Gut Microbes and Its Physiological Role in Fish: Adaptive Strategies for Climatic Variability

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Abstract

The gut microbes of fish encompass various effects on the host such as the size of the fish, their metabolism, food, feeding behavior, and immunity. The process is mediated through interaction between microbes and the gut-brain axis. In fish larvae, the microbes are introduced from the egg, surrounding water, and their first feed. However, there is species-specific variation in the colonization of microbial communities. The microbial composition of the gut varies; some dominant microbes are Proteobacteria, Firmicutes, Bacteroidetes, Actinobacteria, and Fusobacteria. The various environmental, ecological, and evolutionary factors affect intestinal microbial communities and their functions. Various intrinsic factors also influence the gut microbes such as phylogeny, sexual state, life stages, trophic status, and genetics. The gut microbial community modulates the host's physiology and the host provides nutrients to the gut microbes. The gut microbial activity depends on the composition and the diversity of gut microbes. The feeding, digestion, and metabolism of the host can be affected by gut microbes. In addition, it also influences stress response, reproduction, development, and immune response. Food and feeding alteration can change the gut microbial community. The inclusion of different proteins, lipids, probiotics, prebiotics, etc. can alter the gut microbes and enhance the health status.

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1 Introduction

Microbes are different microorganisms, present in the environment. Microbiome refers to the characteristic microbial community inhabiting a well-defined habitat with distinct physicochemical parameters (Whipps et al. 1988*)*. Microbes are ubiquitous and present across all life-sustaining habitats on Earth; the differences exist in the varied environment which carries different microbial communities. Microbes are not only present in these external environments, but they are also found to be associated with many eukaryotic hosts (Sullam et al. 2012). The impact of microbial communities on the health of various types of the host such as plants, fish, and terrestrial animals including humans has gained wide attention nowadays (Brugman et al. 2018). The microbiota can offer various benefits to the host by supplementing adequate nutrients, inducing host immune development and metabolism, and protecting the host against invading pathogens (Brugman et al. 2018). Vertebrates' gastrointestinal (GI) tract is a composite microbial ecosystem containing a complex and dynamic association of microorganisms, which have crucial roles in the nutrition and health of the host (Wang et al. 2018). The various environmental factors influence the microbial community composition; at the same time microbes also influence the host environment (Bletz et al. 2017).

2 Gut Microbiota

Gut microbiomes are the microbes present in the intestine. The gut microbiomes of fish encompass various effects on the host such as the overall size of fish, their metabolism, food and feeding behavior, and their immunity (Yukgehnaish et al. 2020). The gut microbes are dynamic. These microbiomes are either transient or persistent, depending on the duration they live in the gut microbiota (Prasanth et al. 2018). The persistent microbiota lives in association with the gut wall and has a symbiont relationship with the host (Zhang et al. 2016). The transient microbiota comes through external sources such as food and does not live for a longer period in the stomach (Yukgehnaish et al. 2020).

3 Origin and Sources of Gut Microbes

Various factors control the gut microbial content of an infant. In fishes, the origin of gut microbes is still in the infant stage. In humans, it has been suggested that the gut microbes might have been introduced through the birth canal, pass through the oral cavity to the placenta, or subsequently introduced through the gastrointestinal tract in infants during breastfeeding (Prince et al. 2014; Gueimonde et al. 2006). In fish larvae, the entrance of microbes occurs from the egg, the adjacent water, and their initial feed (Egerton et al. 2018). However, there is species-specific variation in the colonization of microbial communities (Egerton et al. 2018). The species-specific variation in the microbial community in the larvae represents the variation of egg glycoprotein (Larsen 2014). The variation of these microbes depends on the variation of the surrounding environment from where the microbes are being attached to the egg surface. The chorion-attached bacteria subsequently colonize the gut of the newly developed larvae (Larsen 2014). The colonization of bacteria further diversifies when the larvae take the water from the environment (Lauzon et al. 2010). The feeding habit of fish also influences their microbial diversity and changes as the larvae develop into fry, fingerling, and adults (Ringø and Birkbeck 1999; Egerton et al. 2018). It has been observed that this microbial population becomes stable within the first 50 days in various species (Larsen 2014).

4 Diversity of Gut Microbes

The variability is one of the remarkable features of GI microbiota in fishes. It is not yet fully understood the complex process involved in the regulations of these bacterial populations in the GI tract of fish. Few studies have been focused on fishes such as Rainbow trout, Common carp, Atlantic cod, Atlantic salmon, Grass carp, and Zebrafish (Wang et al. 2018). The microbial composition of the gut varies although some dominant microbes are Actinobacteria, Bacteroidetes, Firmicutes, Fusobacteria, and Proteobacteria (Eichmiller et al. 2016). The various environmental, ecological, and evolutionary factors affect intestinal microbial communities and their functions. Various intrinsic factors also influence the gut microbes such as phylogeny, sexual state, life stage, trophic status, and genetics (Egerton et al. 2018). Closely related mammals having similar diets are found to harbor similar gut microbes (Sullam et al. 2012). The diversity of gut microbes also varies between fish species and within fish species. The composition of gut bacteria in fishes can be determined by the habitat, trophic level, and possibly host phylogeny shape (Sullam et al. 2012). Various research proved that the microbial flora composition varies (Table 1) in different fish species owing to their nutrition, intestinal microenvironment, age, geography, environmental factors, stress, etc. (Verschuere et al. 2000; Skrodenyte-Arbaciauskiene et al. 2008). The variation of gut microbiota depends up on the type of fish species and environmental conditions such as developmental stage of fish, feeding regime, seasonal variation, temperature, pH, nutrients intake, captive sate, and sexual state which allows the host to perform different functions and enables the host to thrive in various conditions (Hansen and Olafsen 1999; Dhanasiri et al. 2011; Hovda et al. 2012; Miyake et al. 2015; Apajalahti 2005; Cordero et al. 2015). The most influencing factor to affect the diversity of fish is trophic status, habitat of the fish, and host ancestry (Sullam et al. 2012).

Table 1 Microbial diversity in different fish species

Fish species	Dominant bacteria	References
Freshwater		
Salmo trutta fario	Aeromonas, *Buttiauxella agrestis*, *Budvicia aquatica*, *Erwinia persicinus*, *Obesumbacterium proteus*	Skrodenyte-Arbaciauskiene et al. (2006)
Onchorhyncus mykiss	Proteobacteria, Actinobacteria, Fusobacteria	Navarrete et al. (2012)
	Bacteroidetes, Fusobacteria, Proteobacteria, Firmicutes, and Actinobacteria	Michl et al. (2017)
	Tenericutes, Firmicutes, Proteobacteria, Bacteroidetes	Lyons et al. (2017)
Silurus meridionalis	Tenericutes, Fusobacteria, Proteobacteria, and Bacteroidetes	Zhang et al. (2018)
Aristichthys nobilis	Firmicutes, Methylocaldum, and Bacillus	Zeng et al. (2020)
Hypophthalmichthys molitrix	Cyanobacteria, Proteobacteria, Actinobacteria, Bacteroidetes	Ye et al. (2014)
	Anaerospora	Zeng et al. (2020)
Danio rerio	Aeromonas, Pseudomonas	Bates et al. (2006)
	Lactobacillus plantarum, *Lactobacillus fermentum*	Russo et al. (2015)
	Planctomycetes, Fusobacteria, Verrucomicrobia	Koo et al. (2017)
Ctenopharyngodon idella	Proteobacteria, Firmicutes, Actinobacteria	Han et al. (2010)
	Proteobacteria and Cyanobacteria	Zeng et al. (2020)
Gambusia affinis	Proteobacteria and Flavobacteria	Carlson et al. (2017)
Carassius auratus	Fusobacteria, Proteobacteria, Bacteriodetes	Li et al. (2017)
	Firmicutes, Methylocaldum, and Bacillus	Zeng et al. (2020)
Silurus asotus	Aeromonas, Flavobacterium, Bacteroides, Pseudomonas	Di Maiuta et al. (2013)
Lagodon rhomboides	Clostridium, Mycoplasma, Photobacterium	Ransom (2008)
Oreochromis niloticus	Firmicutes, Actinobacteria, Proteobacteria	Zhai et al. (2017)
Morone saxatilis	Aeromonas, Pseudomonas, Vibrio	MacFarlane et al. (1986)
Paralichthys lethostigma	Clostridium, Photobacterium	Givens et al. (2015)
Salmo salar	*Acinetobacter junii*, Mycoplasma, Lactobacillus	Holben et al. (2002)
	Escherichia, Propionibacterium	Green et al. (2013)
Acipenser baerii	*Cetobacterium somerae*	Geraylou et al. (2013)
Morone saxatilis	Aeromonas, Pseudomonas, Vibrio	MacFarlane et al. (1986)
Ictalurus punctatus	Bacteroidetes, Firmicutes, Fusobacteria, Proteobacteria	Gatesoupe et al. (2016)
Astyanax mexicanus	Gammaproteobacteria, Firmicutes, Bacteroidetes, and Betaproteobacteria	Ornelas-García et al. (2018)

