

IMPORTANCE OF GUT MICROBIOTA IN FISH – A REVIEW

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The microbiota are normally involved in numerous factors concerned with the health of the fishes in their environment and many of them can also cause threats to the same. In fish, the gut microbiota inhabiting the gastrointestinal tract influence the physiology, nutrition, life span, immunity, besides acting as a barrier against pathogens. Although gut microbiotas are present in all the fish, their composition varies based on their life stages, the environment in which they live, diet, seasons, trophic levels, etc. There are numerous studies related to the intestinal microbiota of freshwater, marine fish and in various life stages of fish. But the knowledge on the microbiota in aquatic ecosystem is yet to be explored. Researches in this field will pave way to the develop techniques to manipulate the gut microbiota of the desired fish species of culture to improve their growth and production. This review is intended to provide collective information on the gut microbiota in fish, their development, dynamics in the living environment and their manipulation towards improving production and sustainability in the field of fisheries.

Key words: Freshwater fish, Gut microbiota, Manipulation of gut microbiota, Marine fish

Introduction

Fishes are poikilothermic aquatic animals that consist of a vast range of vertebrates to invertebrates of the animal kingdom. Fish are considered as sources of low-fat high-quality protein; rich in omega-3 fatty acids, vitamins like B₂ and D and minerals such as iron, calcium, phosphorus, iodine, magnesium, zinc and potassium. The consumption of fish has been increased by increasing the world's population from the mid of the 20th century. According to FAO (2020), in per capita terms, there is increase of fish consumption from 9.0 kg in 1961 to 20.2 kg in 2015, at an average rate of 1.5% increase per year. The estimate for 2016 and 2017 was about 20.3 and 20.5 kg respectively. Such demand was contributed by the total global fish production of 170.9 MMT through 90.9 MMT of capture

fisheries and 80.0 MMT of aquaculture. The aquaculture sector, contributed by both inland and marine sector produced 51.4 MMT and 28.7 MMT, respectively contributing up to 46.8% of total fish production.

Fish possess bacterial flora on or in their skin and its various organs (Austin, 2002). Generally, the bacterial genera isolated are related to the environment of the fish and varies with numerous factors such as the salinity and the load of bacterial communities in the water. The bacteria recovered from the surface of skin and gills may be temporary rather than resident on the surface of the fish. Gut microbiota of fish appear to vary with the complications in the digestive system. The microbiota present in the gut is the representation

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of those from the surrounding environment or the diet fed which can survive and multiply within intestinal tract, there is also evidence for a different intestinal microflora in some species (Cahill, 1990). Gut microbiota can influence development, life span, physiology, immunity, and barriers against the pathogen in fish (Yan *et al.*, 2016). Hence, the components that direct the intrusion of microbes in the fish gut will give an underlying advance towards anticipating and treating fish diseases (Xiong *et al.*, 2019).

Several factors may affect the microbiota of the fish gut. The changes in external factors like age, diet, environment and trophic levels can alter the gut microbiota of the fish (Liu *et al.*, 2016; Stephens *et al.*, 2016; Michl *et al.*, 2017; Wang *et al.*, 2018). To study the gut microbiomes in fish, various methods are being adopted for the examination of the confederation of microorganisms. In the past, the culture-dependent methods (Ringo *et al.*, 2003; Romero and Navarrete, 2006), denaturing gradient gel electrophoresis and temporal temperature gradient gel electrophoresis techniques (Reveco *et al.*, 2014) revealed a very low fraction of the significant microorganisms. But, today there are wide varieties of culture-independent technique available for the analysis of microbiota of fish (Tarnecki *et al.*, 2017). By knowing the importance of microbial communities in the fish body, we can manipulate these communities to bring out the best possible role to be expressed in their body for the benefit of fish health.

Historical overview of gut microbiota of fish

The collective genomes within the microorganisms inhabiting a particular environment were termed as a microbiome (Burokas *et al.*, 2015). Higher vertebrates harbour these microbial communities in their body from the skin surface to the gastrointestinal tract (Sandrini *et al.*, 2015). The studies on such a complex form of microorganisms in fishes started as early as the 1930s (Reed and Spence, 1929; Gibbons, 1933) in which they investigated

the skin and gut microbial communities. The study was further explored by the influence of intestinal flora in fish on fasting (Margolis, 1953). Understanding the importance of these microbiomes has led to several studies in fish viz. changes in the gut microbiota with response to the diet (Sera *et al.*, 1972), variation in the gut microbiota of the farmed fish (Gilmour *et al.*, 1976), the influence of the gut microbiome by the surrounding environment and the intake of diet (Cahill, 1990). One of the limitations in the isolation and culture of gut microbiota using culture-dependent methods is that, only 10% of microorganisms has been studied.

Gut microbiota of freshwater fish

Considerable differences in the composition of intestinal microbial flora in marine and freshwater fish are described by Izvekova *et al.* (2007). The gut microbial composition of the freshwater fish differs due to the varying environmental conditions of their habitat. *Acinetobacter*, *Aeromonas*, *Flavobacterium*, *Lactococcus*, *Pseudomonas*, obligate anaerobes (*Bacteroides*, *Clostridium* and *Fusobacterium*) and members of family *Enterobacteriaceae* dominate the gut of freshwater species (Gómez and Balcazar, 2008). A limited number of bacterial taxa found in the intestines of some fish species may indicate not only a low diversity of these bacteria but may also be due to insufficient knowledge about them. Herbivorous and omnivorous freshwater fish shows shorter gut transit times with low levels of short chained fatty acids (SCFA) in the gut, which are produced during the conversion of unassimilable algal constituents by the gut microbes (German *et al.*, 2010) than some of their marine counterparts. The highest level of SCFA was reported in the posterior intestine of *Oreochromis* sp. Free living Amoebae are ubiquitous in freshwater fish *Oreochromis niloticus* (Milanez *et al.*, 2017) and its infection poses a public health problems due to possible human consumption. Beneficial gut microbiota reported in various freshwater fish are presented in Table.1

