Effects of Black Soldier Fly, *Hermetia illucens* (Linnaeus, 1758), Larvae Incorporated Feed on Histomorphology, Gut Microbiota and Blood Chemistry of Cultured Fishes: A Review

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Abstract

Inadequate availability and unreasonable prices made fish meal an unreliable feed ingredient in aquaculture. Consequently, researchers have tested different plant and animal-derived protein sources as an option over the fish meal. The black soldier fly, *Hermetia illucens* (Linnaeus, 1758), larva, has been identified as a reliable protein source for fish meal replacement. Many studies have revealed the growth and microbiological impacts of *H. illucens* larvae as a protein source in finfish culture. However, a review of knowledge on histopathology, haematology and microbial changes modulated by *H. illucens* larvae when incorporated as a feed ingredient in finfish aquaculture is not available. Therefore, this study reviews the effects on the histopathology, haematology and gut-microbial properties of finfish fed diet incorporated with *H. illucens* larvae. A review of different finfish species tested up to 100 % inclusion of *H. illucens* larvae meal in their diets revealed mixed results in blood chemistry, gut microbiota, and gut histology. Most studies stated common positive effects such as reduced plasma cholesterol levels, increased microbial diversity, and increased intestinal absorption up to 50 % incorporation level. Despite the possibility of incorporating *H. illucens* larvae meal without any negative impacts on some carnivore fish species, most studies disclosed adverse effects beyond 50 % fish meal replacement due to high chitin and crude fat levels in *H. illucens* larval diets.

Keywords: fishmeal, haematology, microbiology, microflora

Introduction

Fishmeal has remained the primary feed ingredient for protein supplementation in the aquaculture industry for decades due to its high digestibility and balanced nutritional attributes. Fishmeal is widely accepted as a suitable source for animal feeds since it is a rich source of proteins, lipids, minerals, and vitamins. Millions of tonnes of fishmeal are usually manufactured from wild-caught, small marine fish that contain a high percentage of bones and oil (Miles and Chapman, 2012). Fears have been raised regarding using fishmeals in aquaculture with concerns of adding more pressure to wild fisheries (Allan, 2004). With predictions of further growth in the aquaculture sector (Brugère and Ridler, 2004; Terova et al., 2021), there is an ongoing argument that the practice of feeding 'fish to fish' is inefficient and wasteful (Milewski, 2002).

The expectations of aquaculture producers to reduce feed costs and purchase animal proteins with health benefits and low risk of contaminants (Naylor et al., 2009) have led to an increased focus on alternatives for fishmeal (Olsen and Hasan, 2012). Numerous possibilities have been discovered to replace fishmeal with protein, derived from a range of non-fish sources such as by-products from land animal processing, microalgae, zooplankton, plants, bacteria and insects (Priyadarshana et al., 2021).

Insects possess the capacity to upgrade low-quality organic material, require minimal water and cultivable land, and emit little greenhouse gases (van Huis, 2013). Among the potential insect species for aquaculture feed preparation, *Hermetia illucens* (Linnaeus, 1758), was identified as a suitable fishmeal replacer due to its suitability for large-scale production (Li et al., 2020) and balanced amino acid profile similar to fishmeal (Barroso et al., 2014). The fat level and fatty acid profile of black soldier fly larvae (BSFL) were highly variable with the nature of the substrate used for them to grow (St-Hilaire et al., 2007). However, Priyadarshana et al. (2021) observed varying degrees of success in studies on several finfish species in which fish meal was substituted with different levels of BSFL meal. These positive and negative effects of BSFL inclusion seem to be modulated by gut microbiota (Rimoldi et al., 2019; Terova et al., 2019), haematology (Magalhães et al., 2017; Abdel-Tawwab et al., 2020) and histomorphology (Lock et al., 2016; Li et al., 2019) of the digestive system in various finfish species. This review presents the effects of BSFL incorporated diets on gut microbiota, haematology and histomorphology of the digestive system in finfish aquaculture.

