



PROBING INTO THE IMPACTS OF ENDOGENOUS AND EXOGENOUS SHORT-CHAIN FATTY ACIDS (SCFAS) IN FISH HEALTH AND GROWTH – A REVIEW

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Abstract

Short-chain fatty acids (SCFAs) are small organic acids that exist in the fish gastrointestinal tract, mainly acetate, propionate, and butyrate. These SCFAs are produced through anaerobic fermentation of dietary non-digestible carbohydrates by gut microbes. Though enough studies have been devoted to showcasing the potential of SCFAs in human nutrition, the research on their production, potential, and existence in fish has been comparatively limited until recently. This review aims to provide a comprehensive overview of the current knowledge regarding SCFAs in aquaculture. It starts with commenting on the different sources, such as substrate and microbial species that are responsible for the production of SCFAs and their transportation and ends up depicting the relationship between biofloc technology and SCFA production. This review also discusses the factors influencing SCFA production, such as environment, diet, and feeding habits of fish. Furthermore, the biological functions of SCFAs have been highlighted, and critical findings were compiled, including immunomodulatory effects, physiological response, gut health, and immunity.

Key words: organic acids, gut microbes, fermentation, antibiotics, aquaculture

List of abbreviations:

ALPI – intestinal alkaline phosphatase, AXOS – arabinooligosaccharides, CAT – catalase, CHO – carbohydrate, CO-A – coenzyme A, FABP – fatty acid binding protein, FCR – feed conversion ratio, FOS – fructooligosaccharides, GI – gastrointestinal, GOS – galactooligosaccharides, IKK β – inhibitor of κ B kinase beta, IKK γ – inhibitor of κ B kinase gamma, I κ B α – inhibitor of κ B alpha, IL – interleukin, IMC – Indian major carps, IMO – isomaltooligosaccharides, INF – interferon, LMWPs – low molecular weight polysaccharides, Lyz – lysozyme, MAPK – mitogen activated protein kinase, MOS – mannanoligosaccharides, MRS broth – de Man, Rogosa, and Sharpe broth, NF- κ B – nuclear factor-kappa B, OTUs – operational taxonomic units, PCNA – proliferating cell nuclear antigen, PER – protein efficiency ratio, SCFAs – short-chain fatty acids, scFOS – short-chain fructooligosaccharides, SGR – specific growth rate, SOD – superoxide dismutase, TNF – tumor necrosis factor, XOS – xylooligosaccharides.

The global demand for fish meat is more significant than that for poultry, pork, and beef products (Tacon and Metian, 2013), which is an ideal source of high-quality and easily digestible proteins, essential fatty acids, vitamins, and minerals. Culture fisheries have replaced capture fisheries due to their enormous growth in satisfying human needs (Guerreiro et al., 2018 a). Some issues arise in the cultural practices to improve the species' health and growth performance, enhance the host immune system, and improve the digestibility of the nutrients, etc. (Nawaz et al., 2018). In addition, the most important factors, such as stress and diseases, affect the successful practices of aquafarming (Subramanian et al., 2013). Antibiotics are used commercially in aquaculture to tackle the above problems (Wongsasak et al., 2015). However, the banned practice of using antibiotics due to its adverse effects including the occurrence of resistant pathogens and accumulation of antibiotic residues in the culture species triggered the researchers to find non-antibiotic compounds that can promote health and growth performance.

Interestingly, the intestine of the animal is considered an ideal environment for the colonization and proliferation of beneficial bacteria, which have a significant role in maintaining the host's health through various mechanisms (Wang et al., 2018), including enhancement of the immune system, defense against pathogens, effective utilization of feed, and production of metabolites such as short-chain fatty acids, vitamins, etc. In particular, the influence of gut microbiota on dietary carbohydrate fermentation by microbial metabolism results in the production of short-chain fatty acids (SCFAs) (Piazzon et al., 2017) in the fish gut, which have beneficial effects on the host animal. Short-chain fatty acids are intestinal metabolic compounds consisting of chains that range in length from two to six carbon atoms, with one or two carboxyl groups located at the end of their chains. However, it is essential to note that fish cannot synthesize SCFA directly; instead, SCFAs are produced through the fermentation of natural diets such as algae, plankton, aquatic plants, and commercial diets with plant-based ingredients by gut

microorganisms in anaerobic conditions. In addition, dietary incorporation of specific synthetic sources of SCFA also known as acidifiers, including acetic acid, propionic acid, butyric acid, formic acid, etc., in fish diets provides an ideal environment for the growth of gut microbiota for producing SCFAs. In fish, SCFAs are comprised of acetic acid, propionic acid, and butyric acid, and a small proportion of valeric, isobutyric and isovaleric acids (Hao et al., 2017) produced from microbial anaerobic fermentation of both digestible (monosaccharides, disaccharides, and starch) and non-digestible carbohydrates (cellulose, hemicellulose, and pectin). Among various microorganisms, the production of SCFA is dominated by bacteria in the fish gut microbiome (Rombout et al., 2011). To date, most research has focused on bacterial composition in the fish gut microbiome (Liu et al., 2014; Ng and Koh, 2017; Hoseinifar et al., 2017; Abdel-Mohsen et al., 2018; Guerreiro et al., 2018 b; Wassef et al., 2020; Gallo et al., 2020; Li et al., 2022; Wassef et al., 2023). The composition of the gut microbiome is influenced by diet composition, species type, and environmental conditions. On top of that, Gallo et al. (2020) reported that gut microbiome composition varied with the species despite inhabiting the same geographical location.

Fish gut microbiota have a crucial role in stimulating the immune system (Tian et al., 2017; Wassef et al., 2017, 2020) and promoting growth (Liu et al., 2014; Ng and Koh, 2016; da Silva et al., 2016; Wassef et al., 2017; Guerreiro et al., 2018 b), which were considered a primary application of dietary incorporation of SCFAs in fish diet. In addition, dietary SCFAs improve innate immunity and enhance disease resistance against pathogens by modulating the gut microbiota (Li et al., 2022). There appears to be a synergistic effect between the biofloc system and SCFA production that could benefit fish. This current review will provide a comprehensive information on endogenous and exogenous production of SCFAs and their beneficial effects in promoting the growth and immune mechanism in resisting disease occurrence in fish. It concludes with the scientific gaps that would guide future researchers towards feed additives in improving the growth, health status, and disease prevention of aquatic animals.

Sources of SCFAs in fish diets

In general, the fish gut microbiota ferments food fibers and carbohydrates to synthesize SCFAs which are reduced to short-chain fatty acids. The gut microbiota is crucial for the nutrition and general well-being of fish (Ley et al., 2008) whose composition varies according to the source, serving as the substrate for the synthesis of SCFAs (Ciarlo et al., 2016). Frequently employed plants centered components in aquafeeds, such as the meal of soybeans, bran from corn, rice, and wheat, contain fermentable fibers that the fish's gut microbiota metabolize to form short-chain fatty acids, which are vital nutrients that support the fish growth performance. Furthermore, it was well recognized that adding probiotics, prebiotics,

and resistant starch to the diet might improve fish health and growth through a variety of processes, including serving as a catalyst and a substrate for the fish gut's synthesis of short-chain fatty acids.

Soybean meal

The inclusion of soybean meal is indirectly related to SCFA production due to the modification of the intestinal microbiota of fish. Interestingly, it has been observed that the experimental diets with bioprocessed soybean meal by *Aureobasidium pullulans* included three different fractions: bioprocessed soybean meal after enzymatic treatment, and additionally rinsed or washed bioprocessed soybean meal yielded diverse operational taxonomical units (OTUs) in which *Lactococcus lactis*, typically used for carbohydrate fermentation, was found to be abundant in the gut environment (Fowler et al., 2021). This resulted in better gut interactions and enhanced growth, promoting metabolite production such as SCFAs in hybrid sea bass (Fowler et al., 2021). However, when several experimental dietary regimens were fed, there were barely any modifications in the gut microbiota. On top of that, variations were observed in the bioprocessed soybean meal diet with different fractions in hybrid seabass (Fowler et al., 2021). In summary, while the generation of SCFAs is not the primary focus of this work, it is thought that adding soybeans alters the microbial makeup of fish guts, which may indirectly impact SCFA production. Besides, adding soybean meal to a mixture of lactic acid-producing bacteria, such as *Lactobacillus plantarum* and *L. fermentum* enhanced the amount of total short-chain fatty acids in the diet of Atlantic salmon, with the amounts of acetoacetic acid and succinic acid among them being the most significant levels when compared to other diets (Nimalan et al., 2023).