Table 1. Beneficial gut microbiota reported in various freshwater fish

Host	Dominant gut microbiota	Reference
Nile tilapia (<i>Tilapia nilotica</i>), goldfish (<i>Carassius auratus</i>), and Ayu (<i>Plecoglossus altivelis</i>)	Obligate anaerobes (<i>Bacteroidaceae</i>) were predominant over facultative anaerobes (<i>Vibrionaceae</i> and <i>Enterobacteriaceae</i>)	Sakata <i>et al.</i> , 1980
Japanese eel (<i>Anguilla japonica</i>), carp (<i>Cyprinus carpio</i>), goldfish (<i>Carassius auratus</i>), Ayu (<i>Plecoglossus altivelis</i>), tilapia (<i>Tilapia nilotica</i>) and channel catfish (<i>Ictalurus punctatus</i>)	<i>Bacteroides</i> type A, with the potential of producing vitamin B ₁₂	Sugita <i>et al.</i> , 1991
Ayu (<i>Plecoglossus altivelis</i>), carp (<i>Cyprinus carpio</i>), channel catfish (<i>Ictalurus punctatus</i>), Japanese eel (<i>Anguilla japonica</i>) and Tilapia (<i>Tilapia nilotica</i>)	<i>Aeromonas</i> , <i>Bacteroidaceae</i> and <i>Clostridium</i> strains producing amylase that play an important role in the digestion of starch	Sugita <i>et al.</i> , 1997
Silver carp (<i>Hypophthalmichthys molitrix</i>), common carp (<i>Cyprinus carpio</i>), channel catfish (<i>Ictalurus punctatus</i>) and deep-bodied crucian carp (<i>Carassius cuvieri</i>)	<i>Lactococcus raffinolactis</i> , a predominant intestinal LAB	Hagi <i>et al.</i> , 2004
Goldfish (<i>Carassius auratus</i>), common carp (<i>Cyprinus carpio</i>) and Mozambique tilapia (<i>Oreochromis mossambicus</i>)	<i>Bacteroides</i> type A strains with high vitamin B ₁₂ producing ability, Vancomycin-resistant bacteria such as <i>Cetobacterium somerae</i>	Tsuchiya <i>et al.</i> , 2008
Rohu (<i>Labeo rohita</i>) and catla (<i>Catla catla</i>)	Lactic acid bacteria <i>Enterococcus faecalis</i> and <i>Pediococcus acidilactici</i> to ferment fish processing waste	Rai <i>et al.</i> , 2011
Zebrafish (<i>Danio rerio</i>)	<i>Aeromonas</i> spp., <i>Pseudomonas</i> spp., <i>Plesiomonas</i> spp., <i>Vibrio</i> spp., <i>Shewanella</i> spp. and <i>Cetobacterium</i> spp.	Roeselers <i>et al.</i> , 2011
Rohu (<i>Labeo rohita</i>), Mrigal (<i>Cyrrhinus mirgala</i>) and Tilapia (<i>Oreochromis mossambicus</i>)	<i>Enterobacter asbura</i> , <i>Pichia kudriavzevii</i> , <i>Candida tropicalis</i> and <i>Candida parapsilosis</i> can produce tannase to overcome the antinutritional factors in the feedstuffs.	Mandal and Ghosh, 2013
Channel catfish (<i>Ictalurus punctatus</i>), Largemouth bass (<i>Micropterus salmoides</i>) and Bluegill (<i>Lepomis macrochirus</i>)	<i>Cetobacterium somerae</i> , <i>Plesiomonas shigelloides</i> , <i>Fusobacterium mortiferum</i> and <i>Aeromonas</i> sp.	Larsen <i>et al.</i> , 2014

Table 1 , Cont.

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Host	Dominant gut microbiota	Reference
Mrigal (<i>Cyrrhinus mirgala</i> and Tilapia (<i>Oreochromis niloticus</i>))	<i>Pichia kudriavzevii</i> and <i>Candida rugosa</i> , extracellular enzyme producing yeasts	Banerjee and Ghosh, 2014
Freshwater fishes <i>Schizothorax zarudnyi</i> and <i>Schizocypris altidorsalis</i>	Actinobacteria with their potential to produce biologically active compounds.	Jami <i>et al.</i> , 2015
Grass carp (<i>Ctenopharyngodon idellus</i>)	<i>Dechloromonas</i> , <i>Methylocaldum</i> , <i>Planctomyces</i> , <i>Rhodobacter</i> , <i>Caulobacter</i> , <i>Flavobacterium</i> , and <i>Pseudomonas</i>	Tran <i>et al.</i> , 2018
Freshwater pufferfish (<i>Tetraodon cutcutia</i>)	Gammaproteobacteria, Fosobacteria, Actinobacteria, <i>Anerolineae</i> , Betaproteobacteria, Deinococci, Clostridia and Deltaproteobacteria	Deb <i>et al.</i> ,

Gut microbiota of marine fishes

The fish and other marine animals have their unique interaction with the surrounding environment and the microorganisms inhabiting the environment. The gut of marine fish is dominated by *Alcaligenes*, *Alteromonas*, *Aeromonas*, *Flavobacterium*, *Carnobacterium*, *Moraxella*, *Micrococcus*, *Pseudomonas* and *Vibrio* (Gómez and Balcazar, 2008). A summary of the major bacterial flora composing the gut microbiota of marine fish was reviewed by Llewellyn *et al.* (2014). A review of the intestinal microflora of fish larvae and fry of 24 marine and freshwater fish showed the most frequently reported bacteria were *Vibrio*, *Pseudomonas*, *Cytophaga*, *Flavobacterium* and the family *Enterobacteriaceae* (Ringø and Birkbeck, 1999). While the microbial community changes with life stage and habitat, a relatively stable gut microbiota are established within the first 50 days of life for many species (Larsen *et al.*, 2014). Lactic acid bacteria (mainly *Lactobacillus* sp.) have also been found to be minor components of the gut microflora of both freshwater and marine fish (Izvekova *et al.*, 2007). Table 2 shows the dominant gut microbial communities in marine fish.

Importance of gut microbiota in disease resistance

Gut microbiota are the microorganisms that are colonizing the digestive tract, enveloping the entire scope of the biochemical cycle, and incite a resistant arrangement of the host life form (Gómez and Balcazar, 2008). Numerous beneficial bacterial strains have been created to treat microorganism prompted bacterial maladies, and this current strategy's adequacy has been demonstrated (Verschuere *et al.*, 2000). Some beneficial microbes can create microorganisms that stifle or even destroy the inhibitory compounds (Teplitski *et al.*, 2009). *Lactococcus lactis* isolated from marine fish produced bacteriocin nisin Z, which can restrain the development of the fish microbe *Lactococcus garvieae* at 5 AU mL⁻¹ made it a promising option in the prevention of lactococcosis (Sequeiros *et al.*, 2015). A bacteria *Centroscyllium fabricii* isolated from the deep sea shark was found to have an antagonistic activity in the fish gut (Bindiya *et al.*, 2015).

