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REVIEW

Recent progress in the understanding of the gut microbiota of marine fishes

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Abstract
As the significance of the gut microbiota has become increasingly realized, a large number of related studies have emerged. With respect to the gut microbial composition of fish, the predominant gut microbes and core gut microbiota have been reported by many researchers. Our understanding of fish gut microbiota, especially its functional roles, has fallen far behind that of terrestrial vertebrates, although previous studies using gnotobiotic zebrafish models have revealed that the gut microbiota performs a significant role in gut development, nutrient metabolism and immune responses. Given that environmental factors of marine habitats are very different from those of freshwater habitats, a distinct difference may exist in the gut microbiota between freshwater and marine fish. Therefore, this review aims to address the advances in marine fish gut microbiota in terms of methodologies, the gut microbial composition, and gnotobiotic models of marine fish, the important factors (host genotype and three environmental factors: temperature, salinity and diet) that drive marine fish gut microbiota, and significant roles of the gut microbiota in marine fish.

Keywords Marine fish · Gut microbiota · Gnotobiotic · Influence factors · Gut microbial functions

Introduction

As an important part of digestion and absorption, the gut is also a significant immune and endocrine organ of the host. The gut microbiota is significant for the host as they are closely related to the normal operation of the intestinal functions. Fish is one of the most species-rich, economically and ecologically important vertebrate groups, which is also important for the provision of quality food for human beings. Although much progress has been made in exploring and characterizing the gut microbiota in many fish species, there are still numerous issues to be resolved. Compared to the huge contribution of fish species to total vertebrate diversity, the gut microbiota of fish is still far from being fully understood and exploited. So far, most of the studies on fish gut microbiota are still descriptive, and mainly concerned with the composition of microbial communities. Moreover, our understanding of the fish gut microbiota, especially its functional roles, is still superficial. A large part of our insights into the complicated cross-talk between the gut microbiota and fish host is deduced from terrestrial vertebrates, and obtained from some studies using gnotobiotic zebrafish (*Danio rerio*). This is the most successful and mature model for delineating the functional roles of the gut microbiota in fish. Gnotobiotic animal models comprise one of the most significant in vivo experimental models for investigating the functions of the gut microbiota. Previous studies using gnotobiotic zebrafish have revealed that the gut microbiota performs significant roles in gut development, nutrient metabolism and immune responses (Bates et al. 2006; Koch et al. 2018; Semova et al. 2012). More recently, with the help of next generation sequencing (NGS), we have obtained a better understanding of composition and functional roles of the whole gut microbial community. Moreover, the new information on the gut microbiota revealed that positive and correct manipulation not only can considerably contribute to the continuous research of microbiota in animals, but may

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also substantially benefit the aquaculture industry, which contributes greatly to the supply of fish consumption of the world.

The environmental factors of marine habitats are dramatically different from those of freshwater habitats, and include temperature, salinity, microbes and diets. Given that the gut microorganisms of fish mainly come from surrounding water and diets, it could be expected that a distinct difference would exist in the gut microbiota between freshwater and marine fish, reflecting diverse environmental compositions (Dehler et al. 2017). In this review, we will focus on the advances in marine fish gut microbiota, including methods used in investigating the gut microbiota, the microbial composition, gnotobiotic models, important factors that influence the gut microbiota, and significant roles of the gut microbiota. The comprehensive, detailed and profound insights into marine fish gut microbiota will greatly contribute to the positive manipulation of the gut microbial communities of marine fish, leading to enhancement of marine fish health, promotion of seawater fish productivity and environmental improvement.

Methods used in investigating the gut microbiota of fish

In the process of exploring the fish gut microbiota, knowledge of its composition is insufficient. Instead, the functions are deemed to be more important. Both culture-dependent and culture-independent methods are critical in this process. Additionally, because the host and the gut microbiota may be seen as an interconnected and coregulated system, we should explain the roles of the gut microbiota from two aspects, i.e., the gut microbiota and the host itself. For many years, most of the studies concerning the gut microbiota of fish were performed through traditional culture-dependent methods. Although less than 0.1% of the gut microbes of some fish could be cultured (Wang et al. 2018), the culture-dependent methods were beneficial in revealing intestinal microbial composition and functions. For example, there was benefit in the assays targeting the determination of production and activities of enzymes and other bioactive substances from cultivable microorganisms. In addition, culturomics, which is a new methodology of culture-dependent omics, has been given more attention by researchers. Culturomics is an approach that extensively assesses microbial composition by high-throughput culture (Greub 2012) using multiple culture conditions coupled with the rapid identification of microbial species (Lagier et al. 2018). Culturomics has allowed the culture of hundreds of new microbes related to humans, providing exciting new viewpoints on host–bacteria relationships (Lagier et al. 2018). However, to the best of our knowledge, culturomics has yet to be carried out in studies on the gut microbiota of fish.

Culture-independent molecular based approaches, such as denaturing gradient gel electrophoresis (DGGE), temporal temperature gradient electrophoresis (TTGE), quantitative real-time PCR (qPCR), fluorescence in situ hybridization (FISH), marker gene amplification and sequencing (e.g., 16S rRNA for bacteria and archaea, as well as internal transcribed spacer (ITS) for fungi), and metagenomics have drastically improved our insights into the composition, structure and diversity of the gut microbiota of fish. Moreover, as for the roles of the gut microbiota of fish, the rapid development of culture-independent molecular based omics have provided new avenues to substantially reveal novel and holistic pictures of the gut microbiota functionality and improve our understanding of health and pathogenesis. These omics involve many aspects of the host and the gut microbiota, such as genomics, epigenomics, transcriptomics, proteomics, metabolomics in the host domain, while predicting functional profiling of 16S rRNA gene amplicon sequencing data, metagenomics, metatranscriptomics, metaproteomics and metametabolomics in the gut microbiota domain. However, some drawbacks of omics should not be ignored. For example, the host pollution in the gut microbiota metagenomics and metatranscriptomics is very high. In addition, there is a considerable overlap between the host metabolomics and the gut microbiota metametabolomics. Hence, the sources of many gut metabolites are hard to be assigned, i.e., either to the host or the gut microbiota. Nonetheless, omics have really helped make great progress in the study of the gut microbiota, especially when using multi-omics approaches, which are integrative analyses of multiple kinds of omics data.