The high fat and chitin content in BSFL were the possible causes behind the diverse growth performances in different finfish species (Priyadarshana et al., 2021). The digestive tract sections in fish exhibit many adaptations in both structure and function related to their feeding habits and evolutionary position (Moraes and de Almeida, 2020). Especially in the case of chitin-like nitrogenous polysaccharides, they must be further broken down by chitinolytic enzymes i.e., chitinases and chitobiases, before being utilised. Though some fish inherit the ability to break down chitin governed by chitinolytic enzymes, most fish do not exhibit that ability (Ringø et al., 2012). Thus, the investigation of the use of BSFL as a dietary component on intrinsic factors, i.e., gut microbiota, haematology and histomorphology of the digestive system, is essential to illustrate the diverse growth performances (Priyadarshana et al., 2021).

Effects of *H. illucens* Larval Meal Incorporated Diets on Histo-morphological, Gut Microbial and Haematological Aspects of Finfish

Effects of H. illucens *larval meal incorporated diets on histomorphology of digestive system of finfish*

Numerous studies have evaluated the effects of incorporating BSFL meal on gut histomorphological, gut microbial and haematological aspects. Table 1 summarises histomorphological changes observed in finfish fed by different levels of BSFL meal.

Effects on histomorphology of digestive system of carnivorous finfish species

Changes in the digestive system of finfish species have been evaluated over different feed ingredients with plant (Agbebi et al., 2013; Ogueji et al., 2020) and animal origins (Akhter, 2015). Finfish species such as North African catfish, *Clarias gariepinus* (Burchell, 1822), tested using different feed ingredients, i.e., craib leaf (*Lysiphyllum strychnifolium* (Craib, 1924)) extracts (Munglue and Dasri, 2015), cashew nut (*Anacardium occidentale* Linnaeus, 1753) meal (Iheanacho et al., 2019), doum plant (*Hyphaene thebaica* (Linnaeus,1753)) fruit powder (Al-Khalaifah et al., 2020) showed many adverse effects on the digestive system of carnivorous finfish (Krogdahl et al., 2003). Positive results in the increase of height and perimeter of gut mucosal folds were obtained with a 30 % BSFL replacement of fishmeal fed to *C. gariepinus* fingerlings (Talamuk, 2016). Nutrient uptake increases with the enlarged mucosal surface area, causing a positive impact (Huiling et al., 2012).

Blood vessel endothelium of Atlantic salmon, *Salmo salar* Linnaeus, 1758, fed up to 100 % BSFL meal incorporated diets, was observed normal, without any signs of perivenule bleeding and vacuolisation in parenchyma (Lock et al., 2016). Furthermore, the midgut epithelium was normal, no loss of structural changes or inflammation in the muscularis (Lock et al., 2016). Similarly, Li et al. (2019) revealed no evidence of significant histopathological alterations among *S. salar* pre-smolts fed with 100 % BSFL diet. They reported no signs of local inflammatory response with BSFL diet groups. However, a distinct hyper-vacuolisation was observed in the proximal intestine of *S. salar* fed with the fishmeal diet, while that effect was less prevalent in BSFL diet groups (Li et al., 2019; Li et al., 2020). As Ismaiel et al. (2015) reported, the bioactive components in *H. illucens* larvae were the possible reason for intestinal hyper-vacuolisation. Li et al. (2020) reported a substantial effect of steatosis in the proximal and distal intestines of *S. salar*. The root cause of steatosis is poor nutrient absorption, which results in a condition known as floating faeces (Penn, 2011). This nutrient malabsorption or steatosis was predominantly associated with high-fat deposition in the lumen of the intestine (Bonvini et al., 2015).

A noticeable increase in villus width, enterocyte width and microvilli height were observed in juvenile Barramundi *Lates calcarifer* (Bloch, 1790), fed with 45 % poultry by-product meal (PBM) + 10 % *H. illucens* (HI) (Chaklader et al., 2019). Moreover, they observed a remarkable size reduction in adipocytes at the same feeding, whereas no significant effects were observed between control and 90 % PBM + 10 % HI diets (Chaklader et al., 2019).

Up to 64 % incorporation of BSFL meal in juvenile Japanese seabass *Lateolabrax japonicus*, (Cuvier, 1828), diets showed no impairments in microvilli structure, villus length, goblet cell count, muscular thickness (Wang et al., 2019). However, they observed a vacuolar degeneration in the hepatocytes, with the incorporation of BSFL meal beyond 16 %.

Poma et al. (2017) revealed the high chitin content of *H. illucens* meal as a possible cause of vacuolar degeneration. In contrast, the fish meal replacement with soybean meal showed muscle thickness and villus

Table 1. Effects of different per cent inclusion of black soldier fly, *Hermetia illucens*, larvae meal on histomorphology of digestive system of finfish species.

