

Review

Dietary Lauric Acid and Its Derivatives in Aquaculture Nutrition: Sources, Mechanisms of Action, and Physiological Effects

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Abstract

Lauric acid (LA), a medium-chain fatty acid abundant in coconut oil and *Hermetia illucens* larvae, has been reported to promote growth performance and exhibit antimicrobial and immunostimulatory properties. This review examines current studies on its effects on growth performance, intestinal health, microbiota modulation, and immune responses in aquatic species. Studies in finfish and crustaceans were evaluated according to the LA source, distinguishing purified LA, LA derivatives such as monoglycerides, and LA rich ingredients, when considering LA rich ingredients. Overall, LA was associated with changes in growth performance, feed efficiency, survival, intestinal morphology, gut microbiota, and immune and antioxidant responses, although effects varied with source, dose, species, and experimental conditions. Reported effects include increased villus height and goblet cell density, modulation of gut microbiota, altered cytokine expression, increased antioxidant enzyme activity, and reduced lipid peroxidation. Overall, LA appears to be a promising functional component in aquafeeds for finfish and crustacean species. Nevertheless, inconsistent experimental designs, differences in LA sources, and species-specific responses make direct comparisons among studies difficult. Further studies that use standardized experimental protocols, including consistent LA sources, dietary inclusion levels, trial durations and evaluation criteria, are needed to define optimal inclusion levels in different aquatic species.

Keywords: lauric acid; black soldier fly oil; growth performance; intestinal health; gut microbiota; immune response

Key Contribution: This review provides a comprehensive synthesis of current scientific evidence regarding lauric acid, a medium-chain fatty acid abundant in coconut oil and *Hermetia illucens* larvae, as a promising functional component in aquafeeds for fish and crustacean species. Our review examines the effects of lauric acid on growth performance and feed efficiency, intestinal health, microbiota modulation, and immune and antioxidant responses. A key contribution of this review is a comparative analysis across different finfish and crustacean species, evaluating various administration forms, such as purified lauric acid, monoglycerides, and insect-derived meals/oils.



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1. Introduction

Aquaculture remains one of the fastest growing food production sectors globally, with functional feed additives emerging as an important strategy toward achieving the

objectives of the One Health framework by promoting aquatic animal health, improving resilience and promoting more sustainable production practices. The reduced reliance on traditional chemicals and antibiotics and the transition towards sustainable feed additives in the aquaculture industry directly addresses environmental concerns, animal welfare, and human food safety.

The rapidly growing aquaculture industry is continuously seeking sustainable and health-promoting strategies that can promote fish growth, enhance gut health, reduce antibiotics reliance, and mitigate disease pressures without compromising on the production efficiency. Currently, research and development in aquaculture is focusing on finding feed additives in a holistic approach, which can promote growth, immune response, gene expression, antioxidant capacity and intestinal morphology in aquatic organisms [1]. Therefore, within this context, in response to the specific needs of aquaculture (sustainable development, nutrition, health, and disease prevention), medium-chain fatty acid (MCFA)-like LA aligns with the industry's requirements due to its distinct metabolic properties [2].

Lauric acid (C12:0) is the longest member of the medium-chain fatty acid (MCFA) family, which also includes caproic (C6:0), caprylic (C8:0), and capric (C10:0) acids. They have gained significant interest due to their faster absorption in aquatic animals compared to long-chain fatty acids [3]. Although all other MCFAs are rapidly absorbed and metabolized, LA is known to provide an efficient energy source while also exerting antimicrobial, immunomodulatory, and gut health-promoting effects in aquatic animals [2]. Recent studies have reported that dietary MCFAs can improve growth performance, nutrient utilization, intestinal morphology, antioxidant capacity, immune function, and resistance to pathogens in fish and crustacean species, highlighting their potential as functional feed ingredients in sustainable aquaculture [4–8].

Compared to other functional feed additives used in aquaculture, LA combines nutritional and bioactive properties that represent an asset compared to commonly used feed additives like organic acids, probiotics, essential oils, and antimicrobial peptides. Organic acids are primarily incorporated into aquafeeds to improve nutrient digestibility, mineral utilization, intestinal microbial balance, and disease resistance, although their efficacy depends on several factors, including the type of acid, inclusion level, species, and culture conditions [9]. On the other hand, probiotics improve host health through the modulation of the intestinal microbiota, competitive exclusion of pathogens, enhancement of digestive enzyme activity, and improvement of the immune system. However, successful probiotic application requires careful selection of host-specific strains, accurate administration methods, and a suitable dosage, as these factors strongly influence their effectiveness [10]. Essential oils derived from plant sources exhibit antimicrobial properties and can enhance fish immune systems, making them more resistant to diseases, but their usage as feed additives presents challenges due to plant-part chemistry, dose-response effects, inter-species variability, their potential interaction with other feed additives or medications, and appropriate dosage [11]. Likewise, antimicrobial peptides exhibit antimicrobial efficacy and potent immunomodulatory effects, but their practical applications in aquaculture remain constrained by potential regulatory and policy challenges, and their excessive or improper use may lead to microbial resistance [12].

Unlike many of these feed additives, LA is a bioactive lipid that simultaneously contributes metabolic energy while exhibiting antimicrobial and immunomodulatory activities characteristic of MCFAs [2]. Furthermore, LA occurs naturally in several raw materials of increasing interest to aquaculture, including coconut oil, palm kernel oil, and black soldier fly larvae, making it particularly relevant for the development of sustainable aquafeeds based on alternative lipid and protein sources [2].

LA is recognized in aquaculture for its antimicrobial, immunomodulatory, and gut health-promoting properties [13–16]. Additionally, it has been found to be readily absorbed by fish's enterocytes and has demonstrated potent antioxidant and antimicrobial properties against fish pathogens [13,17,18].

Recently, numerous benefits and advantages of LA have been demonstrated in aquatic animals, including improved growth performance, feed utilization, immunophysiological responses, antioxidant capacity, intestinal health, and disease resistance against pathogens [1,14,16]. Similar biological benefits have also been reported in human and terrestrial animal studies, supporting the broad functional potential of this fatty acid [19,20]. Its unique metabolic process, unlike long-chain fatty acids, swiftly crosses the membrane bilayer via non-ionic passive diffusion, allowing it to rapidly reach the mitochondria, where it is involved in the β -oxidation pathway for the supply of energy [21,22]. While in the liver, LA is effectively used for energy production through mitochondrial β -oxidation, therefore facilitating rapid energy supply [23].

According to recent studies, the beneficial effect of LA has been studied in terrestrial animals such as cattle, where topical LA was found to have an acaricidal effect [24]. In poultry, dietary glycerol monolaurate (GML) had a positive impact on young broilers by improving intestinal morphology and barrier function and enhancing lipid metabolism [25,26]. In weaned lambs, dietary GML improved growth performance and also had positive effects on lipid metabolism and antioxidant properties [27]. Additionally, dietary GML has been reported to improve growth performance, antioxidant capacity, lipid metabolism, and intestinal health in aquatic species, indicating its potential as a functional feed additive in aquaculture [5,28–30]. These properties have accelerated the interest in exploring LA as a functional feed additive in aquaculture. However, with the recent inclusion of insect meal in aquafeeds, research attention has increased towards the investigation of insect-derived bioactive compounds, such as LA, and their potential effects on aquatic species.

It is important to highlight the different chemical forms used to administer LA in aquafeeds. It is mostly delivered from LA rich vegetable oils (e.g., coconut and palm kernel oils), glycerol monolaurate, medium-chain triglycerides, free LA (purified), and insect-derived ingredients such as black soldier fly (*Hermetia illucens*) meal or oil. Even though these compounds share LA as a common component, they differ substantially in their overall composition which may influence their biological activity in aquatic species. Purified LA is the unesterified fatty acid is readily available for uptake, whereas GML is its monoglyceride derivative, and MCTs contain LA within triglycerides requiring enzymatic hydrolysis before absorption [3]. Coconut and palm kernel oils have LA as the predominant fatty acid, but they also contain appreciable amounts of other saturated and unsaturated fatty acids that may contribute to their biological effects [3]. Similarly, black soldier fly meal and oil provide LA within a complex biological matrix containing proteins, chitin, antimicrobial peptides, minerals, and other lipids [31], thus making it difficult to attribute observed physiological responses exclusively to LA. Nevertheless, these compounds and ingredients have been reviewed together because they represent the main dietary sources and delivery forms through which LA has been studied in aquaculture.

Despite increasing interest in LA containing ingredients and their applications in the aquaculture industry, several important questions remain unanswered. Therefore, the aim of this review is to synthesize and organize the current knowledge of the effects of LA obtained from BSF meal and oil and LA commercial derivatives, when included in aquafeeds, on growth performance, nutrient utilization, digestive capacity (including digestive enzyme activity), immune response, intestinal microbiota modulation, antimicrobial activity, and intestinal morphology and function in fish and crustacean species. This review also aims to provide a comparative analysis across different aquatic species, as well as

different forms in which lauric acid has been administered when specified. It also identifies the key research gaps and possible future directions with a focus on practical applications in fish species.

2. Chemical and Physical Properties of Lauric Acid

Lauric acid (dodecanoic acid, C12:0) is a medium-chain fatty acid defined by its carbon chain length of C6 to C12 [18,19], with the molecular formula $\text{CH}_3(\text{CH}_2)_{10}\text{COOH}$ and a molecular weight of 200.32 Da. LA exists as a bright white, powdery crystalline solid with a faint characteristic odor reminiscent of bay oil or soap at ambient temperature, with a melting point of 43.2–44.8 °C and a boiling point of approximately 298–299 °C [32].