Gut microbiota with respect to the life stages in fish

The colonization of fish gut begins early in the

Table 2. Dominant gut microbial communities in marine fish

Host	Dominant gut microbiota	Reference
Neritic sharks	<i>Photobacterium damsela</i>	Grimes <i>et al.</i> , 1985
Atlantic salmon (<i>Salmo salar</i>), Long jawed mudsucker (<i>Gillichthys mirabilis</i>)	<i>Tenericutes</i> (<i>Mycoplasma</i> sp.)	Bano <i>et al.</i> , 2007; Llewellyn <i>et al.</i> , 2016
<i>Penaeus monodon</i>	Gamma Proteobacteria	Rungrassamee <i>et al.</i> , 2014, 2016
Pacific white shrimp (<i>Penaeus vannamei</i>)	Gamma Proteobacteria	Rungrassamee <i>et al.</i> , 2016
12 bony fish and 3 sharks	<i>Proteobacteria</i> , <i>Firmicutes</i>	Givens <i>et al.</i> , 2015
Damselfish (<i>Pomacentridae</i>) and Cardinalfish (<i>Apogonidae</i>)	<i>Endozoicomonaceae</i> , <i>Shewanellaceae</i> , <i>Fusobacteriaceae</i> , <i>Vibrionaceae</i> and <i>Pasteurellaceae</i>	Parris <i>et al.</i> , 2016
Rabbitfish (<i>Siganus muscescens</i>)	Firmicutes, Bacteroidetes and delta-Proteobacteria	Nielsen <i>et al.</i> , 2017
Pacific white shrimp (<i>Penaeus vannamei</i>)	Alpha Proteobacteria alongside Planctomycetales	Chen <i>et al.</i> , 2017
Atlantic cod (<i>Gadus morhua</i>)	Firmicutes, Proteobacteria, Bacteroidetes, and Fusobacteria can act as biomarker for oil contamination	Walter <i>et al.</i> , 2019
<i>Dicentrarchus labrax</i> , <i>Sparus aurata</i> , <i>Diplodus puntazzo</i> , <i>Pagrus pagrus</i> , <i>Argyrosomus regius</i>	<i>Pelomonas puraquae</i> , <i>Hydrogenophaga atypica</i> , <i>Atopostipes suicloacalis</i> , <i>Pseudomonas veronii</i> , <i>Propionibacterium</i> (<i>Cutibacterium acnes</i>), <i>Pseudomonas panacis</i> and <i>Delftia acidovorans</i>	Nikouli <i>et al.</i> , 2020

larval stage and is driven towards the achievement of a complex assemblage of gut-associated microorganisms (Nayak, 2010). Microbial colonisation of fish larvae originates from the eggs, the environment and the first feed. The microbiota of the surrounding water dictates which bacteria encounter the eggs and consequently have the opportunities to colonise. Upon hatching, sterile larvae intake the chorion-associated bacteria, which are the first colonisers of the developing gastrointestinal tract (GIT) (Egerton *et al.*, 2018). The GIT of the newly hatched larvae tends to contain a few bacteria. Subsequent bacterial habitats are acquired in the fish larvae for the first time when they begin to drink water to control osmoregulation and the microbiota then becomes further diversified through feeding

(Hansen and Olafsen, 1999). Numerous studies have shown that diet plays a major role in shaping the gut microbial community and from first feeding; cause to substantial diversification (Lauzon *et al.*, 2010). Around 10^8 bacterial cells having a place with more than 500 distinct species are accounted to populate the fish gut, which is overwhelmed by aerobes or facultative anaerobes (Romero and Navarrete, 2006). The diversity of the gut microbiota generally increases as the fish diet changes from predatory to omnivorous and omnivorous to herbivorous (Liu *et al.*, 2016). The gut colonization can be either driven by stochastic (neutral assembly) or deterministic (non-neutral model). Stochastic deduced from random dispersion of microorganisms or events that land

the microorganisms into the intestine that are responsible for the final shape of the gut microbial community and in deterministic, the assembly is acquired by the host selective factors, active dispersal by the host and microbe and microbe-microbe interactions (Talwar *et al.*, 2018). Over a formative time, the colonization of gut was started by seeding from the surrounding environment, then progressively determined by the non-neutral factors as the fish matures from larvae to adult (Yan *et al.*, 2016). Therefore, the studies suggested stochastic factors as a determinant in colonization of the GI tract. The gut microbial community can change with a variety of factors affecting the host, including changing environmental conditions such as temperature and salinity (Macfarlane and Englyst, 1986), developmental stage (Romero and Navarrete, 2006), digestive physiology (Cahill, 1990) and feeding strategy (Uchii *et al.*, 2006). Some of the gut microfloras appear to be temporary, while other bacterial floras seem to be permanent residents (Kim *et al.*, 2007). Herbivorous fish like pinfish *Lagodon rhomboides* under-goes an ontogenetic diet shift, while transitioning from carnivorous juveniles to either omnivorous or herbivorous adults (Gallagher *et al.*, 2001).

Likewise, the growth, development and migration in anadromous Atlantic salmon *Salmo salar* involve a radical shift across an ecological and trophic spectrum (Orlov *et al.*, 2006). Accompanying the behavioural, physiological and dietary adaptations are necessary to cope up with the transition between freshwater and marine environments (McCormick *et al.*, 2013). The ecological succession of gut microbial communities during development and migration of wild teleost is an excellent system to explore the contribution of host and environmental factors in shaping the microbiome recruitment, particularly in euryhaline species (Schmidt *et al.*, 2015). The study of Xia *et al.* (2014) provided the first perception into the fish gut microbiota

and its changes during starvation. A detailed study on interactions between gut microbiota and hosts under such dynamic conditions will through new light on how the hosts and microbes respond to the dynamic environment. Nikouli *et al.* (2020) provided evidence on adult farmed fish in the Mediterranean sea have a divergent and species-specific gut microbiota profile, that are shaped independently of the similar environmental conditions under which they grow.

Herbivorous marine fish species having higher intestinal short-chain fatty acid concentrations depend on the intestinal microbiota to convert the unassimilable algal constituents to metabolically useful short-chain fatty acids (White *et al.*, 2010), and these fish displays metabolic specializations to the hindgut fermentation (Willmott *et al.*, 2005). Absorption of such short-chain fatty acid in fish is driven by an osmotic gradient between the intestine and blood (Titus and Ahearn, 1992), and so the concentration of these end products of anaerobic metabolism of microbiome in the posterior gut can serve as a rough indicator on potential importance of microbial digestion. Proteobacteria has far and wide presence in the gut microbiota of the aquatic invertebrates and are dominant in crustacean gut (Rungrasamee, 2014; Holt *et al.*, 2020). The phylum proteobacterium is highly diverse in genetics, morphology and physiology (Stackebrandt *et al.*, 1988). Crustaceans predominantly consist of *Vibrio* and *Photobacterium* spp. which have additionally classified sequences attributed to other high-level taxa: Bacteroidetes, Firmicutes, Fusobacteria and Actinobacteria in *Penaeus monodon* (Rungrasamee *et al.*, 2014). Numerous *Vibrio* spp. produce chitinolytic enzymes (Sugita and Ito, 2006), which may express their strength in a chitin-rich environment like crustacean gut by giving a niche substrate for their use. However, the enzymatic capability of a few *Vibrio* spp. may contribute to negative impacts on the carapace of the animals and other health

implications such as red disease, tail necrosis, loose shell syndrome (Jayasree *et al.*, 2006). Microbial profiles are likely impacted by the longitudinal axis of the gut itself as various morphologies and functions along the gut will induce differential pressures on the microbial selection (Holt *et al.*, 2020). These interior variations show comparable taxa in the gut of

wild and farmed *P. monodon* (Rungrasamee *et al.*, 2014). *Penaeus vannamei* guts from various farms were more likely similar to each other despite differences in the microbial community structure of their respective rearing environment (Zoqratt *et al.*, 2018). Table 3 provides the details of the factors that are affecting the microbial communities in fish.