(continued)

Table 1 (continued)

Fish species	Dominant bacteria	References
Marine water		
Odax pullus	Clostridium, *Eubacterium desmolans*, Papillibacter	Clements et al. (2007)
Sardinella longiceps	Achromobacter, Vibrio, Pseudomonas	Karthiayani and Mahadeva Iyer (1967)
Scomber scombrus	Psychrobacter, Vibrio, Shewanella	Svanevik and Lunestad (2011)
Trematomus bernacchii,	Proteobacteria, Actinobacteria, Firmicutes, Thermi, Bacteroidetes Tenericutes	Yan et al. (2016)
Gadus morhua	Aeromonas, Cytophaga, Pseudomonas, Lactobacillus	Strøm and Ringø (1993)
Gillichthys mirabilis	Mycoplasma	Bano et al. (2007)
Clupea harengus	Flavobacterium, Pseudomonas	Hansen et al. (1992)
	Psychrobacter, Alteromonas	Curson et al. (2010)
Syngnathus scovelli	Proteobacteria	Ransom (2008)
Chanos chanos	Vibrio, Pseudomonas	Fernandez et al. (1996)
Dicentrarchus labrax	Moraxella, Vibrio, Acinetobacter	Gatesoupe et al. (1997)
	Proteobacteria, Bacteroidetes, Actinobacteria, Firmicutes	Gajardo et al. (2017)
Sparus aurata	Pseudomonas	Floris et al. (2013)
Hippoglossus hippoglossus	*Photobacterium phosphoreum* (adults)	Verner-Jeffreys et al. (2003)
Pagrus major	Cytophaga, Aeromonas, Pseudomonas, Vibrio	Muroga et al. (1987)
Hermosilla azurea	Faecalibacterium, Enterovibrio, Bacteroides, Desulfovibrio	Fidopiastis et al. (2006)
Solea solea	Moraxella, Pseudomonas, Flavobacterium	Campbell and Buswell (1983)
Scophthalmus maximus	*Vibrio alginolyticus*, *Vibrio anguillarum*, *Vibrio harveyii*, Pseudomonas, Acinetobacter	Munro et al. (1994)
	Vibrio, Acinetobacter, Moraxello	Gatesoupe et al. (1997)
Sebastes schlegeli	Acinetobacter, *V. alginolyticus*, *V. anguillarum*, Pseudomonas	Tanasomwang and Muroga (1989)
Acanthopagrus schlegeli	Aeromonas, Pseudomonas, Vibrio	Muroga et al. (1987)
Cynoscion nebulosus	*Escherichia coli*	Ransom (2008)

(continued)

Table 1 (continued)

Fish species	Dominant bacteria	References
Gadus morhua	Pseudoalteromonas, Microbacterium, Roseobacter	Reid et al. (2009), Aschfalk and Muller (2002)
	Clostridium perfringens, *Vibrio* sp.	Star et al. (2013)
Sciaenops ocellatus	Cetobacterium, Vibrio, Photobacterium	Ransom (2008), Givens et al. (2015)
Paralichthys lethostigma	Clostridium, Photobacterium	Ransom (2008), Givens et al. (2015)
Acanthurus sp.	Epulopiscium	Miyake et al. (2015)
Pomatomus saltatrix	*Vibrio* sp., Pseudomonas	Newman et al. (1972)
Notothenia coriiceps, Chaenocephalus aceratus	*Vibrio* sp., Photobacterium	Ward et al. (2009)
Solea senegalensis	*Vibrio ichthyoenteri*	Martin-Antonio et al. (2007)
Kyphosus sydneyanus	*Clostridium* sp.	Moran et al. (2005)
Salmo trutta trutta	*Aeromonas sobria*, Pseudomonas	Skrodenyte-Arbačiauskiene et al. (2008)
Fugu niphobles	Flavobacterium, Vibrio, Pseudomonas	Sugita et al. (1989)
Plecoglossus altivelis	Gammaproteobacteria, Alphaproteobacteria, Firmicutes, and Bacteroides	Nie et al. (2017)
Andamia tetradactylus	Spirochaetes and Tenericutes	Yoshida et al. (2022)
Reef associated		
Acanthurus nigricans, Chlorurus sordidus, Lutjanus bohar	Proteobacterium, *Vibrio ponticus*, *Vibrio fortis*	Smriga et al. (2010)
Aplodactylus arctidens	Clostridium, *Eubacterium desmolans*, Papillibacter	Clements et al. (2007)
Epinephelus coioides	Pseudomonas, Bacillus, Acinetobacter, Vibrio	Sun et al. (2009)
Pomacentrus moluccensis	*Vibrio harveyi*, Shewanella, Endozoicomonas	Parris et al. (2016)
P. amboinensis		
P. wardii		
P. bankanensis		
P. nagasakiensis		
P. chrysurus		
Siganus fuscescens	Proteobacteria, Cyanobacteria, and Firmicutes	Nielsen et al. (2017)

4.1 Trophic Level

The gut microbes of the fishes change with the trophic status of the fish and correlate it with the availability of natural food and their feeding behavior (Liu et al. 2016). The understanding of fish gut microbiota and their role in the digestion of food is vital (Wang et al. 2018). This will help to accelerate the digestion and health of fish for the culture of various fish species. Various studies have been done to find the gut microbial composition of fish with different feeding habits (Givens et al. 2015). It has been found that the gut microbial content of herbivores is distinct from carnivorous fish (Liu et al. 2016). The planktivorous and benthivorous showed unique microbial content for different fish species in their gut (Uchii et al. 2006). However, the bacterial diversity is found lesser in carnivores, and gradually increases in omnivores and herbivores (Wang et al. 2018). The gut microbiota varies with species belonging to the same trophic level as observed in herbivorous fishes like silver carp, bighead, and grass carp (Li et al. 2018).

The digestive tract of herbivorous fish harbors anaerobic bacteria of the phylum Firmicutes and class Clostridia (Mouchet et al. 2012). The dominance of Firmicutes in the gastrointestinal tract has been observed in many fish species (Clements et al. 2007; Miyake et al. 2015). The microbes repeatedly occur in omnivores, planktivores, and carnivores are Aeromonas, Pseudomonas, and Vibrionaceae (Egerton et al. 2018). The microbes such as *Pseudomonas* spp., Aeromonas, and *Photobacterium* spp. produce digestive enzymes such as proteases and chitinases which help in digestion (MacDonald et al. 1986; Itoi et al. 2006). However, the diversity of these microbes varies with habitat, season, feeding and sex, and age.

4.2 Genetic and Sex of the Host

The composition of microbes varies within and between species. The interspecies variation in gut microbial diversity has been observed for snout bream, bighead carp, grass carp, and silver carp (Li et al. 2018). The variation in gut microbes between sex has also been observed for stickleback (*Gasterosteus aculeatus*), which might be due to sex-specific microbial interaction of feed variation (Bolnick et al. 2014). But only a few studies prevail in the area and its mechanism is poorly understood.

However, among the genetics and environment, the environment has more influence on the diet composition of fishes. It has been observed that different fish species (Channel catfish and blue catfish) even in the same environmental condition may harbor the same gut microbial content (Lokesh et al. 2018).

4.3 Age of the Fish

The microbial diversity changes with the age of fish. The reason might be due to the diet variation and hormonal changes in different life stages of fish (Cantas et al. 2012). The gut microbial diversity is increased with age in catfishes (Zhang et al.