Finfish species	BSFL inclusion level (% of fish meal replacement)	Effects on histomorphology of digestive system	Reference
North African catfish *Clarias gariepinus* (Burchell, 1822) fingerling	Up to 30 %	No negative effects until 30 % inclusion. Slightly increased mucosal fold height and perimeter with BSFL incorporation up to 30 %	Talamuk (2016)
Barramundi *Lates calcarifer* (Bloch, 1790) juvenile	10 %	No negative effects until 45 % poultry byproduct meal (PBM) + 10 % HI (*H. illucens*) inclusion. Increased villus and enterocyte width and microvilli height at 45 % PBM + 10 % HI	Chaklader et al. (2019)
Siberian sturgeon *Acipenser baerii* Brandt, 1869 juvenile	Up to 50 %	No negative effects on liver and spiral valve histology until 37.5 % defatted BSFL meal inclusion. Reduced thickness in muscular layer at 15 % BSFL incorporation.	Caimi et al. (2020); Józefiak et al. (2019a)
Atlantic salmon *Salmo salar* Linnaeus, 1758 post-smolt, pre-smolt	Up to 100 %	No negative effects until 100 % inclusion. No signs of hyper-vacuolisation with BSFL incorporation. Insignificant mild hepatic steatosis at 100 % fishmeal replacement	Lock et al. (2016); Li et al. (2019); Li et al. (2020)
Japanese seabass *Lateolabrax japonicus* (Cuvier, 1828) juvenile	Up to 64 %	No impairments observed in villus length, villus width, inherent thickness, muscular thickness and goblet cells per villus up to 64 %. Slight vacuolar degeneration in hepatocytes beyond 16 %	Wang et al. (2019)
Common carp *Cyprinus carpio* Linnaeus, 1758 juvenile	Up to 100 %	No negative effects until 50 % inclusion. Mild hepatic necrosis in liver beyond 50 % and irregular shaped hepatocytes, and apoptotic cells with small pyknotic nuclei at 100 % fishmeal replacement	Li et al. (2017)
Rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) fry, juvenile	Up to 75 %	No negative effects until 50 % inclusion. Mucosal cell count augmentation and thickened muscularis up to 75 % BSFL incorporation. Higher liver lipid accumulation beyond 50 % inclusion	Renna et al. (2017); Elia et al. (2018); Dumas et al. (2018); Cardinaletti et al. (2019);
Zebra danio *Danio rerio* (Hamilton, 1822) whole life cycle	Up to 100 %	No negative effects until 50 % inclusion. No intestinal inflammation was observed even at 100 % BSFL incorporation. General hepatic steatosis beyond 75 % inclusion and intracellular lipid accumulation at 14 and 21-days of feeding	Vargas et al. (2018); Zarantoniello et al. (2019)

height reduction (Zhang et al., 2018). Ostaszewska et al. (2010) revealed that deficiencies in the amino acid profile as the possible reason for the adverse conditions in the intestinal epithelium. As Alegbeleye et al. (2011) described, retarded absorption of amino acids correlated with the high chitin contents, especially in insect meals.

No significant alterations were reported in the intestinal structure, i.e., villus height of submucosa of rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792), fed with BSFL meal incorporated diets up to 50 % (Renna et al., 2017). Mild changes in glycogen deposition in the liver, white pulp hyperplasia and haemosiderosis in the spleen were observed among fishmeal and BSFL meal diet groups. However, up to 50 % of BSFL meal incorporation showed no substantial changes in gut histopathology, i.e., mucins and villus fragments, in *O. mykiss* (Elia et al., 2018).