The gut microbial composition of marine fish

Various microbes, such as protozoa, fungi, viruses, archaea and bacteria, reside in the fish gut. However, bacteria comprise the predominant members (Merrifield and Rodiles 2015). The residents in the gut may be divided into allochthonous (free living, transient and associated with the digesta) and autochthonous (colonize the mucosal surface of the gut). Additionally, the density and composition of the microbiota varying among different parts of fish gastrointestinal tract have been well documented (Egerton et al. 2018; Wang et al. 2018). In their review, Wang et al. (2018) reported that the predominant intestinal microbes of marine fish are facultative anaerobes, comprising *Vibrio*, *Pseudomonas*, *Acinetobacter*, *Corynebacterium*, *Alteromonas*, *Flavobacterium* and *Micrococcus*. In general, considering the different trophic level of marine fish, Firmicutes usually dominate the gut of marine herbivorous fish, whereas Proteobacteria are often predominant in the gut of marine non-herbivorous fish (Egerton et al. 2018). Some researchers expect that the entire microenvironment in the gut would be powerfully affected by the predominant microbes (Romero et al. 2014). However, in the process of studying the gut microbiota, rare microorganisms may be the ignored critical players, which could regulate the diverse interactions within the gut. Rare species are increasingly considered to be significant drivers of microbiome functions (Jousset et al. 2017). An enlightening study of Rolig et al. (2015) showed that numerically minor component *Shewanella* significantly lowered zebrafish intestinal neutrophil response by secreting an anti-inflammatory factor, suggesting that the host immune system could be potently affected by rarer species in the gut microbiota.

Indeed, the concept of "core gut microbiota" has also been proposed by many researchers (Ghanbari et al. 2015; Roeselers et al. 2011; Wong et al. 2013). Significantly, the identification of the core microbiota shows a certain degree of plasticity by preserving microorganisms required for minimum function of the gut environment (Dehler et al. 2017). However, to date, it is unclear whether a core gut microbiota presents in all kinds of fish or, if so, at what phylogenetic level. Moreover, the core microbiota cannot fully represent the health status of the host; there is still a tremendous gap in the clear understanding of the exact role of specific gut microbiota. This suggests that more attention should be paid to the functional contribution of the whole gut microbiota to the host. Furthermore, some resident members are opportunistic pathogens, e.g., *Vibrio alginolyticus*, which affects grouper (*Epinephelus coioides*) (Samad et al. 2014), rockfish (*Sebastes schlegeli*) (Kim et al. 1999) and silver sea bream (*Sparus sarba*) (Li et al. 2016). However, the organism may exert beneficial effects, notably as a probiotic. In this role, *V. alginolyticus* was demonstrated to protect Atlantic salmon (*Salmo salar*) against some fish pathogenic bacteria (Austin et al. 1995). Hence, the boundary between a pathogen and a symbiont is often blurred. Moreover, comparisons between healthy and diseased fish may be used to characterize health-associated microbes in the gut via determining which taxa are responsible for the changing health status, especially when including healthy wild fish in such comparisons. Though such comparisons may only find subtleties in the microbial communities, the influences of minor differences may be better delineated by studying the potential functions exerted by these subtle communities. Ultimately, improved understanding of health-associated microbial communities in the gut will provide new avenues to restore the disease-associated microbiota to a healthy state.

Gnotobiotic models of marine fish

Gnotobiotic models, which are defined as animals reared under axenic conditions or with specific microbial species (Pham et al. 2008), have been used widely for determining the functions of the intestinal microbiota in a diverse range of animals. Actually, compared with other fish species, the most commonly used gnotobiotic model is zebrafish, which has attractive attributes, namely transparent body, high fecundity, large brood size, external fertilization, rapid external development, and abundant genomic information (Leulier et al. 2017; Pham et al. 2008). The use of gnotobiotic models has greatly facilitated the determination of the interactions among the host, microbiota and environmental factors, and contributed to positive modulation of the gut microbiota.

However, zebrafish is a freshwater fish, and it is difficult to reflect the characteristics of marine fish. There is a serious lack of representative species of marine fish, although some gnotobiotic models of marine fish have been developed, such as European sea bass (*Dicentrarchus labrax*) (Rekecki et al. 2009; Schaeck et al. 2016a) and Atlantic cod (*Gadus morhua*) (Forberg et al. 2011). It is notable that gnotobiotic models of several marine fish species have unique advantages over the gnotobiotic zebrafish model. For example, European sea bass is an important economic fish species. Therefore, it is a very meaningful model for determining the pathogenic mechanisms or screening effective probiotics for use in marine aquaculture. Moreover, threespine stickleback (*Gasterosteus aculeatus*), which is another important model fish, possesses complex traits in the repeated evolution process from ancestral marine to derived freshwater forms (Milligan-Myhre et al. 2016). Also, the fish inhabits many marine, estuarine and freshwater habitats (Hohenlohe et al. 2010), and has a great advantage in studying how natural genetic variation shapes the gut microbiota of fish. This allows researchers to sample a great deal of host genetic variations in an easily handled gnotobiotic experimental system (Small et al. 2017). Some of these gnotobiotic marine fish models have been used in studying the effects of microbes on host development (Rekecki et al. 2009), investigating the host natural genetic variation that leads to different innate immune responses to the gut microbiota (Milligan-Myhre et al. 2016), testing probiotic candidates (Aerts et al. 2018; Schaeck et al. 2016b, 2017) and exploring host–pathogen interactions (Li et al. 2015; Rekecki et al. 2012). However, the development and applications of gnotobiotic marine fish models are still in their infancy and lag far behind those for zebrafish. Unfortunately, there are still many limitations that are difficult to resolve in gnotobiotic models of marine fish. Firstly, using gnotobiotic marine fish models is mainly dependent on the ability to easily breed and raise gnotobiotic marine fish; this is difficult. Secondly, it is hard to maintain the gnotobiotic status for a long time. Thirdly, the specific nutritional requirements of gnotobiotic marine fish are largely unknown. Therefore, providing gnotobiotic marine fish with adequate nutrition is a huge challenge. Lastly, considering the high diversity of marine fish and their habitats, the existing kinds of gnotobiotic marine fish models are too limited to fully reflect the characteristics of each marine fish. Therefore, a great deal of effort should be put into finding the most representative marine fish species to establish gnotobiotic models, and further ensure that multigenerational lines may be maintained in these gnotobiotic models.