Its defining physicochemical characteristic is amphiphilicity: the molecule possesses a polar, hydrophilic carboxylic head group and a nonpolar, hydrophobic twelve carbon alkyl tail [12]. This structural organisation governs its partitioning between aqueous and lipid phases and contributes to its ability to interact with biological membranes. The monoglyceride derivative GML differs from free LA because esterification of the carboxyl group prevents its acid–base ionization. GML has demonstrated stronger antimicrobial activity than free LA against some microorganisms under specific experimental conditions, although its membrane-disruptive activity is also influenced by pH and the surrounding physicochemical environment [33].

As a weak acid, LA undergoes reversible proton dissociation in aqueous solution, with an apparent pK_a of approximately 6.9–7.0 under relevant aqueous conditions. Consequently, pH determines the relative proportions of protonated LA (RCOOH) and its deprotonated form, the laurate anion (RCOO^-), thereby influencing its solubility, aggregation behavior, membrane interactions, and antimicrobial activity. Near its apparent pK_a , protonated and deprotonated forms can coexist and form self-associated structures while maintaining an equilibrium with monomeric LA. The monomeric fraction is particularly relevant to membrane interactions because protonated LA can partition into lipid bilayers and alter membrane organization. This structure governs its partitioning between aqueous and lipid phases and contributes to its ability to interact with biological membranes. [34].

3. Sources of Lauric Acid

Lauric acid is heterogeneously distributed across different natural lipid sources, occurring at particularly high concentrations in certain plant lipids. Coconut oil (*Cocos nucifera*) (46–54% of the total fatty acids) and palm kernel oil (*Elaeis guineensis*) (45–50% of the total fatty acids) are the most prominent sources, making these oils the primary terrestrial lipid reservoirs of LA for animal nutrition and industrial applications [3]. In addition to coconut and palm kernel oil, other plant lipid sources, such as *Attalea speciosa* and *Astrocaryum murumuru*, also contain substantial amounts of LA (47.4% and 40% LA content, respectively), although their use in aquafeeds is less widespread [35]. While present in small quantities, LA is also present in animal-derived fats, goat milk 3.1%, and cow milk (2.9%) [35]. In these sources, LA is predominantly esterified to triacylglycerols (TAGs), which are hydrolyzed by intestinal lipases during digestion, releasing free LA and 2-monoacylglycerols, which are subsequently absorbed by enterocytes. As a medium-chain fatty acid, LA exhibits absorption and metabolic characteristics that differ from those of long-chain fatty acids, contributing to its relatively rapid utilization and oxidation, hence its bioavailability [36,37].

Apart from tropical plant oils, it is also present in high concentrations in black soldier fly larvae (BSFL) [35,38]. BSF can be reared on a large variety of organic materials and by-products such as food waste, fruit waste, rice straw, sewage sludge, pig, poultry, and chicken manure, cow dung, and palm decanter cake from oil palm mills [34,39–42]. However, the fatty acid composition of BSF larvae is not constant and can be influenced by several factors,

such as rearing substrate (fat and carbohydrate content), developmental stage, larval nutrition status, processing conditions, and processing method [41,43–45]. Consequently, although LA is generally the major fatty acid in BSFL, its relative abundance can vary substantially among production conditions. For example, LA has been reported to account for approximately 52% of total fatty acids under some rearing conditions [40,46], while values as high as 76.1% of the total fatty acids have been reported in larvae reared on fruit waste [47].

BSF oil therefore represents a potentially valuable source of LA, although its composition should be considered when comparing it with conventional LA rich oils such as coconut and palm kernel oils. In terms of the sustainability, BSF production offers potential advantages through the valorization of organic wastes and the production of biomass with limited land requirements; however, its environmental performance depends on the rearing substrate, energy inputs, processing practices, and other farm production conditions. Therefore, while its bioconversion of organic waste streams saves land and reduces waste, energy consumption for drying, climate control for rearing, especially in temperate climates, and direct gas emissions are key impact drivers [48].

Natural sources of LA are usually included in aquafeed formulations for fish and crustaceans either directly (as a lipid ingredient) or indirectly (i.e., insect meal). The inclusion of these dietary components in aquafeeds must be carefully balanced for their high saturated fatty acid content by considering species-specific nutrient requirements.

4. Metabolism of Lauric Acid in Aquatic Species

The digestion, absorption, transport, and metabolism of dietary fatty acids vary greatly based mainly on their chain length and physiological traits of the host species [49]. In general, MCFAs have faster absorption in aquatic animals compared to long-chain fatty acids, which are predominantly re-esterified into TAGs within enterocytes, incorporated into chylomicrons, and delivered to the liver via the lymphatic system before storage or use for energy [3,28]. In contrast, MCFAs rapidly enter the portal vein, which accelerates their uptake and oxidation by the liver [36]. MCFAs do not depend on membrane transporters for cellular uptake and can therefore be directly transported to the mitochondrial membrane without the assistance of carnitine [36]. There are several ways in which LA is rapidly metabolized in the liver. β -oxidation accounts for the major pathway for MCFA metabolism, producing acetyl-CoA, which enters the citric acid cycle, where intermediates such as oxaloacetate and malate are diverted for glucose production [28]. Increased levels of nicotinamide adenine dinucleotide (NADH) acts as an allosteric inhibitor of the cycle which causes the increased production of ketone bodies [3].

Even though the liver produces acetyl-CoA, it has insufficient β -ketoacyl-CoA transferase, thus making it unable to utilize the ketone bodies. The ketone bodies are therefore transported to other tissues such as the brain, muscle, and heart that have enzymes to convert ketone bodies to acetyl-CoA to serve as an energy source [36]. As reviewed by Hoseinifar et al. [3], the rapid β -oxidation mechanism is important in aquaculture to enhance the protein-sparing effect, in order to optimize dietary protein for use in muscle growth and not energy production.

Although lipid digestion and absorption have been extensively studied in teleosts, studies specifically investigating the intestinal absorption and metabolic fate of LA remain scarce. As a result, the current understanding of LA metabolism in fish is largely extrapolated from general studies of fish lipid digestion and mammalian studies of MCFA metabolism.

It is important to note that although the absorption pattern of MCFAs in aquatic animals might be similar to that of mammals, limited studies have been done specifically in

this field. A study on Atlantic salmon reported that medium-chain triglycerides, including LA, are mainly absorbed in the pyloric caeca and are also highly digestible compared to long-chain fatty acids [50], indicating that fish can also efficiently absorb MCFAs from the gut. The hepatic oxidation metabolic feature of LA is often used to explain the rapid turnover and lower adipose deposition of MCFAs in vertebrate systems, but this trend may vary in fish with high lipid storage, such as rainbow trout (*Oncorhynchus mykiss*) [51]. For example, rainbow trout fed diets including coconut oil (estimated 6.7% LA in the diet) had higher whole-body retention of LA compared to those fed diets containing fish oil, suggesting that LA tissue deposition rather than its oxidation is a significant metabolic outcome in this species [52].

5. Effects of Lauric Acid on Growth Performance and Feed Utilization

Dietary inclusion of purified LA, coconut oil, insect oil, insect meal, and other related MCFAs (monolaurin and mixed monoglycerides) has been investigated in several aquaculture species with variable effects on growth, feed utilization, and efficiency. As reviewed by Liu et al. [2], incorporating these fatty acids into the diets of aquatic animals can enhance weight gain rate, feed conversion ratio (FCR), and survival rates while at the same time reducing morphometric indices such as viscerosomatic, hepatosomatic, and mesenteric fat indices. Several studies have also investigated the effects of insect oil, which contains LA, and its impact on growth performance when substituted or supplemented with fish oils (FO) and vegetable oils in different fish species. Insect oils have also been tested on carnivorous fish species, which are usually fed diets with higher dietary lipid levels than omnivorous species. A relatively high dietary inclusion levels of insect oils, particularly black soldier fly oil (BSFO), exhibited promising fish performance, similar to FO or other traditional oil alternatives.

Direct studies on the growth promoting effects of LA come primarily from studies using purified LA. The growth promoting effects of LA in black seabream (*Acanthopagrus schlegelii*) have been investigated extensively. Dietary supplementation of 0.1% and 0.8% purified LA led to a significant increase in the final body weight (FBW), specific growth rate (SGR), feed efficiency (FE), and hepatosomatic index (HSI) compared to the control diet [18]. Building on these findings, a subsequent study was done by the same authors with lower dietary LA inclusion levels, in which they observed significantly higher FBW, SGR, and protein efficiency ratio (PER) in the same species fed diets supplemented with a limited amount of LA (0.04%) [1]. These two studies demonstrated clear growth promoting effects of LA in black sea bream, suggesting that even at low inclusion levels, LA can have a positive impact in the growth performance of this fish species. Likewise, in European seabass (*Dicentrarchus labrax*), a positive linear relation was observed between LA supplementation (0.5%, 1% and 2%) and growth rate and feed intake [16], thus linking dietary LA to feed stimulant properties. A study on zebrafish (*Danio rerio*), dietary supplementation with 0.05% LA led to significant enhancements in final body length, FBW, weight gain, SGR, and condition factor compared to the unsupplemented control diet [53], thus confirming that even at low inclusion levels, LA can still benefit growth in teleost species.