Table 3. Factors that are affecting the microbial communities in fish

Factors	Findings	Reference
Age	Microbial diversity increases with host-age.	Wang <i>et al.</i> , 2018
	Age has a significant influence on the intestinal microbiota; water microbiota strongly influence gut microbiota at early life stages.	Bledsoe <i>et al.</i> , 2016
Diet	Gut microbial diversity decreases as the source of nutrient derivation in the diet are restricted.	Michl <i>et al.</i> , 2017
	Gut microbiome composition as well as metabolite profiles are significantly altered by host species and feeding behaviour.	Li <i>et al.</i> , 2017a
	Colonisation with significantly different adherent and non-adherent communities; non-adherent microbiome are much diverse and diet-dependent than adherent microbiome.	Gajardo <i>et al.</i> , 2017
	Gut microbiome differs by diet treatment but communities in biofilters remain stable independent of diet; gut communities less diverse than those of water and biofilters.	Schmidt <i>et al.</i> , 2016
Environment	Gut microbial diversity increases as the fish develop and is less affected by the surrounding environment than by host diet and development.	Li <i>et al.</i> , 2017b
	Gut environment and other host development processes shape the microbiome.	Yan <i>et al.</i> , 2016
	Water microbial communities strongly shape those in the gut thereby resulting in a correlation between water and gut microbial community dynamics.	Giatsis <i>et al.</i> , 2015
	Environmental factors more strongly influence microbiome at early life stages.	Stephens <i>et al.</i> , 2016
	The microbiome is significantly altered even at a low level of environmental changes but has strong resilience power.	Narrowe <i>et al.</i> , 2015
Host factors	Presence of core gut microbial flora regardless of the habitat type will indicate the operational host selective forces.	Dehler <i>et al.</i> , 2017
	Similar gut microbiota regardless of source; shaped by host factors; differences in composition highlight the habitat-specific taxa.	Lyons <i>et al.</i> , 2017

Table 3, Cont.

Cont. Table 3.

Factors	Findings	Reference
	Gut microbial communities in different species are not exactly the same but also not different altogether.	Song <i>et al.</i> , 2016
External factors	Probiotic administration for a short period significantly affects the gut microbiota composition at later stages of life.	Giatsis <i>et al.</i> , 2016
	Diet, time of sampling and host-specific factors also influence the microbes.	Zarkasi <i>et al.</i> , 2016
Host factors	The gut microbiome is dependent upon the host life history or genetic background; different nutritional stresses affect host-microbiome and health differently.	Gatesoupe <i>et al.</i> , 2016
Trophic levels	Trophic level strongly influences the microbiome composition of fish from the same habitats supported by evidence of a large core gut microbiota in multiple species.	Liu <i>et al.</i> , 2016
Geographical distance	Geographical distance has less impact on gut microbiome; diversity and identity of microbial communities are more strongly determined by life-cycle stage.	Llewellyn <i>et al.</i> , 2016

Methods for manipulation of gut microbiota

The methods of manipulation of gut microbiota in fish include the alteration of dietary proteins and lipids, as well as the addition of probiotics and prebiotics in the diet.

Proteins: The source of proteins (Desai *et al.*, 2012), their quantity (Geurden *et al.*, 2014) and chemical structure (Kotzamanis *et al.*, 2007) of proteins can influence the gut microbial composition. Peptides and glycopeptides, released through protein digestion can modulate the condition and activity of the intestinal cells as well as the microbiota of the gut (Świątecka *et al.*, 2012). Short peptides can be added to the diet that can directly manipulate gut microbial composition by providing suitable substrates for bacteria thus encouraging their proliferation (Kotzamanis *et al.*, 2007). Some peptides produce antimicrobial activity and help to protect against pathogenic bacteria (Sila *et al.*, 2014).

Lipids: It has been confirmed that the increased lipid concentrations resulted in a more diverse gut microbial community in fish (Ringø and Birkbeck, 1999). The studies of Lødemel *et al.* (2001) have shown that the use of plant oils can improve fish's

resistance to pathogenic bacteria as these natural plant oils are deficient in marine polyunsaturated fatty acids, arachidonic acid, eicosapentaenoic acid and docosahexaenoic acid.

Probiotics: Probiotics are live beneficial microorganisms which when administered in adequate amounts confer various health benefits on the host. Several studies have confirmed that the gut microbial communities can be manipulated with the application of probiotics (Asaduzzaman *et al.*, 2018; Siriyappagounder *et al.*, 2018).

Prebiotics: The term 'dietary prebiotics', was defined as "a selectively fermented ingredient, that results in specific changes in the composition and/or activity of the gastrointestinal microbiota, thus conferring benefit(s) upon host health" (Gibson *et al.*, 2010). Galactooligosaccharides, arabinoxylo-oligosaccharides, fructooligosaccharides, chito-oligosaccharide, mannanoligosaccharides, inulin, and levan were the common prebiotics used in aquaculture (Ringø *et al.*, 2014).

Conclusion

The research findings on the gut microbiome of the fish, thus, far as provided an understanding

on the gut microbial communities of various freshwater and marine fish, mechanisms in the development of the fish gut microbiota, the variation in their composition to the different environmental conditions of the water, diet, seasons, and trophic levels. This knowledge will pave way for the exploration of gut microbial

manipulation techniques for increasing production, finding new advanced techniques to study the microbial communities that are normally difficult to culture or identification.

Conflict of interest: The authors declare that there is no conflict of interest.

