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PROOF
REVIEW

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Vegetable Oil Inclusion in Aquafeeds: Implications for Growth and Final Carcass Quality in Finfish Culture

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Abstract

The rapid expansion of the aquaculture sector in recent years, coupled with heightened public awareness regarding the nutritional benefits of seafood consumption, has established aquatic species as a pivotal source of animal protein globally. However, the global intensification of aquaculture production has precipitated a surge in the demand for fish oil within aquafeeds. This trajectory appears unsustainable and economically unviable in the long term, as global fish oil stocks are finite and diminishing. Dietary lipids are indispensable for maintaining the physiological health and optimizing the growth performance of aquatic species, serving as the primary source of n-3 and n-6 essential fatty acids. Consequently, aquaculturists and researchers are actively seeking suitable alternative lipid sources to substitute fish oil in aquafeed formulations. This study demonstrates that the substitution of fish oil with vegetable oils can enhance the sustainability of aquaculture production while simultaneously augmenting the profitability of farming operations. Extant literature indicates that a diverse array of vegetable oils including palm oil, coconut oil, sunflower oil, among others can be utilized as viable substitutes for fish oil without exerting deleterious effects on fish growth performance. Nevertheless, resultant alterations in the fatty acid profile of the muscle tissue, which constitutes the edible portion for human consumption, warrant critical attention and strategic management.

Introduction

Aquaculture represents a cornerstone of the global food production industry and plays an instrumental role in ensuring international food security. Furthermore, approximately 40 million individuals are engaged in various facets of the aquaculture sector (Yadav et al., 2019). The advancement of intensive aquaculture systems necessitates the formulation of high-quality feeds, within which lipids serve as a critical component (Ayisi et al., 2019). Lipids are regarded as indispensable nutrients in fish diets, participating in energy provision via triglycerides, the maintenance of membrane structural integrity through phospholipids, and the supply of essential fatty acids (EFAs) and eicosanoid precursors required for cellular regulatory processes (Menoyo et al., 2007). Moreover, lipids are vital for the absorption of fat-soluble vitamins (A, D, E, and K) and dietary pigments (NRC, 2011). The significance of fatty acids in fish nutrition can be evaluated through three primary lenses: physiological maintenance, optimal growth performance, and the final nutritional quality of the product (Mata-Sotres et al., 2021).

Fish oil (FO) provides a rich source of polyunsaturated fatty acids (PUFA), particularly long-chain highly unsaturated fatty acids (HUFA), and has traditionally served as the primary lipid source in aquafeeds (Ayisi et al., 2019). However, the rapid expansion of the aquaculture industry and the shift toward intensive farming have increased the reliance on

formulated diets. Projections indicate that the continued development of the aquaculture sector, if solely reliant on FO derived from marine pelagic fish, is practically unfeasible (Turchini & Francis, 2009). Consequently, the heavy dependence on FO has emerged as a major concern for the industry (Mourente & Bell, 2006). The limited supply of oils rich in n-3 long-chain polyunsaturated fatty acids (n-3 LC-PUFA) driven by stagnant production and rising demand from other sectors such as human nutraceuticals can no longer satisfy the requirements for sustainable growth in aquaculture and feed production (Mock et al., 2019). This traditional reliance poses a significant barrier to the sustainable expansion of salmonid, marine fish, and shrimp farming. To mitigate this dependency, substantial research has focused on sustainable alternatives, including vegetable oils (VO) and terrestrial animal fats. Vegetable oils are considered suitable FO substitutes due to their widespread availability, cost-effectiveness, and absence of environmental contaminants such as dioxins (Chen et al*.,* 2017; Xie et al*.,* 2018). Nevertheless, a fundamental distinction remains: FO is abundant in LC-PUFAs, specifically eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), which are critical for cellular structure (Greene & Selivonchik, 1990). In contrast, VOs are rich in C18 PUFAs, such as α -linolenic acid (ALA) and linoleic acid (LA) (Nayak et al., 2017). These fatty acids are of particular importance as they can serve as substrates for the biosynthesis of more biologically active LC-PUFAs (Senadheera et al*.,* 2010).

The capacity of C18 PUFAs to meet EFA requirements depends on the presence of fatty acid desaturase (Fads) and elongase (Elovl) enzymes within the organism. Consequently, EFA requirements vary across species based on their endogenous ability to bioconvert C18 PUFAs into LC-PUFAs. In brief, while C18 PUFAs can fulfill the EFA requirements of most freshwater and salmonid species, many marine species characterized by limited or absent biosynthetic capacity exhibit a strict dietary requirement for preformed LC-PUFAs (Xie et al., 2018). These LC-PUFAs are essential components of plasma membranes and play fundamental roles in growth, development, reproduction, stress resistance, immune response, and neural function (Nayak et al., 2017; Xie et al*.,* 2018). The objective of this review is to examine the influence of vegetable oils on the expression of genes involved in lipid metabolism. Furthermore, this article evaluates the impact of VO inclusion on growth performance, feed utilization efficiency, body composition, fatty acid profiles, and the immunological status of fish.

Oils

Lipids are broadly categorized into two primary classifications: vegetable oils and animal fats. Vegetable oils are derived from botanical sources, including soybean, peanut, and sunflower oils, among others. The byproduct remaining after oil extraction commonly referred to as oil cake or meal serves as a significant protein constituent in aquafeed formulations. Conversely, animal-derived lipids encompass fats extracted from various faunal sources. These include fish oil as well as rendered fats sourced from poultry, bovine, and porcine slaughterhouse byproducts (Yadav et al., 2019).

Vegetable Oils in Aquafeed Formulations

Vegetable oils extensively utilized in aquafeed production encompass a diverse range of lipid sources, including palm, coconut, soybean, corn, camelina, perilla, cottonseed, and linseed oils, among others. Although these botanical lipids exhibit heterogeneous fatty acid profiles, they are characteristically devoid of long-chain omega-3 polyunsaturated fatty acids (n-3 LC-PUFAs). Conversely, they possess substantial concentrations of alternative fatty acids, such as n-3 PUFAs, n-6 PUFAs, monounsaturated fatty acids (MUFAs), and saturated fatty acids (SFAs). Specifically, olive, rapeseed, and canola oils are distinguished by their high MUFA content, whereas sunflower, corn, and soybean oils are predominantly rich in n-6 PUFAs. Furthermore, tropical oils such as palm and coconut are characterized by a high proportion of SFAs, while linseed and perilla oils serve as significant sources of n-3 PUFAs (Ayisi et al., 2019). The comparative fatty acid compositions (SFAs, MUFAs, and PUFAs) of selected vegetable oils are illustrated in Figure 1.

Linseed Oil (Flaxseed Oil)

Linseed (flaxseed), derived from *Linum usitatissimum* L., typically contains approximately 36% to 40% lipids and serves as a potent source of essential n-3 fatty acids, specifically α-linolenic acid (ALA). Beyond its lipid profile, linseed is a rich source of lignans (phytoestrogenic components), minerals, vitamins, and dietary fibers. Furthermore, linseed meal the residual byproduct after oil extraction constitutes a viable protein source for livestock nutrition and is extensively utilized in developed nations (Oomah, 2001). While linseed possesses low concentrations of saturated fatty acids (SFAs), its unsaturated fatty acid profile is characterized by an n-6 to n-3 ratio of approximately 0.3:1. This stands in stark contrast to the majority of vegetable oils, in which n-6 fatty acids generally predominate over the n -3 series. Both n -3 and n-6 fatty acids are distinguished by the position of their terminal double bonds and are indispensable for metabolic processes and the biosynthesis of eicosanoids. As primary precursors, linoleic acid (LA) and ALA must be supplied in sufficient quantities via the diet to maintain physiological homeostasis. Linseed oil represents one of the most concentrated botanical sources of n-3 fatty acids within the limited range of terrestrial alternatives. It contains approximately 53% ALA but is devoid of long-

chain highly unsaturated fatty acids (HUFAs), such as eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA), and arachidonic acid (ArA) (NRC, 1993). Notably, freshwater teleosts, including rainbow trout *Oncorhynchus mykiss*, possess the enzymatic capacity for the bioconversion of LA to ArA and ALA to EPA and DHA.

In a study by Dupont-Cyr et al. (2022), the effects of substituting fish oil (FO) with linseed oil (LO) on muscle fatty acid composition, growth performance, and feed utilization were evaluated in Arctic charr *Salvelinus alpinus*, brook charr *S. fontinalis*, and their reciprocal hybrids. The experimental design involved four groups subjected to two distinct dietary lipid sources (100% LO or 100% FO). The results indicated that growth performance, feed intake, and muscle protein content were not significantly influenced by dietary LO. However, the lipid source significantly modulated the muscle fatty acid profile; substituting FO with LO led to a moderate reduction in EPA and DHA (25.5% and 18.4%, respectively) and a substantial increase in ALA (177%) across the four experimental groups. These findings suggest that muscle fatty acid profiles are primarily dictated by dietary intake. Furthermore, interspecific hybridization did not appear to impact the expression of key enzymes involved in HUFA biosynthesis. The study concluded that linseed oil can be effectively utilized as a fish oil substitute in aquafeeds without deleterious effects on growth, feed efficiency, or the proximate composition of muscle tissue.

