deteriorating their growth rates, feed conversion ratio, or mortality (Miller et al., 2006). Salmon fed only Schizochytrium oil had an equal fillet DHA concentration to those fed by FOs; such an effect cannot be achieved using vegetable oils (Sprague et al., 2015). Moreover, larvae fed DHA-rich algal oils showed increased rates of eye development, swim bladder inflation, and survival rates compared to FO-based diets (Koven et al., 2023).

Challenge: High cost remains the biggest hurdle. The heterotrophic process involves sterile conditions, pure substrates (glucose), and further processing (isolation and harvesting), making the process 2–5 times more expensive than FO (Naylor et al., 2021). Economies of scale and less costly substrates, such as molasses, are being explored to cut costs.

Genetically Modified Oilseed Crops

Oilseed metabolic engineering for EPA/DHA is one of the most important technical innovations in recent years. Through the metabolic manipulation of the oilseed crops, by transferring algal or fungal genes encoding desaturase and/or elongase into camelina (*Camelina sativa*), canola (*Brassica napus*), or soybean, oilseeds could be obtained with EPA and DHA levels similar to those of FO (Napier et al., 2019). Aquaterra® (earlier known as DHA canola oil) has approximately 10-12% EPA and 8-10% DHA, which is on par with FO. The large-scale feeding experiment conducted with Atlantic salmon proved that complete substitution of FO with genetically modified canola oil resulted in equal growth, efficiency, and fillet quality without any presence of a transgene in fish tissues (Betancor et al., 2017). Meta-analysis of several studies showed no effects on growth, mortality, or health parameters of various species (Tocher et al., 2019).

Regulatory status: Aquaterra® has received regulatory approval in the USA (FDA GRAS

notification), Canada (CFIA), Australia, and New Zealand but remains restricted in the European Union due to GM labeling requirements and consumer resistance. As of 2024, limited commercial adoption continues due to the higher cost than FO and consumer perception issues (Malcorps et al., 2021). Second-generation GM crops under development aim to produce oils with higher DHA: EPA ratios (optimal for marine fish) and to stack traits for pest resistance and drought tolerance (Napier et al., 2019).

Insect Oils

The use of insects as an environmentally friendly protein and fat source for animal feed production is becoming increasingly popular. Among all insects, *Hermetia illucens* is the most researched one because of its fast growth rate, high feed conversion efficiency, and ability to convert various organic wastes into valuable biomass (Ewald et al., 2020). Black soldier fly larvae oil (BSFLO) consists of 30–40% lipids, primarily lauric acid (C12:0, 35–45%), followed by smaller percentages of palmitic, oleic, and linoleic acids. The key advantage of this oil is its very low percentage of EPA and DHA. Nonetheless, this oil composition can be adjusted through the type of substrate used during larval growth; feeding the larvae with fish offal or microalgae can increase the amount of EPA/DHA up to 5–10% (Ewald et al., 2020; Liland et al., 2017).

Studies have reported successful incorporation of BSFLO in diets of rainbow trout, Atlantic salmon, and European sea bass at levels of 25–50% of dietary lipids without any growth impairment (Liland et al., 2017). Increasing levels of BSFLO above 75–100% result in decreased growth performance and changes in the fatty acid composition of fillets; thus, they require fortification with DHA-rich resources (Liland et al., 2017). Alternative insects: larval oil from houseflies (*Musca domestica*), yellow mealworms (*Tenebrio molitor*), and cricket oil have been investigated, but with lower lipid content and poor profiles. Environmental benefits: The rearing of

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insects has low land use, low water requirements, valorization of organic waste, and generates fewer greenhouse gases compared to livestock farming. Studies on life cycle assessment have shown that BSFLO has a 50–70% reduced carbon footprint compared to FO (Malcorps et al., 2019). Despite its nutritional advantages, black soldier fly larvae oil presents several feed-manufacturing challenges. Its high lauric acid content can increase lipid crystallization during storage and processing, potentially affecting oil flow properties, pellet binding characteristics, and vacuum-coating efficiency. These engineering constraints should be considered alongside biological performance when evaluating commercial adoption.

Single-Cell Oils (Yeast, Fungi, Bacteria)

The oil-forming capacity of microorganisms (yeasts, fungi, and bacteria) may reach over 20% of biomass and provide a basis for scaling up the fermentation oil production process, which is not dependent on agriculture or fisheries. *Yeasts*: *Yarrowia lipolytica* is currently the most studied oleaginous yeast. It has been engineered to synthesize EPA (15–20% of total FA) (Xue et al., 2018). *Rhodospiridium toruloides* and *Lipomyces starkeyi* are being researched as lipid-carotenoid co-producing organisms. The lipids produced by yeasts do not contain DHA; therefore, additional enzymes should be expressed along with the algal ones.