REFERENCES

- Asaduzzaman M, Sofia E, Shakil A, Haque NF, Khan MNA *et al.*, 2018. Host gut-derived probiotic bacteria promote hypertrophic muscle progression and up regulate growth-related gene expression of slow-growing Malaysian Mahseer *Tortambroides*. *Aquacult Rep*, 9: 37-45, doi: 10.1016/j.aqrep.2017.12.001
- Austin B, 2002. The bacterial microflora of fish. *The Sci World J*, 2: 558-572, doi: 10.1100/tsw.2002.137
- Banerjee S and Ghosh K, 2014. Enumeration of gut associated extracellular enzyme-producing yeasts in some freshwater fishes. *J Appl Ichthyol*, 30(5): 986-993, doi: 10.1111/jai.12457
- Bano N, DeRae Smith A, Bennett W, Vasquez L and Hollibaugh JT, 2007. Dominance of mycoplasma in the guts of the Long-Jawed Mudsucker, *Gillichthys mirabilis*, from five California salt marshes. *Environ Microbiol*, 9(10): 2636-2641, doi: 10.1111/j.1462-2920.2007.01381.x
- Bindiya ES, Tina KJ, Raghul SS and Bhat SG, 2015. Characterization of deep sea fish gut bacteria with antagonistic potential from *Centroscyllium fabricii* (Deep Sea Shark). *Probiotics Antimicrob Proteins*, 7(2): 157-163, doi: 10.1007/s12602-015-9190-x
- Bledsoe JW, Peterson BC, Swanson KS and Small BC, 2016. Ontogenetic characterization of the intestinal microbiota of channel catfish through 16S rRNA gene sequencing reveals insights on temporal shifts and the influence of environmental microbes. *PLoS One*, 11(11): e0166379, doi: 10.1371/journal.pone.0166379
- Burokas A, Moloney RD, Dinan TG and Cryan JF, 2015. Microbiota regulation of the mammalian gut-brain axis. *Adv Appl Microbiol*, 91: 1-62, doi: 10.1016/bs.aambs.2015.02.001
- Cahill MM, 1990. Bacterial flora of fishes: A review. *Microb Ecol*, 19(1): 21-41, doi: 10.1007/BF02015051
- Chen WY, Ng TH, Wu JH, Chen JW and Wang HC, 2017. Microbiome dynamics in a shrimp grow-out pond with possible outbreak of acute hepatopancreatic necrosis disease. *Sci Rep*, 7(1): 9395, doi: 10.1038/s41598-017-09923-6
- Deb S, Das L and Das SK, 2020. Composition and functional characterization of the gut microbiome of freshwater pufferfish (*Tetraodon cutcutia*). *Arch Microbiol*, 202(10): 2761-2770, doi: 10.1007/s00203-020-01997-7
- Dehler CE, Secombes CJ and Martin AM, 2017. Seawater transfer alters the intestinal microbiota profiles of Atlantic salmon (*Salmo salar* L.). *Sci Rep*, 7(1): 13877, doi: 10.1038/s41598-017-13249-8
- Desai AR, Links MG, Collins SA, Mansfield GS, Drew MD *et al.*, 2012. Effects of plant-based diets on the distal gut microbiome of rainbow trout (*Oncorhynchus mykiss*). *Aquaculture*, 350: 134-142, doi: 10.1016/j.aquaculture.2012.04.005
- Egerton S, Culloty S, Whooley J, Stanton C and Ross RP, 2018. The gut microbiota of marine fish. *Front Microbiol*, 9: 873, doi: 10.3389/fmicb.2018.00873
- FAO 2020. Fisheries and Aquaculture topics. Fact Sheets. Text by Jean- Francois Pulvenis. In: FAO Fisheries Division [online], Rome. The State of World Fisheries and Aquaculture (SOFIA), <http://www.fao.org/fishery/> [17 Sept 2020]
- Gajardo K, Jaramillo-Torres A, Kortner TM, Merrifield DL, Tinsley J *et al.*, 2017. Alternative protein sources in the diet modulate microbiota and functionality in the distal intestine of Atlantic salmon (*Salmo salar*). *Appl Environ Microbiol*, 83(5): e02615-16, doi: 10.1128/AEM.02615-16
- Gallagher ML, Luczkovich JJ and Stellwag EJ, 2001.

- Characterization of the ultrastructure of the gastrointestinal tract mucosa, stomach contents and liver enzyme activity of the pinfish during development. *J Fish Biol*, 58(6): 1704-1713, doi: 10.1111/j.1095-8649.2001.tb02324.x
- Gatesoupe FJ, Huelva C, Le Bayon N, Le Delliou H, Madec L *et al.*, 2016. The highly variable microbiota associated to intestinal mucosa correlates with growth and hypoxia resistance of sea bass, *Dicentrarchus labrax*, submitted to different nutritional histories. *BMC Microbiol*, 16(1): 266, doi: 10.1186/s12866-016-0885-2
- German DP, Nagle BC, Villeda JM, Ruiz AM, Thomso AW *et al.*, 2010. Evolution of herbivory in a carnivorous clade of minnows (*Teleostei: Cyprinidae*): effects on gut size and digestive physiology. *Physiol Biochem Zool*, 83(1): 1-18, doi: 10.1086/648510
- Geurden I, Mennigen J, Plagnes-Juan E, Veron V, Cerezo T *et al.*, 2014. High or low dietary carbohydrate: protein ratios during first-feeding affect glucose metabolism and intestinal microbiota in juvenile rainbow trout. *J Exp Biol*, 217(19): 3396-3406, doi: 10.1242/jeb.106062
- Giatsis C, Sipkema D, Smidt H, Heilig H, Benvenuti G *et al.*, 2015. The impact of rearing environment on the development of gut microbiota in tilapia larvae. *Sci Rep*, 5(1): 18206, doi: 10.1038/srep18206
- Giatsis C, Sipkema D, Ramiro-Garcia J, Bacanu GM, Abernathy J *et al.*, 2016. Probiotic legacy effects on gut microbial assembly in tilapia larvae. *Sci Rep*, 6: 33965, doi: 10.1038/srep33965
- Gibbons NE, 1933. The slime and intestinal flora of some marine fishes. *Contrib Can Biol Fish*, 8(1): 275-290, doi: 10.1139/f33-022
- Gibson GR, Scott KP, Rastall RA, Tuohy KM, Hotchkiss A *et al.*, 2010. Dietary prebiotics: current status and new definition. *Food Sci Technol Bull Funct Foods*, 7(1): 1-19, doi: 10.1616/1476-2137.15880
- Gilmour A, McCallum MF and Allan MC, 1976. The bacteriology of power station effluent used to farm marine fish. *Aquaculture*, 7(4): 357-362, doi: 10.1016/0044-8486(76)90132-0
- Givens CE, Ransom B, Bano N and Hollibaugh JT, 2015. Comparison of the gut microbiomes of 12 bony fish and 3 shark species. *Mar Ecol Prog Ser*, 518: 209-223, doi: 10.3354/meps11034
- Gómez GD and Balcázar JL, 2008. A review on the interactions between gut microbiota and innate immunity of fish. *FEMS Immunol Med Microbiol*, 52(2): 145-154, doi: 10.1111/j.1574-695X.2007.00343.x
- Grimes DJ, Brayton P, Colwell RR and Gruber SH, 1985. *Vibrios* as autochthonous flora of neritic sharks. *Syst Appl Microbiol*, 6(2): 221-226, doi: 10.1016/S0723-2020(85)80056-4
- Hagi T, Tanaka D, Iwamura Y and Hoshino T, 2004. Diversity and seasonal changes in lactic acid bacteria in the intestinal tract of cultured freshwater fish. *Aquaculture*, 234(1-4): 335-346, doi: 10.1016/j.aquaculture.2004.01.018
- Hansen GH and Olafsen JA, 1999. Bacterial interactions in early life stages of marine cold water fish. *Microb Ecol*, 38(1): 1-26, doi: 10.1007/s002489900158
- Holt CC, Bass D, Stentiford GD and van der Giezen M, 2020. Understanding the role of the shrimp gut microbiome in health and disease. *J Invertebr Pathol*: 107387, doi: 10.1016/j.jip.2020.107387
- Izvekova GI, Izvekov EI and Plotnikov AO, 2007. Symbiotic microflora in fishes of different ecological groups. *Biol Bull*, 34(6): 610-618, doi: 10.1134/S106235900706012X
- Jami M, Ghanbari M, Kneifel W and Domig KJ, 2015. Phylogenetic diversity and biological activity of culturable Actinobacteria isolated from freshwater fish gut microbiota. *Microbiol Res*, 175: 6-15, doi: 10.1016/j.micres.2015.01.009
- Jayasree L, Janakiram P and Madhavi R, 2006. Characterization of *Vibrio* spp. associated with diseased shrimp from culture ponds of Andhra Pradesh (India). *J World Aquacult Soc*, 37(4): 523-532, doi: 10.1111/j.1749-7345.2006.00066.x
- Kim DH, Brunt J and Austin B, 2007. Microbial diversity of intestinal contents and mucus in rainbow trout (*Oncorhynchus mykiss*). *J Appl Microbiol*, 102(6): 1654-1664, doi: 10.1111/j.1365-2672.2006.03185.x
- Kotzamanis YP, Gisbert E, Gatesoupe FJ, Infante JZ and Cahu C, 2007. Effects of different dietary levels of fish protein hydrolysates on growth, digestive enzymes, gut microbiota, and resistance to *Vibrio anguillarum* in European sea bass (*Dicentrarchus labrax*) larvae. *Comp Biochem Physiol A Mol Integr Physiol*, 147(1): 205-214, doi: 10.1016/j.cbpa.2006.12.037