2018). In Atlantic salmon also gut microbes vary between embryo and hatchlings, and hatchings exhibited more microbial diversity (Lokesh et al. 2018).

4.4 Season

The diversity and abundance of gut microbes change with the season (Hagi et al. 2004; Sullam et al. 2012). The variation might be for a short duration or a longer period. The seasonal variation in gut microbes might have influenced due to temperature variation or due to changes in food composition in the gut (Al-Harbi and Uddin 2004). The dominant taxa vary with season (Hagi et al. 2004), and the count of total bacteria peaks during summer and autumn (Macmillan and Santucci 1990; Al-Harbi and Uddin 2004). However Neuman et al. (2016) could not find any relationship between season and change in gut microbial diversity.

4.5 Habitat

The change in habitat affects the gut microbial content. The salinity of water and temperature influence the microbial community. In black molly dominant microbes vary as the salinity increases, whereas in rainbow trout temperature changes the dominant microbes (Schmidt et al. 2015; Huyben et al. 2018). It has been observed that the microbial diversity varies between freshwater and marine habitat fishes (Vatsos 2016). Vibrio is the common microbes occurring in marine habitat fishes whereas in the freshwater fishes Aeromonas and Pseudomonas dominate (Vatsos 2016).

Various pollutants such as pesticides and heavy metals influence the gut microbial composition. In common carp and zebrafish, it has been observed that polystyrene microparticles and waterborne copper influence the microbes associated with the immunity (Meng et al. 2018; Jin et al. 2018).

In the captive state also, the gut microbes depend on many factors such as food ingredients, environment, and social behavior (Egerton et al. 2018). The altered gut microbiota in captive breeding has been reported in many freshwater and marine fish species (Bucio et al. 2006; Nelson et al. 2013). Under captive management, various factors such as stocking density, stress, feed, and use of antibiotics (Verschuere et al. 2000; Navarrete et al. 2008; Clements et al. 2014) can alter the gut microbiota. In the zebrafish model, it has been shown that there are changes in gut microbiota in captive and lab-reared fish; however, some microbes remained the same depending on their historical correlation (Roeselers et al. 2011). Various others also reported that although there are habitat-specific changes, there always exists some core microbiota (Roeselers et al. 2011).

5 Physiological Roles of Gut Microbiota

The gut microbial community modulates the host's physiology, and the host provides nutrients for the gut microbes (Rosenbaum et al. 2015). However, the gut microbial activity depends on the composition and the diversity of gut microbes (Vigneri 2014). The host physiology which can be affected by gut microbes is feeding, digestion, and metabolism; it also influences stress response, reproduction, growth, and immunity (Butt and Volkoff 2019).

5.1 Influence of Microbiota on Feeding and Metabolism

The gut microbes have a major role in the regulation of feeding, digestive process, and metabolism (Duca et al. 2012). In fishes, limited studies have been conducted to identify the effect of microbes on feeding and metabolism (Butt and Volkoff 2019). These microbes secrete short-chain fatty acid, indoles and butyrate, etc. in the form of metabolites and affect digestion and metabolism (Butt and Volkoff 2019). These microbiotas also influence the gut neurotransmitter such as serotonin, dopamine, etc., and affect the function of the gut such as motility, release of enzyme, and feeding behavior (Yano et al. 2015; Strandwitz 2018). The gut neurotransmitter also influences the microbes and modifies the discharge of cytokines (Mittal et al. 2017).

Some of the metabolites regulate the cells of the intestine and regulate their uptake, absorption, etc., and thus affect various metabolism such as adipogenesis (Bäckhed et al. 2004). The gut microbial release also modulates the secretion of gut enzymes and thus gut motility (Cani and Knauf 2016). The released microbial compounds may also circulate to reach the brain or may regulate the release of appetite-regulating peptides which may stimulate the release of central neuropeptides (Cussotto et al. 2018).

In fish also some studies have shown the influence of gut microbiota on metabolism. The microbial community can alter the metabolism pathway of carbohydrate, fat, and protein changes in grass carp (Ni et al. 2013). In zebrafish also it has been observed that change in gut microbes changes the lipid metabolism (Semova et al. 2012).

5.2 Effect of Gut Microbial Activity on Stress Response

Fishes may get stressed due to many factors such as poor water quality, lack of oxygen, temperature, and overcrowding. The stress affects the microbial community composition and changes the gut mucus and adversely affects the nutrient absorption and immunity of the host (Cantas et al. 2012). This may decrease the feeding rate and increase the chances of pathogen infection (Sekirov and Finlay 2009) as observed in goldfish and chinook salmon (Volkoff and Peter 2004; Bernier 2010). The microbes influence the hypothalamic-pituitary-adrenal (HPA) axis which is subjected to hormone control behavioral response such as feeding (Sudo 2014).

5.3 Effect of Gut Microbial Activity on Reproduction

The exact mechanism of gut microbes on reproduction is not clear. Some studies have shown that gut microbes help in gonadal development and reproduction (Butt and Volkoff 2019). In larval fish, the supplementation of probiotics improves their development and gonadal maturation as observed in zebrafish (Avella et al. 2012; Carnevali et al. 2013). In adult zebrafish and goldfish, the probiotic microbes improved gonadosomatic indexes (GSI), produced more eggs, higher reproductive gene expression, and higher reproductive success (Ghosh et al. 2007; Carnevali et al. 2013).

5.4 Effect of Gut Microbial Activity on Development

The gut microbes vary with the developmental stages. It has been found that as the fish grows their microbial diversity increases in grass carp (Wang et al. 2015). In Zebrafish the lack of microbes impaired the development of the gastrointestinal tract and the reversal of microbes may resume the function (Lescak and Milligan-Myhre 2017). The microbes may also influence neuronal development and affect the movement and feeding and ultimately the development of fish (Phelps et al. 2017).

5.5 Effect of Gut Microbial Activity on Immunity

The gut microbes play a critical role in developing the immune response of the host fish. The pathogens are defended by the intestinal microbes in host fishes (Kim et al. 2017). These pathogens could not interrupt the gut barrier and could not hamper the brain and intestine function (Ribet and Cossart 2015). The microbes present in the gut shows a competitive behavior for space with the pathogen, and they also secrete the antimicrobial peptides to disrupt the pathogen (Kim et al. 2017). In rainbow trout, it has been observed that supplementation of beneficial microbes enhances the immunity of the host (Adel et al. 2017).

6 Adaptive Strategy for Climatic Variability

The gut microbiota is allied with the health condition of fish. These microbes can be manipulated to enhance the health status of fish. Food and feeding alteration can change the gut microbial community. The inclusion of different proteins, lipids, probiotics, and prebiotics can alter the microbes of the gut and enhance health status (Egerton et al. 2018). The variation in diet and gut microbiota has been reported by various authors (Delcroix et al. 2015; Zarkasi et al. 2016), and it could be helpful as an adaptive strategy for climatic variations.

6.1 Protein

Protein acts as a source of energy in food. At the same time, the inclusion of different protein diets can also alter the gut microbiota. The type of protein and its quantity can affect the gut microbial structure (Desai et al. 2012; Geurden et al. 2014; Zarkasi et al. 2016). Peptides and glycopeptides produced after protein hydrolysis can make changes in the gut diversity (Swiatecka et al. 2012), and the supply of direct protein hydrolysates can act as a substrate for microbes and enhance their growth (Delcroix et al. 2015). The protein hydrolysate also helps to combat pathogenic bacteria, certain peptides act as antimicrobials whereas some amino acids regulate the immune pathway and synthesis of antibodies (Kiron 2012; Sila et al. 2014; Egerton et al. 2018). Thus they assist to improve the health status of fish.

6.2 Lipids

Lipid is also the main energy basis in fish. It has been found that increasing the lipid content enhances the gut microbial diversity (Lesel et al. 1989). Variation of lipid diet alters the microbial diversity in arctic char (Ringø et al. 2002). It has been shown that change of fish oil to plant-based oil improves the gut microbial community and immunity of fish against pathogens (Lødemel et al. 2001; Ringø et al. 2002). Various microbes isolated from the gut of fishes and invertebrates such as *Shewanella* sp. and *Vibrio* sp. produce polyunsaturated fatty acids (Monroig et al. 2013). These microbes can act as a potential probiotic (Egerton et al. 2018).