Contrary, Cardinaletti et al. (2019) announced a remarkable increase in fat accumulation in the hepatocytes at 50 % BSFL incorporation. Further, they reported a shortened intestinal fold length in the medium tract of the intestine and the presence of goblet cells that produce neutral mucins with BSFL meal incorporation. Furthermore, Dumas et al. (2018) revealed that the villi in the anterior intestine were notably shorter than the control at 26.4 % BSFL incorporation. The villus length correlated with weight gain, fat accumulation and lipid absorption (Taylor et al., 2021); thus, shorter villi might lead to poor growth performances. Up to a 37.5 % BSFL meal incorporation while replacing 50 % dietary fishmeal is suggested for Siberian sturgeon *Acipenser baerii* Brandt, 1869, without any impairments in liver and spiral valve histopathology (Caimi et al., 2020). However, Józefiak et al. (2019a) claimed that the thickness of the mucosal layer remarkably increased in *A. baerii* fed with 15 % *Tenebrio molitor* Linnaeus, 1758. In contrast, the thickness was reduced with 15 % BSFL meal incorporation. Moreover, thickness of the muscular layer also notably increased with *T. molitor,* not with BSFL incorporation. However, thickened muscularis is considered to positively impact digestion and absorption (Sarvestani et al., 2015) and, together with thickened mucosa, serve as an adaptation for better utilisation of insect diets (Guilbard et al., 2007).

Effects on histomorphology of digestive system of omnivorous finfish species

There are several reports evaluating the effects of different feed ingredients on the gut histomorphology of omnivorous fish. For instance, *Cyprinus carpio* Linnaeus, 1758, has been tested by feeding plant protein sources such as soybean meal (Zhang et al., 2012). Furthermore, some studies focused on using animal protein sources such as *Musca domestica* Linnaeus, 1758, larva (Ogunji et al., 2011) and defatted *Bombyx mori* Linnaeus, 1758, pupae (Zhang et al., 2013) for omnivorous finfish species. However, feeding trials regarding BSFL meal on *C. carpio* juveniles discovered some mild hepatic necrotic signs in the liver at 75 % and 100 %. Moreover, debris was found in the microvilli beyond 50 % fishmeal replacement by BSFL meal (Li et al., 2017).

Hepatic steatosis is an excessive accumulation of triglycerides in the hepatocytes (Wang et al., 2006). The hepatic steatosis was found among zebrafish *Danio rerio* (Hamilton, 1822) at 100 % (Vargas-Abúndez et al., 2018) and beyond 75 % (Zarantoniello et al., 2020) BSF prepupae incorporated diets. Feeding BSF prepupae grown on corn meal-fruit and vegetable mixture (50:50) resulted in intracellular lipid accumulation in *D. rerio* at 14 and 21-days of feeding (Vargas-Abúndez et al., 2018). However, no intestinal inflammation was observed among *D. rerio,* even up to a 100 % BSFL meal incorporation (Zarantoniello et al., 2020). Ample amounts of medium-chain saturated fatty acids (MCSFA) in insect diets were found as a potential cause of the hindered inflammatory activity (Lichtenstein et al., 2010). Moreover, Vargas-Abúndez et al. (2018) found a vast number of mucous cells in the intestine of *D. rerio* fed with BSF prepupae that are grown on corn meal-fruit and vegetable mixture (50:50). Increased mucosal cell count is an indication of the intestinal inflammation (Söderholm et al., 2002).

It can be concluded that micro morphological alterations and inflammatory activities in the finfish intestine are mainly associated with the chitin levels in BSFL meals. In addition, the high-fat content in BSFL meals directly influenced hepatocytic lipid accumulation. Therefore, incorporation levels beyond 75 % were ineffective for most finfish species (Zarantoniello et al., 2019).

Effects of H. illucens *larval meal incorporated diets on finfish gut microbiota*

Several reports evaluate the influence of different dietary ingredients on the gut microbiota of different livestock species (Borrelli et al., 2017; Kawasaki et al., 2019) and finfish species (Ringø and Olsen, 1999; Bolnick et al., 2014; Ringø et al., 2016). Moreover, the gut microbiota of *H. illucens* larvae has also been investigated, and Actinobacteria (*Actinomyces* spp.), Firmicutes (*Bacillus* spp.), Proteobacteria (*Providencia* spp.), Bacteroidetes (*Dysgonomonas* spp.) were found to be the key inhabitants (Bruno et al., 2019). Table 2 shows the effects of BSFL meal incorporated diets on finfish gut microbiota.

Effects on gut microbiota of carnivorous finfish species

Mycoplasma (Zarkasi et al., 2014; Jin et al., 2019), *Aliivibrio* (Karlsen et al., 2017; Fogarty et al., 2019) and *Borrelia* spp. (Godoy et al., 2015; Zarkasi et al., 2016) have been identified as the key intestinal inhabitants of the wild and captively reared *S. salar*.