- Larsen AM, Mohammed HH and Arias CR, 2014. Characterization of the gut microbiota of three commercially valuable warmwater fish species. *J Appl Microbiol*, 116(6): 1396-1404, doi: 10.1111/jam.12475
- Lauzon HL, Gudmundsdottir S, Petursdottir SK, Reynisson E, Steinarsson A *et al.*, 2010. Microbiota of Atlantic cod (*Gadus morhua* L.) rearing systems at pre- and post-hatch stages and the effect of different treatments. *J Appl Microbiol*, 109(5): 1775-1789, doi: 10.1111/j.1365-2672.2010.04806.x
- Li T, Long M, Li H, Gatesoupe FJ, Zhang X *et al.*, 2017a. Multi-omics analysis reveals a correlation between the host phylogeny, gut microbiota and metabolite profiles in cyprinid fishes. *Front Microbiol*, 8: 454, doi: 10.3389/fmicb.2017.00454
- Li X, Zhou L, Yu Y, Ni J, Xu W *et al.*, 2017b. Composition of gut microbiota in the gibel carp (*Carassius auratus gibelio*) varies with host development. *Microb Ecol*, 74(1): 239-249, doi: 10.1007/s00248-016-0924-4
- Liu H, Guo X, Gooneratne R, Lai R, Zeng C *et al.*, 2016. The gut microbiome and degradation enzyme activity of wild freshwater fishes influenced by their trophic levels. *Sci Rep*, 6: 24340, doi: 10.1038/srep24340
- Llewellyn MS, Boutin S, Hoseinifar SH and Derome N, 2014. Teleost microbiomes: the state of the art in their characterization, manipulation and importance in aquaculture and fisheries. *Front Microbiol*, 5: 207, doi: 10.3389/fmicb.2014.00207
- Llewellyn MS, McGinnity P, Dionne M, Letourneau J, Thonier F *et al.*, 2016. The biogeography of the Atlantic salmon (*Salmo salar*) gut microbiome. *ISME J*, 10(5): 1280-1284, doi: 10.1038/ismej.2015.189
- Lødemel JB, Mayhew TM, Myklebust R, Olsen RE, Espelid S *et al.*, 2001. Effect of three dietary oils on disease susceptibility in Arctic charr (*Salvelinus alpinus* L.) during cohabitant challenge with *Aeromonas salmonicida* ssp. *salmonicida*. *Aquacult Res*, 32(12): 935-945, doi: 10.1046/j.1365-2109.2001.00621.x
- Lyons PP, Turnbull JF, Dawson KA and Crumlish M, 2017. Phylogenetic and functional characterization of the distal intestinal microbiome of rainbow trout *Oncorhynchus mykiss* from both farm and aquarium settings. *J Appl Microbiol*, 122(2): 347-363, doi: 10.1111/jam.13347
- Macfarlane GT and Englyst HN, 1986. Starch utilization by the human large intestinal microflora. *J Appl Bacteriol*, 60(3): 195-201, doi: 10.1111/j.1365-2672.1986.tb01073.x
- Mandal S and Ghosh K, 2013. Isolation of tannase-producing microbiota from the gastrointestinal tracts of some freshwater fish. *J Appl Ichthyol*, 29(1): 145-153, doi: 10.1111/j.1439-0426.2012.02054.x
- Margolis L, 1953. The effect of fasting on the bacterial flora of the intestine of fish. *J Fish Res Board Can*, 10(2): 62-63, doi: 10.1139/f53-003
- McCormick SD, Sheehan TF, Björnsson BT, Lipsky C, Kocik JF *et al.*, 2013. Physiological and endocrine changes in Atlantic salmon smolts during hatchery rearing, downstream migration, and ocean entry. *Can J Fish Aquat Sci*, 70(1): 105-118, doi: 10.1139/cjfas-2012-0151
- Michl SC, Ratten JM, Beyer M, Hasler M, LaRoche J *et al.*, 2017. The malleable gut microbiome of juvenile rainbow trout (*Oncorhynchus mykiss*): diet-dependent shifts of bacterial community structures. *PloS One*, 12(5): e0177735, doi: 10.1371/journal.pone.0177735
- Milanez GD, Masangkay FR, Thomas RC, Ordonez MOGO, Bernales GQ *et al.*, 2017. Molecular identification of *Vermamoeba vermiformis* from freshwater fish in lake Taal, Philippines. *Exp Parasitol*, 183: 201-206, doi: 10.1016/j.exppara.2017.09.009
- Narrowe AB, Albuthi-Lantz M, Smith EP, Bower KJ, Roane TM *et al.*, 2015. Perturbation and restoration of the fathead minnow gut microbiome after low-level triclosan exposure. *Microbiome*, 3(1): 6, doi: 10.1186/s40168-015-0069-6
- Nayak SK, 2010. Role of gastrointestinal microbiota in fish. *Aquacult Res*, 41(11): 1553-1573, doi: 10.1111/j.1365-2109.2010.02546.x
- Nielsen S, Walburn JW, Verges A, Thomas T and Egan S, 2017. Microbiome patterns across the gastrointestinal tract of the rabbitfish *Siganus fuscescens*. *Peer J*, 5: e3317, doi: 10.7717/peerj.3317