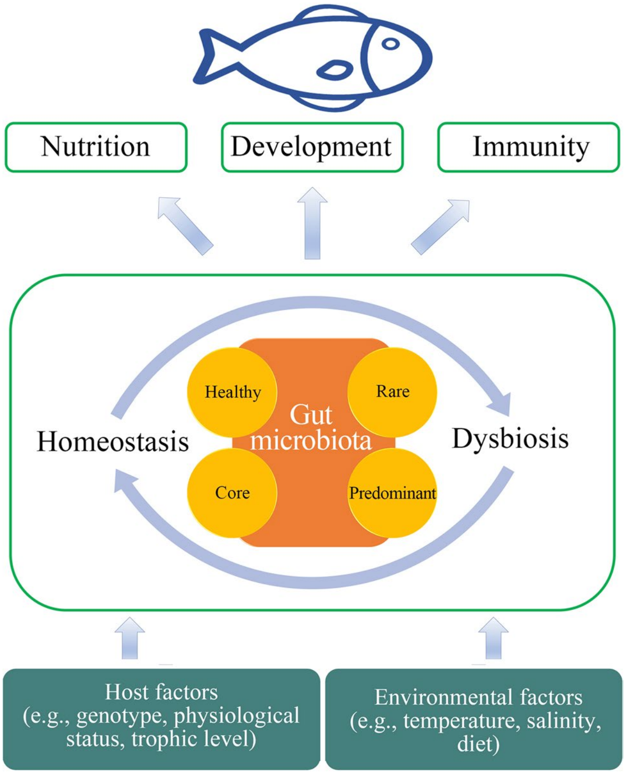

Fig. 1 Factors influencing the gut microbiota of marine fish. When various influence factors are at normal levels, the gut microbiota will remain homeostasis. However, if some influence factors are at abnormal levels, the gut microbiota will be dysbiosis. The gut microbiota (whether it is the predominant, rare, core, or healthy gut microbiota) plays an important role in the host, such as nutrition, development and immunity

Factors influencing marine fish gut microbiota

A variety of factors can drive the gut microbiota of marine fish, including host factors (such as genotype, physiological status and trophic level) and environmental factors (for example, diet, water temperature and salinity) (Egerton et al. 2018; Gatesoupe et al. 2016; Guerreiro et al. 2016; Liu et al. 2019a; Smith et al. 2015) (Fig. 1). Indeed, the composition and structure of marine fish gut microbiota are the result of the joint action of many factors. Consequently, it is difficult to be sure which factor plays a decisive role. Here, we will focus on the host genotype, water temperature and salinity, and diet.

Host genotype

Getting insights from animal models and human research, it is well established that the host exerts control in selecting and regulating its microbiota (Kostic et al. 2013). This is the same for fish (Legrand et al. 2020). The fish genotype covaried with the gut microbiota composition and the populations with greater genetic divergences showed more divergences in the gut microbiota (Smith et al. 2015). Smith et al. (2015) demonstrated that internal sorting processes (host genotype) may contribute more to population level differences in the gut microbiota of threespine stickleback than colonization processes (transient environmental effects). Using the gnotobiotic threespine stickleback model, Milligan-Myhre et al. (2016) found that no matter that fish were exposed to complex communities of microbes or exposed to a gut isolate *Pseudomonas* KMM0021, the ancestral oceanic population generated a stronger innate immune response to the gut microbiota than the derived freshwater population. This revealed that different immune responses to the gut microorganisms can exist in closely related populations. Consistently, in Atlantic salmon, Webster et al. (2018) found that population genetic variation was correlated with structure and diversity of the gut microbiome. In addition to the intraspecific level, host genetics plays a role in shaping the gut microbiota at the interspecific level (Fietz et al. 2018). Intriguingly, the major histocompatibility complex (MHC) II was considered to be conserved among jawed vertebrates. However, Star et al. (2011) reported that Atlantic cod lacks the genes for MHC II. This system takes responsibility for the classical adaptive immune response against parasitic and bacterial infections by activating CD4$^+$ T cells in other vertebrates (Star and Jentoft 2012). Hence, the absence of MHC II may influence the interactions between Atlantic cod and its microbial community (Star et al. 2013), which to some extent indicates the host-specific selection of the gut microbiota. Also, Riiser et al. (2018) speculated that lacking differentiation in the intestinal microbiome of Atlantic cod may be related to the lack of MHC II.