Fungi: The most studied fungal oleaginous strain is *Mortierella alpina*. It produces arachidonic acid (20:4n-6, or ARA; 30–40%). ARA is considered a critical fatty acid for reproductive processes and immune response in marine fishes. It is generally insufficient in FO and vegetable oil; therefore, *M. alpina* oil can be used as a valuable additive. *Bacteria*: *Rhodococcus opacus* and *Streptomyces spp.* accumulate triacylglycerols (>50% dry weight) yet synthesize mostly saturated and mono-unsaturated fatty acids (Sullivan et al., 2018). Autotrophic bacteria (e.g., *C. autoethanogenum*), which can ferment gases (CO₂, CO, H₂) and are currently at the early development

stage of single-cell oil production, have been mentioned. *Scalability*: Industrial-scale (100,000–500,000 liters) fermentation for oil production using yeast and algae has been developed commercially. Costs remain the limiting factor, where economic viability will only be possible when the feedstocks cost 200 per ton, and the oil yield exceeds 0.25 g of oil/g carbon.

Byproduct and circular economy-based lipids

A circular bioeconomy is a process that maximizes resources by recovering the lipids from byproducts before turning them into waste. Some major byproduct sources include the following: Fish byproducts: Byproducts such as heads, frames, viscera, skins, and trimmings from farmed and wild-caught fish make up 30-60% of total fish mass. These byproducts are known to have high-quality FO with a content of 10-20% oil and fatty acid composition comparable to FO obtained from whole fish (Malcorps et al., 2019). The annual byproduct output from Norwegian salmon processing alone stands at approximately 200,000 tons, of which 20,000-30,000 tons of oil can be recovered.

Slaughtering byproducts and rendering plant byproducts: Animal fats extracted from slaughterhouses are being used for lower-quality purposes, but refining and deodorizing them might enhance their suitability as aquafeed. Food waste: Lipids from grease traps, waste vegetable oils, and food manufacturing waste (e.g., bakery waste oils) can be obtained relatively cheaply yet must be treated to eliminate contaminants such as water, solid waste, and peroxides. In biorefinery facilities, they can be transformed into feed lipids (Malcorps et al., 2019). Grains and spent brewery yeast: After protein and fiber are separated, lipids in trace amounts (3–8%) can be extracted from beer production byproducts. Using an established infrastructure for ethanol production facilities is advantageous for the process (Oliveira et al., 2024). Because some environmental impacts are assigned to the primary products, the environmental footprints (in g CO₂e/kg oil) of lipids derived from

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byproducts are significantly lower than those of FO, according to the LCA methodology (Malcorps et al., 2019).

Advances in formulation, processing, and emerging technologies

Lipid blending strategies

No alternative lipid is suitable to replace FO from every perspective. Thus, blending has emerged as a solution to provide optimal fatty acid composition, reduce feed costs, and supply essential fatty acids. Blending schemes typically include a baseline oil blend such as rapeseed, palm, and linseed oils containing appropriate n-3 and n-6 C18 PUFAs. The addition of oils rich in DHA (algae, *GM canola*, or *Thraustochytrids*) meets the needs of marine fish. The inclusion of animal fat or insect oil can decrease the costs of warm-water species. The addition of phospholipids (soy lecithin or egg lecithin) to broodstock and larvae diets can be beneficial. Optimal mixing formulas can be designed through mathematical models (linear programming or genetic algorithms) to meet the target fatty acid profile at minimal cost, taking into account actual market prices. A possible formula is 40:30:30 rapeseed, poultry fat, and algal oils, which can replace 100% FO in salmon diets with fillet DHA levels > 0.5% (Glencross, 2009; Torstensen et al., 2005).