6.3 Probiotics

Probiotics are live microorganisms that supply health benefits to the host. These microorganisms are used as a substitute for antibiotics in aquaculture (Abelli et al. 2009). Among microorganisms, the gram-negative bacteria, gram-positive bacteria, bacteriophages, and yeasts could be used as probiotics (Akhter et al. 2015). Bacillus and Lactobacillus are the most recurrently used probiotics in aquaculture (Merrifield and Carnevali 2014). These microbes help to increase the growth rate and modulate the immune reaction of the host (Lobo et al. 2014; Cordero et al. 2015). In the aquaculture sector, these probiotics help to improve the health and nutritional status and reduce the cost (El-Haroun et al. 2006). However it is difficult to process, store, and feed the probiotics in aquaculture (Merrifield et al. 2010).

6.4 Prebiotic

Prebiotics are the substrates used to confer a health benefit in host fishes in a selective mode (Cremon et al. 2018). The commonly used prebiotics are fructooligosaccharides, mannan-oligosaccharides, inulin, and *trans*-galactooligosaccharides (Ringø et al. 2016). The prebiotic also helps to improve the growth, feed conversion, nutrient uptake, and immunity of fish (Bongers and van den Heuvel 2003; Torrecillas et al. 2007; Adel et al. 2016). However, the success of prebiotic administration depends on the age of the fish, species of fish culture condition, and dose of prebiotics (Torrecillas et al. 2014).

7 Next-Generation Sequencing Study of Gut Microbes

A detailed understanding between intestinal microbiota and their host fish can depict the function and dysfunction of the host organism. Conventional culture-dependent studies on fish intestinal microbiota were conducted over the last decades (Cahill 1990). However, these microbiotas only indicate $<0.1\%$ of the total microbial community in the intestine of host fishes with low cultivability (Romero and Navarrete 2006; Navarrete et al. 2009; Zhou et al. 2014; Ghanbari et al. 2015). With the advancement in DNA sequencing and bioinformatics, extensive molecular ecology-based methods on the 16S and 23S rRNA genes have become more frequently used recently.

The next-generation sequencing (NGS) technology based on the 16S and 23S rRNA and the development of various bioinformatics software has advanced the knowledge of these microbial taxa. More efficient and budget-friendly approaches to NGS technologies have gained wide attention for studying the high dense gut microbiota composition and its genetic potential (Ghanbari et al. 2015). The emerging rapid and reliable NGS techniques can enrich the knowledge of the fish gut microbial community with promising results.

8 Conclusion

Fish gut microbes affect the physiology, immunity, and growth of fish. The gut microbial composition of fish varies in different fish species and within fish species differs in different life stages. The various intrinsic and extrinsic factors also influence the gut microbes and their activity. Fish gut microbial composition differed depending on species, sex, habitat, and feeding behavior. The gut microbial manipulation through prebiotics has the potential to promote the growth and health condition of fish.

References

Abelli L, Randelli E, Carnevali O, Picchietti S (2009) Stimulation of gut immune system by early administration of probiotic strains in *Dicentrarchus labrax* and *Sparus aurata*. Ann N Y Acad Sci 1163:340–342. https://doi.org/10.1111/j.1749-6632.2008.03670.x

Adel M, Nayak S, Lazado CC, Yeganeh S (2016) Effects of dietary prebiotic GroBiotic®—a on growth performance, plasma thyroid hormones and mucosal immunity of great sturgeon, Husohuso (Linnaeus, 1758). J Appl Ichthyol 32:825–831. https://doi.org/10.1111/jai.13153

Adel M, Lazado CC, Safari R, Yeganeh S, Zorriehzahra MJ (2017) AqualaseR, a yeast-based in-feed probiotic, modulates intestinal microbiota, immunity and growth of rainbow trout Oncorhynchus mykiss. Aquac Res 48:1815–1826. https://doi.org/10.1111/are.13019

Akhter N, Wu B, Memon AM, Mohsin M (2015) Probiotics and prebiotics associated with aquaculture: a review. Fish Shellfish Immunol 45:733–741. https://doi.org/10.1016/j.fsi.2015.05.038

Al-Harbi AH, Uddin MN (2004) Seasonal variation in the intestinal bacterial flora of hybrid tilapia (Oreochromis niloticus × Oreochromis aureus) cultured in earthen ponds in Saudi Arabia. Aquaculture 229:37–44. https://doi.org/10.1016/S0044-8486(03)00388-0

Apajalahti J (2005) Comparative gut microflora, metabolic challenges, and potential opportunities. J Appl Poult Res 14(2):444–453

Aschfalk A, Muller W (2002) Clostridium perfringens toxin types from wild-caught Atlantic cod (Gadus morhua L.), determined by PCR and ELISA. Can J Microbiol 48:365–368

Avella MA, Place A, Du SJ, Williams E, Silvi S, Zohar Y et al (2012) Lactobacillus rhamnosus accelerates zebrafish backbone calcification and gonadal differentiation through effects on the GnRH and IGF systems. PLoS One 7:e45572. https://doi.org/10.1371/journal.pone.004557258

Bäckhed F, Ding H, Wang T, Hooper LV, Koh GY, Nagy A et al (2004) The gut microbiota as an environmental factor that regulates fat storage. Proc Natl Acad Sci U S A 101:15718–15723. https://doi.org/10.1073/pnas.0407076101

Bano N, deRae Smith A, Bennett W, Vasquez L, Hollibaugh JT (2007) Dominance of Mycoplasma in the guts of the long-jawed mudsucker, Gillichthys mirabilis, from five California salt marshes. Environ Microbiol 9:2636–2641

Bates JM, Mittge E, Kuhlman J, Baden KN, Cheesman SE, Guillemin K (2006) Distinct signals from the microbiota promote different aspects of zebrafish gut differentiation. Dev Biol 297: 374–386

Bernier NJ (2010) Food intake regulation and disorders. Fish Dis Disord 2:238–266. https://doi.org/10.1079/9781845935535.0238

Bletz MC, Archer H, Harris RN, McKenzie VJ, Rabemananjara FC, Rakotoarison A, Vences M (2017) Host ecology rather than host phylogeny drives amphibian skin microbial community structure in the biodiversity hotspot of Madagascar. Front Microbiol 8:1530

Bolnick DI, Snowberg LK, Hirsch PE, Lauber CL, Org E, Parks B et al (2014) Individual diet has sex-dependent effects on vertebrate gut microbiota. Nat Commun 5:ncomms5500. https://doi.org/10.1038/ncomms5500

Bongers A, van den Heuvel EG (2003) Prebiotics and the bioavailability of minerals and trace elements. Food Rev Int 19:397–422. https://doi.org/10.1081/FRI120025482

Brugman S, Ikeda-Ohtsubo W, Braber S, Folkerts G, Pieterse CM, Bakker PA (2018) A comparative review on microbiota manipulation: lessons from fish, plants, livestock, and human research. Front Nutr 5:80

Bucio A, Hartemink R, Schrama JW, Verreth J, Rombouts FM (2006) Presence of lactobacilli in the intestinal content of freshwater fish from a river and from a farm with a recirculation system. Food Microbiol 23:476–482. https://doi.org/10.1016/j.fm.2005.06.001

Butt RL, Volkoff H (2019) Gut microbiota and energy homeostasis in fish. Front Endocrinol 10:9

Cahill MM (1990) Bacterial flora of fishes: a review. Microb Ecol 19:21–41. https://doi.org/10.1007/BF02015051

Campbell AC, Buswell JA (1983) The intestinal microflora of farmed Dover sole (Solea solea) at different stages of fish development. J Appl Microbiol 55:215–223. https://doi.org/10.1111/j.1365-2672.1983.tb01318.x

Cani PD, Knauf C (2016) How gut microbes talk to organs: the role of endocrine and nervous routes. Mol Metabol 5:743–752. https://doi.org/10.1016/j.molmet.2016.05.011

Cantas L, Sorby JR, Alestrom P, Sorum H (2012) Culturable gut microbiota diversity in zebrafish. Zebrafish 9:26–37. https://doi.org/10.1089/zeb.2011.0712