Water temperature and salinity

Fish are poikilothermic organisms that are exposed to seasonal or daily temperature fluctuations in natural environments. Temperature could influence the gut microbiota of poikilotherms through modulation of the host metabolic responses or a direct effect on the gut microbial community (Soriano et al. 2018). Turbot (*Scophthalmus maximus*) reared at 15 °C had lower intestinal bacterial richness and diversity than those reared at 20 °C (Guerreiro et al. 2016). Water temperature corresponded to changes in Atlantic salmon gut microbiome both with α-diversity and β-diversity indices (Nguyen et al. 2020). Also, Horlick et al. (2020) and Soriano et al. (2018) found a temperature-related change in the gut microbiota of yellowtail kingfish (*Seriola lalandi*). Through a seasonal study, Hatje et al. (2014) reported that the persistence and prevalence of *Vibrio* and *Pseudomonas* species in the gut of Atlantic salmon were caused mainly by water temperature. Similarly, previous studies showed that lactic acid bacteria (LAB) count of hindgut feces of Atlantic salmon decreased in response to elevated water temperatures (Neuman et al. 2016, 2018).

Salinity may also exert major impacts on the fish gut microbiota, particularly in the case of some euryhaline marine fish. Salinity is the major variable that determines environmental microbial community composition, worldwide (Lozupone and Knight 2007). This means that fish may encounter different microbes in different salinity environments, which may influence the fish gut microbiota. Additionally, salinity change-associated shift in the intestinal microbiota is likely to have resulted from the host response to salinity stress and the effects of subsequent stress on the intestinal microbiota (Zhang et al. 2016). The fish intestine is an important osmoregulatory organ (Wong et al. 2014), and when the intestine exerts osmoregulatory functions, the intestinal habitat niches for microbes may change. This could contribute to altering the intestinal microbiota (Dehler et al. 2017). Liu et al. (2019a) reported that the intestinal microbiota of Golden pompano (*Trachinotus ovatus*) was very different in each salinity (5, 15, 25 and 35) group. The results of the study of Hamilton et al. (2019) on wild Arctic charr (*Salvelinus alpinus*) populations showed salinity-mediated turnover in the intestinal microbiota. Interesting insights may be acquired from two comparable studies investigating the effect of salinity stress on the gut microbiota of Atlantic salmon. Dehler et al. (2017) reported that compared with freshwater fish, seawater fish have a lower α-diversity and higher abundance of Firmicutes (55.6%). However, Rudi et al. (2018) found that the α-diversity is higher in seawater fish, which are dominated also by Firmicutes (> 80%). The exact mechanisms behind this distinctive difference deserve further investigations.

Diet

Diet composition – these include proteins (Gajardo et al. 2017; Nyman et al. 2017; Parma et al. 2016; Schmidt et al. 2016), lipids (Castro et al. 2019; You et al. 2019; Yu et al. 2019), carbohydrates (Gatesoupe et al. 2014; Zhao et al. 2020), vitamins (Huang et al. 2019; Xun et al. 2019), probiotics (Jaramillo-Torres et al. 2019; Lauzon et al. 2010), prebiotics (Gupta et al. 2019; Li et al. 2019b; Su et al. 2017), and many other additives (Dai et al. 2020; Luo et al. 2020; Piazzon et al. 2017), and diet processing technologies (Barreto-Curiel et al. 2018)—may induce changes in the gut microbiota of marine fish. More detailed effects of diet on the gut microbiota of aquatic animals may be found in the review by Ringø et al. (2016). As it is well recognized, many marine fish species are carnivorous that prefer fish meal more so than plant proteins. To reduce the use of expensive fishmeal, many studies have been conducted to investigate the effects of alternative protein sources for fish meal on marine fish. These include dietary plant protein sources for feeding to turbot (Chen et al. 2018; Li et al. 2019a, 2020; Liu et al. 2019b), Atlantic salmon (Bakke-McKellep et al. 2007; Green et al. 2013; Reveco et al. 2014), gilthead sea bream (*Sparus aurata*) (Estruch et al. 2015), yellow drum (*Nibea albiflora*) (Tan et al. 2020), and large yellow croaker (*Larimichthys crocea*) (Wang et al. 2019b). These studies showed that the gut microbiota and overall health of marine fish could be affected by plant proteins as substitutes for fish meal. It is noteworthy that our previous studies on turbot have demonstrated that adding moderate amounts of anti-nutritional factors (e.g., glycinin, daidzein, xylan and stachyose) to diet could positively shape the gut microbiota and promote the host's health; however, too much is harmful (Hu et al. 2015a, b; Li et al. 2017; Ou et al. 2019; Yang et al. 2018, 2019). Therefore, replacing fish meal with plant protein sources and applying anti-nutritional factors in aquafeed must be more carefully considered.

Functions of marine fish gut microbiota

The gut microbes affect the host in many ways, including involvement in a variety of physiological activities. Moreover, the mechanisms governing the host-gut microbiota interactions and how these mechanisms exert effects on the host phenotypes are very complicated. Therefore, the full and in-depth understanding of the functional contributions of the gut microbiota will provide tantalizing new prospects for optimizing and maintaining the host's health through targeted regulation of the gut microbiota. The following section will be focused on the roles of the gut microbiota in nutrition (Table 1), development (Table 2) and immunity (Table 3) of marine fish.

Nutritional function

Many residents in the gut have enzymes that contribute to utilizing some ingredients of diets, especially some otherwise indigestible components. Many marine fish species are carnivorous, and enzymes contributing to protein digestion play a vital role in their digestive and absorptive process. Moreover in general, carbohydrate utilization varies in different fish species, with omnivores or herbivores tolerating higher levels of dietary carbohydrates than carnivores (Oliva-Teles 2012). Therefore, microbes, which are capable of degrading cellulose, starch and other carbohydrates, could be used as potential probiotics for carnivorous fish. Many marine fish gut-derived bacterial strains possess enzymes that aid in digestion, and include amylases, proteases, cellulases and lipases (Liu et al. 2020; Niu et al. 2019; Ramirez and Dixon 2003). The digestive enzyme-producing microbes isolated from fish guts have been comprehensively reviewed by Ray et al. (2012). In addition, the supplementation with probiotics could elevate intestinal digestive enzyme activities of marine fish. For example, compared with controls, i.e., without probiotics, juvenile olive flounder (*Paralichthys olivaceus*) fed with *Bacillus* sp. SJ-10 had significantly