Sunflower Oil

Sunflower *Helianthus annuus* L. represents one of the four predominant global edible oils, alongside soybean, rapeseed, and cottonseed oils. It is characterized by an exceptionally high polyunsaturated fatty acid (PUFA) content, ranging from 85% to 95%, and is particularly enriched with linoleic acid (LA), which constitutes approximately 68% to 72% of its total fatty acid profile. Furthermore, sunflower oil (SFO) contains essential natural antioxidants, including alpha-tocopherol and vitamins A, D, and E, which collectively enhance its oxidative stability (Asghar et al*.,* 2024). In a 90-day nutritional trial conducted by Asghar et al. (2024), the physiological effects of substituting fish oil (FO) with SFO were investigated in Rohu *Labeo rohita*. Five experimental diets were formulated with varying FO-to-SFO replacement levels (0%, 25%, 50%, 75%, and 100%). The results demonstrated that the survival rate (SR), hepatosomatic index (HSI), viscerosomatic index (VSI), and whole-body proximate composition remained unaffected by SFO inclusion. However, dietary substitution significantly modulated the fatty acid profiles of both the muscle and hepatic tissues. Specifically, an increase in dietary SFO led to a reduction in saturated fatty acids (SFAs) alongside a concomitant increase in monounsaturated fatty acids (MUFAs) and LA. Conversely, the proportions of alpha-linolenic acid (ALA), docosahexaenoic acid (DHA), and eicosapentaenoic acid (EPA) declined in correlation with higher SFO inclusion levels. Hematological parameters, including red blood cell (RBC) count, hemoglobin (Hb) concentration, and hematocrit (Hct) levels, showed no significant alterations. Regarding serum biochemistry, globulin (GLO) levels decreased significantly, whereas alanine transaminase (ALT) and aspartate transaminase (AST) activities exhibited non-significant increases. Total protein (TP) levels rose at 100% SFO inclusion, and albumin (ALB) concentrations increased at both 75% and 100% replacement levels. While cholesterol (CHOL), triacylglycerol (TG), and high-density lipoprotein (HDL) levels were not significantly impacted, low-density lipoprotein (LDL) levels increased significantly compared to the control group. Cortisol (CORT) and glucose (GLU) levels remained relatively stable with non-significant fluctuations.

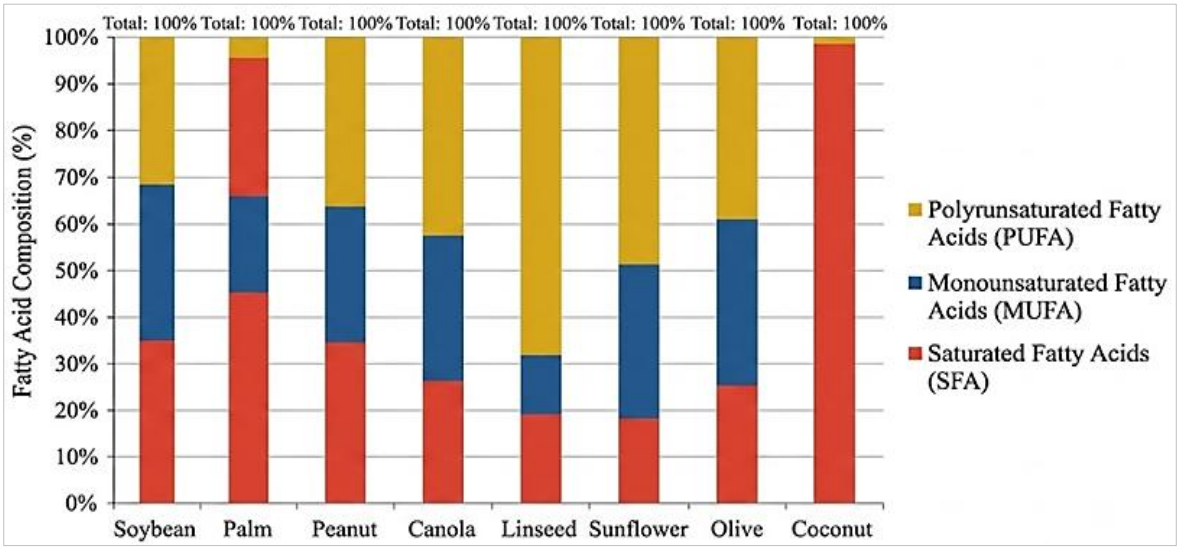

Figure 1. Saturated fatty acids (SFA), monounsaturated fatty acids (MUFA) and polyunsaturated fatty acids (PUFA) of important vegetable oils.

The antioxidant defense system, including the activities of superoxide dismutase (SOD), glutathione peroxidase (GSH-Px), and catalase (CAT) in the liver and serum, was not significantly affected; however, malondialdehyde (MDA) levels a marker of lipid peroxidation decreased significantly. In conclusion, while the muscle and hepatic fatty acid profiles were modified by the diet, FO can be replaced by SFO up to 100% in *L. rohita* diets without compromising growth performance or general health status, offering a promising sustainable alternative in aquafeed production.

Coconut Oil

Coconut, botanically identified as *Cocos nucifera*, is cultivated globally and serves as a significant source of saturated fatty acids (SFAs). Lauric acid, a predominant constituent of coconut oil (CO), has been characterized as possessing potent antiviral, antiprotozoal, and antibacterial properties, while simultaneously enhancing metabolic rate. A notable advantage of CO is its exceptional oxidative stability; it is recognized as one of the most stable lipids, exhibiting high resistance to rancidity. Unlike the majority of vegetable oils, coconut oil maintains its structural integrity and is not readily degraded by elevated temperatures (Aderolu & Akinremi, 2009). In terms of its biochemical profile, CO is characterized by a high concentration of lauric acid (C12:0), followed by myristic acid (C14:0), which averages approximately 17.19%. Other saturated constituents present at relatively high levels include palmitic acid (C16:0), caprylic acid (C8:0), and capric acid (C10:0), with average total fatty acid contributions of 8.80%, 6.76%, and 6.37%, respectively. Conversely, unsaturated fatty acids are present in relatively low proportions, with oleic acid ranging from 5.25% to 10.54% and linoleic acid spanning 0.79% to 2.58% (Mikołajczak, 2017). Ballestrazzi et al. (2006) investigated the dietary replacement of fish oil (FO) with refined coconut oil in rainbow trout *Oncorhynchus mykiss* over a 231-day period. Four experimental diets were formulated with escalating levels of CO: Diet A (0%), Diet B (6%), Diet C (12%), and Diet D (13%) as partial or total FO substitutes. The results indicated robust growth performance, with daily weight gain exceeding 3 g/day and a feed conversion ratio (FCR) of less than 1.5 across all treatment groups. While no significant differences were observed in primary carcass traits or whole-body proximate composition, the total energy content of the fish fed Diet D exhibited a significant increase.

Olive Oil

Olive oil, derived from *Olea europaea*, is a lipid source characterized by its high concentrations of fat-soluble vitamins (notably Vitamin E), phenolic compounds, and triacylglycerols rich in monounsaturated fatty acids (MUFAs). In the context of aquatic nutrition, olive oil is distinguished by its high digestibility, with oleic acid serving as its primary monounsaturated fatty acid constituent (Blatchly et al., 2017). Nutritionists and researchers posit that diets enriched with MUFA-heavy oils specifically those high in oleic acid offer significant nutritional advantages and may also mitigate the deleterious effects of ultraviolet radiation on dermal tissues (Rodrigues et al*.,* 2015). In a study by Sáez-Royuela et al. (2022), a 90-day experimental trial was conducted to evaluate the effects of partial and total replacement of cod liver oil (FO) with a vegetable oil (VO) blend. This blend comprised 30% linseed oil, 20% corn oil, and 50% olive oil, and was evaluated in tench (*Tinca tinca* Linnaeus, 1758). Six experimental diets were formulated with varying VO replacement levels: 0%, 20%, 40%, 60%, 80%, and 100%.

Across all experimental cohorts, a 100% survival rate was recorded, and no significant differences were observed in growth performance parameters, including total length (TL), body weight (W), specific growth rate (SGR), feed conversion ratio (FCR), and biomass gain (BG). Compared to the control group, the whole-body lipid content significantly decreased in the 100% VO replacement group. While no significant variations were detected in the total whole-body concentrations of saturated fatty acids (SFAs), MUFAs, or polyunsaturated fatty acids (PUFAs), the α -linolenic acid (ALA) content increased alongside FO replacement, becoming significantly higher than the control at the 40% substitution level. Furthermore, nutritional indices specifically the sum PUFA /SFA and n-6/n -3 ratios increased in correlation with higher VO inclusion, whereas the combined EPA + DHA content exhibited a concomitant decline.