Carlson JM, Leonard AB, Hyde ER, Petrosino JF, Primm TP (2017) Microbiome disruption and recovery in the fish Gambusia affinis following exposure to broad-spectrum antibiotic. Infect Drug Resist 10:143

Carnevali O, Avella MA, Gioacchini G (2013) Effects of probiotic administration on zebrafish development and reproduction. Gen Comp Endocrinol 188:297–302. https://doi.org/10.1016/j.ygcen.2013.02.022

Clements KD, Pasch IB, Moran D, Turner SJ (2007) Clostridia dominate 16S rRNA gene libraries prepared from the hindgut of temperate marine herbivorous fishes. Mar Biol 150:1431–1440. https://doi.org/10.1007/s00227-006-0443-9

Clements KD, Angert ER, Montgomery WL, Choat JH (2014) Intestinal microbiota in fishes: what's known and what's not. Mol Ecol 23:1891–1898. https://doi.org/10.1111/mec.12699

Cordero H, Guardiola FA, Tapia-Paniagua ST, Cuesta A, Meseguer J, Balebona MC et al (2015) Modulation of immunity and gut microbiota after dietary administration of alginate encapsulated Shewanella putrefaciens Pdp11 to gilthead seabream (Sparus aurata L.). Fish Shellfish Immunol 45:608–618. https://doi.org/10.1016/j.fsi.2015.05.010

Cremon C, Barbaro MR, Ventura M, Barbara G (2018) Pre-and probiotic overview. Curr Opin Pharmacol 43:87–92

Curson AR, Sullivan MJ, Todd JD, Johnston AW (2010) Identification of genes for dimethyl sulfide production in bacteria in the gut of Atlantic Hrring (Clupea harengus). ISME J 4:144–146. https://doi.org/10.1038/ismej.2009.93

Cussotto S, Sandhu KV, Dinan TG, Cryan JF (2018) The neuroendocrinology of the microbiota-gut-brain axis: a behavioural perspective. Front Neuroendocrinol 51:80–101. https://doi.org/10.1016/j.yfrne.2018.04.002

Delcroix J, Gatesoupe FJ, Desbruyères E, Huelvan C, Le Delliou H, Le Gall MM, Quazuguel P et al (2015) The effects of dietary marine protein hydrolysates on the development of sea bass larvae, Dicentrarchus labrax, and associated microbiota. Aquac Nutr 21:98–104. https://doi.org/10.1111/anu.12139

Desai AR, Links MG, Collins SA, Mansfield GS, Drew MD, Van Kessel AG et al (2012) Effects of plant-based diets on the distal gut microbiome of rainbow trout (Oncorhynchus mykiss). Aquaculture 350:134–142. https://doi.org/10.1016/j.aquaculture.2012.04.005

Dhanasiri AK, Brunvold L, Brinchmann MF, Korsnes K, Bergh O, Kiron V (2011) Changes in the intestinal microbiota of wild Atlantic cod Gadus morhua L. upon captive rearing. Microb Ecol 61:20–30. https://doi.org/10.1007/s00248-010-9673-y

Di Maiuta N, Schwarzentruber P, Schenker M, Schoelkopf J (2013) Microbial population dynamics in the faeces of woodeating loricariid catfishes. Lett Appl Microbiol 56:401–407

Duca FA, Swartz TD, Sakar Y, Covasa M (2012) Increased oral detection, but decreased intestinal signaling for fats in mice lacking gut microbiota. PLoS One 7:e39748. https://doi.org/10.1371/journal.pone.0039748

Egerton S, Culloty S, Whooley J, Stanton C, Ross RP (2018) The gut microbiota of marine fish. Front Microbiol 9:873. https://doi.org/10.3389/fmicb.2018.00873

Eichmiller JJ, Hamilton MJ, Staley C, Sadowsky MJ, Sorensen PW (2016) Environment shapes the fecal microbiome of invasive carp species. Microbiome 4:44. https://doi.org/10.1186/s40168-016-0190-1

El-Haroun E, Goda AS, Chowdhury K (2006) Effect of dietary probiotic Biogen R supplementation as a growth promoter on growth performance and feed utilization of Nile tilapia Oreochromis niloticus (L.). Aquac Res 37:1473–1480. https://doi.org/10.1111/j.1365-2109.2006.01584.x

Fernandez RD, Tendencia EA, Leano EM, Duray MN (1996) Bacterial flora of milkfish, Chanos chanos, eggs and larvae. Fish Pathol 31:123–128. https://doi.org/10.3147/jsfp.31.123

Fidopiastis PM, Bezdek DJ, Horn MH, Kandel JS (2006) Characterizing the resident, fermentative microbial consortium in the hindgut of the temperate-zone herbivorous fish, Hermosilla azurea (Teleostei: Kyphosidae). Mar Biol 148:631–642

Floris R, Manca S, Fois N (2013) Microbial ecology of intestinal tract of gilthead sea bream (Sparus aurata Linnaeus, 1758) from two coastal lagoons of Sardinia (Italy). Trans Waters Bull 7:4–12

Gajardo K, Jaramillo-Torres A, Kortner TM, Merrifield DL, Tinsley J, Bakke AM, Krogdahl Å (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–e02616

Gatesoupe F-J, Infante JLZ, Cahu C, Quazuguel P (1997) Early weaning of seabass larvae, Dicentrarchus labrax: the effect on microbiota, with particular attention to iron supply and exoenzymes. Aquaculture 158:117–127. https://doi.org/10.1016/S0044-8486(97)00179-8

Gatesoupe FJ, Huelvan C, Le Bayon N, Le Delliou H, Madec L, Mouchel O, Quazuguel P, Mazurais D, Zambonino-Infante JL (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):1–13

Geraylou Z, Souffreau C, Rurangwa E, Maes GE, Spanier KI, Courtin CM et al (2013) Prebiotic effects of arabinoxylan oligosaccharides on juvenile Siberian sturgeon (Acipenser baerii) with emphasis on the modulation of the gut microbiota using 454 pyrosequencing. FEMS Microbiol Ecol 86:357–371

Geurden I, Mennigen J, Plagnes-Juan E, Veron V, Cerezo T, Mazurais D 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 217:3396–3406. https://doi.org/10.1242/jeb.106062

Ghanbari M, Kneifel W, Domig KJ (2015) A new view of the fish gut microbiome: advances from next-generation sequencing. Aquaculture 448:464–475. https://doi.org/10.1016/j.aquaculture.2015.06.033

Ghosh S, Sinha A, Sahu C (2007) Effect of probiotic on reproductive performance in female livebearing ornamental fish. Aquac Res 38:518–526. https://doi.org/10.1111/j.1365-2109.2007.01696.x

Givens CE, Ransom B, Bano N, Hollibaugh JT (2015) Comparison of the gut microbiomes of 12 bony fish and 3 shark species. Mar Ecol Prog Ser 518:209–223

Green TJ, Smullen R, Barnes AC (2013) Dietary soybean protein concentrate-induced intestinal disorder in marine farmed Atlantic salmon, Salmo salar is associated with alterations in gut microbiota. Vet Microbiol 166:286–292

Gueimonde M, Sakata S, Kalliomäki M, Isolauri E, Benno Y, Salminen S (2006) Effect of maternal consumption of lactobacillus GG on transfer and establishment of fecal bifidobacterial microbiota in neonates. J Pediatr Gastroenterol Nutr 42(2):166–170

Hagi T, Tanaka D, Iwamura Y, Hoshino T (2004) Diversity and seasonal changes in lactic acid bacteria in the intestinal tract of cultured freshwater fish. Aquaculture 234:335–346. https://doi.org/10.1016/j.aquaculture.2004.01.018

Han S, Liu Y, Zhou Z, He S, Cao Y, Shi P et al (2010) Analysis of bacterial diversity in the intestine of grass carp (Ctenopharyngodon idellus) based on 16S rDNA gene sequences. Aquac Res 42: 47–56

Hansen G, Olafsen J (1999) Bacterial interactions in early life stages of marine cold water fish. Microb Ecol 38:1–26. https://doi.org/10.1007/s002489900158

Hansen G, Strøm E, Olafsen J (1992) Effect of different holding regimens on the intestinal microflora of herring (Clupea harengus) larvae. Appl Environ Microbiol 58:461–470