Studies on LA derivatives should be considered separately from that obtained with purified LA. In black sea bream, GML at 0.04% increased FBW, weight gain, SGR, and PER [28]. Similarly, common carp (*Cyprinus carpio*) fed diets supplemented with GML (0.05% and 0.1%) showed increased FBW, feed intake, weight gain, and SGR [5]. This improved growth performance could be attributed to the ability of GML to prolong the residence time of food in the intestine, thus promoting digestion and absorption of nutrients, thereby enhancing growth [54,55]. In Nile tilapia (*Oreochromis niloticus*), the highest growth and feed efficiency were observed when diets were supplemented with graded levels

of alpha-monolaurin (0.4% and 0.6% in the diet) [56]. Gilthead seabream (*Sparus aurata*) recorded higher FBW, feed intake, and SGR when fed diets supplemented with 0.3% sodium salt of coconut fatty acid distillate, which is rich in LA [4]; the authors argue that this growth-promoting action could be attributed to the increased growth hormone content and insulin-like growth factors, upregulated expression of the *alpi* gene, and the increased complexity of intestinal folds in the main absorptive intestinal segment. Even though these results indicate that both purified LA and its derivatives may have growth promoting effects, they should not be considered equivalent to free LA because differences in chemical form and metabolism may influence their biological effects. Thus, evidence from purified LA and its derivatives supports a potential role for LA derived compounds in growth promotion, while their effects should not be interpreted as one.

Studies on BSFO and BSF meal, rather than purified LA, have generally reported no adverse effects of inclusion on growth performance in several fish species. However, these studies should be interpreted more cautiously because these materials contain LA together with other fatty acids and, in the case of BSF meal, protein, chitin, minerals, and other bioactive compounds. Rainbow trout fed a diet with 2.5%, 5%, and 10% BSFO inclusion to replace FO (estimated 0.6, 1.2, and 2.4% LA of the diet) reported no adverse effects on growth performance and somatic indices [57]. Even though the dietary treatment in this study significantly affected FCR overall; this effect was attributable to differences among the BSFLM treatments rather than among the BSFO treatments. FCR did not differ significantly among the 2.5, 5.0, and 10% BSFO diets. Similarly, it has been reported that up to 16% BSFO in the diet (estimated 1.4% LA in the total diet) could replace FO and soybean oil (SBO) without affecting diet palatability, growth performance, and feed utilization in rainbow trout, but increased the FBW and HSI [58]. Furthermore, the growth performance parameters of rainbow trout fed spirulina-enriched BSF diets (0.4–2.5% LA of total FA) were not impaired by the dietary treatments [59]. Similarly, 4% BSF oil (LA not reported) yielded no significant differences in feed intake, FBW, HSI, and weight gain in rainbow trout [60]. In Atlantic salmon (*Salmon salar*), Belghit et al. [17] utilized BSFO from BSF raised on organic waste streams and on *Ascophyllum nodosum* seaweed (19–29% LA of the total FA in the diet). However, no negative effects on feed intake, as well as FBW, feed FCR and protein efficiency were reported. A study by Goda et al. [61] demonstrated that substituting SBO with BSFO (1%) containing 0.04% LA led to optimized growth performance in terms of feed conversion ratio in Nile tilapia fry. Comparable outcomes have also been reported in hybrid red tilapia (*Oreochromis* sp.), where a dietary inclusion of 1.91% BSFO, corresponding to 7.2% LA of total FA in the diet, resulted in the greatest growth performance in terms of FBW and weight gain, but no significant differences were observed in the SGR, FCR, apparent protein digestibility, and somatic indices [62].

While the beneficial effects of LA have been well documented across a range of teleost species, research in invertebrates, particularly crustaceans is still in its early stages, with comparatively few studies available in the literature. In contrast, in crustaceans, purified LA supplementation in the diet (0.009–0.291% LA) did not significantly affect growth performance parameters in swimming crab (*Portunus trituberculatus*) [14], indicating that the response may be species-specific and influenced by differences in digestive biology.

The mechanisms by which LA supplementation may affect growth and feed utilization are multifactorial rather than reflecting a single mode of action. One is that MCFAs directly enter the liver via the portal vein and is rapidly metabolized, thus providing readily available energy that can support growth; however, the extent to which this occurs still remains insufficiently characterized in fish. In addition, direct evidence in zebrafish, Nile tilapia, and black seabream indicates that LA supplementation can enhance digestive enzyme activities and upregulate growth-related genes, including growth hormone (*gh*) and

insulin-like growth factor 1 (*igf-1*), suggesting potential links between improved digestive function and growth endocrine regulation [53]. In black sea bream, dietary supplementation of LA has also been associated with improved growth and feed efficiency alongside increased intestinal villus height, goblet cell abundance, and changes in gut microbial composition, suggesting that modulation of intestinal morphology and microbiota may further contribute to improved digestive efficiency, nutrient utilization, and hence improved growth [1,18]. Furthermore, LA has the ability to enhance digestive function as it acts as a natural acidifier by lowering intestinal pH and promoting beneficial gut bacteria, thus improving overall fish health and performance (Figure 1) [1,16,18]. However, these mechanisms do not establish a direct pathway, and evidence for increased feed intake or intestinal acidification as mechanisms of LA mediated growth promotion in fish remains limited. Thus, current evidence supports the possibility that LA may influence growth through interacting effects on energy metabolism, digestive function, intestinal microbiota, and intestinal structure, whereas the roles of feed intake, intestinal acidification, and GH/IGF-1 signalling require further mechanistic investigation.

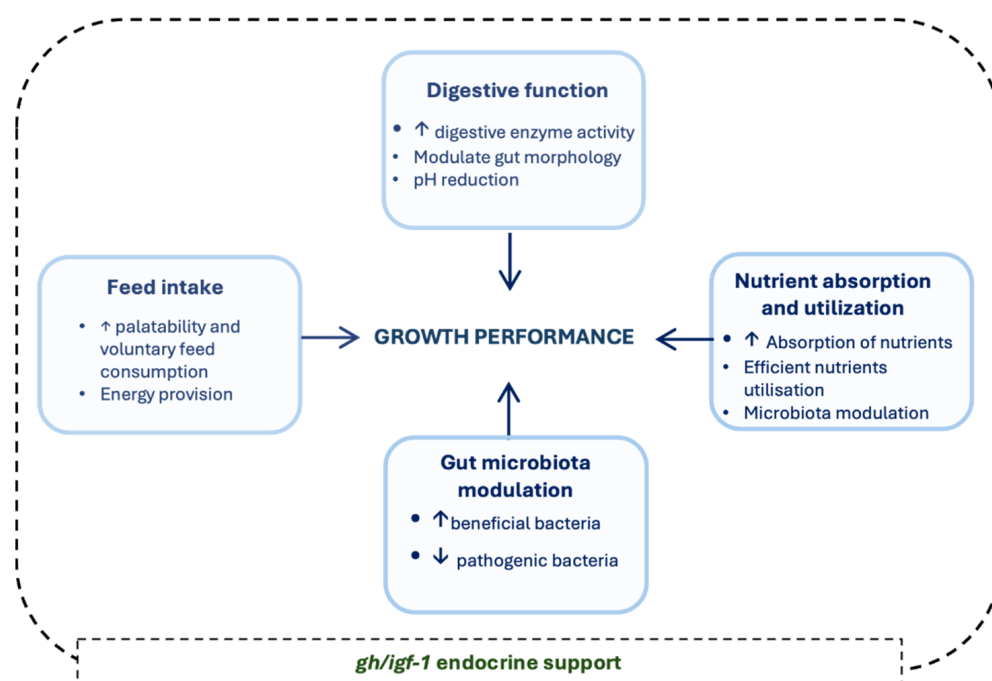


Figure 1. Proposed mechanisms under which dietary lauric acid may influence growth performance in aquatic species.

Overall, the above-mentioned studies, summarized in Table 1, suggest that free LA, its derivatives, and LA containing ingredients like BSF meal and oil can exert a positive effect on growth performance in certain finfish species. Furthermore, it seems that the efficacy of LA in aquafeeds is characterized by its distinct dose-response relationship, following a non-linear distribution. Low to moderate inclusion levels led to positive responses in growth performance and feed efficiency while higher levels may have neutral or diminished effects and vice versa. For example, in zebrafish, the best growth performance indices were observed at 0.05–0.1% instead of 0.2% of LA [53].

Table 1. Studies summarizing the effects of dietary lauric acid or lauric acid-rich ingredients and MCFAs on growth performance and nutrient utilization in different aquatic species.