- Nikouli E, Meziti A, Smeti E, Antonopoulou E, Ment E *et al.*, 2020. Gut microbiota of five sympatrically farmed marine fish species in the Aegean Sea. *Microb Ecol*, PMID: 32840670, doi: 10.1007/s00248-020-01580-z
- Orlov AV, Gerasimov YV and Lapshin OM, 2006. The feeding behaviour of cultured and wild Atlantic salmon, *Salmo salar* L., in the Louvenga River, Kola Peninsula, Russia. *ICES J Mar Sci*, 63(7): 1297-1303, doi: 10.1016/j.icesjms.2006.05.004
- Parris DJ, Brooker RM, Morgan MA, Dixon DL and Stewart FJ, 2016. Whole gut microbiome composition of damselfish and cardinalfish before and after reef settlement. *Peer J*, 4: e2412, doi: 10.7717/peerj.2412
- Rai AK, Jini R, Swapna HC, Sachindra NM, Bhaskar N *et al.*, 2011. Application of native lactic acid bacteria (LAB) for fermentative recovery of lipids and proteins from fish processing wastes: bioactivities of fermentation products. *J Aquat Food Prod Technol*, 20(1): 32-44, doi: 10.1080/10498850.2010.528174
- Reed GB and Spence CM, 1929. The intestinal and slime flora of the haddock: a preliminary report. *Contrib Can Biol Fish*, 4(1): 257-264, doi: 10.1139/f29-019
- Reveco FE, Øverland M, Romarheim OH and Mydland LT, 2014. Intestinal bacterial community structure differs between healthy and inflamed intestines in Atlantic salmon (*Salmo salar* L.). *Aquaculture*, 420: 262-269, doi: 10.1016/j.aquaculture.2013.11.007
- Ringø E and Birkbeck TH, 1999. Intestinal microflora of fish and fry: a review. *Aquacult Res*, 30(2): 73-93
- Ringø E, Olsen RE, Mayhew TM and Myklebust R, 2003. Electron microscopy of the intestinal microflora of fish. *Aquaculture*, 227(1-4): 395-415, doi: 10.1016/j.aquaculture.2003.05.001
- Ringø E, Dimitroglou A, Hoseinifar SH and Davies SJ, 2014. Prebiotics in finfish: an update. In: *Aquaculture nutrition: Gut Health, Probiotics and Prebiotics*, Merrifield DL, Ringø E (edn.), Wiley, pp360-400
- Roeselers G, Mittge EK, Stephens WZ, Parichy DM, Cavanaugh CM *et al.*, 2011. Evidence for a core gut microbiota in the zebrafish. *ISME J*, 5(10): 1595-1608, doi: 10.1038/ismej.2011.38
- Romero J and Navarrete P, 2006. 16S rDNA-based analysis of dominant bacterial populations associated with early life stages of coho salmon (*Oncorhynchus kisutch*). *Microb Ecol*, 51(4): 422-430, doi: 10.1007/s00248-006-9037-9
- Rungrasamee W, Klanchui A, Maibunkaew S, Chaiyapechara S, Jiravanichpaisal P *et al.*, 2014. Characterization of intestinal bacteria in wild and domesticated adult black tiger shrimp (*Penaeus monodon*). *PloS One*, 9(3): e91853, doi: 10.1371/journal.pone.0091853
- Rungrasamee W, Klanchui A, Maibunkaew S and Karoonuthaisiri N, 2016. Bacterial dynamics in intestines of the black tiger shrimp and the Pacific white shrimp during *Vibrio harveyi* exposure. *J Invertebr Pathol*, 133: 12-19, doi: 10.1016/j.jip.2015.11.004
- Sakata T, Sugita H, Mitsuoka T, Kakimoto D and Kadota H, 1980. Isolation and distribution of obligate anaerobic bacteria from the intestines of freshwater fish. *Bull Jap Soc Sci Fish*, 46(10): 1249-1255, doi: 10.2331/suisan.46.1249
- Sandrini S, Aldriwesh M, Alruways M and Freestone P, 2015. Microbial endocrinology: host-bacteria communication within the gut microbiome. *J Endocrinol*, 225(2): R21-R34, doi: 10.1530/JOE-14-0615
- Schmidt VT, Smith KF, Melvin DW and Amaral-Zettler LA, 2015. Community assembly of a euryhaline fish microbiome during salinity acclimation. *Mol Ecol*, 24(10): 2537-2550, doi: 10.1111/mec.13177
- Schmidt V, Amaral-Zettler L, Davidson J, Summerfelt S and Good C, 2016. Influence of fishmeal-free diets on microbial communities in Atlantic salmon (*Salmo salar*) recirculation aquaculture systems. *Appl Environ Microbiol*, 82(15): 4470-4481, doi: 10.1128/AEM.00902-16
- Sequeiros C, Garcés ME, Vallejo M, Marguet ER and Olivera NL, 2015. Potential aquaculture probiont *Lactococcus lactis* TW34 produces nisin Z and inhibits the fish pathogen *Lactococcus garvieae*. *Arch Microbiol*, 197(3): 449-458, doi: 10.1007/s00203-014-1076-x
- Sera H, Ishida Y and Kadota H, 1972. Bacterial-flora in digestive tracts of marine fish-IV. Effect of H⁺ concentration and gastric juices on indigenous bacteria. *Bull Jap Soc Sci Fish*, 38(8): 859-863