When *S. salar* was fed with a 10 % BSFL diet, at the phylum level, the results showed a higher abundance of Firmicutes, Actinobacteria, Proteobacteria and Tenericutes in intestinal digesta samples. Spirochaetes, Proteobacteria, Firmicutes, Tenericutes and Actinobacteria were the major inhabitants in intestinal mucosa samples (Li et al., 2021). The above-mentioned microbial groups have also been reported in BSFL gut microflora (Bruno et al., 2019). The abundance of Actinobacteria (*Actinomyces*) (Beier and Bertilsson, 2013) and Firmicutes (*Bacillus*) (Cody, 1989), was almost positively related to chitin degradation.

In contrast to the findings of Li et al. (2021), chitinase activity or the presence of chitinolytic bacteria were not found in the midgut of turbot *Psetta maxima* (Linnaeus, 1758) with up to 76 % BSFL incorporation in their diets, even though they primarily feed on crustaceans. The absence of chitinolytic bacteria in *P. maxima* could be due to prolonged exposure to chitin-free diets (Kroeckel et al., 2012).

Monopterus albus (Zuiew, 1793) fed with 7.5 % fishmeal replaced (15.78 % BSFL incorporation) diets showed an increase in *Proteobacteria* spp., where the increment was significant at the 7.5 % fishmeal replacement. Further, Hu et al. (2020) reported a reducing trend in *Firmicute* spp. where the reduction was remarkable at the 7.5 % fishmeal replacement. The Proteobacteria to Firmicutes ratio was related to dietary lipid assimilation (Marques et al., 2015).

Intestinal mucosa of *O. mykiss* fed with partially defatted BSFL meal (up to 50 %), showed a notably higher microbial diversification, with the highest biodiversity at 25 % BSFL group. Proteobacteria and

Table 2. Effects of different per cent inclusion of black soldier fly larvae (BSFL) meal on the gut microbiota of diverse finfish species.

Finfish species	BSFL inclusion rate (% of fish meal replacement)	Effects on gut microbiota	Reference
Atlantic salmon *Salmo salar* Linnaeus, 1758 sea water phase	10 %	No negative effects until 10 % inclusion. Clear differences in microbial communities of intestinal digesta and mucosa	Li et al. (2021)
Asian swamp eel *Monopterus albus* (Zuiew, 1793) juvenile	Up to 7.5 %	No negative effects until 7.5 % fishmeal replacement Remarkable increase in gut Proteobacteria and reduction in gut Firmicutes	Hu et al. (2020)
Rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) fry, juvenile	Up to 50 %	No negative effects until 50 % inclusion. Increased microbial diversity with the BSFL incorporation	Bruni et al. (2018); Huyben et al. (2019); Józefiak et al. (2019b); Rimoldi et al. (2019); Terova et al. (2019)
Turbot *Psetta maxima* (Linnaeus, 1758) juvenile	Up to 76 %	No negative effects until 76 % inclusion. No chitinase enzyme activity or chitin degrading bacteria	Kroeckel et al. (2012)
Zebra danio *Danio rerio* (Hamilton, 1822) whole life cycle	100 %	Increased gut microbial alpha diversity with the incorporation of *H. illucens* meals	Zarantoniello et al. (2019)

Actinobacteria phyla dominated the intestinal mucosa samples. However, amongst those phyla, *Aeromonas rivipollensis* was the only group of abundant microbes in the fish meal incorporated diet group. In contrast, *Acinetobacter* spp., *Brevundimonas* spp., *Pseudomonas* spp., *Carnobacterium divergens*, *Citrobacter gilleni*, *Curtobacterium flaccumfaciens*, *Delftia acidovoran*, and *Kluyvera intermedia* were predominantly found in BSFL diet groups. The phyla Proteobacteria and Firmicutes dominated the digesta samples of *O. mykiss* juveniles (Bruni et al., 2018). Further, at the phylum level, the abundance of Firmicutes in *O. mykiss* gut was notably increased with a 30 % BSFL and defatted BSFL diet groups. Moreover, the Actinomycetales and Lactobacillales order increased in the 30 % pre-pupae and larvae diet groups (Huyben et al., 2019). As reported by Rimoldi et al. (2019), a higher bacterial diversity was also associated with the incorporation of BSFL (up to 30 %) into the diets of *O. mykiss*, where *Mycoplasma* was the predominant genera. However, a reduction in the relative abundance of genera-*Proteobacteria* was observed. At the same time, the abundance of Actinobacteria phylum remarkably increased with the BSF prepupae diet groups of up to 30 %.