Table 1 Studies related to the nutritional functions of the gut microbiota of marine fish

Species	Noteworthy results	Reference
Southern flounder (*Paralichthys lethostigma*)	Some intestinal isolates of *Clostridium* showed enzyme activities of alkaline and acid phosphatases, esterase lipase (C8), phosphohydrolase and leucine arylamidase	Ramirez and Dixon (2003)
Olive flounder (*Paralichthys olivaceus*)	*Bacillus licheniformis* KCCM 43270 isolated from the intestine can secrete amylase, protease, cellulase and lipase	Niu et al. (2019)
Golden pompano (*Trachinotus ovatus*)	*Bacillus pumilus* A97 derived from the intestine have protease activity and amylase activity	Liu et al. (2020)
Olive flounder	*Bacillus* sp. SJ-10 significantly increased activities of intestinal amylase, trypsin and lipase, and *Lactobacillus plantarum* significantly increased the activities of intestinal trypsin and lipase	Jang et al. (2019)
Yellowtail kingfish (*Seriola lalandi*)	Pathways about amino acid metabolism were more abundant in the gut microbiota of wild fish while more abundant of carbohydrate metabolism in farmed fish	Ramírez and Romero (2017b)
Fine flounder (*Paralichthys adspersus*)	The intestinal microbiota of cultured fish had significantly increased pathways related to the pentose phosphate pathway as well as the amino sugar and nucleotide sugar metabolism. While wild fish manifested more noteworthy functional pathways (unsaturated fatty acids, SCFAs, biotin)	Ramírez and Romero (2017a)
Rabbitfish (*Siganus fuscescens*)	Levels of SCFAs (the index of microbial fermentation activity) within the hindgut were similar in both tropical and temperate populations	Jones et al. (2018)
Surgeonfishes	Multi-omics methods detailed the importance of giant enteric symbionts belonging to members of "*Epulopiscium*" bacterial lineage with respect of their functional roles in digesting algal polysaccharides	Ngugi et al. (2017)
Maroon clownfish (*Premnas biaculeatus*)	In predicted metagenome, unfed-state time points enriched in functions related to metabolism, degradation, or biosynthesis. In metatranscriptome, the unfed state was also dominated by functions related to metabolism	Parris et al. (2019)
Olive flounder	The metabolome results showed that intestinal isolate *Lactococcus lactis* WFLU12 significantly elevated concentrations of some beneficial metabolites in the intestine. Also, it has genes encoding enzymes that contribute to the production of these metabolites	Nguyen et al. (2018)
Atlantic salmon (*Salmo salar*)	The functions of oxidative phosphorylation and citrate cycle in the intestinal microbiota were increased in the freshwater stage	Dehler et al. (2017)

Table 2 Studies related to the roles of the gut microbiota of marine fish in host development

Species	Noteworthy results	Reference
Senegalese sole (*Solea senegalensis*)	*Shewanella putrefaciens* Pdp11 promoted early metamorphosis and enhanced growth performance	Lobo et al. (2014)
European sea bass (*Dicentrarchus labrax*)	*Lactobacillus delbrueckii delbrueckii* significantly increased the gene expression of IGF-I (Insulin-like Growth Factor-I), and significantly inhibited the transcription of myostatin (MSTN)	Carnevali et al. (2006)
Senegalese sole	*Shewanella putrefaciens* Pdp11 up-regulated the transcriptions of GH (growth hormone) and IGF-IR (insulin-like growth factor-I receptor)	Jurado et al. (2018)
European sea bass	*Pediococcus acidilactici* can improve skeletal conformation	Lamari et al. (2013)
European sea bass	Probiotic increased intestinal alkaline phosphatase activity	Tovar-Ramırez et al. (2004)
Senegalese sole	Probiotic increased intestinal alkaline phosphatase activity	Sáenz de Rodrigáñez et al. (2009)
Threespine stickleback (*Gasterosteus aculeatus*)	Oceanic population monoassociated with gut isolate *Pseudomonas* KMM0021 raised the odds of possessing a more developed gut compared with germ-free group	Milligan-Myhre et al. (2016)
Olive flounder (*Paralichthys olivaceus*)	The length of intestinal villi and microvilli increased in the probiotic-supplemented groups	Jang et al. (2019)
Golden pompano (*Trachinotus ovatus*)	Indigenous *Bacillus pumilus* A97 significantly increased intestinal villus lengths and villus widths	Liu et al. (2020)
Olive flounder	*Lactococcus lactis* BFE920 significantly increased intestinal gene expression level of occludin and significantly lowered gut permeability	Beck et al. (2016)
Pacific red snapper (*Lutjanus peru*)	*Lactobacillus sakei* increased more mixed mucin (neutral + acid) goblet cells in the intestine	Reyes-Becerril et al. (2014)
European sea bass	Conventional static larvae were shorter, smaller and had a less developed gastrointestinal tract than germ-free static larvae, but the gastrointestinal tract morphology is not really qualitatively different between them	Rekecki et al. (2009)
Atlantic salmon (*Salmo salar*)	*Lactobacillus delbrueckii* subsp. *lactis* maintained a healthy intestinal barrier, whereas *Aeromonas salmonicida* subsp. *salmonicida* damaged intestinal integrity	Salinas et al. (2008)

higher activities of amylase, trypsin and lipase in the intestine. In comparison, the activities of intestinal trypsin and lipase were significantly increased in fish fed with *Lactobacillus plantarum* (Jang et al. 2019). Currently, formulated diets for farmed marine carnivorous fish contain numerous carbohydrates. Therefore, the nutritional functions of their gut microbiota shift to help the host better digest these high-carbohydrate formulated diets. A previous study showed that pathways about amino acid metabolism were more abundant in the gut microbiota of wild yellowtail kingfish but more abundant for carbohydrate metabolism in farmed fish. This apparent difference may be attributed to different diets, namely common protein-rich prey (e.g., squid, shrimp and fish) for wild fish and artificial carbohydrate-rich feed for farmed fish (Ramírez and Romero 2017b). Consistently as compared with wild fine flounder (*Paralichthys adspersus*) (commonly fed on anchovy (*Engraulis ringens*) and crustaceans), predicted functions demonstrated that the intestinal microbiota of cultured flounder (fed with the artificial diet containing 11% carbohydrates) had significantly increased pathways related to the pentose phosphate pathway and amino sugar and nucleotide sugar metabolism (Ramírez and Romero 2017a).