Corn bran

It is a byproduct of corn milling that contains soluble fibers called pectin and hemicellulose, which the microbiota of the intestines has been exhibited to ferment (Mua and Jackson, 1997; Rose et al., 2010; Yang et al., 2013). As a result, SCFAs are produced during the fermentation process. There is limited research on how dietary supplementation with corn bran affects fish SCFA production. Significant quantities of acetate, propionate, and butyrate were produced in an *in vitro* investigation focused on fermenting particular fibers, including arabinoxylan from corn bran. The production rates were measured at 156.66, 16.30, and 10.29 micromoles per 100 milligrams of carbohydrates, respectively (Yang et al., 2013). Similarly, the *in vitro* fermentation of pectin derived from corn bran resulted in the production of acetate, propionate, and butyrate at rates of 178.07, 2.06, and 9.65 micromoles per 100 milligrams of carbohydrates (Yang et al., 2013).

Wheat bran

Another excellent source with rich, complex dietary fibers like cellulose, hemicellulose, and lignin that are

difficult for the small intestine to digest is wheat bran, and it is a fantastic source of SCFAs. Instead, it will be degraded by the anaerobic gut bacteria in the fish intestine via the fermentation process. The *in vitro* investigation on the fermentation of wheat bran by pig gut microbial inoculant revealed elevated propionate production, however, this rise was limited to the first forty-eight hours of the *in vitro* method of fermentation (Wang et al., 2004).

Rice bran

It has been used as a potential source of carbohydrates (12–15% crude fiber) for several commercial herbivorous fish species (Kumar et al., 2017). Dietary fibers from rice bran have been reported to modulate specific bacteria and promote SCFA production in which acetate, propionate, and butyrate alone contribute 95% of total SCFA content (Yao et al., 2022).

Algae and seaweed

Another important natural source of SCFAs, packed with complex polysaccharides that the gut bacteria may digest. Fish species, the composition of the gut microbiota, and the consumption of various algae and seaweed species together affect the extent to which SCFAs are produced and utilized. Many studies state the prebiotic effects of seaweeds and microalgae in SCFA production. For instance, the dietary supplementation of marine microalgae such as *Dunaliella salina* and *Nannochloropsis salina* enhanced the production of butyric acid accounting for 12.03% and 4.87% of total SCFA content, respectively (Chen et al., 2020). The synthesis of SCFAs, especially acetate and propionic acids, is increased by the use of polysaccharides, which are low in molecular weight, shortly called as LMWPs (low molecular weight polysaccharides), which are generated from agar and alginates from seaweeds. This suggests that LMWPs may be a valuable and efficient source of prebiotics (Ramnani et al., 2012).

Aquatic plants

Aquatic plants are another source of dietary fiber in fish diets, contributing to overall health and growth promotion. Firstly, duckweeds are the smallest free-floating aquatic plants utilized by various livestock species, including fish, as a nutrient-rich feed source (Baek et al., 2021). The investigation on *Lemna minor* by Negesse et al. (2009) showed that there were 16.6 millimoles of SCFAs overall, of which two and three carbon short chains accounted for 11.8 and 3.1 mM, respectively. The function of water hyacinth (water lily) as food for several fish species, including IMC, has been the subject of numerous research studies focusing on substituting fish meal. There are no publications mentioning the use of water hyacinth as a dietary supplement to increase the synthesis of SCFAs. However, the *in vitro* fermentation conducted by Banakar et al. (2017) on water hyacinth leaves and petioles by using ruminal fluid of cattle as inoculum, revealed a considerable amount of SCFA production, sug-

gesting that water hyacinth may be utilized as a source of SCFAs in ruminants. In addition, water lettuce (*Pistia striatiotes*) is another floating freshwater aquatic plant that contains significant amounts of fibers and nutrients which is believed to contribute to the SCFA production in fish gut. Despite *Azolla* (water fern) containing essential amino acids, vitamins, minerals and growth-promoting metabolites compared to other crops and macrophyte plants, it is being under-utilized. The efficiency of pulverized azolla as a prebiotic source was determined by comparing the relative growth rate of *Lactobacillus rhamnosus* in MRS broth containing azolla and inulin as a source (Cruz et al., 2023). After 24 hours of incubation, pulverized azolla showed more growth than inulin. This concludes that *Azolla pinnata* is elucidated as a candidate source for better SCFA production, which could be incorporated into the fish diet for overall growth performance (Cruz et al., 2023). Lastly, certain by-products from food and agricultural industries, such as fruit and vegetable residues containing fermentable substrates, can contribute to SCFA production when included in fish diets (Annunziata et al., 2020; Shah et al., 2023).

Probiotics

As defined by Fuller (1989), probiotics are feed supplements that include live microbial cultures that enhance the host animal's gut microbial equilibrium. It is known that the indigestible carbohydrate components that are obtained from the small intestine are fermented by probiotic bacteria to yield SCFAs. In Malaysian mah-seer, the dietary host-derived probiotic bacteria (*Bacillus* sp. AHG22, *Shewanella* sp. AFG21, and *Alcaligenes* sp. AFG22) (*Tor tambroides*) demonstrated enhanced synthesis of volatile short-chain fatty acids in the gastrointestinal tract when compared to a control diet (Asaduzzaman et al., 2018). Generally, *L. lactis* is not found in the GI tract but is often used as a probiotic in olive flounder (*Paralichthys olivaceus*), which also results in high SCFAs, citrulline, vitamins and taurine production (Nguyen et al., 2018). In addition, probiotics may alter the microbial metabolism in the distal parts of the intestine to enhance the formation of short-chain fatty acids, which may enhance the absorption of water and sodium and decrease colonic motility (Ige, 2013). Furthermore, *Bifidobacterium* strains in newly weaned pigs lower the net breakdown of protein, ammonia, and isovaleric acid generation (Modesto et al., 2009).

Prebiotics

Prebiotics, monosaccharides, oligosaccharides, or polysaccharides, constitute a synthetic source with notable impact. These components, which remain indigestible, play a crucial role in fostering favorable effects on the host organism. Specifically, they undergo metabolism to generate short-chain fatty acids through the activity of health-promoting bacteria like *Lactobacillus* and *Bifidobacterium* in the hindgut microbiota (Ringø et al., 2010). Numerous research endeavors

have explored the effects of various prebiotics, including fructooligosaccharides (FOS), inulin, mannanoligosaccharides (MOS), galactooligosaccharides (GOS), short-chain fructooligosaccharides (scFOS), xylooligosaccharides (XOS), arabinoxylooligosaccharides (AXOS), GroBiotic-A, and isomaltooligosaccharides (IMO) in fish. Among these, arabinoxylooligosaccharides produced enhanced acetate, propionate, and total SCFAs in Siberian sturgeon and African catfish (Ringø et al., 2010; Rurangwa et al., 2008). In giant freshwater prawns, the inclusion of 0.4% fructooligosaccharides resulted in increased acetic and propionic acid levels (Fernández et al., 2016). Furthermore, inulin was identified to modify the composition of gut microbiota, resulting in elevated acetic and propionic acid production, although it did not impact butyric acid production in Nile tilapia (Wang et al., 2021).

Resistant starch

It is widely being discussed as a potential synthetic source of SCFAs serving as a prebiotic in the production of SCFAs, particularly acetate, butyrate, and propionate through anaerobic fermentation in the fish hindgut, which has beneficial effects on host organisms (Li et al., 2020). For example, two test diets containing potato starch as resistant starch at 8% and 16% were studied in pigs. The diet with 16% potato starch showed an increase in the production of butyric acid and total SCFAs. As a result, the high levels of butyric acid in the large intestine led to increased crypt depths, which is indicative of enhanced cell proliferation (Hedemann and Bach Knudsen, 2007). In juvenile European seabass, lupin meal (non-starch polysaccharide), waxy maize (99% amylopectin), and amylo maize (70% amylose, 30% amylopectin) were investigated to measure the SCFAs, particularly acetate in the fecal matter. It has been found that lupin meal which is rich in non-starch polysaccharides is fully metabolized and resulted in high acetate content in the fecal matter. Furthermore, amylo maize and waxy maize were also partly metabolized and showed acetate content but less than lupin meal in the fecal matter (Gatesoupe et al., 2014).