Palm Oil (PO)

Palm oil (PO) is an edible vegetable oil derived from the fruit of the oil palm tree *Elaeis guineensis*. PO occupies a unique position among vegetable oils due to its high concentration of saturated fatty acids (SFAs), specifically 10–16% at the sn-2 position of the triglyceride molecule. Furthermore, PO contains significant quantities of diacylglycerols (5–8%) and free fatty acids (FFAs), both of which exert a substantial influence on its physical properties. The lipid profile of PO typically comprises 50% SFAs predominantly palmitic acid (PA, 44%) and minor amounts of stearic acid (5%) alongside 40% monounsaturated fatty acids (MUFAs), primarily oleic acid, and 10% polyunsaturated fatty acids (PUFAs), mainly linoleic acid (Gee, 2007). In a study by Larbi Ayisi et al. (2017), the effects of substituting fish oil (FO) with PO were evaluated in juvenile Nile tilapia *Oreochromis niloticus*. The specimens were administered five experimental diets involving 0%, 25%, 50%, 75%, and 100% PO replacement over an 8-week period. The results demonstrated that growth performance and feed utilization were not

compromised by either partial or total substitution of FO with PO. While protease activity remained unaffected, the activities of lipase and amylase exhibited significant alterations following FO replacement. Regarding physiological and immunological markers, no significant differences were observed in catalase (CAT), superoxide dismutase (SOD), or lysozyme (LYZ) activities across treatments. However, serum malondialdehyde (MDA) levels in fish fed the 100% PO diet were significantly lower than in all other groups, whereas the total antioxidant capacity (TAC) was significantly higher in the 0% PO group. Furthermore, fish fed diets containing 0%, 25%, and 50% PO exhibited significantly higher glutathione reductase (GR) activity compared to those in the 75% and 100% PO groups. Respiratory burst (RB) activity was significantly lower in the 0% PO group than in the 75% and 100% PO groups. Additionally, total protein (TP) levels were significantly lower in the 0% PO group compared to the 50% and 75% PO cohorts. While fish fed PO-based diets demonstrated a resistance to *Streptococcus iniae* comparable to those fed FO-based diets, hepatic function appeared to be compromised at higher inclusion levels. This was evidenced by significant elevations in aspartate aminotransferase (AST) and alkaline phosphatase (ALP). Moreover, AST, TP, triacylglycerol (TAG), and low-density lipoprotein cholesterol (LDL-C) were significantly higher in groups receiving elevated levels of PO. Consequently, the administration of PO-inclusive diets to juvenile tilapia may adversely affect antioxidant parameters and innate immunity, as indicated by the reduction in LYZ, TAC, GR, MDA, CAT, SOD, and GSHpx.

Perilla Seed Oil

Perilla seed oil, derived from *Perilla frutescens*, is characterized by an exceptionally high concentration of n-3 series fatty acids, with alpha-linolenic acid (LNA) accounting for approximately 55% to 66% of the total fatty acid content (Eckert et al., 2011). Furthermore, it serves as a critical biochemical precursor for the biosynthesis of long-chain n-3 polyunsaturated fatty acids (LC-PUFAs), specifically docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) (Diwakar et al., 2008). In a study conducted by Carbonera et al. (2014), the researchers evaluated the effects of replacing dietary sunflower oil with perilla oil in Nile tilapia *Oreochromis niloticus*, GIFT strain over a period of 0, 10, 20, and 30 days. The results indicated a substantial increase in total n-3 fatty acids within the muscle tissue, rising from 63.6 to 181.5 mg g^{-1}. Concurrently, a reduction in total n-6 fatty acid concentrations was observed, decreasing from 256.6 to 196.1 mg g^{-1}. Among the n-3 fatty acids, the concentrations of ALA and DHA increased by factors of 9.4 and 1.9, respectively, following 30 days of perilla oil supplementation. Furthermore, the n-6/n-3 ratio, as well as the polyunsaturated to saturated fatty acid (PUFA/SFA) and polyunsaturated to monounsaturated fatty acid (PUFA/MUFA) ratios, exhibited a trend toward stabilization after 20 days of the perilla oil-enriched diet. The inclusion of perilla oil as a dietary lipid source for 20 to 30 days induced significant modifications in the fatty acid profile of the fish muscle tissue, thereby substantially enhancing its nutritional value for human consumption.

Canola Oil

Canola oil (CO) is the commercial designation for oil derived from specific cultivars of rapeseed *Brassica napus* characterized by low erucic acid concentrations. CO typically offers a more cost-effective and readily available alternative to fish oil (FO) in global markets. This lipid source is particularly rich in monounsaturated fatty acids (MUFAs), α -linolenic acid (ALA), and linoleic acid (LA), with oleic acid (OA) being the predominant constituent. These fatty acids are efficiently catabolized via mitochondrial ß-oxidation. Furthermore, SFAs and MUFAs are metabolically prioritized over polyunsaturated fatty acids (PUFAs) for energy production (Fukada et al., 2017). The n-3 to n-6 ratio of CO is approximately 1:2 (Simopoulos, 1999). Previous research indicates that the dietary substitution of 75% FO in Australasian snapper *Pagrus auratus* and 70% FO in red sea bream *Pagrus major* with CO did not adversely affect growth performance (Fukada et al., 2017). Building on this foundation, Salavatian et al. (2023) investigated the impacts of substituting FO with CO on the growth performance and carcass biochemical composition of juvenile common carp *Cyprinus carpio*. In their study, CO replaced FO at four inclusion levels: 0%, 25%, 50%, and 75%. The experimental results revealed no significant differences among treatments regarding the feed conversion ratio (FCR), protein efficiency ratio (PER), specific growth rate (SGR), body weight gain (BWG), total length increase, average daily gain (ADG), survival rate, or final biometric parameters (final length and weight). While carcass moisture content remained statistically uniform across all groups, significant variations were observed in the crude protein, ash, and lipid content of the muscle tissue.

Soybean Oil (SBO)

Currently, soybean oil (SBO), derived from *Glycine max*, is extensively utilized in freshwater aquaculture formulations due to its increasing global production and cost-effectiveness. SBO is characterized by a high concentration of polyunsaturated fatty acids (PUFAs), particularly linoleic acid (LA) (Li et al., 2016). The lipid profile typically comprises 24% monounsaturated fatty acids (MUFAs, primarily oleic acid), 61% PUFAs (predominantly linoleic acid), and 15% saturated fatty acids (SFAs), resulting in an approximate SFA:MUFA:PUFA ratio of 15:24:58. In a study by He et al. (2021), the effects of replacing fish oil (FO) with SBO were investigated in orange-spotted grouper

Epinephelus coioides. The researchers evaluated growth performance, tissue fatty acid (FA) composition, plasma constituents, hepatic metabolic enzyme activities, and the mRNA expression levels of genes associated with lipid metabolism. Five experimental diets were formulated with escalating SBO inclusion levels (0, 250, 500, 750, and 1000 g kg^{-1}).

The results indicated that growth performance, whole-body composition, and muscle protein and lipid content remained unaffected by the dietary treatments. Similarly, increasing dietary SBO inclusion exerted no significant impact on plasma constituents or hepatic metabolic enzyme activities, with the notable exceptions of acetyl-CoA carboxylase (ACC) and hepatic lipase (HL). These enzymes exhibited linear and quadratic responses to SBO inclusion, reaching peak activities at inclusion levels of 1000 and 250 g kg^{-1}, respectively. Nevertheless, the fatty acid profiles of the dorsal muscle and liver generally mirrored the fatty acid composition of the diets. Furthermore, the mRNA expression levels of several hepatic genes (fas, acc, g6pd, lpl, ppar α, cpt-1, srebp-1c, delta 6fad, and elovl5) showed positive linear or quadratic responses to dietary SBO levels. Conversely, a negative linear or quadratic response was observed for the mRNA levels of hsl and atgl in the liver as SBO inclusion increased. The expression levels of scd and fabp were not significantly influenced by dietary SBO. These findings suggest that FO can be entirely substituted with SBO without detrimental effects on growth. However, SBO inclusion exceeding 500 g kg^{-1} may compromise the fatty acid profile of the liver and muscle tissue in this fish species. Table 1 presents the comparative fatty acid compositions of selected vegetable oils and prominent fish oils (Fabiszewska & Bialecka-Florjanczyk., 2014).

Vegetable Oil Economic Dynamics

The primary objective of intensive aquaculture is the optimization of profitability. A critical determinant influencing feed costs, and consequently the overall economic efficiency of a facility, is the selection of lipid sources integrated into the diet formulation. Various oils exhibit distinct price points; therefore, identifying a cost-effective oil that simultaneously promotes positive growth performance is considered a fundamental strategy for sustainable fish nutrition (Ayisi et al*.,* 2019). The market prices for several vegetable oils commonly utilized in aquafeed formulations are presented below (Figure 2).

Global Vegetable Oil Production Dynamics

Vegetable oils have been identified as viable substitutes for fish oil in aquafeed formulations, a shift driven not only by their comparative cost-effectiveness but also by their sustainable production metrics (Ayisi et al., 2019). The total cultivation area dedicated to oilseed crops constituting approximately 7% of global agricultural output has exhibited a substantial expansion in recent years. Of the approximately 500 million tonnes of global oilseed production, soybeans predominate with a 60% market share (360 million tonnes), while sunflower seeds account for 8–9% of the total volume. Consequently, developments within the soybean sector exert a profound influence on broader oilseed markets and their derivatives. Regarding extracted lipid output, palm oil comprises nearly 33% of global vegetable oil production, whereas sunflower oil represents only 9%. According to data from the United States Department of Agriculture (USDA), total global oilseed production reached 532 million tonnes in 2014. This aggregate output consisted of 315 million tonnes of soybeans, 71 million tonnes of rapeseed, 45 million tonnes of cottonseed, 40 million tonnes of sunflower seeds, and 61 million tonnes derived from other oilseed crops. Concurrently, global crude vegetable oil production amounted to 176 million tonnes, comprising 63 million tonnes of palm oil, 47 million tonnes of soybean oil, 27 million tonnes of rapeseed oil, 15 million tonnes of sunflower oil, and 19 million tonnes from other lipid sources (Baysal, 2020). The temporal trends in global oil production are illustrated in Figure 3.

As delineated in Figure 4, Indonesia occupies the premier rank in global vegetable oil production. This leading position is followed sequentially by China, Malaysia, the European Union, the United States, Argentina, and Brazil (Baysal, 2020).