Holben W, Williams P, Saarinen M, Särkilahti L, Apajalahti J (2002) Phylogenetic analysis of intestinal microflora indicates a novel Mycoplasma phylotype in farmed and wild salmon. Microb Ecol 44:175–185

Hovda MB, Fontanillas R, McGurk C, Obach A, Rosnes JT (2012) Seasonal variations in the intestinal microbiota of farmed Atlantic salmon (Salmo salar L.). Aquac Res 43:154–159. https://doi.org/10.1111/j.1365-2109.2011.02805.x

Huyben D, Sun L, Moccia R, Kiessling A, Dicksved J, Lundh T (2018) Dietary live yeast and increased water temperature influence the gut microbiota of rainbow trout. J Appl Microbiol 124:1377–1392. https://doi.org/10.1111/jam.13738

Itoi S, Okamura T, Koyama Y, Sugita H (2006) Chitinolytic bacteria in the intestinal tract of Japanese coastal fishes. Can J Microbiol 52:1158–1163. https://doi.org/10.1139/w06-082

Jin Y, Xia J, Pan Z, Yang J, Wang W, Fu Z (2018) Polystyrene microplastics induce microbiota dysbiosis and inflammation in the gut of adult zebrafish. Environ Pollut 235:322–329. https://doi.org/10.1016/j.envpol.2017.12.088

Karthiayani T, Mahadeva Iyer K (1967) Quantitative and qualitative studies on the bacterial flora of fresh sardines. Fish Technol 4:89–97

Kim S, Covington A, Pamer EG (2017) The intestinal microbiota: antibiotics, colonization resistance, and enteric pathogens. Immunol Rev 279:90–105. https://doi.org/10.1111/imr.12563

Kiron V (2012) Fish immune system and its nutritional modulation for preventive health care. Anim Feed Sci Technol 173:111–133. https://doi.org/10.1016/j.anifeedsci.2011.12.015

Koo H, Hakim JA, Powell ML, Kumar R, Eipers PG, Morrow CD, Crowley M, Lefkowitz EJ, Watts SA, Bej AK (2017) Metagenomics approach to the study of the gut microbiome structure and function in zebrafish Danio rerio fed with gluten formulated diet. J Microbiol Methods 135: 69–76

Larsen AM (2014) Studies on the microbiota of fishes and the factors influencing their composition. Auburn University, Auburn

Lauzon HL, Gudmundsdottir S, Petursdottir SK, Reynisson E, Steinarsson A, Oddgeirsson M et al (2010) Microbiota of Atlantic cod (Gadus morhua L.) rearing systems at pre- and posthatch stages and the effect of different treatments. J Appl Microbiol 109(5):1775–1789

Lescak EA, Milligan-Myhre KC (2017) Teleosts as model organisms to understand host-microbe interactions. J Bacteriol 199:e00868-16. https://doi.org/10.1128/JB.00868-16

Lesel R, De La Noüe J, Choubert G (1989) Fecal bacterial flora of rainbow trout under antibiotic treatment: effect of the number of pyloric caeca and the lipid content of food. In: De Pauw N, Jaspers E, Ackefors H, Wilkins N (eds) Aquaculture: a biotechnology in progress, vol 1. European Aquaculture Society, Bredene, p 592

Li T et al (2017) Bacterial signatures of “red-operculum” disease in the gut of crucian carp (Carassius auratus). Microbial Ecol 74:510–521. https://doi.org/10.1007/s00248-017-0967-1

Li X, Yu Y, Li C, Yan Q (2018) Comparative study on the gut microbiotas of four economically important Asian carp species. Sci China Life Sci 11:1–10. https://doi.org/10.1007/s11427-016-9296-5

Liu Y, Yao Y, Li H, Qiao F, Wu J, Du ZY et al (2016) Influence of endogenous and exogenous estrogenic endocrine on intestinal microbiota in zebrafish. PLoS One 11:e0163895. https://doi.org/10.1371/journal.pone.0163895

Lobo C, Moreno-Ventas X, Tapia-Paniagua S, Rodríguez C, Moriñigo MA, de La Banda IG (2014) Dietary probiotic supplementation (Shewanella putrefaciens Pdp11) modulates gut microbiota and promotes growth and condition in Senegalese sole larviculture. Fish Physiol Biochem 40: 295–309. https://doi.org/10.1007/s10695-013-9844-0

Lødemel JB, Mayhew TM, Myklebust R, Olsen RE, Espelid S, Ringø E (2001) Effect of three dietary oils on disease susceptibility in Arctic charr (Salvelinus alpinus L.) during cohabitant challenge with Aeromonas salmonicida ssp. salmonicida. Aquac Res 32:935–945. https://doi.org/10.1046/j.1365-2109.2001.00621.x

Lokesh J, Kiron V, Sipkema D, Fernandes JMO, Moum T (2018) Succession of embryonic and the intestinal bacterial communities of Atlantic salmon (Salmo salar) reveals stage-specific microbial signatures. Microbiol Open 13:e00672. https://doi.org/10.1002/mbo3.672

Lyons PP, Turnbull JF, Dawson KA, 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 122:347–363. https://doi.org/10.1111/jam.13347

MacDonald N, Stark J, Austin B (1986) Bacterial microflora in the gastrointestinal tract of Dover sole (Solea solea L.), with emphasis on the possible role of bacteria in the nutrition of the host. FEMS Microbiol Lett 35:107–111. https://doi.org/10.1111/j.1574-6968.1986.tb01508.x

MacFarlane RD, McLaughlin JJ, Bullock G (1986) Quantitative and qualitative studies of gut flora in striped bass from estuarine and coastal marine environments. J Wildl Dis 22:344–348

Macmillan JR, Santucci T (1990) Seasonal trends in intestinal bacterial flora of farm-raised channel catfish. J Aquat Anim Health 2:217–222. https://doi.org/10.1577/1548-8667(1990)0022.3.CO;2

Martin-Antonio B, Manchado M, Infante C, Zerolo R, Labella A, Alonso C et al (2007) Intestinal microbiota variation in Senegalese sole (Solea senegalensis) under different feeding regimes. Aquac Res 38:1213–1222

Meng XL, Li S, Qin CB, Zhu ZX, Hu WP, Yang LP et al (2018) Intestinal microbiota and lipid metabolism responses in the common carp (Cyprinus carpio L.) following copper exposure. Ecotoxicol Environ Saf 160:257–264. https://doi.org/10.1016/j.ecoenv.2018.05.050

Merrifield DL, Carnevali O (2014) Probiotic modulation of the gut microbiota of fish. In: Merrifield D, Ringø E (eds) Aquaculture nutrition: gut health, probiotics and prebiotics. John Wiley & Sons, Ltd., Chichester, pp 185–222

Merrifield DL, Dimitroglou A, Foey A, Davies SJ, Baker RT, Bøgwald J et al (2010) The current status and future focus of probiotic and prebiotic applications for salmonids. Aquaculture 302: 1–18. https://doi.org/10.1016/j.aquaculture.2010.02.007

Michl SC, Ratten JM, Beyer M, Hasler M, LaRoche J, Schulz C (2017) The malleable gut microbiome of juvenile rainbow trout (Oncorhynchus mykiss): diet-dependent shifts of bacterial community structures. PLoS One 12(5):e0177735

Mittal R, Debs LH, Patel AP, Nguyen D, Patel K, O'Connor G et al (2017) Neurotransmitters: the critical modulators regulating gut-brain axis. J Cell 232:2359

Miyake S, Ngugi DK, Stingl U (2015) Diet strongly influences the gut microbiota of surgeonfishes. Mol Ecol 24:656–672. https://doi.org/10.1111/mec.13050

Monroig Ó, Tocher DR, Navarro JC (2013) Biosynthesis of polyunsaturated fatty acids in marine invertebrates: recent advances in molecular mechanisms. Mar Drugs 11:3998–4018. https://doi.org/10.3390/md11103998

Moran D, Turner S, Clements K (2005) Ontogenetic development of the gastrointestinal microbiota in the marine herbivorous fish Kyphosus sydneyanus. Microb Ecol 49:590–597