In addition to marine carnivorous fish, piscine herbivores attract much attention in regard to their nutritional ecology, which has remained largely unknown. Clarification is needed to explain the roles of the gut microorganisms of marine herbivorous fish in the gut digestive processes. The work of Sullam et al. (2012) suggested that the gut bacterial communities of marine herbivorous fish show close relationships to those of mammals. Through fermentation, the gastrointestinal microbes provide SCFAs for marine herbivorous fish (Clements and Choat 1995; Mountfort et al. 2002). For example, in rabbitfish (*Siganus fuscescens*), similar levels of SCFAs within the hindgut were observed from tropical to temperate populations (Jones et al. 2018). Interesting insights may be gained from herbivorous surgeonfishes whose major food source is marine algae. Using multi-omics methods, Ngugi et al. (2017) detailed the importance of giant enteric symbionts belonging to the "*Epulopiscium*"

Table 3 Studies related to the immunological roles of the gut microbiota of marine fish

Species	Noteworthy results	Reference
Olive flounder (*Paralichthys olivaceus*)	Host-derived nisin Z- and colicin V-producing probiotic *Lactococcus lactis* WFLU12 showed well competitive exclusion activities against *Streptococcus parauberis* in the intestine	Nguyen et al. (2017)
Fine flounder (*Paralichthys adspersus*)	Compared with wild fish, predicted functions showed that the biosynthesis of ansamycins is more abundant in the intestinal microbiota of cultured fish	Ramírez and Romero (2017a)
Gilthead sea bream (*Sparus aurata*)	Dietary supplementation of probiotics at the early feeding state increased the number of Ig^+ cells and acidophilic granulocytes in the GALT	Picchietti et al. (2007)
European sea bass (*Dicentrarchus labrax*)	Developing fish fed with autochthonous intestinal *Lactobacillus delbrueckii* ssp. *delbrueckii* (AS13B) had significantly higher density of intestinal T cells and acidophilic granulocytes	Picchietti et al. (2009)
Olive flounder	Hindgut indigenous *Lactobacillus plantarum* FGL0001 significantly upregulated intestinal gene expressions of IL-6, IL-8, and TNF-α, and enhanced the survival rate after challenge with *Streptococcus iniae*	Beck et al. (2015)
Golden pompano (*Trachinotus ovatus*)	Serum lysozyme activity and total protein, intestinal gene expression of TLR8 and kidney gene expression of TLR9, as well as disease resistance against *Vibrio ponticus* were all significantly increased by autochthonous intestinal strain *Bacillus pumilus* A97	Liu et al. (2020)
Atlantic salmon (*Salmo salar*)	*Pediococcus acidilactici* MA18/5 M significantly elevated gene expressions of PCNA, TNF-α, and genes related to antiviral protection in the distal intestine during the seawater stage, and increase resistance against IPNV after seawater transfer	Jaramillo-Torres et al. (2019)
Atlantic salmon	The levels of serum ACP and IgM, as well as resistance against *Aeromonas salmonicida* were up-regulated by a probiotic complex consisting of *Bacillus velezensis* V4 and *Rhodotorula mucilaginosa*	Wang et al. (2019a)

Gut-associated lymphoid tissue: GALT; interleukin-6: IL-6; interleukin-8: IL-8; tumor necrosis factor α: TNF-α; toll-like receptor 8: TLR8; toll-like receptor 9: TLR9; proliferating cell nuclear antigen: PCNA; infectious pancreatic necrosis virus: IPNV; acid phosphatase: ACP; immunoglobulin M: IgM

bacterial lineage colonizing these fish with respect of their functional roles in digesting algal polysaccharides. At last, they concluded that the acquisition of a specific enteric microbiota specialized to the host diets is a key niche-partitioning driver in shaping the nutritional ecology of marine herbivorous fish.

Parris et al. (2019) used a multi-omics approach to investigate functional differences of the intestinal microbiota between fed and unfed maroon clownfish (*Premnas biaculeatus*), which is a marine omnivorous fish. In the predicted metagenome, unfed-state time points enriched in functions related to metabolism, degradation, or biosynthesis, e.g., amino acid metabolism, fatty acid metabolism, secondary bile acid production, sphingolipid biosynthesis, and the degradation of many organic compounds. Consistently, metatranscriptome sequencing of the unfed state was dominated by functions related to metabolism, significantly amino acid metabolism and carbohydrate metabolism (pyruvate metabolism and the citric acid cycle, fermentation or the metabolism of fermentation intermediates, and the degradation of cellulose or other complex organic molecules).

It is emphasized that gut microbes have enzymes which generate some beneficial metabolites (such as amino acids, unsaturated fatty acids, short chain fatty acids (SCFAs) and vitamins). Using metabolome technology, Nguyen et al. (2018) found that dietary administration of *Lactococcus lactis* WFLU12, which was isolated from the intestine of olive flounder, significantly elevated concentrations of some beneficial metabolites, for example, citrulline, taurine, tricarboxylic acid cycle (TCA) intermediates, vitamins and SCFAs in the intestine of olive flounder. Also, they found that this probiotic strain has genes encoding enzymes that contribute to the production of these metabolites. Hence, they speculated that these increased metabolites may result from administration of this probiotic strain. In addition, predicted functions indicated that compared with cultured fine flounder, the intestinal microbiota of wild flounder manifested more noteworthy functional pathways (unsaturated fatty acids, SCFAs, biotin) (Ramírez and Romero 2017a). Furthermore, substantial differences in nutritional function of the gut microbiota occur in some specific conditions (for example, transfer from freshwater to seawater) that can help the host better adapt to the environment. In Atlantic salmon, the functions of oxidative phosphorylation and citrate cycle in the intestinal microbiota were increased in the freshwater stage, revealing that the host obtains more free energy that could be used for the requisite changes during smoltification and energy needs during the subsequent osmoregulatory adaptation in the seawater stage (Dehler et al. 2017).