The effect of vegetable oils in feed on fish growth and survival

In recent years, aquaculture nutritionists have increasingly investigated the viability of substituting fish oil (FO) with vegetable oils (VO), specifically evaluating the influence of these lipid sources on growth performance and feed utilization efficiency. Generally, the substitution of FO with VO does not exert deleterious effects on various cultured species, including black carp *Mylopharyngodon piceus* (Sun et al., 2011), Atlantic salmon (*Salmo salar*) (Menoyo et al., 2005), hybrid sturgeon *Acipenser baerii* × *Acipenser schrenckii* (Liu et al., 2018), cobia *Rachycentron canadum* (Trushenski et al., 2011), and Murray cod *Maccullochella peelii peelii* (Francis et al., 2006). Conversely, empirical evidence suggests that partial or total FO replacement can enhance growth performance, feed utilization, and survival rates in specific species, such as the rabbitfish *Siganus canaliculatus* (Xu et al., 2012) and striped catfish *Pangasius hypophthalmus* (Asdari et al., 2011). These favorable outcomes are likely attributable to the capacity of specific VOs to satisfy the essential fatty acid (EFA) requirements necessary for somatic growth. For instance, Peng et al. (2014) substituted dietary FO with soybean oil in juvenile turbot *Scophthalmus maximus* and observed that growth performance was not compromised by the dietary lipid source, concluding that up to 66.7% of FO

Table 1. Fatty acid composition of some selected vegetable and fish oils (Nascimento et al., 2015)

		Vegetable oils (percentage of total fatty acids in the oil)										
Fatty acid	Fatty acid name	Corn	Olive	Canola	Sunflower	Sesame	Flax seed	Peanuts	Fih liver	Tun fish	Anchovies	Hydrolyzed oil
C14:0	Myristic acid	0.03	0	0.05	0.07	0.02	0	0.03	2-6	5-ND	2.7-11.5	6.33
C15:0	Pentadecanoic acid								0.5-ND	2-ND	1.5-ND	
C16:0	Palmitic acid	11.06	10.27	4.05	6.62	9.32	5.87	9.47	7-14	14-24	13-22	19.67
C16:1(n-7)	Palmitoleic acid	0.13	0.81	0.24	0.13	0.15	0.07	0.13	4.5-11.5	12.5-ND	4-12	5.77
C17:0	Margaric acid	0.06	0.07	0.05	0.04	0.04	0.06	0.07	NA	3.5-ND	2-ND	0.72
C17:1	Margaroleic acid	0.03	0.13	0.09	0.03	0	0	0.05				
C18:0	Stearic acid	1.78	3.15	1.93	3.27	5.77	4.35	3.53	1-4	7.5-ND	7-1	4.91
C18:1(n-7)	Vaccenic acid								2-7	7-ND	1.7-3.7	
C18:1 (n-9)	Oleic acid	28.38	77.86	64.47	30.4	40.05	20.38	59.26	12-21	10-25	3.6-17	12.65
C18:2 (n-6)	Linoleic acid	56.31	6.17	18.47	58.25	43.19	15.85	19.96	0.05-3	3-ND	3.5-ND	0.20
C18:3 (n-3)	Linolenic acid	0.8	0.63	8.08	0.05	0	52.65	0.5	2-ND	2-ND	7-ND	0.2
C18:3 (n-6)	γ-linolenic acid								NA	4-ND	5-ND	2.0
C18:4 (n-3)	Stearidonic acid								0.5-4.5	2-ND	5-ND	
C20:0	Arachidic acid	0.41	0.41	0.58	0.24	0.62	0.16	1.47	NA	2.5-ND	1.8-ND	
C20:1 (n-9)	Eicosenoic acid	0.98	0.29	1.26	0.16	0.19	0.10	1.15	5-17	2.5-ND	4-ND	1.96
C20:1 (n-11)	Eicosenoic acid								1-5.5	3-ND	4-ND	
C20:4 (n-6)	Arachidonic acid								1.5-ND	3-ND	2.5-ND	
C20:4 (n-3)	Eicosatetraenoic acid								2-ND	1-ND	2-ND	
C20:5 (n-3)	Eicosapentaenoic acid								7-16	2.5-9	5-26	
C21:5 (n-3)	Heneicosapentaenoic								1.5-ND	1-ND	4-ND	
C22:0	Behenic acid	0.12	0.11	0.3	0.78	0.13	0.16	2.62				
C22:1 (n-9)	Erucic acid	0	0	0.07	0.04	0	0	0.21	1.5-ND	2-ND	2.3-ND	
C22:1 (n-11)	Cetoleic acid									1-ND	5.6-ND	
C22:5 (n-3)	Docosapentaenoic acid (DPA)									3-ND	4-ND	
C22:6 (n-3)	Docosahexaenoic acid (DHA)									21-42.5	4-26.5	0.44
C24:0	Lignoceric acid	0.17	0.05	0.16	0.24	0.08	0.12	1.39				
C24:1	Nervonic acid	0	0	0.12	0	0	0	0				

ND = not detected, defined as ≤0.05%, NA = Not applicable or unavailable.

could be successfully replaced. Similarly, Guler and Yildiz (2010) demonstrated that optimal growth and feed efficiency in rainbow trout *Oncorhynchus mykiss* were achieved when 50% of the dietary FO was replaced with cottonseed oil. Investigating alternative lipid sources, Demir et al. (2014) evaluated the effects of partial or total replacement of FO with unrefined peanut oil (PO) on the growth and physiological parameters of Mozambique tilapia (*Oreochromis mossambicus*; initial weight 6.36 ± 0.19 g) over a 60-day trial. Fish fed diets containing 50% PO exhibited superior weight gain and feed efficiency compared to other experimental treatments. In a related domestic study, Jalili et al. (2013) examined the impact of substituting FO with a vegetable oil blend comprising canola, linseed, and safflower oils (at a ratio of 40:30:30, respectively) on the proximate composition and muscle fatty acid profile of rainbow trout. The results indicated that while the total replacement of FO significantly increased the concentrations of vaccenic, linoleic, and linolenic acids, it led to a significant reduction in myristic, palmitic, oleic, arachidonic (ARA), eicosapentaenoic (EPA), and docosahexaenoic (DHA) acids within the muscle tissue. Crucially, however, the complete substitution of FO with these vegetable oil sources did not induce adverse effects on growth indices, nutritional efficiency, or the muscle proximate composition. Agh et al. (2012) investigated the synergistic effects of substituting dietary fish meal (FM) and fish oil (FO) with plant-based derivatives on the growth performance of rainbow trout *Oncorhynchus mykiss*. Their findings indicated that the simultaneous replacement of 100% FM with plant proteins and 80% FO did not induce significant statistical deviations in growth indices or feed consumption. However, a specific dietary formulation comprising 60% FM substitution with plant proteins and 80% VO

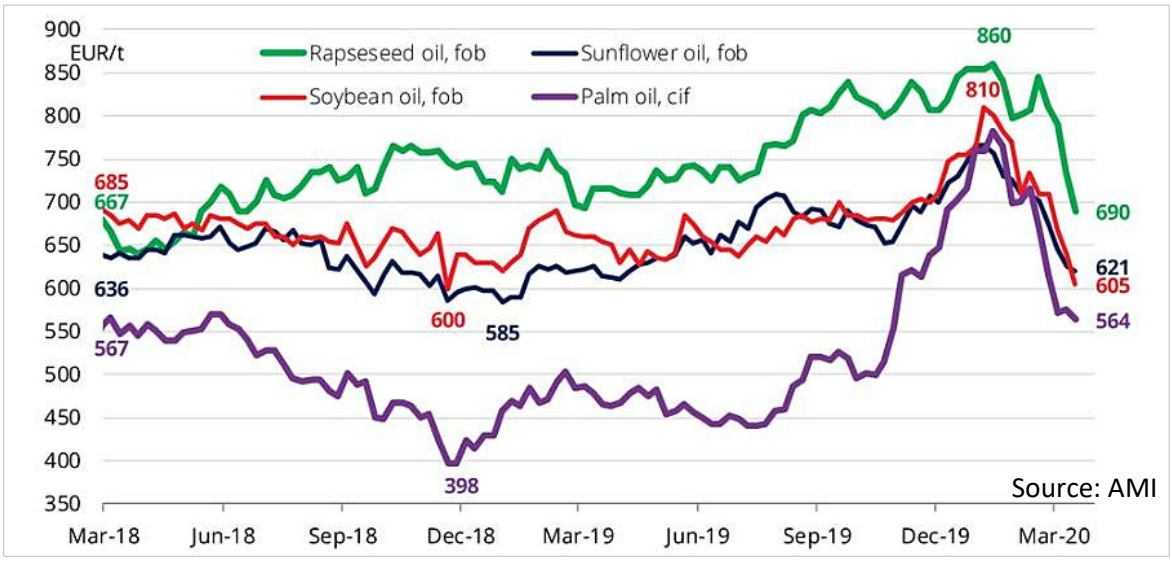

Figure 2. Wholesale prices of vegetable oils (euros per metric ton).