Furthermore, it was emphasised that the BSF prepupa meals positively modify fish gut microbiota in terms of richness and diversity while increasing the host-beneficial bacteria, i.e., lactic acid and butyrate-producing bacteria counts (Terova et al., 2019). Moreover, Aerococcaceae, Lactobacillaceae, Enterococcaceae and Leuconostocacea were the most common LAB families found in BSFL-fed *O. mykiss*. In addition, Rimoldi et al. (2019) reported reduced counts of Gram-negative bacteria, namely *Shewanellaceae*, *Neisseriaceae* and *Enterobacteriaceae* at 20 % BSFL meal incorporation. However, the phyla Actinobacteria, Firmicutes, Proteobacteria and Tenericute mainly dominated the core gut microbiota of *O. mykiss* (Desai et al., 2012; Wong et al., 2013; Ingerslev et al., 2014a; Ingerslev et al., 2014b; Lyons et al., 2017a; Lyons et al., 2017b).

Especially, LAB in finfish gut microbiota has a positive impact on health, as they are capable of secreting bacteriocin-like compounds which can suppress pathogenic microbial activities (Merrifield et al., 2010; Dimitroglou et al., 2011; Gudiña et al., 2015). Similarly, the incorporation of insect meals of *Blatta lateralis* (Walker, 1868), *H. illucens*, *Gryllodes sigillatus* (Walker, 1868) and *T. molitor* Linnaeus, 1758, led to a high gut microbial diversity and amplification of beneficial bacteria in *O. mykiss* (Józefiak et al., 2019b). Moreover, the abundance of *Clostridium* spp. i.e., *C. coccoides*, was beneficial because they could perform unique functions, including homeostasis regulation in the finfish gut and suppression of invasive microbes (Frank et al., 2007; Ye et al., 2014; Kurakawa et al., 2015). High availability of chitin in the later stages of BSF, i.e., early and late prepupa (Xiao et al., 2018), and prebiotic properties of fermenting chitin (Rimoldi et al., 2019) in the fish gut were the possible reasons behind higher microbial diversity. In addition, Choi et al. (2012), Wu et al. (2012), Józefiak and Engberg (2017), Vogel et al. (2018), discovered a prominent antimicrobial activity of BSFL meal extracts against Gram-negative bacterial families, i.e., *Shewanellaceae*, *Neisseriaceae* and *Enterobacteriaceae*.

Effects on gut microbiota of omnivorous finfish species

Reports of much higher diversity in the gut microbiota of omnivorous finfish species occur similar to the carnivorous finfish species. Beyond 50 % of full-fat BSF prepupal meal incorporation in zebrafish diets showed the highest gut microbial alpha diversity. Further, the availability of *Vibrio* and *Mycoplasmataceae* was retarded with the incorporation of BSF prepupal meal, whereas *Cetobacterium* spp. was the most prevalent taxon (Zarantoniello et al., 2019). Brugman et al. (2014) reported that T-lymphocytes in zebrafish gut can suppress the outgrowth of *Vibrio* spp. Furthermore, Zarantoniello et al. (2019) revealed that BSF prepupal meal incorporated diets could stimulate genes (*il10, il1b* and *340 tnfa*) coupled with immune response, and thus, capable of suppressing the activities of virulent pathogens. The high chitin and fat content associated with BSFL meals were the possible reasons for high gut microbial activity (Tran et al., 2015; Sypniewski et al., 2020).

A highly diversified microbial population affects gut health, whereas poor microbial diversity allows the amplification of antagonistic pathogens (Sekirov et al., 2010; Apper et al., 2016). *Acinetobacter* spp. like synergistic bacterial species, plays a vital role in nutrient digestion (Ramírez and Romero, 2017; Wang et al., 2018). Moreover, *Acinetobacter* species secrete amylase, cellulase, chitinase and phytase-like enzymes that inhibit the growth and development of *Vibrio* spp. (Askarian et al., 2012). Besides, *Carnobacterium* spp. can boost specific immunity and promote protein and carbohydrate digestion (Mansfield et al., 2010; Ringø et al., 2010; Al-Hisnawi et al., 2015). Butyrogenic activity associated with *Clostridium* spp. i.e., *C. cluster* also benefits finfish health (Koh et al., 2016; Pryde et al., 2002; Esquivel-Elizondo et al., 2017). Moreover, most studies have revealed that high fat and chitin in BSFL act as the key determinants of the high microbial diversity and the growth of beneficial gut microflora for the host.