The roles in host development

The involvement of the gut microbiota in regulating the host development is an important physiological role of the gut microbiota. Lobo et al. (2014) showed that dietary supplementation of probiotic *Shewanella putrefaciens* Pdp11 promoted early metamorphosis and enhanced growth performance of Senegalese sole (*Solea senegalensis*) larvae. Carnevali et al. (2006) reported that juvenile European sea bass fed with probiotic *Lactobacillus delbrueckii delbrueckii* significantly increased the gene expression of IGF-I (Insulin-like Growth Factor-I) which is synthesized in all tissues and promotes growth and differentiation of muscle and cartilage in various systems, and significantly inhibited the transcription of myostatin (MSTN) which can negatively regulate muscular growth. Moreover, IGF-I is an important factor in the somatotrophic axis, having a role as a mediator of the action of GH (growth hormone) on somatic growth regulation. And the IGF-I binds to a membrane receptor IGF-IR (insulin-like growth factor-I receptor) to play its role (Jurado et al. 2018). Jurado et al. (2018) found that dietary supplementation of probiotic *Shewanella putrefaciens* Pdp11 up-regulated the transcriptions of GH and IGF-IR in Senegalese sole larvae, resulting in an increase in their growth. Moreover, through histological observations and osteocalcin gene expression analysis, Lamari et al. (2013) confirmed that dietary inclusion of allochthonous probiotic *Pediococcus acidilactici* could improve skeletal conformation in European sea bass larvae, although the mode of action needs further elucidation.

Delineating the functional roles of the gut microbiota in marine fish gut development are still in its infancy. Yet, some intestinal enzymes are good indicators of intestinal development. An example includes alkaline phosphatase, which mainly lies on the enterocyte brush border membrane (Hauville et al. 2016). Increased intestinal alkaline phosphatase activity by dietary probiotic administration have been reported in European sea bass (Tovar-Ramırez et al. 2004) and Senegalese sole (Sáenz de Rodrigáñez et al. 2009). Milligan-Myhre et al. (2016) reported that oceanic populations of threespine stickleback monoassociated with *Pseudomonas* KMM0021, which was isolated from stickleback gut, raised the odds of possessing a more developed gut by 2.017 times compared with a germ-free group. Besides, dietary supplementation of probiotics may increase the length and width of intestinal villi and the microvilli of juvenile marine fish (Jang et al. 2019; Liu et al. 2020). During gut development, the intestinal barrier integrity is gradually enhanced. Moreover, the intestinal tight junctions and mucus are important for intestinal barrier integrity. Olive flounder fed with *Lactococcus lactis* BFE920 had significantly higher intestinal gene expression of occludin, which is a significant member involved in tight junctions, and exhibited significantly lower gut permeability (Beck et al. 2016). Pacific red snapper (*Lutjanus peru*) fed with *Lactobacillus sakei* had more mixed mucin (neutral + acid) goblet cells in the intestine (Reyes-Becerril et al. 2014). However, some studies showed inconsistent results. Morphometrical and stereological approaches revealed that conventional static sea bass larvae were shorter, smaller and had a less developed gastrointestinal tract than germ-free static sea bass larvae. Yet, the gastrointestinal tract morphology of conventional larvae did not really qualitatively differ from those of germ-free larvae by light microscopy (Rekecki et al. 2009). These authors speculated that the reason for this result might be that germ-free fish did not possess any microbes which could compete for nutrients or produce toxic products. Besides, some pathogenic bacteria are capable of damaging the intestinal epithelium. Salinas et al. (2008) demonstrated that a healthy intestinal barrier was observed in Atlantic salmon foregut incubated with probiotic *Lactobacillus delbrueckii* subsp. *Lactis*. Conversely, a damaged intestinal integrity was found in the foregut incubated only with *Aeromonas salmonicida* subsp. *salmonicida*; however, the damaging effects of *Aeromonas* was prevented by pre-incubation of the foregut with *L. delbrueckii* subsp. *lactis*. Indeed, damage of fish intestinal mucosal barrier caused by imbalance of host-gut microbiota symbiosis and infection of enteric pathogen can hamper fish gut development.

The negative effects caused by plant-based protein sources on farmed marine fish notably the intense intestinal inflammatory response that can destroy the intestinal epithelium results in poor intestinal development. Consequently, many studies have focused on exploring functional feed additives that counteract these adverse effects and positively shape the gut microbiota, as well as studying the causal relationship between the gut microbiota and enteritis (Bakke-McKellep et al. 2007; Liu et al. 2018, 2019b). However, most of these studies provide only an apparent association between the gut microbiota and enteritis. The exact roles of the gut microbiota in repairment, renewal and development of the intestinal epithelium in enteritis are still poorly understood and merit further investigations. Similarly, replacing fish oil with vegetable oils may lead to intestinal inflammation, gut microbiota dysbiosis and intestinal mucosal barrier damage in marine fish (You et al. 2019). Therefore, it is likely to be a long time before vegetable oils may be used safely and efficiently with marine fish.