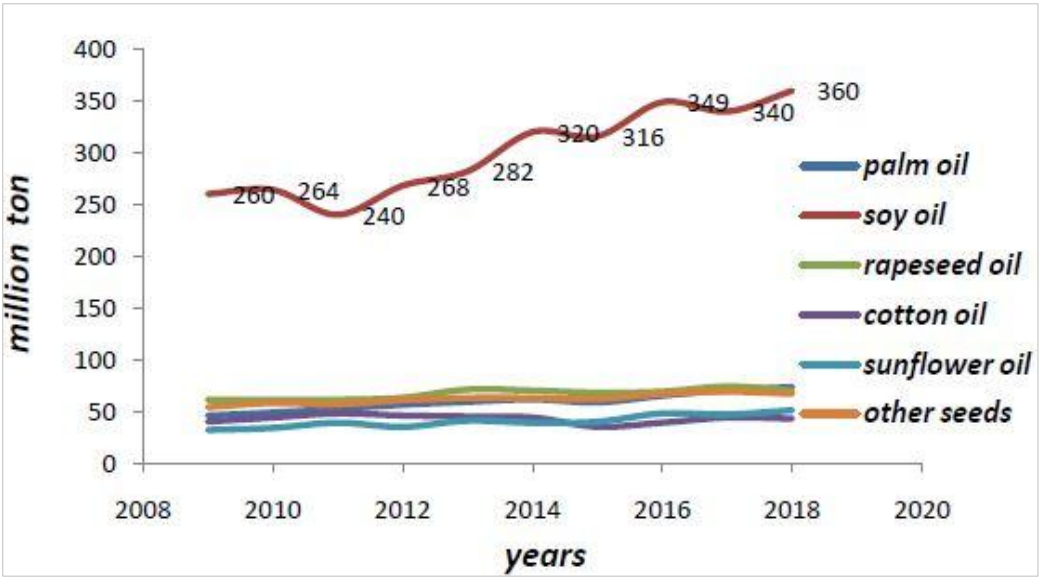

Figure 3. Vegetable oil production by year in the world.

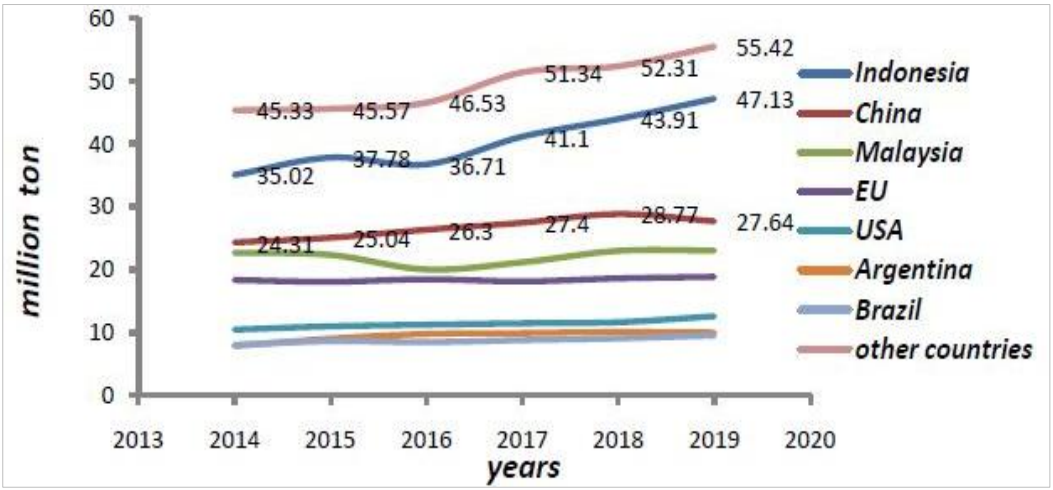

Figure 4. Vegetable oil production by country.

inclusion resulted in superior weight gain and specific growth rate (SGR), alongside a significant reduction in the feed conversion ratio (FCR) compared to other experimental cohorts. In a parallel investigation, Jalili et al. (2012a) evaluated the impact of replacing FO with various vegetable lipid sources in rainbow trout diets formulated with defatted fish meal. The experimental treatments included Kilka oil (FO, control), canola oil (CO), safflower oil (SO), and a blended formulation of 70% SO and 30% linseed oil (SLO). The results demonstrated no significant divergence in growth performance between the FO and CO groups. Conversely, the total substitution of FO with SO or the SLO blend precipitated a reduction in final biomass and SGR. Regarding physiological indices, the viscerosomatic index (VSI) was significantly elevated in the CO group relative to the control, while the hepatosomatic index (HSI) remained unaffected across treatments. The condition factor (CF) exhibited a complex pattern: it was significantly higher in fish fed CO and SLO diets but significantly depressed in the exclusive SO group.

Further biochemical analysis by Jalili et al. (2012b) revealed that while the substitution of FO with VOs significantly augmented muscle protein and ash content, it led to a marked decrement in fillet lipid content relative to the FO-fed cohort. Expanding the scope to cyprinids, Sonu et al. (2014) assessed the viability of sunflower oil (SFO) as an alternative lipid source for common carp *Cyprinus carpio*. Over a 60-day trial with graded inclusion levels (0%, 25%, 50%, 75%, and 100%), no significant perturbations were observed in weight gain, SGR, or survival rates. Cumulatively, previous studies suggest that VOs can serve as partial or total surrogates for FO without compromising somatic growth or feed utilization (summarized in Table 2). However, the efficacy of VO inclusion is multifactorial, depending heavily on the ontogenetic stage (age/size), feed formulation, species-specific physiological requirements, and the physicochemical properties of the selected oil (specifically digestibility and fatty acid profiles).

More recently, Noaman Hamad et al. (2024) explored the modulation of dietary Monounsaturated Fatty Acids (MUFA) and n-6/n-3 ratios in rainbow trout (*Oncorhynchus mykiss*) fed all-plant protein diets. The study employed seven experimental treatments varying in MUFA levels and Linoleic Acid (LA) to alpha-Linolenic Acid (ALA) ratios over an 8-week period. The experimental design included varied ratios ranging from Treatment 1 (MUFA: 1; LA:ALA: 55.33) to Treatment 7 (MUFA: 5.97; LA:ALA: 33.60). The data indicated that fish in Treatment 1 exhibited the lowest growth indices, whereas Treatment 6 yielded the highest growth performance. Building on this, MahmoudiKia et al. (2025) evaluated the complete replacement of FO with a vegetable oil blend (sunflower, linseed, coconut, and olive oils) in a completely plant-based diet for triploid rainbow trout (initial weight 14.5±0.17 g). The study utilized 650 fish distributed randomly across seven experimental treatments mirroring the MUFA and LA:ALA ratios described above. The trial consisted of a 4-month experimental feeding phase followed by a 1-month restoration (finishing) period where fish were re-fed a diet containing fish oil. At the conclusion of both the experimental and finishing phases, no statistically significant differences were observed in the growth indices across the treatment groups. The maintenance of appropriate growth trajectories and the absence of significant disparities among treatments suggest that the utilized vegetable oil blends did not exert negative impacts on the growth, survival, or general health status of the cultured triploid trout.

The Influence of Dietary Vegetable Oils on the Fatty Acid Profile of Fish Tissues

Extensive research has investigated the impact of substituting dietary lipids with vegetable oils (VO) on the carcass composition and fatty acid profiles of teleost fish. The substitution of fish oil (FO) with VO invariably modulates the fatty acid signature of the final product, thereby influencing the nutritional quality of the fillet to

Table 2. Effect of using vegetable oils in feed on growth performance and nutritional indices of different fish species (Ayisi et al., 2019)