SCFAs and their salts

Numerous studies, including those conducted by Lückstädt (2008 a, b), Nuez-Ortín (2013), Koh et al. (2016), Ng and Koh (2017), Hoseinifar et al. (2017), Tran et al. (2020), Sardar (2020), Wassef et al. (2023), Martins et al. (2023) among others have meticulously examined short-chain fatty acids and their salts, revealing their advantageous impact on host animals, notably fish. These investigations have delved into various aspects, elucidating the positive influence of SCFAs and their salts on crucial factors such as growth performance, enhanced mineral bioavailability, heightened enzyme activities, nutrient substitution, digesta composition, feed digestibility, and the intricate composition of gut microbiota. This discourse aims to provide

a comprehensive insight into the physiological effects of dietary inclusion of specific SCFAs, namely acetate, butyrate, propionate, formate, and their corresponding salts on fish physiology, which will be expounded upon in subsequent discussion.

Fish gut microbiota composition and its mechanism of production and absorption of SCFAs

The dynamic nature of fish gut microbiota is characterized by a classification into transient and persistent microbes, determined by the duration of their stay within the gastrointestinal tract (Bhatt et al., 2018). Transient microbes, entering through the ingested food, fail to colonize the gut mucosal or epithelial layers, while resident microbes establish a symbiotic relationship within the colon membrane (Zhang et al., 2016). The microbial composition within the GI tract is contingent upon the prevalence and composition of microorganisms in the rearing water, environment, and the fish diet. In addition, the gut's bacterial load depends on the host's life stage. For instance, the gut bacteria load is initially lower (approximately 10^2 CFU larva⁻¹) in fish larvae than in adult fish, and it has been found that the bacterial load is increased (to $>10^5$ CFU larva⁻¹) once it begins to show morphological development by active feeding (Nayak, 2010). Moreover, the gut microbiota composition differs among feeding habits, as highlighted by Yukgehnash et al. (2020), who conducted a comprehensive review focusing on distinct bacterial compositions associated with various feeding habits and trophic levels. Despite the fact that the diversity of gut microbiota was dominated by bacteria in the fish gut (Rombout et al., 2011), Gatesoupe et al. (2014) reported the presence of yeast in the fish gut microbiota. This finding was supported by the summary of Romero et al. (2014), who described the variety of yeast species isolated from the GI tract of various fish.

Although ample information is available regarding the biosynthesis of SCFAs in humans and other mammals, research on SCFA production in aquatic animals remains limited. The schematic representation of the potential mechanism underlying SCFA production in fish is illustrated in Figure 2. Fish exhibit a higher concentration of SCFAs (most abundantly acetate, propionate, and butyrate) in the distal gut region (Desai et al., 2012; Romero et al., 2014; Ringø et al., 2016; Asaduzzaman et al., 2018). Notably, the levels of acetate, propionate and butyrate are lower in the stomach (1.1, 0.0, 0.0 mM) than in the colon part of the fish (37.5, 12.8, 1.3 mM), where they are readily absorbed and utilized as an energy source (Mountfort et al., 2002; Nuez-Ortín, 2013). Furthermore, certain undigested amino acids (valine, leucine, and isoleucine) and proteins undergo fermentation, giving rise to metabolites such as branched-chain fatty acids (isobutyrate, isovalerate, 2-methyl butyrate), phenols, amines, thiols, and indole (Canfora et al., 2015; Hao et al., 2017). The substrate-dependent fermentation process adds complexity to assessing the SCFA ratio, which varies not only

among fish species but also within the gut of a single species (Ohira et al., 2017). Additionally, the biosynthesis of SCFAs is influenced by the feeding habits of fish. For instance, marine herbivorous species exhibit higher SCFA

levels than freshwater herbivores, and when comparing marine species, carnivorous species show higher SCFA production, followed by herbivorous and omnivorous species (Hao et al., 2017).

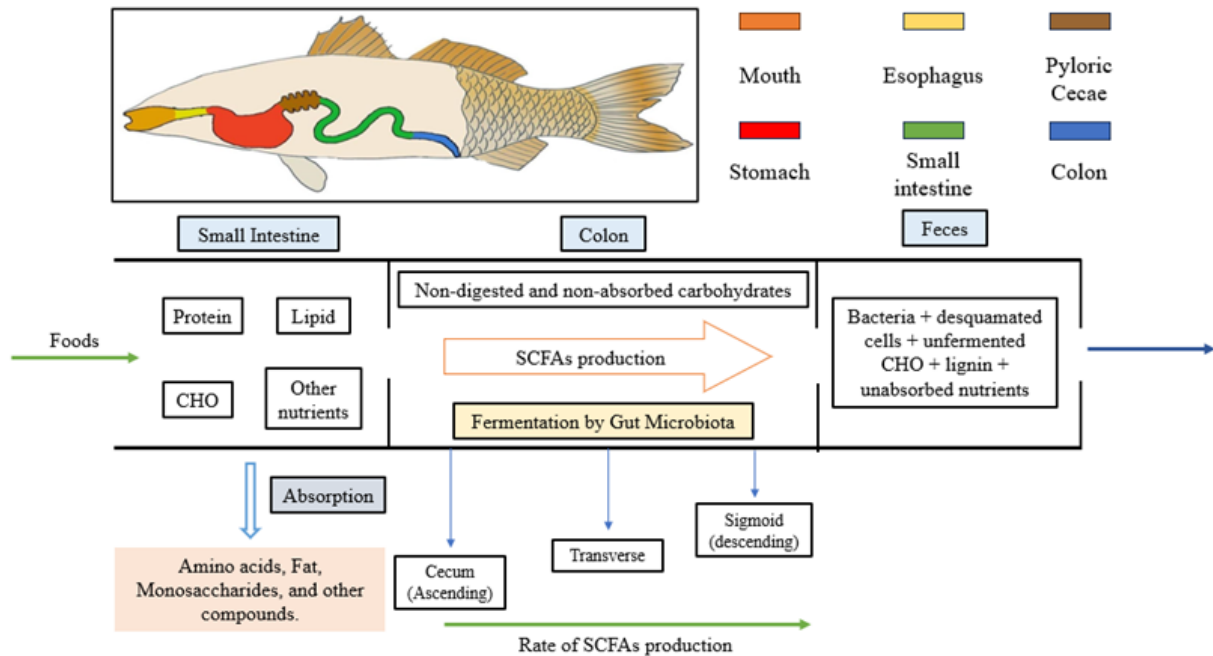


Figure 1. Sketch diagrams showing SCFA production in fish

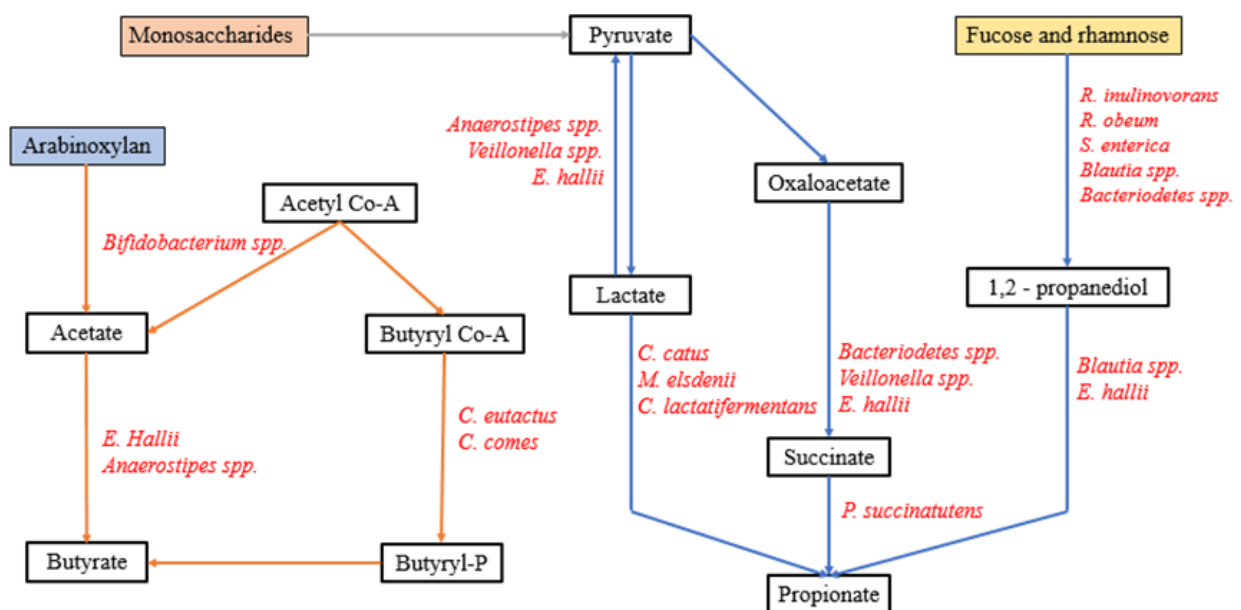


Figure 2. Flowchart representation of bacterial composition responsible for SCFA production (modified from Tran et al., 2020)