Effects of H. illucens *larval meal incorporated diets on finfish haematology*

Several studies were conducted to elucidate the effect of BSFL meal on the haematological parameters of finfish species, as summarised in Table 3.

Effects on carnivorous finfish haematology

Unique haematological properties were observed among different finfish species such as *Argyrosomus regius* (Asso, 1801), *C. gariepinus*, *Oreochromis niloticus* (Linnaeus, 1758), hybrid, *Sparus aurata* Linnaeus, 1758, and *Totoaba macdonaldi* (Gilbert, 1890), for the dietary ingredients; soybean (Trejo-Escamilla et al., 2017), spirulina (Raji et al., 2018), canola (Zhou and Yue, 2010), poultry by-product (Karapanagiotidis et al., 2018) and chicken feathers (Psofakis et al., 2020). The blood chemistry of finfish has also been investigated using insect-based protein sources. As claimed by Freccia et al. (2016), overall performance together with plasma protein concentrations notably increased with the incorporation of speckled cockroach (*Nauphoeta cinerea* (Olivier, 1789)) in the diets of Nile-tilapia.

Incorporating 75 % BSFL in the diet of *C. gariepinus* revealed that haematological parameters (haemoglobin content, white blood cell (WBC) and erythrocyte (RBC) count, mean corpuscular volume (MCV), packed cell volume (PCV), mean corpuscular hemoglobin (MCH), mean corpuscular hemoglobin concentration (MCHC), lymphocytes, monocytes and neutrophils) remained unaffected (Fawole et al., 2020). However, triglyceride and total bilirubin contents were markedly lower in 50 % BSFL diet group.

Haemoglobin, haematocrit, MCV, MCH, MCHC, total serum protein, albumin, globulin, serum alanine aminotransferase, aspartate and plasma cell counts were not affected in European bass, *Dicentrarchus labrax* (Linnaeus, 1758), fry with up to 50 % fish meal replacement by BSFL meal (Abdel-Tawwab et al., 2020). Despite the cholesterol, the rest of the plasma metabolites, i.e., plasma glucose, total proteins, and triglycerides, remained unaffected for the fishmeal and BSFL meal diets (up to 45 % fishmeal replacement) fed to *D. labrax*. Plasma cholesterol levels were remarkably reduced with the replacement of fishmeal by 45 % (Magalhães et al., 2017). Similarly, plasma cholesterol, triacylglycerol, high-density lipoprotein cholesterol and malondialdehyde levels of *L. japonicus* were comparably lower in the defatted BSFL meal diet of up to 64 % than fishmeal diet group (Wang et al., 2019).

The presence of chitin (Diener et al., 2009) and MCSFA (Li et al., 2017) in diets was investigated as a possible cause of plasma cholesterol depletion. Chitosan, a chitin derivative, can bind with cholesterol micelles (Khoushab and Yamabhai, 2010) to restrict cholesterol uptake (Shiau and Yu, 1999; Chen et al., 2015). However, according to Hu et al. (2017), plasma cholesterol and nitric oxide (NO) levels significantly increased at a 30 % fishmeal replacement with BSFL meal in yellow catfish *Pelteobagrus fulvidraco* (Richardson, 1846), while the inhibition of superoxide radical anion formation was significantly reduced (Hu et al., 2017). Kaushik et al. (1995) described that dietary cholesterol content significantly influences plasma cholesterol levels. Nitric oxide is a harmful compound that can cause oxidative stress in organisms (Turko et al., 2001). Park et al., (2014) reported a high radical scavenging activity in BSFL and BSF pupa extracts and, therefore, can arrest the formation of NO. Nonetheless, Hu et al. (2017) reported that at a 30 % fish meal replacement rate, the antioxidant activity of BSFL was insufficient to suppress NO formation in *P. fulvidraco*.

Table 3. Effects of different per cent inclusion of black soldier fly (BSFL) meal on haematology of different finfish species.