Vegetable Oil Source	Replacement Level (%)	Species	Initial Weight (g)	Benefits of fish oil replacement with vegetable oils	Negative effects of fish oil replacement
Palm Oil	0, 33.33, 66.67, 100	*Oreochromis niloticus*	9.09	Significantly reduced mortality and improved survival rate in the 100% replacement diet; maintained carcass quality traits; and preserved fillet sensory and organoleptic properties.	Decreased PUFA and omega-3 fatty acid levels in liver and skeletal muscle; increased saturated fatty acid deposition.
	0, 25, 50, 75, 100	*Cirrhinus mrigala*	2.16	Enhanced oxidative stability of feed due to abundant antioxidant compounds (tocotrienols); safe inclusion up to 25% without negative effects on growth.	Replacement levels above 25% caused marked growth retardation, reduced daily weight gain, and impaired feed efficiency.
	100	*Larimichthys crocea*	245.29	Enhanced specific growth rate and lipid utilization efficiency in replacement treatments; no negative effects on condition factor, carcass weight, or tissue color.	Marked reduction in essential PUFA accumulation in edible tissues.
	0, 1, 1.5, 2	*Clarias gariepinus*	15.14	A highly stable and economical lipid source with enhanced feed stability against thermal oxidation.	Decreased omega-3/omega-6 fatty acid ratio in fillet tissue.
Soybean Oil	0, 60, 80, 100	*Acanthopagrus schlegeli*	20.26	Safe and effective replacement up to 80% with no adverse effects on growth performance; markedly reduced feed production costs.	100% replacement decreased feed efficiency and compromised growth due to limited omega-3 biosynthesis.
	0, 25, 75, 100	*Pelteobagrus vachelli*	1.00	25% replacement (MO1 diet) maintained growth performance and enhanced serum lysozyme, C3, C4, and total IgM levels.	Shifted fillet fatty acid profile toward higher linoleic acid and reduced omega-3/omega-6 ratio; impaired hepatic indices at replacement levels above 25%.
	0, 20, 32, 56, 100	*Megalobrama amblycephala*	0.3	Enhanced somatic growth and feed efficiency at the optimal 20% replacement level.	Replacement beyond the optimal level impaired protein efficiency and induced unfavorable hepatic metabolic responses.
	33.3, 66.7, 100	*Scophthalmus maximus L*	5.88	Safe replacement up to 66.7% with no negative effects on survival or condition factor; reduced feed lipid peroxidation risk.	100% replacement significantly impaired specific growth rate and induced hepatic steatosis via FAS upregulation and CPT I downregulation.
	100	*Larimichthys crocea*	13.77	Improved somatic growth and feed efficiency; cost-effective diets formulated with plant protein sources.	Marked depletion of long-chain omega-3 PUFA reserves in fillet tissues.
Cottonseed Oil	0, 50, 60, 70	*Sparus aurata*	4.00	No adverse effects on carcass traits, protein efficiency, or growth up to 60% replacement; improved feed shelf life due to high vitamin content.	At 70% replacement, growth and feed efficiency slightly declined due to potential effects of free gossypol; increased visceral index.
Peanut Oil	0, 50, 100	*Oreochromis mossambicus*	6.36	Replacement up to 50% maintained growth performance without affecting blood and immune parameters; reduced blood glucose and cholesterol levels.	Complete replacement (100%) may reduce carcass yield and beneficial omega-3 fatty acids.
	0, 25, 50, 75, 100	*Oncorhynchus mykiss*	60.51	Sustainable replacement up to 50% without adverse effects on specific growth parameters.	Above 50% dietary replacement, long-chain PUFA deficiency threatens fillet tissue quality.
	100	*Acipenser gueldenstaedtii*	1.39	Improved growth rate and nutrient utilization efficiency through balanced intestinal digestive enzyme secretion.	Severe depletion of muscle long-chain omega-3 fatty acid reserves due to insufficient biosynthetic capacity.
Linseed (Flaxseed) Oil	0, 25, 50, 75, 100	*Oreochromis niloticus*	22.00	Replacement up to 50% maximized somatic growth through efficient use of plant fatty acid precursors.	Replacement levels above 50% reduced growth due to saturation of hepatic desaturase pathways.
	33.3, 50, 66.7	*Puntius gonionotus*	12.1	Replacement up to 33.3% maintained growth performance; this oil increased the expression of delta-6 desaturase genes in the liver and intestine, thereby promoting endogenous omega-3 biosynthesis.)	Levels above 33.3% reduced growth rate and increased feed conversion ratio due to insufficient endogenous biosynthesis.
	0, 25, 50, 75	*Anoplopoma fimbria*	153.4	Replacement up to 75% improved feed efficiency and enhanced growth.	Complete replacement increases the potential for hepatic and skin-related challenges.
	0, 50, 100	*Oncorhynchus mykiss*	16.5	Stable somatic growth and feed efficiency at both 50% and 100% replacement levels; no adverse changes in serum biochemical parameters.	Significant changes in muscle fatty acid profiles through high deposition of plant-derived alpha-linolenic acid.
Echium Oil	0, 50	*Sparus aurata*	265.05	50% replacement caused no negative effects on growth performance, feed efficiency, or liver function.	Reduced natural EPA and DHA levels in fillets compared with the control.
Rapeseed (Canola) Oil	0, 100	*Dicentrarchus labrax*	35.4	100% replacement enhanced growth and nutrient utilization efficiency; improved protein-sparing effect through increased oleic acid β-oxidation.	Marked reduction in omega-3 PUFA levels in liver and muscle tissues.

varying degrees (Ayisi et al., 2017). For instance, the inclusion of 8% olive pomace as a replacement for dietary FO resulted in a marked reduction in eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) concentrations in gilthead seabream *Sparus aurata*. In the majority of reported cases, the fatty acid compositions of muscle tissue, hepatic tissue, and whole-body homogenates exhibit a high degree of plasticity, directly mirroring the fatty acid profile of the diet (Apraku et al., 2017; Yılmaz & Eroldoğan, 2015). However, this correlation is not absolute; instances exist where dietary lipid composition does not linearly dictate tissue fatty acid profiles. Such discrepancies across studies may be attributed to multifactorial variables, including the nutritional status of the fish during the rearing period, species-specific metabolic capabilities, fish size, and the duration of the feeding trial (Li et al., 2015).

The partial or total replacement of fish oil (FO) with vegetable oils (VO) has the potential to significantly modulate carcass composition, though results vary across scientific literature. For instance, replacing FO with rapeseed oil in the diet of Atlantic salmon *Salmo salar* resulted in increased whole-body protein content and protein retention (Karalazo et al., 2011). This protein-sparing effect may be attributed to the presence of monounsaturated fatty acids (MUFA), such as oleic acid (OA), in vegetable oils. These fatty acids are often preferentially utilized for adenosine triphosphate (ATP) production via beta-oxidation, thereby sparing amino acids for somatic growth (Turchini et al., 2009).

Conversely, numerous studies indicate that substituting FO with VO does not necessarily alter proximate body composition. Li et al. (2015) reported that replacing FO with linseed oil in tilapia diets induced no significant changes in whole-body protein, lipid, or ash content. Similarly, the substitution of FO with linseed oil in silver barb *Barbonymus gonionotus* exerted no discernible impact on carcass composition. Furthermore, the inclusion of soybean oil as a substitute for FO did not affect the proximate composition of black sea bream *Acanthopagrus schlegelii*, gilthead sea bream *Sparus aurata*, or turbot *Scophthalmus maximus*.

These discrepancies across studies may be ascribed to multifactorial variables, including the experimental duration, lipid sources, dietary lipid levels, fish species, developmental stage, and rearing conditions. Additionally, the feed manufacturing process specifically, the distinction between pelleting and extrusion can critically influence the final physiological outcomes (Ayisi et al., 2019).

A recent study by MahmoudiKia et al. (2025) demonstrated that the ratio of n-6 to n-3 polyunsaturated fatty acids (n-6 PUFA/n-3 PUFA) in fish muscle significantly increased in Treatment 5 (fish fed a diet containing 55% MUFA with an LA:ALA ratio of 8) compared to the control group across both experimental periods. During the initial rearing phase, the muscle concentrations of docosahexaenoic acid (DHA), eicosapentaenoic acid (EPA), and total PUFA were significantly reduced in all treatment groups relative to the control. However, a subsequent finishing period utilizing an FO-based diet successfully restored the aforementioned fatty acid profiles in the muscle tissue, although muscle DHA levels in Treatment 5 remained significantly lower than those of the control group. Physiologically, farmed rainbow trout *Oncorhynchus mykiss* demonstrated the capacity for the elongation and desaturation of linoleic acid (LA) to arachidonic acid (ArA), and alpha-linolenic acid (ALA) to EPA and subsequently DHA. This biosynthetic capability is evidenced by the observation that LA and ALA concentrations were lower in the muscle tissue than in the experimental diets, confirming that rainbow trout possess an effective enzymatic pathway for bioconverting 18-carbon fatty acids derived from vegetable oils. Consequently, implementing a short-term finishing feeding strategy with an FO-containing diet serves as a viable method to restore muscle fatty acid profiles, thereby enhancing the nutritional value of the final product.

Impacts of Vegetable Oil Substitution on Serum Metabolites, Antioxidant Capacity, Immune Response, and Fish Health

Ensuring long-term sustainability in aquaculture necessitates the maintenance of healthy stocks characterized by optimal immunocompetence (Montero et al., 2003). Consequently, it is imperative to verify that aquafeeds not only fulfill the nutritional requirements for balanced growth specifically regarding essential fatty acids (EFAs) but also reinforce, or at the very least do not compromise, the fish immune system. In light of this, numerous longitudinal studies have employed a wide array of parameters to elucidate how the utilization of vegetable oils (VOs) modulates fish health and immune functionality

Hematological parameters and serum biochemical profiles constitute critical indicators of the general physiological status of fish (El–Kasheif et al., 2011). Indeed, the overall health assessment of fish is predominantly determined via serum biochemical analysis. Blood analysis serves as a robust diagnostic tool, providing reliable data regarding metabolic disorders, nutritional deficiencies, adaptive responses to environmental stimuli, and chronic stress status (Peres et al., 2013). Ochang (2011) reported that the hematological parameters of Nile tilapia (*Oreochromis niloticus*) were significantly modulated by the substitution of dietary fish oil (FO) with soybean oil, noting marked alterations in erythrocyte counts and total cholesterol levels. Similarly, in African catfish (*Heterobranchus longifilis*), total protein, glucose concentrations, and the activities of serum aspartate aminotransferase (AST) and alanine aminotransferase (ALT) were influenced by the replacement of FO with palm oil (Babalola & Apata, 2012). These findings

suggest that the inclusion of diverse vegetable oils in the diets of various fish species can induce distinct shifts in hematological indices.

Scientific evidence indicates that dietary nutrients and additives possess the capacity to stimulate the fish immune system, thereby enhancing disease resistance (Viswanath, 2012). In fish, the innate (non-specific) immune system plays a more pivotal role in disease resistance than the adaptive immune system. The substitution of FO with VO influences eicosanoid biosynthesis and the functional integrity of immune cells. Furthermore, this substitution is known to alter the fatty acid composition of immune cells, as well as humoral immune processes, including serum lysozyme and alternative complement pathway activities. Moreover, the expression of immune-related genes is modulated when FO is replaced by plant-based lipid sources (Ayisi et al., 2019). These immunological shifts may be attributed to an imbalance in the n-3/n-6 fatty acid ratio resulting from such dietary substitutions. Investigations into the effects of replacing FO with unrefined peanut oil on the serum indices of Common carp (*Cyprinus carpio*) revealed that serum total protein and globulin levels increased concomitantly with rising dietary peanut oil content. Notably, triglyceride levels were significantly elevated in fish fed diets containing 100% peanut oil (Yıldırım et al., 2013). Conversely, Demir et al. (2014) observed that serum glucose levels decreased in tilapia when 50% or 100% of FO was replaced with peanut oil. Furthermore, serum cholesterol levels were lower in groups fed diets with 50% and 100% peanut oil substitution.