Species	Lauric Acid Dose	Lauric Acid Source	Replacement	Effects	Reference
<i>Oncorhynchus mykiss</i>	Estimated 0.6, 1.2, 2.4% LA of the diet	BSF oil	FM and FO replacement	↔Feed intake, FCR, HSI, FBW, TGC, weight gain, survival	[57]
<i>Oncorhynchus mykiss</i>	Estimated 1.4% total diet	BSF oil	FO and SBO replacement	↔feed intake, FCR, PER, K, HSI	[58]
<i>Oncorhynchus mykiss</i>	Reported 0.4–2.5% of total FAs	Spirulina-enriched BSF	FO and FM replacement	↔FBW, RGR, SGR, FCR, K, VSI	[59]
<i>Oncorhynchus mykiss</i>	NR	BSF oil	FO replacement	↔feed intake, FBW, FCR, VSI, HSI, weight gain	[60]
<i>Salmo salar</i>	Reported 19–29% of the total FAs	BSF meal and oil	FM and VO replacement	↔growth and feed intake	[17]
<i>Acanthopagrus schlegelii</i>	0.1–0.8%	Purified LA	Dietary supplement	↑WGR, SGR, FE	[18]
<i>Acanthopagrus schlegelii</i>	0.01, 0.02, 0.04, 0.08, 0.16%	Purified LA	Dietary supplement	↑FBW, WG, SGR, PER (0.04%) ↔IBW, MFI, PPV, CF, HSI, IPV, VSI, SR	[1]
<i>Acanthopagrus schlegelii</i>	0.01, 0.02, 0.04, 0.08, 0.16%	Glycerol monolaurate	Dietary supplement	↑FBW, WG, SGR, PER (0.04%)	[28]
<i>Sparus aurata</i>	0.3%	DICOSAN [®] , Norel	Dietary supplement	↑feed intake, FBW, WG	[4]
<i>Dicentrarchus labrax</i>	0.5, 1, 2%	Purified LA	Dietary supplement	↑feed intake (2%) ↔FBW, WG, growth index, PER, FE	[16]
<i>Cyprinus carpio</i>	0.05–0.1%	Glycerol monolaurate	Dietary supplement	↑FBW, SGR, WGR, FI ↔somatic indices	[5]
<i>Oreochromis niloticus</i>	0.4–0.6%	Alpha-monolaurin	Dietary supplement	↑FBW, WG, SGR, PER, survival Improved FCR	[56]
<i>Oreochromis niloticus</i>	Reported 0.04, 0.081, 0.12, 0.16%	BSF oil	SBO	↑FBW, WG, PER, PPV, ER (0.4%) ↓FBW, WG, PER, FCR (75% and 100% BSFO inclusion)	[61]
<i>Oreochromis</i> sp.	Reported 7.2% (% total FAs)	BSF oil	FO	↔SGR, FCR, VSI, HSI ↑FBW, WG (25% inclusion) ↔%Protein ADC	[62]
<i>Danio rerio</i>	0.05, 0.1, 0.2%	Purified LA	Dietary supplement	↑FBW, WG, SGR, K, final length (0.05% group) ↓FBW, WG, SGR, K, final length (0.2% group)	[53]
<i>Portunus trituberculatus</i>	0.009, 0.04, 0.08, 0.1, 0.15, 0.29%	Purified LA	Dietary supplement	↔FW, WG (%), SR, SGR ↔FE	[14]

Abbreviations: LA: lauric acid, NR: not reported, FAs: fatty acids, FW: final weight, WGR: weight-gain rate, SGR: specific growth rate, FCR: feed conversion ratio, FE: feed efficiency, K: condition factor, HSI: hepatosomatic index, TGC: thermal-unit growth coefficient, VSI: viscerosomatic index, PER: protein efficiency ratio, WG: weight gain, PPV: protein productive value, FI: feed intake, ADC: apparent protein digestibility.

These species-specific differences likely suggest the variations in digestive physiology, fatty acid metabolic pathways and tolerance to MCFAs. Carnivorous species with high lipid digestibility may respond to LA differently than omnivorous and herbivorous species.

For example, MCFAs in Atlantic salmon, a strictly carnivorous species, have the potential to increase chyme enzyme activity and protein digestibility, thus affecting lipid metabolism [7]. In contrast, herbivorous species respond differently to high-lipid diets. Increasing dietary lipid levels from 2% to 10% in grass carp (*Ctenopharyngodon idella*) resulted in reduced feed intake and decreased growth performance and feed efficiency, along with hepatic lipid accumulation and changes in lipoprotein synthesis [63].

6. Effects of Lauric Acid on Digestive Functionality

Digestive functionality encompasses an integrated system of biological processes, including digestive enzyme activity, digestive capacity, intestinal structure, and gut microbial composition, which altogether determine the efficiency of nutrient digestion and absorption. A fish's feeding habit and behavior largely determines its digestive tract structure and the composition of its microbial flora [64]. At the enzymatic level, key digestive enzymes act across distinct regions of the gastrointestinal tract, and their activities serve as measurable indicators of digestive efficiency. Pepsin initiates protein digestion in the stomach, while in the pyloric caeca and proximal intestine, trypsin, chymotrypsin, lipase, and amylase hydrolyze proteins, lipids, and carbohydrates. At the intestinal brush border, alkaline phosphatase, leucine aminopeptidase, maltase and sucrase complete nutrient digestion before absorption [65]. Beyond the digestive enzymes, the intestinal structure, particularly the intestinal villus, plays a key role in the digestion and absorption of food materials, and goblet cells producing mucus protect the epithelium's underlying layers while also serving as a transport medium for food materials across the layers [18,66]. It has been reported that digestive enzyme activities can be regulated by the composition of diets [67–71].

6.1. Effects of Lauric Acid on Digestive Enzyme Activity

A variety of enzymes play an important role in the digestion of food materials. These enzymes present in the fish intestine play a crucial role in breaking down nutrients, and the dietary habits and adaptations of fish are important in determining the function and distribution of these enzymes [72–77]. In carnivorous species, the principle digestive enzymes include proteases such as pepsin, usually active in the stomach, and pancreatic enzymes, including trypsin, chymotrypsin, and lipase, secreted into the pyloric caeca and the proximal intestine. Intestinal brush-border enzymes such as alkaline phosphatase and aminopeptidases are also key indicators of enterocyte differentiation and functional absorptive capacity [72,73]. Apart from structural modifications, functional indicators such as digestive enzyme activity can also provide critical insights into how dietary lipids, particularly MCFAs like LA, influence gastrointestinal performance in fish. Studies on digestive enzyme activities influenced by LA in fish diets are emerging but still remain limited.

Studies using purified LA have generally reported limited effects on digestive enzyme activity. Ullah et al. [1] reported no significant differences in the specific activities of trypsin and amylase, and a lower specific lipase activity, in black seabream fed diets supplemented with 0.01–0.16% LA. A subsequent study carried out by the same authors in 2022, with higher levels of LA (0.1 and 0.8%), also reported no significant differences in the specific enzyme activities of lipase, amylase, and trypsin activities in the stomach, midgut, and hindgut, and slightly reduced lipase activity in the foregut compared to the control diet [18].

In contrast, studies using LA derivatives have reported significant effects on digestive enzymes activity. Dietary alpha-monolaurin (0.2–0.6%) increased the total activity of lipase and amylase in Nile tilapia. The authors argue that this improvement in digestive enzyme activity can be attributed to the growth promoting effects of alpha-monolaurin [56].

Furthermore, studies using BSF larval meal should likewise be distinguished from studies using purified LA, as observed changes may reflect the combined effect of BSF

derived ingredients rather than that of LA alone. In gilthead seabream, 15% defatted BSF meal inclusion (corresponding to 0.5% LA in the diet) resulted in significantly higher specific activities of amylase, trypsin, and chymotrypsin in the posterior intestine, compared to the control diet [74].

The effects of LA on total and specific activities of digestive enzymes may arise from multiple mechanisms and may also be species-specific. Altogether, these findings suggest that LA and MCFA supplementation can enhance the total and specific digestive enzyme activity in some fish species, but outcomes are inconsistent and are context-dependent. Digestive effect responses appear to depend on species, enzyme type, inclusion level, and particularly the chemical form or dietary source through which LA is supplied. Potential mechanisms include the rapid digestion and absorption for rapid energy intake by enterocytes, since they are not incorporated into chylomicrons [75]. Although bile acids are essential for lipid emulsification, micelle formation, and lipid absorption in fish, there is currently insufficient evidence that dietary LA directly alters bile acid secretion or bile acid-mediated lipid digestion. However, studies on mammalian intestinal models suggest that bile acid micelles can facilitate LA uptake, indicating that the absorption of LA should not be considered completely independent of bile salts [76].

The available morphological studies further indicate that LA or LA containing ingredients can influence intestinal architecture, including villus height and goblet cell characteristics. Morphological responses should therefore be interpreted alongside functional indicators such as digestive enzyme activity, nutrient transporter expression, apparent nutrient digestibility, and growth performance. For example, a recent study in black sea bream found significant changes in intestinal villus morphology following purified LA supplementation, while digestive enzyme activities were not significantly affected, illustrating that structural changes do not necessarily translate into altered digestive function [1]. A comprehensive table on the effects of LA on the total and specific digestive enzyme activity of fish species is reported in Table 2.

Table 2. Studies summarizing the effects of dietary lauric acid or lauric acid-rich ingredients and MCFA derivatives on the digestive enzyme activities in different finfish species.