In the fish gut, acetate emerges as the predominant short-chain fatty acid compared to propionate and butyrate, with the latter two being produced by more specialized bacterial strains (Martin-Gallausiaux et al., 2021). The colonic microbiota plays a pivotal role in shaping both the overall availability and the degree of polymerization of non-digestible carbohydrates or hexose oligosaccharides. Consequently, this intricate microbial community orchestrates the synthesis of acetate, propionate, and butyrate as principal end-products alongside the minor generation of lactate, succinate, and salt of capric acid, along with carbon dioxide and water (Roy et al., 2006). Acetate, as the primary metabolic yield, is exclusively derived from pyruvate or arabinoxylan through the acetyl Co-A pathway (also known as the Wood-Ljungdahl pathway), and facilitated by *Bifidobacterium* spp. within the gut (Reichardt et al., 2018). Butyrate synthesis entails diverse compounds such as lactate, acetate, amino acids, and various carbohydrates. This intricate process is governed by either the concatenated pathway of butyryl Co-A and acetate Co-A transferase or the butyrate kinase pathway (Martin-Gallausiaux et al., 2021). Similarly, the production of propionic acid involves distinct pathways, such as the acrylate pathway (utilizing lactate), succinate pathway (involving succinate), or propanediol pathway (utilizing rhamnose and fucose), as elucidated by Ríos-Covián et al. (2016). Tran et al. (2020) have comprehensively illustrated the diverse bacteria responsible for synthesizing all three major SCFAs – acetate, propionate, and butyrate as shown in Figure 2.

The extent of research on the absorption of SCFAs in aquatic species remains limited. Nevertheless, Titus and Ahearn (1992) noted a mode of transportation involving anionic exchange facilitated by bicarbonate, transferring SCFAs from the lumen to the blood in tilapia. Acetate absorbed into the bloodstream via colonic capillaries reportedly contributes to skeletal muscle formation and lipid synthesis (Asaduzzaman et al., 2018). Similarly, butyrate is used as a fuel source for colonocytes, and propionate is a substrate in gluconeogenesis (Morrison and Preston, 2016). In human studies, the absorption pattern of SCFAs reveals a rapid uptake in the anterior region of the colon, with a subsequent decrease toward the distal end, as illustrated in Figure 1. Incubation investigations highlight a concentration-dependent uptake of SCFAs, with a significant impact observed at a concentration of 100 mmol, influencing SCFA movement into the blood from the colon. Interestingly, this transport is not saturable up to a concentration of 120 mmol. The transport mechanisms of SCFAs encompass both active (apical carrier-mediated) and passive systems (non-ionic diffuser) (Kles and Chang, 2006; Krajmalnik-Brown et al., 2012; Den Besten et al., 2013; Liu et al., 2021). Due to the protonated form of SCFAs in the colon at pH 5.5–7.5, where the pKa is 4.8, the predominant mode of transport is non-ionic diffusion. In the colon, SCFAs stimulate the absorption of sodium ions and water, activating the Na⁺/K⁺ exchanger (NHE3). Notably, dietary butyrate has

been found to enhance sodium absorption six fold (Roy et al., 2006). In the anionic form, recent findings indicate that effective SCFA exchange requires carrier transporter proteins such as monocarboxylate transporter (MCT) in the apical membrane (Corrêa-Oliveira et al., 2016).

Factors influencing gut microbiota and SCFA profiles

The microbial composition in the gut, which ferments the non-digestible CHO, proteins and other substrates, will depend on various factors, including environment, types of diet, habitat, feeding behavior, etc. (Kihara et al., 2008; Sullam et al., 2012; Walker et al., 2005; Wu et al., 2012; Ye et al., 2014; Flint et al., 2015; Liu et al., 2016; Li et al., 2017; Hao et al., 2017; Talwar et al., 2018). The degree to which it affects the gut microbiota in synthesizing SCFAs is challenging to determine. However, it is believed that the changes in the gut microbiota will alter the SCFA profile in the gut.

Environmental factors

A comparative study on the water quality and gut microbial composition gave a better understanding of the influence of the environment on the composition of fish gut microbiota. The World Health Organization (2015) stated that shared operational taxonomic units (OTUs) between gut and water ecosystems will be a possible mechanism for microbial diversity in the gut. Furthermore, a meta-analysis focusing on the modulation of the gut microbiome across diverse species with distinct ecologies revealed that salinity significantly contributes to the variation in microbial diversity within the host gut (Sullam et al., 2012). Notably, Walker et al. (2005) discovered that pH also plays a pivotal role in shaping the gut microbiota. In the context of this phenomenon, an investigation into Amazonian tambaqui (*Colossoma macropomum*), known for its resilience to pH fluctuations, elucidated those alterations in pH levels induced changes in the endogenous gut microbiota. Interestingly, the retrieval of these microbes exhibited remarkable flexibility upon restoring pH levels (Sylvain et al., 2016). Leenhouders et al. (2008) reported that *in vitro* fermentation of native wheat starch and glucose at pH 5–6 approximately favored the proliferation of lactic acid-producing bacteria, including *Bifidobacterium*, *Lactobacillus*, and *Eubacteria* species, which subsequently converted lactic acid into acetic, propionic, and butyric acids in Nile tilapia and European seabass. Additionally, pH emerged as a critical factor in transporting short-chain fatty acids from the lumen to colonocytes as observed in mammals (Sellin, 1998).

Feeding habits

Upon delving into investigations regarding the impact of diet and feeding habit, a distinct pattern emerges, elucidating the influence of various factors on the production of short-chain fatty acids in fish. The feeding habits of different species, the type of substrate in the fish diet, supplementary acidifiers, and microorganisms (prebiotics) have been identified as significant contributors to SCFA

production. Ye et al. (2014) found that the diversity of gut microbiota diminishes in the sequence of herbivorous > omnivorous > carnivorous. For example, the bacteria known to decompose cellulose, including *Anoxybacillus*, *Leuconostoc*, *Clostridium*, *Actinomyces*, and *Citrobacter*, were found in grass carp (Wu et al., 2012). Conversely, lipase and protease-synthesizing bacteria called *Halomonas* were observed in carnivorous fish (Liu et al., 2016). Furthermore, the biosynthesis of SCFAs was influenced by the feeding habits of fish. For instance, marine herbivorous species are reported to have higher levels of SCFAs than freshwater herbivores. While comparing the species in marine habitats, the SCFA production was higher in carnivorous followed by herbivorous and omnivorous (Hao et al., 2017). Freshwater carnivorous fish, specifically *Pagrus minor*, exhibit an elevated level of SCFAs in the colon compared to herbivorous (Kihara et al., 2008). Notably, there was a positive correlation between feeding behavior and the composition of gut microbes. Along this line, Li et al. (2017) stated that filter-feeding fish possess a more diverse gut microbe composition due to increased water consumption and extensive coverage through rapid swimming.