Maintaining the pro-oxidant/antioxidant balance is crucial for ensuring the health of cultured fish species (Aluwong et al*.,* 2013). During pathogen invasion, fish, akin to other organisms, require protection against cellular damage induced by reactive oxygen species (ROS). Antioxidant enzymes, such as glutathione S-transferase (GST), glutathione peroxidase (GPx), catalase (CAT), and superoxide dismutase (SOD), are responsible for mitigating oxidative stress (Saddick et al., 2017). In a study by Wang et al. 2016, the replacement of dietary FO with varying levels of linseed oil in juvenile turbot *Scophthalmus maximus* L. did not exert a significant effect on total serum SOD activity. A similar study by Lin & Shiau (2007) demonstrated that serum SOD and CAT activities increased in grouper fed a blend of FO and corn oil. These results align with findings by Sun et al. (2011), wherein the replacement of FO with rapeseed oil in black carp (*Mylopharyngodon piceus*) diets was investigated. However, the substitution of FO with linseed oil or soybean oil did not affect serum lysozyme activity in gilthead sea bream (*Sparus aurata*) (Montero et al., 2008). This is consistent with Mozanzadeh et al*.* (2016), who reported that feeding juvenile *Sparidentex hasta* with canola or sunflower oil as FO substitutes did not alter serum lysozyme activity, whereas a blend of FO and these vegetable oils significantly enhanced lysozyme activity. The elevated lysozyme activity observed in diets containing a mixture of FO and VO may be attributed to an optimized ratio of n-3 and n-6 long-chain polyunsaturated fatty acids (LC-PUFA).

Effects of Vegetable Oils on Lipid Metabolism Gene Expression

The influence of dietary vegetable oils (VO) on the expression of genes associated with lipid and fatty acid metabolism varies significantly across different fish species. For instance, Nayak et al. (2017) observed significantly upregulated mRNA expression levels of Delta6-fatty acid desaturase (*fads2d6*) in the liver, muscle, and intestine of silver barb *Barbonymus gonionotus* fed linseed oil (LO) diets compared to those fed fish oil (FO) based diets. Similarly, Ayisi & Zhao (2017) reported that substituting FO with palm oil in Nile tilapia *Oreochromis niloticus* diets modulated several genes responsible for lipid metabolism. They established a positive correlation between dietary palm oil inclusion levels and the expression of fatty acid synthase (*FAS*), acetyl-CoA carboxylase (*ACC*), stearoyl-CoA desaturase-1 (*SCD1*), and acyl-CoA synthetase (*ACYL*). Furthermore, Li et al. (2015), upon replacing FO with soybean oil (SO) in blunt snout bream *Megalobrama amblycephala*, noted that increasing SO content upregulated acyl-CoA Delta9-desaturase expression while downregulating peroxisome proliferator-activated receptors alpha (*PPARalpha*) and beta (*PPARbeta*). Both PPARs play pivotal role in lipid metabolism (Dressel et al., 2003). These transcription factors are instrumental in fatty acid catabolism, functioning by regulating the gene expression of enzymes involved in fatty acid oxidation (Zheng et al., 2014). Li et al*.* (2015) demonstrated that the highest hepatic expression of *PPAR alpha* and *PPAR*occurred in fish fed diets containing 20% SO, with expression levels declining as SO inclusion increased from 20% to 100%. In a related study, Cruz-Garcia et al. (2011) found that the substitution of FO with VO resulted in the downregulation of liver X receptor (*LXR*) expression in gilthead sea bream (*Sparus aurata* L.). This finding corroborated earlier research by Cruz-Garcia et al. (2009), which also reported downregulated hepatic *LXR* mRNA expression in salmonids fed VO-based diets. LXR is fundamental to fatty acid, cholesterol, and glucose metabolism, acting primarily as a cholesterol sensor (Steffensen & Gustafsson, 2004). Such investigations are critical for the advancement of the aquaculture industry. Understanding how alternative VO sources modulate lipid metabolism gene expression allows for better control over physiological processes, thereby ensuring sustainable aquaculture practices. However, lipid metabolism is an inherently complex process, susceptible to influence by various factors, including the dietary content of other macronutrients such as proteins and carbohydrates. Furthermore, the discrepancies observed across various studies may be

attributed to differences in species, experimental duration, feeding protocols, and the nutritional status of the fish (Ayisi et al., 2019).

Next-Generation Alternative Lipids

Development of HUFA-Rich Vegetable Oils by Genetic Engineering: The Camelina Revolution

Advances in genetic engineering technology have transformed oilseed crops into novel sources of essential fatty acids for aquaculture. Among these, camelina (*Camelina sativa*) is recognized as one of the most promising oilseed crops due to its favorable agronomic adaptability, low input requirements, and high suitability for genetic manipulation. By transferring genes from the long-chain omega-3 fatty acid biosynthetic pathway, researchers have successfully developed transgenic camelina varieties whose oil contains significant amounts of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) fatty acids naturally derived primarily from marine sources (Betancor et al., 2021).

Nutritional studies on European seabass (*Dicentrarchus labrax*) have demonstrated that completely replacing fish oil with transgenic camelina oil is feasible without any negative effects on growth, feed conversion ratio (FCR), or nutritional efficiency. Furthermore, using this oil maintains or even increases the concentration of EPA and DHA in fish tissues, thereby improving the nutritional value of the fillet. Although a temporary reduction in feed intake was observed at the beginning of the feeding period likely due to the presence of glucosinolates in the crude camelina oil this effect was transient and did not significantly affect final growth performance. Consequently, transgenic camelina can be considered one of the most important achievements of genetic engineering in developing sustainable aquaculture feeds. By reducing dependence on limited fish oil stocks, it enables the sustainable production of long-chain omega-3 fatty acids and represents a major step toward the sustainability of the aquaculture industry (Betancor et al., 2021).

The production of camelina containing long-chain omega-3 fatty acids was achieved by transferring seven genes encoding fatty acid desaturase and elongase enzymes from various marine microalgae species, enabling the genetically modified (GM) camelina plants to synthesize EPA and DHA (Ruiz-Lopez et al., 2014). Notably, the presence of balanced amounts of EPA in transgenic camelina oils can modulate the activity of endogenous fatty acid biosynthetic pathways rather than completely shutting them down. This indicates a metabolic equilibrium in which the fish maintains a portion of its internal biosynthetic capacity while simultaneously receiving essential fatty acids from the diet (Betancor et al., 2016).

Seaweeds as Sustainable Sources of Lipids and Essential Fatty Acids in Aquafeeds

The inclusion of seaweeds in aquafeeds can supply bioactive compounds that improve growth performance, enhance the immune system, increase disease resistance, mitigate stress effects, and promote gut health, ultimately leading to enhanced performance in farmed fish and shrimp (Abdel-Latif et al., 2023). Marine macroalgae have garnered significant attention as promising plant-based sources of polyunsaturated fatty acids (PUFAs), particularly eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Jaworowska & Murtaza, 2022). Unlike many terrestrial plants, certain seaweeds are capable of synthesizing these fatty acids. The concentrations of EPA and DHA vary depending on the taxonomic group and species, accounting for approximately 1% to 21% and 2% to 17% of total fatty acids, respectively (Table 3) (Jaworowska & Murtaza, 2022). Consequently, seaweeds represent a potential and sustainable source of EPA and DHA, particularly for reducing dependence on conventional marine-derived ingredients (Jaworowska et al., 2026).

One of the primary advantages of macroalgae compared to terrestrial crops is their minimal requirement for conventional agricultural inputs. These organisms do not require freshwater, arable land, or chemical fertilizers for growth; therefore, they can be produced with lower consumption of limited resources under conditions associated with a reduced carbon footprint (Khan et al., 2024). These attributes align the cultivation and exploitation of seaweeds with the concept of a Sustainable Blue Economy an approach that emphasizes the responsible and sustainable use of ocean resources to generate economic value, preserve the environment, and support the long-term development of coastal communities (Duarte et al.,

Table 3. Total lipid content and n-3 and n-6 FA in Selected Marine Seaweeds (Jaworowska et al., 2026)

Seaweed	Total Lipids (g/100 g DW)	EPA (%)	DHA (%)	Total n-3 (%)	Total n-6 (%)	n-6/n-3 Ratio
Rhodophyta	1.47	33.33	0.24	28.20	2.36	0.08
Palmaria palmata	1.03	32.18	0.27	27.58	2.04	0.07
Porphyra spp.	3.20	38.91	0.02	38.01	13.68	0.36
Ochrophyta	1.58	7.12	0.05	18.98	19.66	1.04
Fucus vesiculosus	1.60	8.48	0.03	14.72	21.10	1.43
Himanthalia elongata	1.92	7.78	0.05	22.07	20.44	0.93
Laminaria digitata	1.42	13.76	0.06	25.80	14.08	0.55
Undaria pinnatifida	2.42	13.00	0.05	41.79	20.27	0.48
Saccharina japonica	1.31	5.01	0.04	11.46	21.24	1.85
Sargassum fusiforme	1.12	4.21	0.03	13.79	15.86	1.15

2023). Accordingly, utilizing seaweeds or their derived products as fish oil replacements in aquafeeds has emerged as a promising strategy for advancing sustainable aquaculture systems. This approach can alleviate pressure on wild fish stocks used for fish oil production while meeting the essential fatty acid requirements of cultured aquatic species and satisfying the growing global demand for sustainable seafood (Duarte et al., 2023).