Species	Lauric Acid Dose	Lauric Acid Source	Replacement	Effects	Reference
<i>Acanthopagrus schlegelii</i>	0.01, 0.02, 0.04, 0.08, 0.16%	Purified LA	Dietary supplement	↔specific trypsin and amylase activity ↓specific lipase activity (0.02% and 0.04%)	[1]
<i>Acanthopagrus schlegelii</i>	0.1–0.8%	Purified LA	Dietary supplement	↔specific lipase, amylase, or trypsin activity (stomach, midgut, hindgut); ↓specific foregut lipase activity (0.1%)	[18]
<i>Acanthopagrus schlegelii</i>	0.01, 0.02, 0.04, 0.08, 0.16%	Glycerol monolaurate	Dietary supplement	↔specific trypsin and amylase activity ↓specific lipase activity (0.02% and 0.04% GML)	[28]
<i>Sparus aurata</i>	NR	BSF meal	VO	↑specific amylase, trypsin, chymotrypsin and activity	[74]
<i>Oreochromis niloticus</i>	0.2–0.6%	α-Monolaurin	Dietary supplement	↑total lipase and amylase activity (0.6%)	[56]

Abbreviations: LA: lauric acid, BSF: black soldier fly, NR: not reported, VO: vegetable oil blend, FO: fish oil.

6.2. Effects of Lauric Acid on Intestinal Health: Morphology, Barrier Function, Functional Indicators/Intestinal Turnover, and Microbiota

In the gastrointestinal tract, aquafeeds are converted to simple nutrient forms which are subsequently absorbed and distributed throughout the body [38]. The structural integrity of the intestinal mucosal barrier is essential for optimal animal performance because it significantly contributes to digestion, nutrient absorption, and immunological enhancement [77]. Epithelial cells are involved in absorption and digestion, while goblet cells secrete mucus for food lubrication and the movement of various components between the layers while simultaneously protecting the underlying layers [66,78]. Therefore, the structural and functional integrity of the intestinal epithelium is crucial for growth performance, feed efficiency, and disease resistance. Dietary interventions that modulate intestinal function and morphology are also able to exert systemic changes that go beyond the digestive processes in animals. LA has been proposed to affect intestinal structure and function through direct interactions in the epithelium and indirect modifications of intestinal microbiota, but data supporting this are still limited.

6.2.1. Effects of Lauric Acid on Intestinal Morphology

Intestinal morphological features are usually an indication of intestinal health, development, and gut functionality [38]. Modification of intestinal morphology, particularly villi architecture and goblet cell composition, is one of the most consistently reported intestinal effects of dietary LA in fish.

The effects of purified LA on intestinal morphology and function in black seabream have been extensively studied by [1,18,28]. Supplementing black seabream diets with as little as 0.1% LA was sufficient to produce significant increases in villus height and villus surface area in juvenile black seabream compared to the control diet [18]. Notably, the same authors further demonstrated that even at a lower inclusion level of 0.04% LA in the diet, improvements in villus height, crypt depth, villus height-to-crypt depth ratio, and goblet cell-to-villus height ratio were still observed [1,28]. Increased villus height may increase the potential absorptive surface area but does not by itself demonstrate enhanced nutrient absorption. Potential effects on epithelial differentiation, brush border function, nutrient transporter activity, and mucin turnover therefore remain plausible but insufficiently demonstrated in fish.

Similarly, in Nile tilapia, the dietary inclusion of 0.4% and 0.6% alpha-monolaurin increased intestinal villus height and villus width, while only 0.6% increased the intervilli distance [56]. The authors attribute improved feed utilization in the study to the beneficial effects of the nutrients on the intestinal morphology.

The findings from these studies suggest that dietary purified LA and its derivatives play a role in increasing intestinal villus height. However, it is important to note that increased villus height may increase the potential absorptive surface area, but it does not inherently guarantee improved nutrient absorption or growth performance. These morphological changes and adaptations should be interpreted alongside other functional indicators such as digestive enzyme activities and nutrient transporters. For example, an increase in fold height in the absence of improvements in digestibility or growth should be considered a structural response rather than improved absorptive function.

6.2.2. Goblet Cells and Barrier Protection

The luminal surface of the gastrointestinal tract mucosal layer is covered by a mucus layer that protects the mucosa from dehydration and physical damage, serving as a physical barrier between the underlying epithelium and luminal substances that could include pathogenic bacteria, viruses, and parasites [79]. Goblet cells are the main source of mucins

and are present throughout the gastrointestinal tract [80]. A number of external factors such as nutrition (dietary composition, feed additives), physiological conditions, e.g., developmental stage, and immunological conditions such as pathogenic infections and intestinal inflammation have a significant impact on goblet cell density [81,82]. Goblet cell density and mucus composition are considered important indicators of intestinal health, but few studies have investigated their changes in fish fed diets containing LA.

In black seabream juveniles, 0.1% purified LA dietary supplementation led to increased goblet cell density [18]. Similarly, in a complementary study on the same species by the same authors [1], dietary supplementation with a lower level of purified LA (0.04%) led to an enhanced intestinal function in terms of increased crypt depth, crypt depth-to-villus height ratio and an increase in the ratio between goblet cells and the villus height. A subsequent study using 0.04% GML in the same species reported comparable changes in fore-intestinal villus height, crypt depth, villus height-to-crypt depth ratio, and the number of goblet cells per villus [28]. In Nile tilapia, dietary α -monolaurin at 0.6% also increased goblet cell number [56], providing further evidence for an effect of this LA derivative. In contrast, feeding rainbow trout with diets including 5% full-fat BSF meal providing approximately 0.23% LA in the diet resulted in a reduction in the cumulative histological score, including goblet cells [83]. However, this response cannot be attributed specifically to 0.23% LA reported in the study because BSF meal contains multiple nutritional and bioactive components.

Therefore, the current studies suggest that the mechanisms underlying LA induced changes in goblet cell density and composition have not been fully explored and understood yet. A possible hypothesis could be the indirect effects linked to changes in overall epithelial structure, thus leading to enhanced intestinal integrity. Currently, direct evidence in fish is lacking, highlighting a significant knowledge gap. As summarized in Table 3, LA, its derivatives and insect meal have some positive effects on intestinal morphology and function.

Table 3. Studies summarizing the effects of dietary lauric acid or lauric acid-rich ingredients and MCFA derivatives on intestinal morphology and histological parameters in aquaculture species.

Species	Lauric Acid Dose	Lauric Acid Source	Replacement	Effects	References
<i>Acanthopagrus schlegelii</i>	0.1–0.8%	Purified LA	Dietary supplement	↑villus height, villus surface area, goblet cell density (0.1%)	[18]
<i>Acanthopagrus schlegelii</i>	0.01, 0.02, 0.04, 0.08, 0.16%	Purified LA	Dietary supplement	↑crypt depth, crypt depth-to-villus height ratio, goblet cells-to-villus height ratio (0.04%)	[1,28]
<i>Oncorhynchus mykiss</i>	Reported 0.23%	BSF meal	SBM	↓cumulative histological score ↑histological conditions	[83]
<i>Oreochromis niloticus</i>	0.2–0.6%	α -Monolaurin	Dietary supplement	↑Villus height, villus length, intervilli distance, goblet cell number (0.6%)	[56]

Abbreviations: LA: lauric acid, BSF: black soldier fly, SBM: soybean meal.

6.2.3. Effects of Lauric Acid on Intestinal Microbial Communities

Gut microbiota in fish is crucial for host physiology, normal gastrointestinal functionality, immunity, and overall health [84,85]. One of the most effective ways to manipulate gut microbiota composition is through the diet [38]. Probiotics, prebiotics, and functional feed

additives such as MCFAs are increasingly being studied for their potential to selectively modulate microbial community composition in a way that still promotes animal health and performance [2]. The formation of certain microbial clades is favored or inhibited by specific dietary components and nutrients, which may significantly affect host health and resistance to diseases [86,87]. The composition of gut microbiota may be affected by dietary lipid levels [14], and specifically, MCFAs, which have been studied extensively for their antimicrobial properties [22,88]. In this context, dietary manipulation of intestinal microbiota has emerged as a promising nutritional strategy in aquaculture.

Direct experimental studies on the effects of dietary LA on fish gut microbiota composition, though very limited, suggest that LA inclusion can alter the relative abundance of microbial taxa. In black seabream, dietary supplementation with 0.1% purified LA resulted in a significant increase in *Firmicutes*, *Clostridia*, and *Bacilli*, although the diversity indices did not differ significantly [18]. These results provide direct evidence that purified LA can modify the composition of the gut microbiota in this species.

Changes in intestinal microbial communities have also been reported following supplementation with monolaurin. Specifically, in gilthead seabream, dietary 1-monoglycerides reduced the abundance of *Gammaproteobacteria* [89]. Similarly, dietary GML at 0.07% led to an increase in the microbial diversity, markedly increasing phyla Fusobacteria and downregulating some Gram-positive bacteria in zebrafish [29], while supplementation at 0.24% and 0.3% resulted in an increase in the alpha diversity at the genus level, particularly *Bacillus* in hybrid grouper (*Epinephelus fuscoguttatus* × *Epinephelus lanceolatus*) [30].

Several studies have also reported changes in gut microbiota following BSF meal or oil inclusion; however, these findings represent effects of complex insect-derived ingredients rather than direct evidence for LA. In gilthead seabream, inclusion of BSF meal altered the relative abundance of several bacterial genera, including *Cetobacterium*, *Oceanobacillus*, and *Paenibacillus* [90], while other studies reported changes in microbial richness and alpha diversity following different levels of BSF meal inclusion (11% and 15% BSF meal, estimated 1 and 1.4% LA) [91]. Similarly, defatted BSF meal inclusion (15–45% in the diet of gilthead seabream, estimated 0.5 and 1.5% LA) altered the abundance of *Oceanobacillus*, *Lederbergia*, *Bacillus*, and *Corynebacterium* in the digesta while decreasing *Lactobacillus* and *Caldalkalibacillus* abundance [74]. In Atlantic salmon, dietary inclusion of BSF-derived ingredients has also been associated with changes in microbial community composition, including increased *Corynebacterium* and *Bacillaceae* while decreasing the abundance of Gram-negative *Gammaproteobacteria*, *Vibrionaceae*, and *Photobacterium* [92]. Similarly, in invertebrates such as swimming crab, 0.12% dietary LA increased microbial richness and abundance, 0.03% and 0.9% reduced the relative abundance of Proteobacteria, and 0.03–0.12% LA was also found to have a significant inhibitory effect on *Vibrionaceae* and resulted in a significant increase in *Rhodobacteriaceae* [14].