Enzymatic Pre-Treatment and Digestibility Enhancement

Lipid digestibility depends on fatty acid composition (saturation level), chain length, and anti-nutritional factors. Cold-water fish have difficulty breaking down saturated fatty acids (palmitic acid and stearic acid) because of reduced bile salt content and lipase activity at lower temperatures (12-15°C). Lipase treatment of dietary triglycerides via exogenous lipases such as microbial lipases (for instance, *Candida rugosa* and *Rhizopus oryzae*) leads to the conversion of fats into free fatty acids and monoacylglycerols, which increases fat absorption in larvae with underdeveloped pancreatic functions (Kolkovski et

al., 2000). Treatment of lecithin with phospholipase A2 results in lysolecithin, an emulsifier with high emulsifying properties and better overall lipid digestibility (Coutteau *et al.*, 2000). The use of solid-state fermentation of oilseeds with lipase-producing fungi (such as *Aspergillus niger*) can increase oil extraction efficiency and decrease anti-nutritional factors (saponins, phytates, tannins, and enzyme inhibitors), thereby improving nutrient availability and lipid utilization.

Emulsifiers and Surfactants

Fish larvae (first 2-4 weeks after hatching) have underdeveloped digestive systems that lack fully developed stomachs, pepsin activity, and adequate bile salt production. Dietary addition of emulsifiers enhances lipid digestion, dispersion, and micelle formation, resulting in better absorption: Phosphatidylcholine (soy lecithin, 60-70%), the most widely used dietary emulsifier for larval diets (Coutteau *et al.*, 2000). Lysolecithin, an enzymatically altered form of lecithin, has an increased hydrophilicity-lipophilicity balance (HLB), making it a more efficient emulsifier for saturated fatty acids. Bile salts (sodium taurocholate and sodium glycocholate) act effectively as emulsifiers, albeit at high costs not practical for commercial feed production.

Encapsulation and Oxidative Stability

LC-PUFAs (EPA and DHA) are prone to autoxidation because of their many bis-allylic hydrogen atoms and can lead to the formation of off-flavor and toxic oxidation compounds (malondialdehyde and 4-hydroxynonenal). Oxidative stability is essential during the manufacture of feed (extrusion up to 150°C), storage (weeks to months), and the ingestion process (exposure to water).

The following microencapsulation techniques provide physical protection to LC-PUFA from oxidative attack: Atomization (spray-drying): encapsulation of oil droplets with carbohydrate (maltodextrin, starch) or protein (gelatin, whey) shells. A common method employed to make larval

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diets. Complex concentration: Encapsulation of oil particles by a polymeric shell composed of oppositely charged polymers (e.g., gelatin and gum arabic). Gives rise to stable capsules that withstand heating and shearing (Oliveira *et al.*, 2024). Liposomes: Oil droplets encapsulated with a phospholipid bilayer; improved delivery of LC-PUFA to enterocytes in larvae (Koven *et al.*, 2023). Nanofiber and Electrospraying: Nanoscale fibers or particulates for delivery. Antioxidant protection: Supplementation of fish feed with antioxidant nutrients (*tocopherols, tocotrienols, astaxanthin, rosemary extract, and green tea catechins*) provides synergistic antioxidative action. *Alpha-tocopherol* (vitamin E) is particularly crucial as a chain-breaking antioxidant in biomembranes and lipoproteins.

Extrusion and Pellet Quality

However, feeding formulations with high fat content (20–40%) pose some challenges in extrusion because oil acts as a plasticizer to the starch and protein complex, resulting in poor pellet strength and higher fines. High-fat extrusion systems include the following: Vacuum-coated post-extrusion system: Modern vacuum-coating systems facilitate the incorporation of high lipid levels into extruded aquafeeds, and commercial Atlantic salmon grow-out diets may contain up to approximately 40% lipid when post-extrusion oil coating is applied. Pellet quality, oil absorption capacity, and oil retention remain critical processing considerations in such high-energy feeds, whereas conventional processing systems generally accommodate lower lipid inclusion levels (Sørensen, 2012). Fat pre-extrusion addition: Adding 8–15% lipid to the preconditioned mash before extrusion, which enhances lubrication and energy savings. Use of binders: Carboxymethyl cellulose, lignin sulfonate, and wheat gluten help increase pellet density in high-fat formulations (Sørensen, 2012).

Precision Lipid Nutrition

Precision lipid nutrition integrates species-specific EFA requirements, lipidomics, transcriptomics,

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machine learning, and predictive modeling to formulate highly targeted diets that maximize lipid utilization while minimizing feed costs and environmental impacts. There is very little data available on EFA requirements for the majority of aquaculture species, numbering over 600 around the world today. Further studies need to focus on novel species such as cleaner fish, ornamental fish, pangasius, grouper, and cobia, for which information about their lipid nutrition requirements is very scarce. The following methods can assist in the development of precision nutrition techniques: machine learning, factorial modeling, lipidomics, and transcriptomics.