Diet

The dietary nutrients showed considerable influence over the gut microbiota composition and production of SCFAs (Flint et al., 2015). In aquatic animals, Hao et al. (2017) stated that the type and amount of fiber are directly related to the type and amount of SCFAs produced. The scarcity of fiber for fermentation prompts the utilization of other nutrients for gut microbiota proliferation (Koh et al., 2016). Notably, the source of nutrients, whether plant-based or animal-based, further shapes gut microbiota composition (Talwar et al., 2018). For instance, Michl et al. (2017) showed that the abundance of specific bacterial orders varies when fed with plant-based (*Lactobacillales*, *Bacillales* and *Pseudomonadales*) or animal-based ingredients (*Bacteroidales*, *Fusobacteriales*, *Clostridiales*, *Alteromonadales*, and *Vibrionales*). Similarly, there was a marked decrease in the total production of SCFAs of about 50% in the grass carp gut when the animal-based diet was replaced with the plant-based diet (Hao et al., 2017). Demonstrating a clear link between gut microbiota composition and SCFA production in fish, studies revealed that dietary components like arabinoxylan enhanced the presence of specific bacteria (*Clostridium*, *Bacillus*, *Lactobacillus*, *Eubacterium*, and *Lactococcus*), which subsequently ended in increased SCFA production in Siberian sturgeon (Geraylou et al., 2012). Moreover, Ringø et al. (2010) conducted an in-depth review of the effects of different dietary components on the gut microbial composition in many fish. The inclusion of prebiotics augments SCFA production by fostering the growth and fermentation of gut microbiota, as reviewed in the *in vitro* and *in vivo* studies on different prebiotics by Tran et al. (2020). Furthermore, the insights into the impact

of prebiotics on SCFA production in aquatic animals were found to be similar to human studies (Asaduzzaman et al., 2018; Hemalatha et al., 2017). For instance, the dietary inclusion of specific microorganisms like *Enterococcus faecalis*, *Alcaligenes* spp. (AFG22), and *Clostridium butyricum* significantly elevated the SCFA level including acetate, butyrate, and propionate in Javanese carp (*Puntius gonionotus*), Malaysian mahseer (*Tar tambroides*), and *Litopenaeus vannamei* (Allameh et al., 2017; Asaduzzaman et al., 2018; Duan et al., 2017).

Dysbiosis

It is characterized by a perturbation in the gut microbial composition resulting from diverse factors such as stress and environmental influences, which significantly impact the production of short-chain fatty acids (Talwar et al., 2018; Montalban-Arques et al., 2015). The dysregulation induced by stress on the intestinal microbiota serves as a pivotal factor influencing SCFA production in vertebrates. In addition, dysbiosis can deplete or harm the beneficial microbes that are naturally present in low concentration, thereby resulting in pathological states in the gut (Montalban-Arques et al., 2015). For instance, the antibiotics induced dysbiosis eliminated both pathogen as well as the mutualist/commensal microbes. As a result, gut microbiota loses its ability to break down complex carbohydrates into SCFAs, stimulating the pathological conditions in the host (McFarland, 2014; Gorkiewicz et al., 2013; Montalban-Arques et al., 2015).

However, there are limited data on the effect of dysbiotic microbiota on the production of SCFAs, fish growth performance and health status. In order to treat dysbiosis, Simpson and Campbell (2015) clearly stated that dietary oligosaccharides could be a potential therapeutic agent. Several human clinical trials have been conducted to assess the efficacy of different prebiotics for the treatment and correction of dysbiotic gut microbiota (Kanauchi et al., 2003; Hanai et al., 2004; Hafer et al., 2007; Benjamin et al., 2011; Joossens et al., 2012; Simpson and Campbell, 2015). Moreover, the ingestion of dietary soluble non-starch polysaccharides could prevent the harmful interactions between the gut epithelium and the microbiome that occur after dysbiosis (Abell et al., 2008; Simpson and Campbell, 2005). Furthermore, the systematic review of McFarland (2014) clearly described the use of probiotics in correcting the dysbiosis of the normal gut microbiota. In fish and mammals, the main mechanism behind the correction of dysbiosis by prebiotics, probiotics, and various dietary fibers is that they may revert the dysbiosis by normalizing the gut microbiome, increasing the production of mucin and antimicrobial peptides, inhibiting the pathogen adhesion to gut epithelium, modulating the immune system (through enhancing the cell mediated responses), and strengthening the mucosal barrier (Ringø et al., 2010; Montalban-Arques et al., 2015; Papadimitriou et al., 2015).

Table 1. The summary of immunomodulatory effects, physiological and growth responses to SCFAs and their salts

Species	SCFAs	Effects	References
1	2	3	4
Arctic charr (<i>Salvelinus alpinus</i>)	Sodium lactate and sodium propionate (1 g/kg)	Na-lactate: increased growth, decreased the amount of lipid, protein, water, and energy in the gut, Na-propionate: growth rate depressed.	Ringø (1991)
	Sodium acetate (1 g/kg)	Promoted the growth, Higher feed intake, Better digestibility.	Ringø (1992)
Rainbow trout (<i>Oncorhynchus mykiss</i>)	Formic acid (10 ml/kg)	Increased the apparent digestibility of P, Reduced the pH, Increased the activity of pepsin, Increased protein digestion and nitrogen retention.	Vielma and Lall (1997)
Atlantic salmon (<i>Salmo salar</i>)	Potassium diformate (KDF) (8 and 14 g/kg) Potassium diformate (0 and 13.5 g/kg)	Better feed efficiency, Improved uniformity within groups. Increased body weight, SGR, dry matter, and gross energy, Increased the protein digestibility, No effects on gut pH.	Christiansen and Lückstädt (2008) Lückstädt (2008 b)
Red hybrid tilapia (<i>Oreochromis</i> sp.)	Potassium diformate (2 g/kg) Sodium salts of acetate, butyrate, propionate, formate (20 g/kg)	Decreased diet pH and reduced the pH of gut digesta, Increased the digestibility of minerals and protein. Not affected the growth and feeding efficiencies, Decreased lipid peroxidation and intestinal SCFAs, Stimulated stress and affected health.	Ng et al. (2009) Ebrahimi et al. (2017)
Red drum (<i>Sciaenops ocellatus</i>)	Potassium diformate (0, 7.5, and 15 g/kg)	Increased growth, feed utilization, and PER, Lowered the pH of diets and stomach contents, Improved the digestive enzymes activities.	Castillo et al. (2014)
Tilapia (<i>Oreochromis niloticus</i>)	Potassium diformate (10 g/kg) Calcium propionate, calcium formate, and sodium acetate (0.922 g/kg) Acetic acid Formic and diformic acid (1 or 2 g/kg) Sodium diformate (3 g/kg)	Improved weight gain and feed efficiency. Increased weight gain, Lower FCR. Increased weight gain and specific growth rate, Lower FCR. Reduced weight gain and specific growth rate, Higher FCR. Improved protein efficiency ratio and protein retention.	Lim et al. (2010) Huan et al. (2018) Fabay et al. (2020) Reda et al. (2016) Liebert et al. (2010)

Table 1 – contd.

1	2	3	4
European seabass (<i>Dicentrarchus labrax</i>)	Poly- β -hydroxybutyrate (20–100 g/kg)	Modulation of intestinal microbiota.	De Schryver et al. (2010)
	Sodium butyrate (2 g/kg)	No change in growth, Stimulated the expressions of IL-1 β , IL-6, IL-8, IL-10 and TNF- α genes, Only TNF- α was significantly upregulated in the distal intestine.	Rimoldi et al. (2016)
	Micro-encapsulated sodium butyrate (2 and 3 g/kg)	Increased growth parameters, Elevated serum immunoglobulin, Increased respiratory burst, phagocytosis, myeloperoxidase, lysozyme, and bactericidal activity, Improved the muscle layer thickness, Increased the goblet cell count and villi length and width.	Abdel-Mohsen et al. (2018)
	Sodium propionate (1, 2, or 3 g/kg)	Increased weight gain, Lower FCR, Elevated the carcass protein content and major blood constituents, Increased the immune indicators, Positively modified gut microbiota, Reduced the total fecal coliform bacteria, Improved fish intestine features (greater villus area and goblet cell count), Stimulated digestive secretion, Enhanced mucus production.	Wassef et al. (2020)
	Sodium diformate (3 and 4 g/kg)	Higher weight gain, specific growth rate, and feed utilization indices, Increased leucocyte count, serum protein, and monocyte and leucocyte percentage, Increased phagocytic and lysozyme activity.	Wassef et al. (2017)
Giant freshwater prawn (<i>Macrobrachium rosenbergii</i>)	Plant nutrients mixture + sodium diformate (3 g/kg)	Normalized physiological conditions, Higher feed intake, weight gain, and lower FCR, Enhanced blood profile, immune response, Increased the striated muscle structure.	Wassef et al. (2021)
	Poly- β -hydroxybutyrate + <i>Artemia</i> nauplii	Increased growth and survival of the larvae.	Nhan et al. (2010)
Rainbow trout (<i>Oncorhynchus mykiss</i>)	Sodium diformate (10 g/kg)	Enhanced the digestibility of lipid, protein, and amino acids.	Morken et al. (2011)
	Sodium formate and butyrate (1 g/kg mixture of Na formate and butyrate at 2:1)	Improved feed utilization and growth rate.	Gao et al. (2011)
	Sodium diformate	Improved the bioavailability of amino acids.	Morken et al. (2012)
Atlantic salmon (<i>Salmo salar</i>) (<i>in vitro</i> study)			

Table 1 – contd.