Immunological roles

The normal function of the gut microbiota is crucial to immunity and homeostasis. Dysbiosis of the gut microbiota could result in immune dysfunction and increased risk of disease. The abuse of antibiotics has caused many bacteria to develop drug resistance, the spread of which has developed into a serious problem threatening and restricting the development of aquaculture. Healthy aquaculture desires natural immune enhancers instead of antibiotics for helping the host resist pathogens while keeping fish healthy and environment friendly. The beneficial microbes in the fish gut may provide the host with some direct and/or indirect immunological benefits. The indirect immunological benefits are correlated with directly preventing the colonization, invasion and infection of pathogens. For example, these roles include competing for nutrients and niches, secreting antimicrobial substances (such as bacteriocins, toxins and siderophores), and modifying the host internal environment (for example, decreasing the intestinal pH). Numerous studies have proved that some strains isolated from the marine fish gut may exert inhibitory effects on pathogens in vitro (Askarian et al. 2012; Cai et al. 1998; Liu et al. 2020; Robertson et al. 2000; Sugita et al. 1997; Westerdahl et al. 1991). Host-derived nisin Z- and colicin V-producing probiotic *Lactococcus lactis* WFLU12 showed profound competitive exclusion activities against *Streptococcus parauberis* in the intestine of olive flounder (Nguyen et al. 2017). As mentioned above, the gut microorganisms of marine fish can produce SCFAs, which decrease the intestinal pH that create a less favorable intestinal environment for several pathogens. Compared with wild fine flounder, predicted functions showed that the biosynthesis of ansamycins is more abundant in the intestinal microbiota of cultured flounder. These compounds may protect cultured fish against bacterial pathogens in the case of high-density intensive aquaculture (Ramírez and Romero 2017a).

The direct immunological benefits are related to the gut microbe-mediated development and maturation of the gut-associated lymphoid tissue (GALT) that not only protects against infections but also regulates immune function in the digestive tract (Rhee et al. 2004) and the gut microbe-mediated enhancement of the host immune responses. The gut microbiota may directly influence the teleost immune system via exposing microbe-associated molecular patterns (MAMPs) and secreting factors. Besides, the gut microbiota and their secreted factors may act locally on the gut mucosal epithelium, or systemically by entering the host circulation, or activating immune cells. Then, these cells move from mucosal sites to systemic lymphoid tissues (Kelly and Salinas 2017). However, the more detailed mechanisms remain greatly elusive and merit further investigations. Some previous studies have proved the promoting effects of marine fish gut microbiota on the development and maturation of the GALT. In gilthead sea bream, dietary supplementation of probiotics at the early feeding state increased the number of Ig^{+} cells and acidophilic granulocytes in the GALT (Picchietti et al. 2007). Autochthonous intestinal *Lactobacillus delbrueckii* ssp. *delbrueckii* (AS13B), which was isolated from adult European sea bass, was administered to developing fish to determine its effects on development and differentiation of the GALT. Here, the results revealed that treated fish had a significantly higher density of intestinal T cells and acidophilic granulocytes compared with controls (Picchietti et al. 2009).

Marine fish gut microbe-mediated enhancement of the host immune responses has been well documented. Compared with the control group, dietary supplementation of indigenous *Lactobacillus plantarum* FGL0001, which was isolated from the hindgut of olive flounder, significantly upregulated intestinal gene expressions of interleukin-6 (IL-6), interleukin-8 (IL-8), and tumor necrosis factor α (TNF-α) of olive flounder, and enhanced the survival rate after challenge with *Streptococcus iniae* (Beck et al. 2015). Compared with the control fish, serum lysozyme activity and total protein, intestinal gene expression of toll-like receptor 8 (TLR8) and kidney gene expression of toll-like receptor 9 (TLR9), and disease resistance against *Vibrio ponticus* were all significantly increased in golden pompano after feeding with an autochthonous intestinal strain of *Bacillus pumilus* A97 (Liu et al. 2020). Dietary inclusion of *Pediococcus acidilactici* MA18/5 M significantly elevated gene expressions of proliferating cell nuclear antigen (PCNA), TNF-α, and genes related to antiviral protection in the distal intestine of Atlantic salmon during the seawater stage, and increased fish resistance against infectious pancreatic necrosis virus (IPNV) after seawater transfer (Jaramillo-Torres et al. 2019). Compared to controls, the levels of serum acid phosphatase (ACP) and immunoglobulin M (IgM), and resistance against *Aeromonas salmonicida* were up-regulated in Atlantic salmon fed with probiotics consisting of *Bacillus velezensis* V4 and *Rhodotorula mucilaginosa* (Wang et al. 2019a).

Conclusions and future prospects

Because of the intimate interaction between the gut microbiota and its host, under normal circumstances, the two may be regarded as symbiotic. Both host factors and environmental factors are responsible for the homeostasis or dysbiosis of the gut microbiota. The marine fish gut microbiota is very diverse, and exerts an important role in the host (such as nutrition, development and immunity). It is necessary to unravel the significant roles of the gut microbiota, whether focused on the predominant, rare, core or healthy gut components. When there is a deeper understanding of the precise mechanisms by which various factors affect the gut microbiota, we may draw on the advantages and avoid the disadvantages, that is, to prevent the imbalance of the gut microbiota and maintain its homeostasis.

Until now, the reproducibility and comparability across studies focusing on the gut microbiota of fish are very poor. To solve these problems, experimental approaches including sample collection and storage, laboratory procedures, sequencing methods and data analyses need to be improved and standardized. In addition, the gnotobiotic-rearing techniques must be advanced as there are deficiencies in the existing gnotobiotic marine fish models. So far, much of our insights into the interactions between the gut microbes and marine fish is limited to bacteria. Unique and complex roles of more various microbial lineages, such as fungi, archaea, viruses and parasites, remain largely uncharacterized, and need further investigations. Moreover, as the interactions between the gut microbiota and its host is very complex, it is necessary to use multi-omics approaches to delineate the roles of unique gut microbial assemblages in the host. Ultimately, studying the roles of the gut microbiota in fish will not only help to fill the gap in basic biology, but also help to optimize fish gut microbiota to promote the development of aquaculture.

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