Finfish species	BSFL inclusion rate (fish meal replacement)	Effects on haematology	Reference
North African catfish *Clarias gariepinus* (Burchell, 1822) fingerling	Up to 75 %	Triglyceride and total bilirubin contents were significantly lower in 50 % BSFL diet group	Fawole et al. (2020)
European seabass *Dicentrarchus labrax* (Linnaeus, 1758) fry, juvenile	Up to 50 %	No negative effects on haematology until 50 % fishmeal replacement. Plasma cholesterol level reduced with the BSFL incorporation	Magalhães et al. (2017); Abdel-Tawwab et al. (2020)
Japanese seabass *Lateolabrax japonicus* (Cuvier, 1828) juvenile	Up to 64 %	Plasma cholesterol, triacylglycerol, high density lipoprotein cholesterol and malondialdehyde levels were reduced at 48 % and 64 % fishmeal replacement	Wang et al. (2019)
Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852) fry, juvenile	-	Plasma cholesterol level and erythrocyte sedimentation rate reduced. Increments in plasma haemoglobin and glucose levels	Ushakova et al. (2016); Ushakova et al. (2018)
Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) fingerlings	Up to 100 %	White blood cell count, erythrocyte count, haemoglobin, haematocrit, mean corpuscular volume, mean corpuscular haemoglobin concentration, red blood cell distribution width and platelet values were not affected up to a 100 % fishmeal replacement	Tippayadara et al. (2021)
Danube sturgeon *Acipenser gueldenstaedtii* Brandt & Ratzeburg, 1833 fry	-	Increased plasma haemoglobin content	Ushakova et al. (2016)
Yellow catfish *Pelteobagrus fulvidraco* (Richardson, 1846) juvenile	Up to 30 %	Plasma cholesterol and nitric oxide (NO) levels significantly increased at a 30 % fishmeal replacement	Hu et al. (2017)

Russian sturgeon *Acipenser gueldenstaedtii* Brandt and Ratzeburg, 1833 juveniles, fed with a 0.2 % probiotic mixture of *Bacillus subtilis* and a homogenate of BSFL, indicated a remarkable increment in the plasma haemoglobin content from 65 to 77 g per litre (Ushakova et al., 2016). Elevated plasma haemoglobin content reflects perfect finfish health and activeness (Ponomarev et al., 2002).

Effects on omnivorous finfish haematology

Tippayadara et al. (2021) stated that the counts of RBC, WBC, haemoglobin, haematocrit, MCV, MCHC, red blood cell distribution width and platelet values were not affected with up to 100 % fishmeal replacement by BSFLM in *O. niloticus*. Nonetheless, for Mozambique tilapia, *Oreochromis mossambicus* (Peters, 1852), the incorporation of BSF prepupae into the diets at 0.5 g.kg^{-1} reduced plasma erythrocyte sedimentation rate (ESR), while increasing plasma haemoglobin and glucose levels (Ushakova et al., 2018). The absence of gut inflammation and pathogenic activities were the major reasons behind the lower ESR. Furthermore, *O. mossambicus* fed a 0.25 % probiotic mixture of *Bacillus subtilis* and a homogenate of BSFL showed a significant reduction in plasma cholesterol levels (Ushakova et al., 2016). However, elevated levels of chitin in BSFL and prepupa meals seemed to act as a beneficial factor regulating blood parameters such as plasma haemoglobin content, RBC, WBC and ESR, within the safe limits and beneficial for finfish blood chemistry.

Conclusion

Species-dependent changes in haematology, gut microbiota, and histomorphology of the digestive system were observed with the incorporation of black soldier fly larvae (BSFL) meal into finfish diets. Even when up to 100 % BSFL meal was incorporated, positive effects on blood chemistry, gut microbiota, and histomorphology of the digestive system were observed. The plasma cholesterol level was significantly reduced in the majority of cases. Amplification of the bacterial diversity was associated with BSFL meal-included diets. In most cases, a significant increase in mucosal thickness and hepatopancreatic lipid accumulation were observed in finfish intestines. Despite a few negative impacts on some omnivore finfish species, gut microbiota, haematology and histomorphology of the digestive system were positively affected by up to 50 % inclusion. However, more studies would be essential for further validation of the BSFL meal as a protein source in finfish aquaculture.

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