These findings suggest that LA can modulate gut microbial communities, potentially through both direct antimicrobial and indirect host-mediated interactions. Directly, undissociated LA and its monoglyceride derivative, monolaurin, can interact with microbial membranes and disrupt membrane integrity, providing a plausible basis for the inhibition of susceptible microorganisms. Indirectly, LA induced modifications in intestinal barrier function, mucus production, immune responses, and the intestinal environment may further influence microbial community structure. In black sea bream, dietary LA altered the abundance of several bacterial taxa alongside changes in antioxidant capacity and intestinal development; however, these responses were measured concurrently and therefore do not establish that antioxidant or epithelial changes directly drove microbial modulation [18]. Therefore, although LA may influence the gut microbiota through multiple interacting pathways, the relative contribution of direct antimicrobial activity compared

to host-mediated effects remains unclear. Moreover, most available aquaculture studies have focused on taxonomic changes rather than functional microbiome or metabolomic outcomes, limiting our understanding of how LA induced microbial changes translate into physiological benefits. These findings position LA as a promising dietary intervention, with great potential for applications in disease prevention and intestinal health maintenance. Table 4 summarizes the effects of LA and LA rich feed ingredients on gut microbiota composition in aquatic species.

Table 4. Studies summarizing the effects of dietary lauric acid or lauric acid-rich ingredients and MCFA derivatives on gut microbiota in aquatic species.

Species	Lauric Acid Dose	Source of LA	Effects	Reference
<i>Sparus aurata</i>	0.5%	Monoglyceride blend	↓ <i>Gammaproteobacteria</i> abundance	[89]
<i>Sparus aurata</i>	Reported 2.81% (DM basis)	BSF meal	↑ <i>Oceanobacillus</i> and <i>Paenibacillus</i> ↓ <i>Cetobacterium</i>	[90]
<i>Sparus aurata</i>	NR	BSF meal	↑microbial richness and alpha diversity	[91]
<i>Sparus aurata</i>	NR	BSF meal	↑ <i>Oceanobacillus</i> , <i>Lederbergia</i> , <i>Bacillus</i> , <i>Corynebacterium</i> ↓ <i>Lactobacillus</i> and <i>Caldalkalibacillus</i>	[74]
<i>Acanthopagrus schlegelii</i>	0.1–0.8%	Purified LA	↑ <i>Firmicutes</i> , <i>Clostridia</i> , and <i>Bacilli</i> (0.1%) ↔diversity indices	[18]
<i>Salmo salar</i>	NR	BSF oil	↑ <i>Corynebacterium</i> and <i>Bacillaceae</i> ↓ <i>Gammaproteobacteria</i> , <i>Vibrionaceae</i> , <i>Photobacterium</i>	[92]
<i>Danio rerio</i>	0.075%	Glycerol monolaurate	↑gut microbial diversity, <i>Fusobacteria</i> ↓Gram-positive bacteria	[29]
<i>Epinephelus fuscoguttatus</i> × <i>E. lanceolatus</i>	0.06, 0.12, 0.18, 0.24, 0.3, 0.36%	Glycerol monolaurate	↑intestinal flora, increased alpha diversity at genus level, <i>Bacillus</i> (0.24, 0.3%)	[30]
<i>Portunus trituberculatus</i>	0.009, 0.04, 0.08, 0.1, 0.15, 0.29%	Purified LA	↑microbial richness, <i>Rhodobacteriaceae</i> , <i>Vibrionaceae</i> (0.15%) ↓ <i>Proteobacteria</i> (0.15%)	[14]

Abbreviations: LA: lauric acid, NR: not reported, DM: dry matter, BSF: black soldier fly.

7. Effects of Lauric Acid on Immune Response

The immune system is crucial for defending the body from disease invasion and promoting overall health. Experimental data support the implication of LA in modulating the immune responses in fish, but these responses vary according to species, dietary form, tissue sampled, and experimental conditions [8,93,94]. There are few studies evaluating the antioxidant potential of LA in fish. Immune responses to dietary LA appear to be species, dose, tissue, and context-dependent. Importantly, the available studies are from different dietary forms, including purified LA, LA derivatives, BSF oil, and BSF meal; thus, these studies should not be considered equivalent evidence for the effects of free LA.

In European seabass, dietary supplementation with 1% purified LA revealed pronounced immunomodulatory effects, with downregulation of inflammatory and regulatory

cytokines such as tumor necrosis factor- α (*tnf- α*), interleukin-1 β (*il-1 β*), and interleukin-10 (*il-10*) in the anterior intestine, which the authors associated with the reduction in circulating white blood cells. The same authors observed that these changes also occurred together with reduced intestinal peroxidation, suggesting a possible change in intestinal homeostasis, rather than a simple stimulation or suppression of immunity [16]. Similarly, dietary supplementation with purified LA at levels up to 0.8% of the diet had no significant effect on total protein, lysozyme, or albumin blood levels in black seabream [1,18,28].

In contrast, dietary inclusion of 0.4 and 0.6% alpha-monolaurin in Nile tilapia, resulted in a linear increase in white blood cell count as well as upregulation of serum immunoglobulin G (IgG), immunoglobulin M (IgM), *il-1 β* , and interferon-gamma (*ifn- γ*), while downregulating the heat shock protein 70 (*hsp70*) gene, suggesting a reduction in cellular stress [56].

In rainbow trout, 16% dietary inclusion of BSFO was associated with significantly elevated serum peroxidase activity and upregulation of renal interleukin-8 (*il-8*) and interferon regulatory factor-1 (*irf-1*), alongside some immunological benefits [58]. However, because BSFO contains numerous fatty acids and other lipids, these immune responses cannot be attributed specifically to LA. In another complementary study using rainbow trout, the marker associated with cellular proliferation and DNA repair, proliferating cell nuclear antigen (*pcna*), was not significantly affected by the inclusion of 4% BSF oil in the diets of rainbow trout, indicating no severe DNA repair or inflammation in the liver [60]. Similarly, neither 5% BSFO in European catfish (*Silurus glanis*) nor 10.5% BSFO (0.7% LA in the diet) in barramundi (*Lates calcarifer*) affected total protein, albumin, or globulin concentrations [95,96]. These results suggest that BSF-derived lipid sources can modify selected immune parameters without producing consistent changes in systemic immune indices.

At the intestinal level, although subtle, some immunomodulatory effects of LA were reported in gilthead seabream. Dietary inclusion of 9.5% BSFO upregulated intestinal anti-inflammatory cytokine *il-10* and the pro-inflammatory gene *tnf- α* but had no effect on plasma innate immune humoral parameters (nitric oxide, antiproteases, proteases, and peroxidase) [97]. Conversely, supplementation with 0.3% sodium salt of coconut fatty acid distillate, rich in LA, resulted in a downregulation of *il-8* in the anterior intestine [4], suggesting an anti-inflammatory effect at a substantially lower level.

Notably, upregulation of inflammatory cytokines should not automatically be interpreted as detrimental, nor should their downregulation necessarily indicate improved immune responses. Interpretation of the physiological responses depends on tissue examined, duration of the response, nutritional and immune status of the fish, and whether the animals are exposed to an inflammatory challenge. A short summary of these studies is presented in Table 5.

Table 5. Studies summarizing the effects of dietary lauric acid or lauric acid-rich ingredients and MCFA derivatives on immune parameters in aquatic animals.

Species	Lauric Acid Dose	Source	Effects	Reference
<i>Oncorhynchus mykiss</i>	Estimated 1.4% LA total diet	BSFO	↑plasma peroxidase activity, renal <i>il-8</i> , <i>tnf-α</i> , and <i>irf-1</i>	[58]
<i>Oncorhynchus mykiss</i>	NR	BSFO	↔ <i>pcna</i>	[60]
<i>Acanthopagrus schlegelii</i>	0.1–0.8%; 0.01–0.16%; LA	Purified LA	↔serum total protein, lysozyme, or albumin levels	[1,18,28]

Table 5. Cont.