Microbial oil technologies

Microbial oils made by gas fermentation are an innovative and sustainable source of FO. Technologies that involve microbes capable of producing biomass from industrial CO₂, CO, and H₂ are an alternative to oils that require agricultural feedstock and fishery sources.

Metabolic engineering and biotechnological innovation

Advances in metabolic engineering have enabled the production of EPA- and DHA-rich oils in oilseed crops and have highlighted the potential of genome editing approaches for enhancing endogenous LC-PUFA biosynthesis in aquatic species. The use of genetic modification to increase the potential of marine fish to biosynthesize EPA and DHA using desaturase and elongase genes is an option that exists. Experiments conducted in laboratories indicate an improvement in the synthesis of LC-PUFAs in transgenic fish, but the use is yet to be commercialized due to the existence of regulations and other issues related to gene escape. The use of genome editing technologies like CRISPR/Cas9 would be a better choice in the future.

Physiological and product quality impacts

Growth performance and feed efficiency

Recent studies suggest that nutritional programming during early developmental stages

Sci. Technol. Arts Res. J., July–Sep, 2026, 15(3), R1-R17 may partially enhance endogenous desaturase and elongase activity in some species, improving subsequent utilization of low-fish-oil diets. Although evidence remains species-specific, this represents a promising complementary strategy alongside alternative lipid sources.

Several meta-analyses have revealed that partial replacement of FO (up to 50–70%) does not impact growth and FCR in commercially cultivated species of fish (Turchini et al., 2009; Glencross, 2009). The complete replacement by vegetable oil results in lower growth (10–25% decrease in specific growth rate) in marine fish but has no effect on the growth of freshwater fish, provided the requirements of EFAs (ALA/LA) are met (Tocher, 2003).

DHA is an essential fatty acid required for normal growth in marine fish. If its deficiency exists, the following processes compensate for DHA loss: higher adjustments in membrane fluidity through incorporation of oleic acid and regulation of gene expression in lipogenic enzymes, but none of these processes can fully substitute for DHA's structural function in neural and retinal tissue. In studies carried out with gilthead sea bream under dietary conditions with no addition of FO and feeding only vegetable oils, lower growth rates (15–20%), poor feed utilization, and mortality were observed (Izquierdo et al., 2015). DHA from algae at a dose of 0.5–1% of the diet restores growth.

Reproductive Performance

Nutrition of broodstock has an essential effect on gamete quality, fecundity, fertilization ability, and larval survival. Lipids, phospholipids, and LC-PUFAs are among the main compounds of yolk and sperm membranes (Izquierdo et al., 2001). ARA has a vital role in reproductive processes as the precursor of prostaglandins responsible for ovulation and spawning processes. Complete replacement of FO by vegetable oils in the broodstock diet leads to decreased egg size, hatching rate, and larval survival in sea bream and sea bass (Ferozekhan et al., 2020). Dietary addition of algal oils (DHA+ARA) improves reproductive

performance. There is a limited number of multigenerational studies (F₀-F₂), although they are extremely required; for example, it was found that zebrafish exposed to two-generation dietary FO replacement with vegetable oils had decreased fecundity and changed expression of desaturase genes (Tocher et al., 2019).

Immune Function and Disease Resistance

LC-PUFAs influence the immune system using several mechanisms that include (i) modulation of membrane fluidity to allow efficient signaling of the receptors; (ii) biosynthesis of eicosanoids such as prostaglandins, leukotrienes, and thromboxanes through metabolism by EPA and ARA; and (iii) the activity of certain transcription factors, including NF- κ B and PPAR γ (Montero et al., 2008). The right balance of the n-3 and n-6 ratios (usually in the proportion of 2:1 to 4:1) stimulates lymphocyte proliferation and enhances macrophage phagocytosis and antibody production. An imbalanced intake of too much n-6 LC-PUFA (soybean oil) results in the accumulation of more pro-inflammatory eicosanoids such as leukotriene B₄ and prostaglandin E₂. In contrast, high intake of dietary EPA/DHA leads to the biosynthesis of resolvins and protectins, which have anti-inflammatory activities (Montero et al., 2008). Implications of the findings: Atlantic salmon, fed on vegetable oil with 75% of fish oil (FO) replaced, had poor resistance to pathogens (*Aeromonas salmonicida* and *Vibrio anguillarum*), leading to death rates of 20-30% against only 5-10% for FO. The inclusion of algal oil (supplying EPA/DHA).