- Sila A, Nedjar-Arroume N, Hedhili K, Chataigné G, Balti R *et al.*, 2014. Antibacterial peptides from barbel muscle protein hydrolysates: activity against some pathogenic bacteria. *LWT-Food Sci Technol*, 55(1): 183-188, doi: 10.1016/j.lwt.2013.07.021
- Siriappagounder P, Galindo-Villegas J, Lokesh J, Mulero V, Fernandes JMO *et al.*, 2018. Exposure to yeast shapes the intestinal bacterial community assembly in zebrafish larvae. *Front Microbiol*, 9: 1868, doi: 10.3389/fmicb.2018.01868
- Song W, Li L, Huang H, Jiang K, Zhang F *et al.*, 2016. The gut microbial community of antarctic fish detected by 16S rRNA gene sequence analysis. *BioMed Res Int*, 2016: 3241529, doi: 10.1155/2016/3241529
- Stackebrandt E, Murray RGE and Trüper HG, 1988. Proteobacteria classis nov., a name for the phylogenetic taxon that includes the “purple bacteria and their relatives”. *Int J Syst Microbiol*, 38(3): 321-325, doi: 10.1099/00207713-38-3-321
- Stephens WZ, Burns AR, Stagaman K, Won S, Rawls JF *et al.*, 2016. The composition of the zebrafish intestinal microbial community varies across development. *ISME J*, 10(3): 644-654, doi: 10.1038/ismej.2015.140
- Sugita H, Miyajima C and Deguchi Y, 1991. The vitamin B12-producing ability of the intestinal microflora of freshwater fish. *Aquaculture*, 92: 267-276, doi: 10.1016/0044-8486(91)90028-6
- Sugita H, Kawasaki J and Deguchi Y, 1997. Production of amylase by the intestinal microflora in cultured freshwater fish. *Lett Appl Microbiol*, 24(2): 105-108, doi: 10.1046/j.1472-765X.1997.00360.x
- Sugita H and Ito Y, 2006. Identification of intestinal bacteria from Japanese flounder (*Paralichthys olivaceus*) and their ability to digest chitin. *Lett Appl Microbiol*, 43(3): 336-342, doi: 10.1111/j.1472-765X.2006.01943.x
- Świątecka D, Markiewicz LH and Wróblewska B, 2012. Experimental immunology pea protein hydrolysate as a factor modulating the adhesion of bacteria to enterocytes, epithelial proliferation and cytokine secretion—an *in vitro* study. *Cen Eur J Immunol*, 37(3): 227-231, doi: 10.5114/ceji.2012.30798
- Talwar C, Nagar S, Lal R and Negi RK, 2018. Fish gut microbiome: current approaches and future perspectives. *Indian J Microbiol*, 58(4): 397-414, doi: 10.1007/s12088-018-0760-y
- Tarnecki AM, Burgos FA, Ray CL and Arias CR, 2017. Fish intestinal microbiome: diversity and symbiosis unravelled by metagenomics. *J Appl Microbiol*, 123(1): 2-17, doi: 10.1111/jam.13415
- Teplitski M, Wright AC and Lorca G, 2009. Biological approaches for controlling shellfish-associated pathogens. *Curr Opin Biotech*, 20(2): 185-190, doi: 10.1016/j.copbio.2009.03.001
- Titus E and Ahearn GA, 1992. Vertebrate gastrointestinal fermentation: transport mechanisms for volatile fatty acids. *Am J Physiol Regul Integr Comp Physiol*, 262(4 Pt 2): R547-R553, doi: 10.1152/ajpregu.1992.262.4.R547
- Tran NT, Zhang J, Xiong F, Wang GT, Li WX *et al.*, 2018. Altered gut microbiota associated with intestinal disease in grass carp (*Ctenopharyngodon idellus*). *World J Microbiol Biotechnol*, 34(6): 71, doi: 10.1007/s11274-018-2447-2
- Tsuchiya C, Sakata T and Sugita H, 2008. Novel ecological niche of *Cetobacterium somerae*, an anaerobic bacterium in the intestinal tracts of freshwater fish. *Lett Appl Microbiol*, 46(1): 43-48, doi: 10.1111/j.1472-765X.2007.02258.x
- Uchii K, Matsui K, Yonekura R, Tani K, Kenzaka T *et al.*, 2006. Genetic and physiological characterization of the intestinal bacterial microbiota of bluegill (*Lepomis macrochirus*) with three different feeding habits. *Microb Ecol*, 51(3): 277-284, doi: 10.1007/s00248-006-9018-z
- Verschuere L, Rombaut G, Sorgeloos P and Verstraete W, 2000. Probiotic bacteria as biological control agents in aquaculture. *Microbiol Mol Biol Rev*, 64(4): 655-671, doi: 10.1128/mmbr.64.4.655-671.2000
- Walter JM, Bagi A and Pampanin DM, 2019. Insights into the potential of the Atlantic cod gut microbiome as biomarker of oil contamination in the marine environment. *Microorganisms*, 7(7): 209, doi: 10.3390/microorganisms7070209
- Wang AR, Ran C, Ringø E and Zhou ZG, 2018. Progress in fish gastrointestinal microbiota research. *Rev Aquacult*, 10(3): 626-640, doi: 10.1111/raq.12191

- White WL, Coveny AH, Robertson J and Clements KD, 2010. Utilisation of mannitol by temperate marine herbivorous fishes. *J Exp Mar Biol Ecol*, 391(1-2): 50-56, doi: 10.1016/j.jembe.2010.06.007
- Willmott ME, Clements KD and Wells RMG, 2005. The influence of diet and gastrointestinal fermentation on key enzymes of substrate utilization in marine teleost fishes. *J Exp Mar Biol Ecol*, 317(1): 97-108, doi: 10.1016/j.jembe.2004.11.008
- Xia JH, Lin G, Fu GH, Wan ZY, Lee M *et al.*, 2014. The intestinal microbiome of fish under starvation. *BMC Genomics*, 15: 266, doi: 10.1186/1471-2164-15-266
- Xiong JB, Nie L and Chen J, 2019. Current understanding on the roles of gut microbiota in fish disease and immunity. *Zool Res*, 40(2): 70, doi: 10.24272/j.issn.2095-8137.2018.069
- Yan Q, Li J, Yu Y, Wang J, He Z *et al.*, 2016. Environmental filtering decreases with fish development for the assembly of gut microbiota. *Environ Microbiol*, 18(12): 4739-4754, doi: 10.1111/1462-2920.13365
- Zarkasi KZ, Taylor RS, Abell GC, Tamplin ML, Glencross BD *et al.*, 2016. Atlantic salmon (*Salmo salar* L.) gastrointestinal microbial community dynamics in relation to digesta properties and diet. *Microb Ecol*, 71(3): 589-603, doi: 10.1007/s00248-015-0728-y
- Zoqratt MZHM, Eng WWH, Thai BT, Austin CM and Gan HM, 2018. Microbiome analysis of Pacific white shrimp gut and rearing water from Malaysia and Vietnam: implications for aquaculture research and management. *PeerJ*, 6: e5826, doi: 10.7717/peerj.5826