Species	Lauric Acid Dose	Source	Effects	Reference
<i>Sparus aurata</i>	Reported 12.1, 23.7, 29.1% LA (total FA)	BSFO	↔humoral innate immune parameters (nitric oxide, antiproteases, proteases, and peroxidase)	[97]
<i>Sparus aurata</i>	Reported 12.1, 23.7, 29.1% LA (total FA)	BSFO	↑ <i>il-10</i> and <i>tnf-α</i> expression in intestine	[97]
<i>Sparus aurata</i>	0.3%	Coconut oil derivative	↓ <i>Il-8</i> ↔ <i>tnf-α</i> and <i>il-1β</i>	[4]
<i>Dicentrarchus labrax</i>	0.5, 1, 2%	Purified LA	↓ <i>tnf-α</i> , <i>il-1β</i> , and <i>il-10</i> (1%)	[16]
<i>Silurus glanis</i>	Reported 11.75, 23.67% LA (total FA)	BSFO	↔total protein, albumin, or globulin levels	[95]
<i>Oreochromis niloticus</i>	0.4 and 0.6%	Alpha-Monolaurin	↑IgG, IgM, <i>il-1β</i> , <i>ifn-γ</i> ↓ <i>hsp70</i> (0.2%)	[56]
<i>Lates calcarifer</i>	NR	BSFO	↔plasma proteins (total protein, albumin, and globulin)	[96]

Abbreviations: LA: lauric acid, 0.5, NR: not reported, FA: fatty acids, BSF: black soldier fly, IgG: immunoglobulin G, IgM: immunoglobulin M.

8. Lauric Acid and Its Effects on Antioxidant Parameters

Oxidative stress is defined as an imbalance between reactive oxygen species (ROS) production and the antioxidant defense system. Inadequate antioxidant defense allows ROS to impair cellular essential functions, ultimately leading to stress induced cell death [98]. Few studies have evaluated the capacity of LA, LA rich ingredients, and other MCFAs to modulate antioxidant defenses in aquatic organisms. These studies remain inconsistent, with outcomes depending on fish species, tissue, LA dose and LA dietary forms.

In black seabream, supplementation with up to 0.1% purified LA resulted in a significant decrease in malondialdehyde (MDA) levels in serum, indicating a reduction in lipid peroxidation, thus a protective antioxidant effect [18]. In a subsequent study, the authors observed similar results, with 0.04% LA supplementation subsequently reducing lipid peroxidation levels, thus corroborating their earlier findings [1]. Additionally, European seabass fed diet containing 1% purified LA showed a decrease in catalase (CAT) and glutathione reductase activities and lipid peroxidation at the intestinal level [16]. This response may reflect a lower oxidative burden and reduced requirement for antioxidant defense since reduced antioxidant enzyme activity occurred alongside reduced lipid peroxidation.

In Nile tilapia, these antioxidant effects have been evaluated at the hepatic level. Dietary inclusion of alpha-monolaurin (0.2%) increased hepatic activities of superoxide dismutase (SOD), CAT, and glutathione peroxidase (GPX), while decreasing lipid peroxidation levels, indicating an enhancement of the enzymatic antioxidant defense system [56]. In gilt-head seabream, dietary inclusion of 4% BSFO, corresponding to 1.9 LA% in the diet based on its reported fatty acid composition resulted in reduced intestinal lipid peroxidation [97]. The authors of this study attributed the positive effect on intestinal antioxidant status to LA found in BSFO.

In invertebrates, little evidence for LA mediated antioxidant effects is available. In whiteleg shrimp (*Litopenaeus vannamei*), dietary inclusion of LA (0.1% and 0.8%) in combination with N-acetyl-L-cysteine significantly enhanced the expression of SOD and glutathione peroxidase (GSH-Px), while reducing MDA at the hepatopancreatic level under high stock-

ing density conditions [15]. Although these results indicate that LA may improve the capacity to mitigate ROS-induced damage in shrimp, the independent contribution of LA cannot be established because N-acetyl-L-cysteine was administered concurrently.

The dose dependent responses reported in aquatic organisms may further explain some of the inconsistencies among studies. At relatively low inclusion levels, LA may induce changes in immune and antioxidant systems that contribute to cellular homeostasis, whereas excessive exposure may increase oxidative or inflammatory stress. Such a hermetic-like response is biologically possible but has not been demonstrated in depth for dietary LA in aquatic species. For example, in swimming crab, 0.1% dietary LA upregulated *cat* and *gpx*, but higher concentrations (0.15 and 0.29%) led to a downregulation of these antioxidant genes in the hepatopancreas [14]. Additionally, MDA levels in the serum remained unaffected in this study, suggesting that at the tested levels, LA was only able to upregulate antioxidant gene expression without a reduction in lipid peroxidation.

Studies linking LA with mitogen-activated protein kinase (MAPK) and nuclear factor erythroid 2-related factor 2 (NRF2) signalling remain limited and are still emerging. In yellow croaker (*Larimichthys crocea*) macrophages, GML suppressed extracellular signal-regulated kinase (ERK)/c-Jun N-terminal kinase (JNK) MAPK signalling and reduced ROS production while increasing *nrf2* expression, supporting a potential connection between LA, inflammatory signalling, and antioxidant defense [99]. However, these findings were obtained in macrophages and should not be generalized as whole fish responses. Studies involving Toll-like receptor (TLR)/nuclear factor- κ B (NF- κ B) signalling pathways to dietary LA still remain to be established.

Overall, LA and LA related compounds can modulate immune and antioxidant responses in aquatic organisms, but the direction and magnitude of these effects depend on the dose, chemical form, tissue, sampling time, and physiological status. Although MAPK, ROS-mediated, and NRF2-dependent responses may contribute to these effects, direct evidence for purified dietary LA in fish still remains limited. Changes in immune and antioxidant markers should therefore be interpreted collectively, and further dose-response and tissue specific studies are needed to establish whether these responses represent adaptive regulation or adverse inflammatory and oxidative stress. The results of the studies on the effects of LA on antioxidant parameters are summarized in Table 6.

Table 6. Studies summarizing the effects of dietary lauric acid or lauric acid-rich ingredients and MCFA derivatives on antioxidant responses in aquatic species.

Species	Lauric Acid Dose	Source	Effects	Reference
<i>Acanthopagrus schlegelii</i>	0.1% LA	Pure lauric acid	↔CAT, SOD, GSH-Px, or T-AOC; ↓lipid peroxidation, MDA	[1,18]
<i>Dicentrarchus labrax</i>	0.5, 1, 2%	Pure lauric acid	↓CAT and glutathione reductase, lipid peroxidation (1%)	[16]
<i>Sparus aurata</i>	Reported 12.1, 23.7, 29.1% LA (total FA)	BSF Oil	↓intestinal lipid peroxidation	[97]
<i>Oreochromis niloticus</i>	0.2, 0.4, 0.6%	Alpha-monolaurin	↑hepatic SOD, CAT, GPx ↓lipid peroxidation (0.2%)	[56]
<i>Litopenaeus vannamei</i>	0.2%	Pure lauric acid	↑SOD and GSH-Px ↓MDA under high stocking density	[15]
<i>Portunus trituberculatus</i>	0.009, 0.04, 0.08, 0.1, 0.15, 0.29%	Pure lauric acid	↑ <i>cat</i> and <i>gpx</i> in hepatopancreas ↓MDA (0.1%)	[14]

Abbreviations: HI: *Hermetia illucens*, LA: lauric acid, FA: fatty acids, SOD: superoxide dismutase, MDA: malondialdehyde, CAT: catalase, GSH-Px: glutathione peroxidase, Gpx: glutathione peroxidase.

9. Antimicrobial Properties of Lauric Acid

The antimicrobial activity of LA is primarily associated with its amphiphilic structure and its ability to interact with microbial membranes [33], although additional intracellular effects have also been reported. Its antimicrobial efficacy is strongly influenced by pH, which determines its ionization state and, consequently, its ability to partition into lipid membranes. At pH values at which a sufficient proportion of LA is present in its undissociated form, the molecule can readily interact with and penetrate microbial phospholipid membranes [33]. This interaction can alter membrane structure and permeability, resulting in the leakage of intracellular components, disruption of membrane-associated functions, and, depending on the extent of damage, loss of cellular homeostasis and cell death [100].

In bacteria, LA and its derivative monolaurin act by disrupting the lipid bilayer, and their incorporation into lipid bilayers can alter membrane organization and induce membrane structural changes, resulting in increased permeability and disruption of essential membrane functions [100]. The antimicrobial activity of fatty acids is also influenced by carbon chain length. The earlier results of Kabara [101] demonstrated that saturated fatty acids exhibited their highest antimicrobial activity against Gram-positive bacteria when the chain length was twelve carbons long. Although susceptibility varies among bacterial species, antimicrobial fatty acids and monoglycerides generally exhibit greater activity against Gram-positive bacteria, whereas the outer membrane of Gram-negative bacteria can act as an additional permeability barrier, reducing access to the cytoplasmic membrane.

In enveloped viruses, LA destabilizes the lipid envelope by solubilizing phospholipids, thereby preventing viral attachment and fusion with host cells and impairing viral replication. Additionally, it can damage viral RNA or DNA and alter membrane permeability and fluidity, ultimately inhibiting viral maturation and causing viral inactivation. The antiviral activity of LA and GML has primarily been associated with their ability to interact with enveloped viruses. A recent experimental study demonstrated that treatment with LA or GML disrupted the envelope structure of cyprinid herpesvirus 2 (CyHV-2), altered its physicochemical properties, compromised virion stability, and reduced its viral infectivity and replication [102]. Therefore, the interaction of these amphiphilic compounds with viral envelope lipids may compromise the structural integrity required for viral infectivity and interfere with processes such as attachment and fusion with host cells.

In fungi, LA binds to ergosterol, the main component of fungal membranes, through van der Waals forces and hydrogen bonding, leading to pore formation that alters membrane integrity and ion balance, ultimately resulting in cell death [103,104].