Mouchet MA, Bouvier C, Bouvier T, Troussellier M, Escalas A, Mouillot D (2012) Genetic difference but functional similarity among fish gut bacterial communities through molecular and biochemical fingerprints. FEMS Microbiol Ecol 79:568–580. https://doi.org/10.1111/j.1574-6941.2011.01241.x

Munro PD, Barbour A, Birkbeck TH (1994) Comparison of the gut bacterial flora of start-feeding larval turbot reared under different conditions. J Appl Microbiol 77:560–566. https://doi.org/10.1111/j.1365-2672.1994.tb04402.x

Muroga K, Higashia M, Keitoku H (1987) The isolation of intestinal microflora of farmed red seabream (Pagrus major) and black seabream (Acanthopagrus schlegeli) at larval and juvenile stages. Aquaculture 65:79–88. https://doi.org/10.1016/0044-8486(87)90272-9

Navarrete P, Mardones P, Opazo R, Espejo R, Romero J (2008) Oxytetracycline treatment reduces bacterial diversity of intestinal microbiota of Atlantic salmon. J Aquat Anim Health 20:177–183. https://doi.org/10.1577/H07-043.1

Navarrete P, Espejo RT, Romero J (2009) Molecular analysis of microbiota along the digestive tract of juvenile Atlantic salmon (Salmo salar L.). Microb Ecol 57:550–561. https://doi.org/10.1007/s00248-008-9448-x

Navarrete P, Magne F, Araneda C, Fuentes P, Barros L, Opazo R et al (2012) PCR-TTGE analysis of 16S rRNA from rainbow trout (Oncorhynchus mykiss) gut microbiota reveals host-specific communities of active bacteria. PLoS One 7:e31335

Nelson TM, Rogers TL, Carlini AR, Brown MV (2013) Diet and phylogeny shape the gut microbiota of Antarctic seals: a comparison of wild and captive animals. Environ Microbiol 15:1132–1145. https://doi.org/10.1111/1462-2920.12022

Neuman C, Hatje E, Zarkasi KZ, Smullen R, Bowman JP, Katouli M (2016) The effect of diet and environmental temperature on the faecal microbiota of farmed Tasmanian Atlantic Salmon (Salmo salar L.). Aquac Res 47:660–672. https://doi.org/10.1111/are.12522

Newman JTJ, Cosenza BJ, Buck JD (1972) Aerobic microflora of the bluefish (Pomatomus saltatrix) intestine. J Fish Res Board Can 29:333–336

Ni J, YanQ YY, Zhang T (2013) Factors influencing the grass carp gut microbiome and its effect on metabolism. FEMS Microbiol Ecol 87:704–714. https://doi.org/10.1111/1574-6941.12256

Nie L, Zhou QJ, Qiao Y, Chen J (2017) Interplay between the gut microbiota and immune responses of ayu (Plecoglossus altivelis) during Vibrio anguillarum infection. Fish Shellfish Immunol 68: 479–487

Nielsen S, Walburn JW, Verges A, Thomas T, Egan S (2017) Microbiome patterns across the gastrointestinal tract of the rabbitfish Siganus fuscescens. PeerJ 5:e3317

Ornelas-García P, Pajares S, Sosa-Jiménez VM, Rétaux S, Miranda-Gamboa RA (2018) Microbiome differences between river-dwelling and cave-adapted populations of the fish Astyanax mexicanus (De Filippi, 1853). PeerJ 6:e5906

Parris DJ, Brooker RM, Morgan MA, Dixson DL, Stewart FJ (2016) Whole gut microbiome composition of damselfish and cardinalfish before and after reef settlement. PeerJ 4:e2412

Phelps D, Brinkman NE, Keely SP, Anneken EM, Catron TR, Betancourt D et al (2017) Microbial colonization is required for normal neurobehavioral development in zebrafish. Sci Rep 7:11244. https://doi.org/10.1038/s41598-017-10517-5

Prasanth B, Venkatesh K, Rajesh P, Gayathri R, Kanchana M, Nurul Amin SM et al (2018) A mini review on immune role of chemokines and its receptors in snakehead murrel Channa striatus. Fish Shellfish Immunol 72:670–678

Prince AL, Antony KM, Chu DM, Aagaard KM (2014) The microbiome, parturition, and timing of birth: more questions than answers. J Reprod Immunol 104–105:12–19. https://doi.org/10.1016/j.jri.2014.03.006

Ransom BL (2008) Intestinal microbial community composition of six Actinopterygii fish species in the southeastern United States. University of Georgia, Athens

Reid HI, Treasurer JW, Adam B, Birkbeck TH (2009) Analysis of bacterial populations in the gut of developing cod larvae and identification of Vibrio logei, Vibrio anguillarum and Vibrio splendidus as pathogens of cod larvae. Aquaculture 288:36–43

Ribet D, Cossart P (2015) How bacterial pathogens colonize their hosts and invade deeper tissues. Microbes Infect 17:173–183. https://doi.org/10.1016/j.micinf.2015.01.004

Ringø E, Birkbeck TH (1999) Intestinal microflora of fish larvae and fry. Aquac Res 30:73–93. https://doi.org/10.1046/j.1365-2109.1999.00302.x

Ringø E, Lødemel JB, Myklebust R, Jensen L, Lund V, Mayhew TM et al (2002) The effects of soybean, linseed and marine oils on aerobic gut microbiota of Arctic charr Salvelinus alpinus L. before and after challenge with Aeromonas salmonicida ssp. salmonicida. Aquac Res 33: 591–606. https://doi.org/10.1046/j.1365-2109.2002.00697.x

Ringø E, Zhou Z, Vecino JLG, Wadsworth S, Romero J, Krogdahl Å et al (2016) Effect of dietary components on the gut microbiota of aquatic animals. A never-ending story? Aquac Nutr 22: 219–282. https://doi.org/10.1111/anu.12346

Roeselers G, Mittge EK, Stephens WZ, Parichy DM, Cavanaugh CM, Guillemin K et al (2011) Evidence for a core gut microbiota in the zebrafish. ISME J 5:1595–1608. https://doi.org/10.1038/ismej.2011.38

Romero J, Navarrete P (2006) 16S rDNA-based analysis of dominant bacterial populations associated with early life stages of coho salmon (Oncorhynchus kisutch). Microb Ecol 51: 422–430. https://doi.org/10.1007/s00248-006-9037-9

Rosenbaum M, Knight R, Leibel RL (2015) The gut microbiota in human energy homeostasis and obesity. Trends Endocrinol Metab 26:493–501. https://doi.org/10.1016/j.tem.2015.07.002

Russo P, Iturria I, Mohedano ML, Caggianiello G, Rainieri S, Fiocco D, Angel Pardo M, López P, Spano G (2015) Zebrafish gut colonization by mCherry-labelled lactic acid bacteria. Appl Microbiol Biotechnol 99(8):3479–3490

Schmidt VT, Smith KF, Melvin DW, Amaral-Zettler LA (2015) Community assembly of a euryhaline fish microbiome during salinity acclimation. Mol Ecol 24:2537–2550. https://doi.org/10.1111/mec.13177

Sekirov I, Finlay BB (2009) The role of the intestinal microbiota in enteric infection. J Physiol 587: 4159–4167. https://doi.org/10.1113/jphysiol.2009.172742

Semova I, Carten JD, Stombaugh J, Mackey LC, Knight R, Farber SA et al (2012) Microbiota regulate intestinal absorption and metabolism of fatty acids in the zebrafish. Cell Host Microbe 12:277–288. https://doi.org/10.1016/j.chom.2012.08.003

Sila A, Nedjar-Arroume N, Hedhili K, Chataigné G, Balti R, Nasri M et al (2014) Antibacterial peptides from barbel muscle protein hydrolysates: activity against some pathogenic bacteria. LWT Food Sci Technol 55:183–188. https://doi.org/10.1016/j.lwt.2013.07.021

Skrodenyte-Arbaciauskiene V, Sruoga A, Butkauskas D (2006) Assessment of microbial diversity in the river trout Salmotrutta fario L. intestinal tract identified by partial 16S rRNA gene sequence analysis. Fish Sci 72:597–602