1	2	3	4
White-leg shrimp (<i>Penaeus vannamei</i>)	Sodium butyrate	Modification of intestinal microbiota and enhanced growth.	da Silva et al. (2013, 2016)
Sea bream (<i>Sparus aurata</i>)	Sodium butyrate (Gustor Aqua® Bp70, BP-70®Norel, and SILOhealth 108Z)	Increased the final weight, Increased the bioavailability of essential amino acids and nucleotide derivatives, Enhanced energy provision to the enteric cells by the decrease in glucose and amino acid oxidation.	Robles et al. (2013)
		Gustor Aqua® Bp70: Increased growth performance, Increased plasma glucose and cortisol at 0.4 % supplementation, Increased the abundance of mucosal folding, infiltration of lymphocytes, and number of granulocytes in the submucosa along the intestine and the accumulation of glycogen in hepatocytes, and stimulated the expression of <i>PCNA</i> and <i>ALPI</i> through the intestinal tract at 0.8%.	Estensoro et al. (2016)
		BP-70®Norel: Increased survival after challenges with <i>Photobacterium damsela</i> subsp. <i>piscicida</i> (Phdp), Increased intestinal microbiota, specifically butyrate-producing bacteria.	Piazzon et al. (2017)
		SILOhealth 108Z: Increased the number of lactic acid bacteria (<i>Lactobacillus</i>), Reduced gammaproteobacteria.	Rimoldi et al. (2016)
Grass carp (<i>Ctenopharyngodon idella</i>)	Sodium butyrate (1 g/kg)	Increased fish growth, intestinal growth and function, Increased lysozyme and acid phosphatase activities, complement (C3 and C4), and immunoglobulin M content, Immune-related genes were regulated, Increased <i>Lactobacillus</i> count and butyrate level and decreased the acetate and propionate level in the gut.	Tian et al. (2017)
Nile tilapia (<i>Oreochromis niloticus</i>)	Calcium propionate (5, 10, and 15 g/kg) Sodium benzoate (10, 20, and 30 g/kg)	10 g/kg – improved growth rate 5, 10, and 15 g/kg – improved feed efficiency, PER, and protein productive values. The count of lymphocytes and monocytes were affected and not affected by the serum enzyme activities, including aspartate aminotransferase and alanine aminotransferase, and phagocytes, At 20 and 30 g/kg, the structure of the liver and kidney has been changed, not affecting the gills.	Hassaan et al. (2014) El-Sayed Ali et al. (2018)
Common carp (<i>Cyprinus carpio</i>)	Microencapsulated sodium butyrate (300 mg/kg)	Increased weight gain, reduced FCR, Stimulated immune response by expressing HSP70, IL-1 β and TNF- α and TNF- β , Improved intestinal conditions, particularly when fed with oxidized oil.	Liu et al. (2014)
Chinese mitten crab (<i>Eriocheir sinensis</i>)	Bio encapsulated poly- β -hydroxybutyrate	Enhanced survival, development rate, and osmotic tolerance.	Sui et al. (2014)

1	2	3	4
White-leg shrimp (<i>Penaeus vannamei</i>)	Sodium propionate (5, 10, and 20 g/kg) Butyrate and propionate (5, 10, and 20 g/kg) Sodium butyrate + <i>Lactobacillus plantarum</i>	Modification of intestinal microbiota and enhanced growth, Increased final weight, feed efficiency, nitrogen retention, protein efficiency ratio, survival and yield, A lower count of <i>Vibrio</i> sp. has been observed.	da Silva et al. (2016)
	Propionic acid (5 g/kg) Formic acid (0, 3, and 6 g/kg)	Not affected the growth performance, immunological parameters, and total heterotrophic bacterial count in the gut, Enhanced the resistance against <i>Vibrio alginolyticus</i> . Enhanced the growth and increased the expression of prophenoloxidase, lysozyme, penaeidin-3a and crustin genes in the hepatopancreas.	Bolivar Ramirez et al. (2017) Pournozaffar et al. (2017)
	Sodium propionate	No changes in growth performance Lower gut bacterial counts, Better survival against <i>Vibrio parahaemolyticus</i> .	Chuchird et al. (2015)
Zebrafish (<i>Danio rerio</i>)		Increased expression of TNF- α , IL-1 β and lysozyme genes. Decreased expression of SOD, CAT, and HSP70 in the liver.	Safari et al. (2016)
Caspian white fish (<i>Rutilus frisii kutum</i>)	Sodium propionate (2.5, 5, 10, and 20 g/kg)	Improved growth performance and feed utilization.	Hoseinifar et al. (2016)
Catfish (<i>Clarias gariepinus</i>)	Sodium butyrate (0, 2 and 20 g/kg)	No effects on weight gain, SGR, PER, and FCR, Altered the bacterial community in hindgut.	Owen et al. (2006)

SGR – specific growth rate, PER – protein efficiency ratio, FCR – feed conversion ratio, SOD – superoxide dismutase, CAT – catalase, TNF- α – tumor necrosis factor- α , TNF- β – tumor necrosis factor- β , IL-1 – interleukin 1, IL-2 – interleukin 2, IL-3 – interleukin 3, IL-4 – interleukin 4, IL-5 – interleukin 5, IL-6 – interleukin 6, IL-8 – interleukin 8, IL-10 – interleukin 10, PCNA – proliferating cell nuclear antigen, ALP – alkaline phosphatase

Immunomodulatory effects of SCFAs and their role in disease resistance

Numerous investigations have been conducted to explore the immunomodulatory effects of short-chain fatty acids and their role in bolstering the immune system for enhanced disease resistance in fish (refer to Table 1). Notably, a study employing the zebrafish tail wounding model revealed that butyrate synthesized in the gut exhibited anti-inflammatory effects in neutrophils and macrophages (Cholan et al., 2020). Furthermore, the incorporation of microencapsulated sodium butyrate into the diet induced alterations in the immune response, as evidenced by changes in anti-inflammatory (TGF- β) and pro-inflammatory (IL-1 β and TNF- α) cytokines in the gut of common carp (Liu et al., 2014). Safari et al. (2016) showed a substantial role of dietary sodium propionate in upregulating mucosal immune genes (TNF- α , IL-1 β , and Lyz) and downregulating antioxidant genes (*SOD* and *CAT*) in zebrafish. Similarly, Zhu et al. (2014) discovered that a blend of SCFAs (formic acid and benzoic acid) down-regulated *SOD* and *CAT* genes in yellowtail catfish. The dietary supplementation of butyrate at 0.8% expressed two genes, including intestinal FA-binding protein (FABP2) and proliferating cell nuclear antigen (PCNA), in the gastrointestinal tract of the host. This supplementation at 0.8% was reported to confer disease resistance against *Photobacterium damsela* subsp. *piscicida* (Phdp) in gilthead seabream, reducing inflammation from bacterial infection and promoting the diversity of butyrate-producing bacteria in the gut, thus restoring gut integrity (Piazzon et al., 2017). In seabass (*Dicentrarchus labrax*), the expression of TNF-1 α was upregulated with 0.2% butyrate supplementation, stimulating both anti-inflammatory genes (IL-10 and TNF-1 α) and pro-inflammatory genes (IL-1 β , IL-6, IL-8), which might be due to the fact that the dietary butyrate supplementation has increased cellular turnover (Rimoldi et al., 2016). Tian et al. (2017) challenged grass carp fed a sodium butyrate diet with *Aeromonas hydrophila*, resulting in lower enteritis morbidity. Furthermore, the study of El-Sayed Ali et al. (2018) showed an increased number of lymphocytes and monocytes in the blood and alteration in the liver and kidney structure (10 and 20 g/kg) when sodium butyrate was included in the diet of Nile tilapia. Many studies have been conducted on immune responses of European seabass (*Dicentrarchus labrax*) supplemented with different SCFA salts, such as sodium butyrate, sodium propionate, sodium diformate, and potassium diformate (Wassef et al., 2017, 2020, 2021, 2023; Abdel-Mohsen et al., 2018). Notably, Abdel-Mohsen et al. (2018) reported that microencapsulated sodium butyrate at a rate of 2 or 3 g/kg increased the serum immunoglobulins, respiratory burst, phagocytosis, myeloperoxidase, lysozyme, and bactericidal activity in *D. labrax* fry (individual body weight, IBW of 0.45 g). Wassef et al. (2020) found that supplementation of sodium propionate (3 or 2 g/kg) increased the efficiency