Experimental studies have reported antibacterial, antifungal, and antiparasitic activity of LA against microorganisms including *Staphylococcus aureus*, *Clostridium* spp., *Escherichia coli*, *Salmonella* spp., *Candida* spp., *Aspergillus* spp., *Penicillium* spp., and *Giardia duodenalis* [105–108]. However, most of these studies originate from terrestrial microorganisms and *in vitro* experiments and therefore demonstrate antimicrobial activity under controlled experimental conditions rather than disease protection in aquatic animals. A few papers have already reported the antimicrobial activity of LA against fish-pathogenic bacteria such as *Aeromonas hydrophila* and *Vibrio* spp., as well as fungi such as *Saprolegnia parasitica* and enveloped viruses [103,109]. Specifically, an *in vitro* study demonstrated that LA effectively inhibited the growth of the fungal pathogen *Saprolegnia parasitica* and the protozoan *Ichthyophthirius multifiliis* [13], while *in vivo* dietary supplementation with coconut oil (1% and 4%) was found to reduce *Aeromonas hydrophila* colonization while promoting the growth of beneficial gut microbiota, such as lactic acid bacteria in zebrafish [110]. Studies of bacterial challenges using LA derivatives are also emerging. For instance, GML (0.05–0.25%) improved the survival of cage-reared juvenile pompano (*Trachinotus ovatus*)

after a *Vibrio parahaemolyticus* challenge (2×10^6 CFU/mL), providing evidence for the protective effect of GML against disease.

From these studies, it is clear that the translation of *in vitro* antimicrobial activity to dietary efficacy still remains unclear. The effective LA concentrations *in vitro* may not be achieved in the intestinal lumen after feed consumption, digestion, absorption, and metabolism in *in vivo* studies. Furthermore, antimicrobial activity *in vitro* should not be interpreted as evidence that dietary LA can reach therapeutically effective concentrations in fish tissues. Further studies on LA in the gastrointestinal tract alongside pathogen challenge tests are required.

Due to these properties, LA could represent a promising alternative for reducing antibiotic use in aquaculture. Its antimicrobial activity is generally attributed to three main mechanisms: (i) disruption of Gram-positive bacterial membranes and lipid-enveloped viruses through physicochemical interactions; (ii) interference with intracellular processes such as transcription and signal transduction; and (iii) alteration of membrane stability and integrity [36]. Although its membrane targeting mechanisms may theoretically involve mechanisms different from those of conventional antimicrobials, there is currently insufficient experimental evidence to conclude that LA has a low likelihood of inducing the development of resistance, especially in aquatic pathogens. Collectively, the studies discussed throughout this review suggest that LA may exert its functional effects in aquatic species through multiple interconnected mechanisms involving energy metabolism, intestinal health, gut microbiota, immune responses, antioxidant defense, and antimicrobial activity, as summarized in Figure 2.

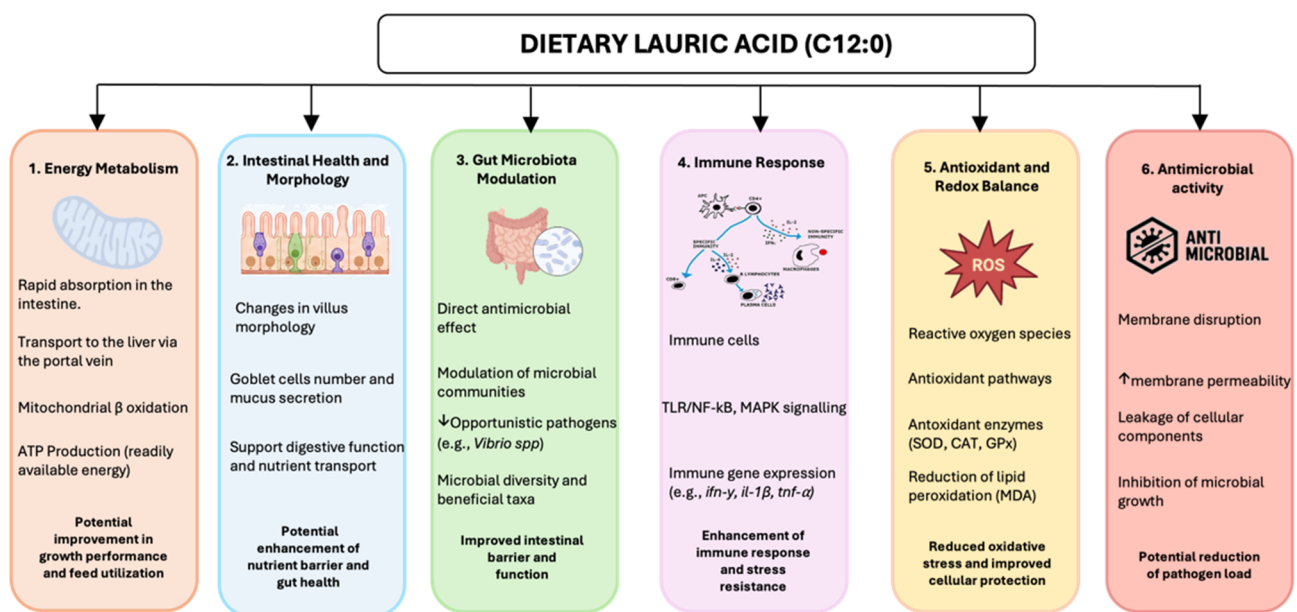


Figure 2. Schematic representation of the proposed mechanisms and functional effects of lauric acid in aquatic species.

10. Conclusions

LA has demonstrated significant potential as a promising feed additive in aquaculture due to its diverse biological benefits and its increasing availability from vegetable sources and alternative sustainable animal origin feed ingredients. The studies reviewed here suggest that LA in the diets of aquaculture species can influence several physiological processes, including growth performance, digestive functionality, intestinal health, immune and antioxidant responses, intestinal microbiota, and disease resistance, either in its purified form, as monoglycerides, or as part of LA rich ingredients such as BSF meal, oil, and

coconut oil. These studies also indicate that the effects of LA are highly dependent on species, dietary inclusion level, experimental conditions, and chemical forms. Nonetheless, the results obtained from purified LA should be distinguished from those obtained from derivatives of LA and LA rich ingredients such as BSF meal, oil and coconut oil.

Dietary LA supplementation has been associated with improvements in growth performance and feed utilization. These effects are attributed to the unique metabolic properties of MCFAs, which are rapidly absorbed and oxidized to provide readily available energy. Nevertheless, a few studies have reported optimal performance at very low inclusion levels, while higher levels often produce neutral or inconsistent responses.

Experimental data have also demonstrated that dietary LA can influence intestinal health and morphology. Different studies reported improvements in intestinal morphology, including increased villus height and goblet cell density, thus enhancing nutrient absorption and gut health. Furthermore, LA and its derivatives have demonstrated the capacity to modulate gut microbiota composition, thus reducing potentially pathogenic bacteria like *Vibrio*, while increasing the microbial richness and diversity, resulting in an enhanced robustness against pathogens.

The effects of LA on immune and antioxidant responses are less consistent but still suggest potential benefits. Some studies reported modulation of immune related gene expression, enhanced total and specific antioxidant enzyme activities, and reduced lipid peroxidation, indicating that LA may contribute to improved stress resistance and immune competence in aquatic organisms. However, findings are not uniform across species and experimental conditions.

The antimicrobial potential of LA is promising but remains insufficiently studied in aquaculture settings. Future studies should therefore determine and validate whether antimicrobial concentrations observed *in vitro* can be achieved in the gastrointestinal tract and evaluate whether dietary LA or its derivatives provide measurable protection against relevant aquatic pathogens and also investigate potential antimicrobial resistance *in vivo*.

Overall, the findings discussed above highlight several research gaps that need to be addressed to fully elucidate the potential of LA as a functional ingredient in aquafeeds. First, the use of complex feed ingredients as a source of LA. Many studies utilize BSF oil or meal, which contain other bioactive compounds such as antimicrobial peptides and chitin; thus, the contribution of LA cannot be separated from these compounds. Secondly, studies differ substantially in LA form (free LA, monoglyceride, insect oil, insect meal, and coconut oil), inclusion level, experimental condition, dietary formulation, and reporting of dietary LA concentrations, limiting direct comparison among studies. Developing standard reporting of LA content and comparable experimental frameworks would greatly improve interpretation of dose-response relationships. Further studies should establish species-specific optimal inclusion levels and evaluate long-term safety, palatability, feed intake, tissue lipid deposition, and potential effects on essential fatty-acid balance.

Nevertheless, LA could represent a valuable dietary component with the potential to support sustainable aquaculture by improving growth performance, intestinal health, and immune responses in aquatic species, while contributing to reduced reliance on antibiotics and chemical additives, supporting the One Health perspective. Future research should focus on elucidating the underlying mechanisms of action, developing optimal inclusion levels for different species and developmental stages, and evaluating their long term efficacy and cost-effectiveness in commercial farming conditions. Even though the studies reviewed here have demonstrated beneficial effects across a range of inclusion levels, the evidence is still insufficient to recommend an optimal inclusion level. Finally, comparative assessments of production costs, availability of ingredients, resource use, and adequate environmental impact assessments are required to determine the economic and sustainability advantages

of LA and LA rich ingredients relative to conventional feed additives and lipid sources. Therefore, economic evaluations are needed to determine the economic feasibility of its large-scale application in aquafeeds [41].

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