Nevertheless, the nutritional value of seaweeds is not restricted to their fatty acid profile, as the concentration and composition of their constituent lipids are also of paramount importance. Total lipid content in macroalgae is heavily influenced by species, environmental conditions, seasonality, age, and developmental stage, typically ranging from less than 1% to approximately 20% of dry weight. Certain species are particularly lipid-rich; for instance, the total lipid content in the green alga *Ulva rigida* is approximately 12%, whereas in certain brown algal species of the genus *Dictyota*, it has been reported to range between 12% and 20% (Hughes et al., 2020). Seasonal variations can also exert a marked effect on lipid accumulation. In species belonging to the genera *Saccharina*, *Laminaria*, and *Alaria esculenta*, peak lipid levels in the fronds are generally observed during the winter months, whereas in species of the genus *Fucus*, maximum total lipid content has been reported in summer, particularly in August (Kim et al., 1996). Furthermore, comparative analyses across different geographical regions indicate that tropical species possess significantly lower total lipid content than cold-water species (Sanchez-Machado et al., 2004). Therefore, species-specific and environmental differences must be carefully considered when selecting appropriate candidates for nutritional exploitation and lipid production.

In addition to essential fatty acids, macroalgae contain a diverse array of bioactive lipid compounds that enhance their practical utility. Studies have demonstrated that lipid extracts derived from various brown, green, and red algal species exhibit potent biological activities, including antioxidant, anti-inflammatory, and antiproliferative properties (Lopes et al., 2020). The presence of these compounds renders seaweeds not only a valuable source of fatty acids but also a suitable candidate for functional feed formulation in aquaculture, particularly because their bioactive constituents may play a vital role in improving the physiological status and environmental stress resistance of aquatic organisms. Overall, the presence of EPA and DHA, diverse lipid profiles, cultivation capacity without extensive reliance on freshwater and arable land, and bioactive properties establish seaweeds as promising options for the development of sustainable and functional resources in the aquaculture industry.

Microalgae as Sustainable Alternatives to Fish Oil in Aquafeeds: Nutritional Efficacy, Bioactive Potential, and Future Perspectives

Fish oil is a critical component of aquafeeds, providing dietary energy as well as long-chain polyunsaturated omega-3 fatty acids (omega-3 LC-PUFAs), particularly eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), which play fundamental roles in neural development, immune function, and overall aquatic health (Tocher, 2015). Although vegetable oils and animal fats have been extensively investigated as alternatives, their inherent lack of EPA and DHA frequently compromises growth performance and the nutritional value of farmed seafood (Alhazzaa et al., 2019). For instance, the omega-3 LC-PUFA content in farmed Atlantic salmon experienced a significant decline between 2006 and 2015, driven largely by the expanded incorporation of alternative lipid sources (Sprague et al., 2016).

To address these nutritional gaps while fostering industry sustainability, researchers have focused on identifying functional feed ingredients capable of maintaining fish health and productivity. Among these, microalgae have emerged as a highly promising alternative to fish oil due to their exceptional nutritional profile and robust capacity for synthesizing omega-3 LC-PUFAs (Abdel-Latif et al., 2022). Certain microalgal strains can allocate between 37% and 67% of their total fatty acids to omega-3 LC-PUFAs (Table 4), thereby satisfying essential fatty acid requirements in aquaculture species. Furthermore, optimization of cultivation parameters such as light intensity and nutrient availability can significantly enhance productivity and modulate fatty acid composition (Chen et al., 2017); for instance, reduced light intensity has been shown to elevate the relative proportions of EPA and DHA in *Pavlova lutheri* cells (Guedes et al., 2010).

Heterotrophic and photosynthetic microalgae, particularly *Schizochytrium* and *Aurantiochytrium* species, are recognized as premier sources of DHA for fish oil replacement. Their inclusion in the diets of commercial species including Atlantic salmon (*Salmo salar*), Nile tilapia (*Oreochromis niloticus*), olive flounder (*Paralichthys olivaceus*), and Pacific white shrimp (*Litopenaeus vannamei*) has demonstrated excellent

Table 4. Fatty Acid Composition of Different Microalgae (% of Total FA) (Ma & Hu, 2024)

Oils	SFAs	MUFAs	LA	AA	ALA	EPA	DHA	ω-6 PUFAs	ω-3 PUFAs
Schizochytrium sp.	35.23	0.9	0.7	2.9	0.1	3.5	31.4	18.17	37.08
Crypthecodinium cohnii	36	11	NA	NA	NA	NA	44.0	NA	44.0
Phaeomonas parva	22.4	4.8	1.8	2.9	0.0	56.0	11.0	4.7	67.0
Glossomastrix chrysoplasta	26.4	10.6	3.9	5.5	0.0	39.2	8.9	9.4	48.1
Fragilidium sp.	23.9	2.0	0.3	0.0	1.8	20.9	26.3	0.6	49.0
Isochrysis galbana	25.3	12.78	1.93	0.15	NA	26.25	11.47	13.55	49.37

efficacy, successfully enabling total replacement of dietary fish oil while improving growth rates, feed conversion ratios (FCR), immune responses, and muscle omega-3 content (Tibbetts et al., 2020; Guimarães et al., 2019; Abdel-Latif et al., 2022). Specifically, *Schizochytrium sp.* (SC) has been utilized to replace up to 80% of fish oil in rainbow trout (*Oncorhynchus mykiss*) diets without adverse effects on growth, with moderate inclusion levels (20%) even yielding enhancements in growth performance, feed efficiency, immune markers, and disease resistance (Lee et al., 2022). Similarly, complete replacement strategies combining vegetable oils with commercial microalgal omega-3 products have been reported with success in rainbow trout (Betiku et al., 2016). Beyond direct fish oil substitution, microalgal biomass could serve as an effective bio-enrichment agent (Roshandel et al., 2025).

Compared to terrestrial oil crops (such as soybean, peanut, and sunflower), photosynthetic microalgae offer profound ecological and operational advantages, including exceptionally rapid growth rates, short cultivation cycles, higher lipid productivity per unit area, and no competition for arable land or freshwater resources (Yang et al., 2025). Alongside EPA and DHA, many strains accumulate valuable levels of alpha-linolenic acid (ALA) and diverse bioactive compounds that exhibit potent antioxidant, anti-inflammatory, and immunostimulatory properties. These attributes not only protect against environmental stressors and pathogens but also position microalgal lipids as premier candidates for functional aquafeed formulations (Yang et al., 2025).

Although high production costs remain a primary constraint restricting the ubiquitous commercial adoption of microalgal additives, ongoing advancements in cultivation technologies, photobioreactor design, and nutrient management continue to improve economic viability (Ma & Hu, 2024). Consequently, microalgae represent a scientifically robust, environmentally sustainable, and highly scalable cornerstone for replacing marine-derived fish oil and advancing the long-term circular bioeconomy of the global aquaculture sector.

Conclusion and Future Perspectives

Dietary fish oil requirements vary significantly between freshwater and marine fish species. Furthermore, fish oil inclusion can modulate certain feed characteristics, particularly palatability. In general, it can be concluded that fish oil is susceptible to substantial substitution with vegetable oils. In the majority of instances, the replacement of fish oil with various vegetable oils whether applied individually or as blends does not exert a detrimental impact on the growth performance of the target species. Nevertheless, empirical outcomes may vary contingent upon the species and developmental stage of the fish, the duration of the feeding trial, and the dietary content of n-3 long-chain polyunsaturated fatty acids (n-3 LC-PUFA). Provided that the diet contains adequate levels of n-3 LC-PUFA, discernible alterations in fish growth performance are generally not anticipated. Notably, the fatty acid profiles of muscle, liver, and whole-body tissues typically mirror the dietary fatty acid composition; consequently, the lipid profiles of these tissues are readily modified when vegetable oils are utilized as substitutes for fish oil. Although extensive research has been conducted on the dietary inclusion of vegetable oils as fish oil alternatives across various species, there appears to be a paucity of data regarding the implications of such substitutions for the genetic architecture and general health status of the fish. Recent advancements in nutritional science have facilitated the integration of nutritional analysis and genomics through the discipline of nutrigenomics, thereby elucidating the influence of diet on differential gene expression (Kumar et al., 2017). This scientific domain investigates the modulation of genetic signaling by nutrients and holds significant potential for optimizing the health, flesh quality, and growth performance of cultured species, reducing feed costs, and ultimately realizing sustainable aquaculture practices (Overturf et al., 2016). Consequently, future nutritional investigations are anticipated to focus on the molecular mechanisms governing growth, immune responses, and the metabolism of lipids and fatty acids. Furthermore, research efforts should not be restricted to specific life stages; the preponderance of existing literature has primarily targeted the juvenile phase. However, it has been demonstrated that nutrient utilization efficiency, gene expression patterns, and somatic composition evolve throughout the ontogeny of the fish (Johansen & Overturf, 2006). Therefore, comprehensive studies addressing the substitution of fish oil with vegetable oils must be conducted across all developmental stages.

Ethical Statement

Only recently published scientific literature has been used with appropriate citation and not any animal subjects were used.

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Author Contribution

All authors were involved in early drafting and editing, reviewing the manuscript.

Conflict of Interest

The authors declare that they have no known competing financial or non-financial, professional, or

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