Fillet Nutritional Quality for Human Health

The main reason for feeding farmed fish with LC-PUFAs is the provision of these beneficial fatty acids to the consumer. Higher EPA+DHA consumption is epidemiologically proven to have benefits, including reducing cardiovascular mortality, improving neurodevelopment, and exhibiting anti-inflammatory properties. Farmed Atlantic salmon is one of the major dietary sources of EPA+DHA consumed by Western populations. On the other hand, a high proportion of FO

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replacement ($\geq 70\%$) with plant-based oils significantly decreases the content of EPA+DHA in the fillet of farmed fish. For example, according to Sprague et al. (2016), full substitution of FO with plant-based oils in farmed Atlantic salmon decreased the fillet concentration of EPA+DHA down to about 0.3-0.5 g/100 g, comparable to the concentration in terrestrial meat.

Successful mitigation strategies

FO in finishing diets (re-feeding): The supplementation of fish oil in feeding for the last 8 to 12 weeks during production can increase EPA+DHA contents by 80 to 90% compared to control, despite using FO-free diets during growth. This is based on quick turnover rates of lipids in salmon muscle. Inclusion of algal or GM oil in diets: The supplementation of algal or GM canola oil maintains the same contents of EPA+DHA as the control without the need for a finishing diet. Species-specific approaches: Tilapia and catfish, wherein EPA+DHA content is not a requirement, do not need to include high vegetable oil in diets.

Lipid Oxidation and Shelf Life

Fats and fillets high in PUFA are susceptible to oxidation, leading to volatile compounds (hexanal, nonanal, and 2,4-decadienal) that cause unpleasant flavors and odors. Consumption of oxidized feed is associated with loss of palatability, reduced nutrient bioavailability, enteritis, and hepatotoxicity (Hamre, 2010). Feed oxidation: During extrusion at 100-150°C, feed is prone to oxidation. The addition of antioxidants can inhibit oxidative damage during processing. After extrusion, coating under vacuum prevents further heating. Storage in nitrogen and vacuum, and the addition of synthetic and natural antioxidants, result in shelf life extending up to 6-12 months.

Fillet oxidation: Oxidation capacity depends on dietary fatty acid content and antioxidant activity. Fillets of fish reared on vegetable oils (low in PUFA) will be less oxidized and have a longer storage time compared to those reared on FO diets. However, fish that are on algal and genetically modified oils (high DHA) will have fillets with

comparable or higher oxidation activity than those raised on FO diets, necessitating careful handling and additional antioxidants. Vitamin E (α -tocopherol) at 200-400 mg/kg feed can prevent fillet oxidation (Hamre, 2010).

Future directions

Advancements in precision nutrition, biotechnology, circular bioeconomy, and new technologies will be crucial to future developments in aquafeed lipid nutrition despite many achievements in the replacement of FO. There are still some challenges in terms of species-specific

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lipid nutrition, sustainability, consumer acceptance, and approval of the products.

Sustainable Bioeconomy Approaches

The concept of the circular bioeconomy entails the reuse of waste streams as feed ingredients. The future can thus see integrated biorefineries and insects feeding on aquaculture waste products, as well as the extraction of lipids from waste streams from food processing. From life cycle assessments, insect oils and byproduct oils appear to be more environmentally friendly than conventional FO (Table 2).

Table 2

Environmental profiles of major lipid sources used in aquafeeds based on life-cycle assessment (LCA) studies.

Lipid Source	Carbon footprint (kg CO ₂ e/kg oil)	Land use (m ² ·yr/kg oil)	Water use (L/kg oil)	LCA boundary
Fish oil (Peruvian anchovy)	2.8	0.5	120	Cradle-to-gate
Rapeseed oil	1.9	12.5	2,500	Cradle-to-gate
Insect oil (BSF, waste-fed)	0.7	0.8	18	Cradle-to-gate
Byproduct fish oil	0.4	0.1	30	Cradle-to-gate

The environmental indicators are adapted from published LCA studies. Most values are reported using cradle-to-gate system boundaries. For byproduct-derived oils, environmental burdens are partially allocated to the primary product (fish fillets or processed food products), resulting in lower footprint estimates. Results should therefore be interpreted as comparative estimates rather than universal values because outcomes vary according to allocation methodology, geographic location, production technology, and feedstock source.

Among the lipid sources compared, insect oil and byproduct fish oil exhibit the lowest carbon, land-use, and water-use footprints. Their superior environmental performance is largely attributable

to waste-stream utilization and resource recovery within circular bioeconomy systems, whereas crop-derived oils generally require higher land and freshwater inputs.