Skrodenyte-Arbačiauskiene V, Sruoga A, Butkauskas D, Skrupskelis K (2008) Phylogenetic analysis of intestinal bacteria of freshwater salmon Salmo salar and sea trout Salmo trutta trutta and diet. Fish Sci 74:1307–1314. https://doi.org/10.1111/j.1444-2906.2008.01656.x

Smriga S, Sandin SA, Azam F (2010) Abundance, diversity, and activity of microbial assemblages associated with coral reef fish guts and feces. FEMS Microbiol Ecol 73:31–42

Star B, Haverkamp TH, Jentoft S, Jakobsen KS (2013) Next generation sequencing shows high variation of the intestinal microbial species composition in Atlantic cod caught at a single location. BMC Microbiol 13:248

Strandwitz P (2018) Neurotransmitter modulation by the gut microbiota. Brain Res 1693:128–133. https://doi.org/10.1016/j.brainres.2018.03.015

Strøm E, Ringø E (1993) Changes in bacterial flora in developing cod, Gadus morhua (L.), larvae after inoculation of lactobacillus plantarum in the water. In: Walther B, Fyhn HJ (eds) Physiological and biochemical aspects of fish larval development. University of Bergen, Bergen, pp 226–228

Sudo N (2014) Microbiome, HPA axis and production of endocrine hormones in the gut. In: Microbial endocrinology: the microbiota-gut-brain axis in health and disease. Springer, New York, pp 177–194

Sugita H, Iwata J, Miyajima C, Kubo T, Noguchi T, Hashimoto K et al (1989) Changes in microflora of a puffer fish Fugu niphobles, with different water temperatures. Mar Biol 101: 299–304

Sullam KE, Essinger SD, Lozupone CA, O'Connor MP, Rosen GL, Knight R et al (2012) Environmental and ecological factors that shape the gut bacterial communities of fish: a meta-analysis. Mol Ecol 21:3363–3378. https://doi.org/10.1111/j.1365-294X.2012.05552.x

Sun Y, Yang H, Ling Z, Chang J, Ye J (2009) Gut microbiota of fast and slow growing grouper Epinephelus coioides. Afr J Microbiol Res 3:637–640

Svanevik CS, Lunestad BT (2011) Characterisation of the microbiota of Atlantic mackerel (Scomber scombrus). Int J Food Microbiol 151:164–170

Swiatecka D, Markiewicz LH, 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. Cent Eur J Immunol 37:227–231. https://doi.org/10.5114/ceji.2012.30798

Tanasomwang V, Muroga K (1989) Intestinal microflora of rockfish Sebastes schlegeli, tiger puffer Takifugu rubripes and red grouper Epinephelus akaara at their larval and juvenile stages. Nippon Suisan Gakkaishi 55:1371–1377

Torrecillas S, Makol A, Caballero M, Montero D, Robaina L, Real F et al (2007) Immune stimulation and improved infection resistance in European sea bass (Dicentrarchus labrax) fed mannan oligosaccharides. Fish Shellfish Immunol 23:969–981. https://doi.org/10.1016/j.fsi.2007.03.007

Torrecillas S, Montero D, Izquierdo M (2014) Improved health and growth of fish fed mannan oligosaccharides: potential mode of action. Fish Shellfish Immunol 36:525–544. https://doi.org/10.1016/j.fsi.2013.12.029

Uchii K, Matsui K, Yonekura R, Tani K, Kenzaka T, Nasu M, Kawabata ZI (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

Vatsos IN (2016) Standardizing the microbiota of fish used in research. Lab Anim 51:353–364. https://doi.org/10.1177/0023677216678825

Verner-Jeffreys DW, Shields RJ, Bricknell IR, Birkbeck TH (2003) Changes in the gut-associated microflora during the development of Atlantic halibut (Hippoglossus hippoglossus L.) larvae in three British hatcheries. Aquaculture 219:21–42

Verschuere L, Rombaut G, Sorgeloos P, Verstraete W (2000) Probiotic bacteria as biological control agents in aquaculture. Microbiol Mol Biol Rev 64:655–671. https://doi.org/10.1128/MMBR.64.4.655-671.2000

Vigneri S (2014) The brain-gut axis: from pathophysiology to possible future strategies of treatment. Brain Disord Ther 3:137. https://doi.org/10.4172/2168-975X.1000137

Volkoff H, Peter RE (2004) Effects of lipopolysaccharide treatment on feeding of goldfish: role of appetite-regulating peptides. Brain Res 998:139–147

Wang W, Wu S, Zheng Y, Cheng Y, Li W, Zou H et al (2015) Characterization of the bacterial community associated with early-developmental stages of grass carp (Ctenopharyngodon idella). Aquac Res 46:2728–2735. https://doi.org/10.1111/are.12428

Wang AR, Ran C, Ringø E, Zhou ZG (2018) Progress in fish gastrointestinal microbiota research. Rev Aquacult 10:626–640. https://doi.org/10.1111/raq.12191

Ward NL, Steven B, Penn K, Methe BA, Detrich WH (2009) Characterization of the intestinal microbiota of two Antarctic notothenioid fish species. Extremophiles 13:679–685

Whipps J, Lewis K, Cooke R (1988) Mycoparasitism and plant disease control. In: Burge M (ed) Fungi in biological control systems. Manchester University Press, Manchester, pp 161–187. ISBN 9780719019791

Yan Q, Li J, Yu Y, Wang J, He Z, Van Nostrand JD, Kempher ML, Wu L, Wang Y, Liao L, Li X, Wu S, Ni J, Wang C, Zhou J (2016) Environmental filtering decreases with fish development for the assembly of gut microbiota. Environ Microbiol 18(12):4739–4754

Yano JM, Yu K, Donaldson GP, Shastri GG, Ann P, Ma L et al (2015) Indigenous bacteria from the gut microbiota regulate host serotonin biosynthesis. Cell 161:264–276. https://doi.org/10.1016/j.cell.2015.02.047

Ye L, Amberg J, Chapman D, Gaikowski M, Liu WT (2014) Fish gut microbiota analysis differentiates physiology and behavior of invasive Asian carp and indigenous American fish. ISME J 8:541–551

Yoshida MA, Tanabe T, Akiyoshi H, Kawamukai M (2022) Gut microbiota analysis of Blenniidae fishes including an algae-eating fish and clear boundary formation among isolated Vibrio strains. Sci Rep 12(1):1–13

Yukgehnaish K, Kumar P, Sivachandran P, Marimuthu K, Arshad A, Paray BA, Arockiaraj J (2020) Gut microbiota metagenomics in aquaculture: factors influencing gut microbiome and its physiological role in fish. Rev Aquac 12(3):1903–1927

Zarkasi KZ, Taylor RS, Abell GC, Tamplin ML, Glencross BD, Bowman JP (2016) Atlantic salmon (Salmo salar L.) gastrointestinal microbial community dynamics in relation to digesta properties and diet. Microb Ecol 71:589–603. https://doi.org/10.1007/s00248-015-0728-y

Zeng A, Tan K, Gong P, Lei P, Guo Z, Wang S et al (2020) Correlation of microbiota in the gut of fish species and water. 3 Biotech 10(11):1–10

Zhai Q, Yu L, Li T, Zhu J, Zhang C, Zhao J, Zhang H, Chen W (2017) Effect of dietary probiotic supplementation on intestinal microbiota and physiological conditions of Nile tilapia (Oreochromis niloticus) under waterborne cadmium exposure. Antonie Van Leeuwenhoek 110:501–513. https://doi.org/10.1007/s10482-016-0819-x

Zhang C, Derrien M, Levenez F, Brazeilles R, Ballal SA, Kim J et al (2016) Ecological robustness of the gut microbiota in response to ingestion of transient food-borne microbes. ISME J 10(9): 2235–2245

Zhang Z, Li D, Refaey MM, Xu W, Tang R, Li L (2018) Host age affects the development of southern catfish gut bacterial community divergent from that in the food and rearing water. Front Microbiol 9:495. https://doi.org/10.3389/fmicb.2018.00495

Zhou Z, Yao B, Romero J, Waines P, Ringø E, Emery M et al (2014) Methodological approaches used to assess fish gastrointestinal communities. In: Merrifield D, Ringø E (eds) Aquaculture nutrition: gut health, probiotics and prebiotics. John Wiley & Sons Ltd., Hoboken