of the immune system by enhancing the major blood constituents and immune function indicators in the same species (IBW of 0.45 $\pm$ 0.23 g). In *D. labrax* (IBW of 4.75 $\pm$ 0.04 g), it has been found that dietary sodium diformate at a dosage of 3 g/kg improved the health status by increasing the leucocyte count, serum proteins, monocyte and lymphocyte percentages, lysozyme activity, and leucocyte phagocytosis (Wassef et al., 2017). Similarly, Wassef et al. (2021) conducted a study on the effect of supplementary sodium diformate in the low fish meal plant-based diet on *D. labrax* (IBW of 13.71 g) in which they have found that the supplementation of sodium diformate (3 g/kg) with the plant-mix diet increased the major blood constituents and serum immunity indicators.

In crustaceans, the studies about the role of SCFAs on the immunomodulatory effects and disease resistance are limited. Nonetheless, in white-leg shrimp (*Penaeus vannamei*), dietary propionate supplementation increased the expression of lysozyme, crustin, prophenoloxidase, and penaeidin-3a genes (Pourmozaffar et al., 2017). Additionally, the serum agglutination titer was observed to be higher with dietary propionate or butyrate supplementation in *Penaeus vannamei* (da Silva et al., 2016). The challenge study with *Vibrio alginolyticus* by feeding the sodium butyrate with *Lactobacillus plantarum* and exhibited improved resistance against the pathogen, with no marked effects on performance, gut microbiota composition, and immunological parameters (Bolívar Ramírez et al., 2017). To summarize with the aforementioned discussion, it is evident that SCFAs are known to augment immune responses by regulating immune cells and immune-related genes. Furthermore, they exert significant effects on the activity of antioxidant enzymes.

On top of that, SCFAs play a crucial role in exhibiting defense against microbial threats to the host and contribute to the maintenance of healthy gut microbiota in the GI. Abu-Elala and Ragaa (2015) found that dietary supplementation of SCFAs (potassium diformate, KDF) possesses antimicrobial effects capable of enhancing health and preventing diseases caused by pathogens. Ng et al. (2009) reported that diets with organic acid blends and a KDF diet reduced the total fecal bacteria in tilapia. In hybrid tilapia, KDF promoted the colonization of specific bacteria in the gut (Zhou et al., 2009). In addition, Wassef et al. (2017) showed that 3 g/kg of supplementary sodium diformate acted as basal health promoter through enhancing leucocyte counts, monocytes and lymphocyte percentages, serum proteins, leucocyte phagocytosis and lysozyme activity in European seabass (*Dicentrarchus labrax*). Chuchird et al. (2015) found that dietary supplementation of 3 and 6 g/kg of formic acid increased survival against *Vibrio parahaemolyticus*, reducing total bacterial count and *Vibrio* load in the intestine of white-leg shrimp (*Penaeus vannamei*) under laboratory conditions. Similarly, white-leg shrimp exhibited inhibitory effects against *Vibrio* sp. when fed propionate, acetate, and butyrate salts (da Silva et al., 2013).

Physiological responses and growth performances of fish fed with SCFAs and their salts

In aquaculture, Hoseinifar et al. (2017) and Ng and Koh (2017) highlighted that short-chain fatty acids are considered safe compounds in aquaculture and are emerging as superior feed additives in fish diets. According to Freitag (2007), SCFAs exert their influence on the physiological status of fish through three primary mechanisms. Firstly, they demonstrate their effects through the administered feed. Secondly, they impact the gastrointestinal tract, and finally, they direct their effects on metabolism. Most SCFAs function by reducing pH, preventing the growth of gram-negative bacteria in the stomach and small intestine through anion production in bacterial cells and acid dissociation. Additionally, SCFAs are incorporated into the feed to mitigate microbial loss by reducing pH (Hoseinifar et al., 2017). Dietary supplementation of SCFAs in fish diets acts as an acidifier and plays a pivotal role in enhancing mineral bioavailability. SCFAs influence mineral bioavailability by modifying mineral absorption metabolism through alterations in gut pH, complex formation via chelation of elements in the intestinal brush border, and increasing the area for absorption by promoting the multiplication of intestinal epithelial cells. Furthermore, SCFAs serve as substrates for energy production during the metabolic process, contributing to ATP production in the citric acid cycle (Hoseinifar et al., 2017). For instance, dietary sodium butyrate increases the energy provision to enteric cells by decreasing the oxidation of glucose and amino acids in *Sparus aurata* (Robles et al., 2013). In addition, it also increased the bioavailability of essential amino acids and nucleotide derivatives. It should be also noted that the *in vitro* study of Morken et al. (2012) showed that the dietary supplementation of sodium diformate resulted in the improved bioavailability of amino acids. They also reported the enhanced digestibility of proteins, lipids and amino acids when fed with sodium diformate at 10 g/kg. In red hybrid tilapia, 0.2% supplementation of potassium diformate (KDF) decreased the pH of diet and gut digesta, and increased the digestibility of minerals, and protein (Ng et al., 2009). Similarly, dietary SCFAs like poly- β -hydroxybutyrate (20–100 g/kg) resulted in modulation in the intestinal microbiota in European seabass (*Dicentrarchus labrax*), as reported in the study of De Schryver et al. (2010). Wassef et al. (2023) reported several studies on the physiological benefits of SCFA salts, such as sodium butyrate, sodium diformate, sodium propionate, and potassium diformate on European seabass (*Dicentrarchus labrax*). These studies demonstrated improvements in mucosal protection, intestinal functions, and inflammatory response and positively modulated the distal-intestine microbiome. Similar effects were observed in white-leg shrimp when fed with sodium propionate at 5, 10, and 20 g/kg (da Silva et al., 2016).

In the 1990s, the utilization of dietary SCFAs gained prominence for their positive effects on fish by enhancing feed efficiency, promoting feed intake and subse-

quent production performances. Notable investigations, as summarized in Table 1, followed Ringø's (1991) study, which demonstrated the significant effects of dietary supplementation of lactate and propionate on the growth performance of Arctic charr (*Salvelinus alpinus*). Similarly, Ringø (1992) explored the impact of acetate supplementation, resulting in enhanced growth in Arctic charr (*Salvelinus alpinus*). In rainbow trout, the supplementation of formic acid (10 ml/kg) showed a marked increase in protein digestion, nitrogen retention, pepsin activity and reduction in pH (Vielma and Lall, 1997). In contrast, a negative effect on feed conversion efficiency (FCE) was observed when rainbow trout were fed an organic acid blend of butyrate and sodium formate at a 1:2 ratio without impacting growth performance (Gao et al., 2011). Christiansen and Lückstädt (2008) reported that the supplementation of KDF at the rate of 8 and 14 g/kg enhanced the feed efficiency with improved uniformity within the group. Similarly, in tilapia (*Oreochromis niloticus*), the weight was gained with improved feed efficiency. It showed increased protein efficiency ratio (PER) and protein retention when fed with KDF at 10 g/kg (Lim et al., 2010) and sodium formate at 3 g/kg (Liebert et al., 2010). Conversely, in red hybrid tilapia (*Oreochromis* spp.), Ebrahimi et al. (2017) have found that incorporating sodium salts of SCFAs (20 g/kg) promoted stress and affected health, possibly due to decreased intestinal SCFAs. However, the growth and feeding efficiency were not affected.