Regulatory and consumer acceptance challenges

The integration of new lipid sources not only requires technology but also relies on consumer and regulatory acceptance. While there is growing acceptance of insect feed ingredients, genetic modification remains controversial in Europe.

Integrated multi-omics approach for aquaculture

Advanced techniques such as lipidomics, transcriptomics, metabolomics, and machine

learning allow for comprehensive analysis of fish lipid metabolism and nutritional conditions. They can detect deficiencies in growth and health effects, leading to more accurate formulations and timely nutritional interventions. As the cost decreases, the integration of multi-omics methods will become increasingly popular in precision aquaculture. Thus, the perspective of aquafeed lipids seems to be a combination of precision nutrition, sustainable alternatives, biotechnology, circular resource use, and molecular technology.

Research priorities for sustainable fish oil (fo) replacement

Despite significant progress in alternative lipid development, there are several key research priorities that need to be addressed before full and sustainable fish-oil replacement can be achieved in different aquaculture systems. Future studies should focus on biological, industrial, and market challenges like the following:

1. Long-term and multigenerational effects of alternative lipid sources on growth, reproductive performance, fecundity, survival of offspring, and possible intergenerational epigenetic modifications.
2. Species-specific EFA requirements, particularly for emerging species. For which nutritional information remains limited.
3. Gut microbiota-lipid interactions and their effects on nutrient utilization, immune competence, and disease resistance.
4. Real-world oxidative stability of novel lipid sources during feed processing, storage, transport, and commercial production conditions.
5. Economics and scalability of microbial oils, insect oils, and genetically engineered lipid sources under commercial production systems.
6. Consumer acceptance and market perception of seafood produced using novel lipid ingredients, including insect-

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derived and genetically modified oil sources.

7. Harmonized regulatory frameworks that facilitate the safe commercialization of genetically modified and genome-edited lipid products while maintaining public confidence.
8. Integration of precision nutrition, multi-omics technologies, artificial intelligence, and sustainability.

By tackling these research priorities, we can more rapidly advance sustainable aquafeed lipid technologies, enabling a reduction in reliance on finite marine stocks while upholding fish performance, product quality, and overall environmental and economic viability.

CONCLUSIONS

Ecological, economic, and scientific drivers are currently compelling the replacement of marine FO with sustainable alternatives across the aquaculture industry. Vegetable oils from plants work for freshwater and diadromous fish, allowing for a complete substitution of FO while ensuring growth rates are sustained, although the content of EPA + DHA in fillets is greatly reduced. Due to their requirement for dietary preformed DHA, the nutritional needs of marine fish cannot be met by a single alternative to FO. However, a combination of inexpensive vegetable oils with other alternatives rich in DHA (algal oils, genetically engineered oilseeds, or oils extracted from marine fish byproducts) allows for a total substitution of FO, as well as for fish health, growth, and high-quality fillets.

Oils from insects and single cells are circular alternatives with positive environmental impacts. Although they are still more expensive than FO at present, they have strong potential to become economically competitive in just one decade, thanks to technological advances. Gas fermentation and genetic engineering of fish may serve as ultimate solutions that would completely free fish farming from dependence on agriculture; however, both involve serious risks and ethical

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considerations. There will not be a single dominant technology in this space. The future aquafeed lipids will be represented by regional and species-specific blends consisting of various sources (land-based, oceanic, insect, and microorganism), dependent on locally available resources and cost efficiency. Personalized feeding made possible by using omics biomarkers and machine learning will allow for formulating feed mixes for specific farms and even groups of fish.

Recommendations

By implementing principles of the circular bioeconomy that allow reusing lipids from other parts of food value chains, aquaculture can significantly decrease reliance on wild fish and, at the same time, offer omega-3-rich seafood to consumers worldwide. The research gaps identified above (multi-generation impact assessment, novel species, gut microbiota, consumer attitudes) need to be addressed through investments in research and collaboration between all stakeholders, including academic institutions, industry representatives, and regulators. With such effort, the goal of sustainable aquaculture free of FO becomes closer to reality.

CRedit author statement

Mekonnen Melesse Diriba: Conceptualization, Methodology, Draft Writing, Data Curation, Data Visualization, Resources, Analysis, Reviewing, and Editing

Declaration of competing interests

The author declares no competing interests.

Ethical Approval

Not Applicable

Data availability

Data sources are appropriately cited in text.

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