Final weight, feed efficiency, PER, nitrogen retention, and survival were increased when fed with a diet containing butyrate and propionate at 5, 10, and 20 g/kg. Similarly, dietary calcium propionate supplementation increased the growth rate (10 g/kg) and feed efficiency, PER, and protein productive values (5, 10 and 15 g/kg) in tilapia (Hassaan et al., 2014). In Caspian white fish, sodium propionate at the rate of 2.5, 5, 10, and 20 g/kg improved the growth performances and feed utilization (Hoseinifar et al., 2016). In addition, Wassef et al. (2023) reported the growth promoting effects (weight gain, specific growth rate, feed utilization) of various exogenous SCFAs, such as sodium butyrate, sodium propionate, sodium diformate in *D. labrax*. Furthermore, Fabay et al. (2022) reviewed the positive effects of several acid sources supplementation (refer to Table 1) on different fish growth performances and feed efficiency. Many investigations have been conducted in studying the growth response of exogenous SCFA supplementation on shellfish. In giant freshwater prawn (*Machrobranchium rosenbergii*) larvae, the supplementation of poly β -hydroxybutyrate with *Artemia* resulted in improved growth and survival (Nhan et al., 2010). Higher growth rates were reported in the same species when fed with the sodium salts of SCFAs, such as fumarate, succinate, propionate, and butyrate, at a rate of 73 mM/kg in the commercial diet (da Silva et al., 2016). Similarly, in *Penaeus vannamei*, da Silva et al. (2016) found that the dietary supplementation of 2% butyrate improved various growth parameters compared

to control groups. Conversely, Pourmozaffar et al. (2017) reported no significant effects on the growth performance when white-leg shrimp were fed with 0.5% propionic acid compared to the control diet.

The potential of SCFAs to improve growth performance, immune response, and disease resistance is influenced by various factors, including dosage, exogenous source, species type, feed composition, and culture conditions. Among these, exogenous sources of SCFAs showed combined effects of growth promotion, immune function and various physiological responses in fish. For example, in *Sparus aurata*, the dietary supplementation of sodium butyrate from different sources, including Gustor Aqua® Bp70 – increased growth, plasma glucose and cortisol (0.4%), the abundance of mucosal folding, infiltration of lymphocytes and number of granulocytes in submucosa along the intestine, accumulation of glycogen in hepatocytes and triggered the expression of *PCNA* and *ALPI* through intestinal tract (0.8%) (Estensoro et al., 2016); BP-70® Norel – increased the survival, resistance against *Photobacterium damsela* subsp. *piscicida* (Phdp) and specific butyric acid-producing bacteria (Piazzon et al., 2017); SILOhealth 108Z – increased the number of lactic acid bacteria (*Lactobacillus*) and reduced gammaproteobacteria (Rimoldi et al., 2016).

Fish gut health and immunity

As discussed above, SCFAs are produced from the non-digestible carbohydrate substrate in the GI tract by the effect of gut microbiota (Magouz et al., 2020). The production of SCFAs has improved the intestine function through activating the intestinal cells to produce mucin and establish tight junctions. This results in better feed utilization and good growth performance (Liu et al., 2017). In addition, it also regulates the diversity and composition of microbiota, which allows only the beneficial microbes to grow and suppress the harmful microbes (Wu et al., 2018; Wassef et al., 2020). Of all the exogenous SCFAs, dietary sodium butyrate has a crucial role in providing numerous positive effects in the host intestine (Abdel-Mohsen et al., 2018; Dawood, 2021).

In grass carp (*Ctenopharyngodon idella*), Tian et al. (2017) reported the effect of dietary sodium butyrate, which resulted in increased activity of digestive enzymes (amylase, trypsin, lipase, chymotrypsin), downregulated the inflammatory and proinflammatory mRNA levels (TNF- α , INF- γ 2, IL-1 β , IL-6, IL-8, IL-15, IL-17D, IL-12, NF- κ B, IKK β , IKK γ , p38MAPK and MAPK), upregulated the immune mRNA levels (β -defensin-1, mucin-2, IL-10, IL-11, TGF- β 1, TGF-2, IL-4 and Ik β a), increased the numbers of *Lactobacillus* and reduced the numbers of *Aeromonas* and *Escherichia coli*. Jesus et al. (2019) reported that dietary sodium butyrate enhanced digestive activities and intestinal morphology. In parallel, Liu et al. (2019) found that the intestinal microbiota composition was modulated in turbot fed with sodium butyrate, and it also upregulated the intestinal gene expression of tight junction proteins (TNF- α and NF κ B). Similarly,

Liu et al. (2014) revealed that dietary sodium butyrate supplementation enhanced the microbial activity, microvillus length, and immune-related genes in common carp. In red hybrid tilapia (*Oreochromis* spp.), the dietary supplementation of sodium butyrate increased the production of short-chain fatty acids (Romano et al., 2016). Furthermore, Dawood et al. (2020) studied the mode of action of sodium butyrate in the intestine of Nile tilapia, which confirms that it has uplifted the digestive enzyme activities, increased the intestinal microbiota diversity, increased the protein level in the tight junction of the intestine, and upregulated the immune-related genes. SCFAs have also increased the area of villi in absorbing the nutrients, which in turn results in better digestibility of feed and availability (Abdel-Mohsen et al., 2018, Wassef et al., 2020, 2023).

Synergistic dynamics between biofloc system and SCFAs in aquaculture

Biofloc formation and SCFA production play an interconnected relationship that influences the microbial community in the fish gut and subsequently health and growth performances of fish. The decomposition of organic matter by the microbes produces SCFAs as by-products by microbes will act as probiotics which have an important role in improving the immune system and disease resistance by protecting the intestinal epithelial cells and in triggering the digestive enzymes (Abdel-Mohsen et al., 2018, Wassef et al., 2020, El-Sayed et al., 2021). As discussed by Khanjani et al. (2022), the bacterial composition and its density in the floc will be influenced by the type of carbon sources, rearing conditions, carbon: nitrogen ratio, cultivated species, stocking density, pH, initial body weight, and salinity which will subsequently affect the production of specific SCFA. Many studies have found that microbial floc could be used for enhancing antifungal antibiotics and in stimulating the immune system due to the fact that it blocks quorum sensing (Avnimelech et al., 2015) and prevents the growth of pathogenic bacteria, ensuring increased probiotic activity (Adel et al., 2017). These synergistic effects have immense potential in ensuring sustainability and increasing the efficiency of aquaculture practices.

Limitations and future studies

All the plant-based ingredients are considered for their nutritional profile, particularly protein, lipids and ANFs. The study concerning the metabolism and utilization of carbohydrates as a source of SCFAs is still lacking in aquatic animals. Though there are enough studies on the effects of various plant feedstuffs in fish, the studies on SCFAs profile and their mechanism in enhancing the growth and immune system of fish while utilizing aquatic plants as feed resources are limited. Future studies are required to understand the mechanistic mode of action of SCFAs in enhancing the immune response of fish. There are many pathways involved in producing SCFAs in the colon, which means that further investigations on the

aquatic species are still required for better understanding. Many research findings have shown the positive relationship between the gut microbiota diversity and composition, and SCFA production in fish. However, the study on the specific microorganism responsible for the specific SCFA is unexplored (Llewellyn et al., 2014). Since the transport mechanism of SCFAs has already been studied in tilapia, all other fishes are believed to have the same. Therefore, future investigations must be done regarding the growth, survival, and replication of SCFA bacteria and their response to the dietary SCFAs in the gut. Many studies have shown the presence of numerous types of bacteria in the floc which has synergistic effect with the SCFA production. Though there is an interconnected relationship between the biofloc and SCFA production, the area of exact mechanism of SCFA production by the specific bacteria from specific carbon source in floc (SCFAs produced in the culture water and acting as acidifier) is still unexplored. It has been found that there exists a gap in exploring the knowledge about the role of SCFAs in enhancing the antioxidant system of aquatic animals at the molecular level. To summarize, this study revealed the vast scope of conducting extensive and intensive research on the effects of SCFAs on various finfish and shellfish species.

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