

Influence of Gut Microbiota on Growth and Development of Fishes

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Abstract: Fishes are the main component of aquaculture market belongs to diverse community of vertebrates. Microbes colonize inside the gut of the animals including fishes. Micro-flora or microbiota harbours inside the fishes have direct effect on fish health by stimulating immune system, aids in the nutrient acquisition and compete with the pathogenic microbes. The gut microflora also involved in development of gastro-intestine, production and provision of vitamins, enhancement nutrient uptake with the help of enzymatic activity. Along with the availability of nutrients, gut flora also helps in the maintenance of mucosal tolerance, disease resistance, and secretion of therapeutic compounds such as anti-cancerous and anti-inflammatory agents. These microbes inside the animals controls diverse metabolic functions such as physiology to immunological processes. The group of microbes involved in the gut flora are Firmicutes, Bacteroidetes, and Actinobacteria and these plays diverse role in health of fishes.

This investigation aims at role of gut microflora on the health of fishes. The interactions of gut microbes with the physiology and metabolism. The major effect brought by the microbes on growth and development of fishes are also investigated in this article.

Keywords: Gut flora, Fish Biology, microbial interactions, Fish health

I. INTRODUCTION

Fishes are the diverse group of animals, which includes poikilothermic aquatic animals, belongs to vertebrates and invertebrates. Fish have special place as the dietary component as it contains several necessary elements such as I, Mg, Zn, K, Ca, P, omega-3 fatty acids, vitamins B₂, vitamins D, essential minerals, etc. Since 19th century demand of fish as dietary components tremendously increased. Among all, the Teleost is having special place in aquaculture industry.

Fishes exposed to microbes through surrounding water and soil and these microbes get colonize on external surface and in internal organs. Diverse group of microbes and symbionts harbours inside the fish having favourable ecological niche and regulates nutrition, environment and age of fishes (Syvokienè et al., 2011). These microbes produces bioactive agents inside the fishes like tetrodotoxin, eicosapentaenoic acid, biotin, vitamin B12 and antimicrobial compounds which helps in benefits of fishes such as pool of enzymes for enhanced digestions (Bairagi et al., 2004). Microbes inside the gastrointestinal region colonize, survive and multiply in this region. These gut flora helps to prevent colonization of pathogens inside the gut (Gomez-Gil et al., 2000; Ringø et al., 2005), improved digestion with the release of diverse enzymes (Ringo and Birkbeck, 1999); increased uptake of nutrient and organic material (Moriarty, 1996) and immune-stimulations (Rengpipat et al., 2000; Bhat et al. 2024).

Fishes are important dietary element of human food as it provides micro and macronutrients necessary for the growth and development of human beings (Mishra 2020a). The catfishes are having demand fish market because of high medicinal value and they are highly nutritious (Mishra, 2020b). The diet and food habits are the important parameters towards availability of natural resources (Kido, 1996). The biochemical estimations of gut content helps in tracking food and feeding habits of fish's results in good management practice of fisheries (Agbabiaka, 2012; Mishra, 2020c). The analysis of food habit reveals type of prey frequently consumed, quantify rate of ingestion and type of individual food



types to get the better idea of fish nutrition (Kariman et al., 2009). The diet of fishes helps to find their position in the food web of ecosystem (Padmakumar et al., 2009), prey-predator size relationship, habitat selection and diet shift during ontogeny (Chippis and Garvey, 2007; Mishra, 2020d).

Fishes often exposed to microbes through water and in sediments. These microbes influence the colonization on external surfaces along with gills. The water and food also taken up by the digestive tract, full of microbes. Microbial colonization commenced at the egg or larval stage until the complete maturity of the fish (Olafsen, 2001). The flora inside the developing fishes depends on the microbial density in the eggs, larvae, food and water. This flora manipulated by addition of probiotic, which can colonize the fishes for shorter or longer period as per the need (Austin, 2002; Robertson et.al. 2000).

Till date there were three chances of microbial exposure to fishes recorded; a) Organisms around the fishes came in close contact with microbes or growth of microbes at wound sites; b) Microbes went inside of fishes with water or food and colonize alimentary canal; and c) microbes present fish's surfaces interfered by antibiotics or natural inhibitory compounds or resident microflora (Austin and Austin, 1987).

II. AUTOCHTHONOUS AND ALLCHTONOUS MICROBIOTA

The microbial colonization or microbiota inside the fish's gut categorize into Autochthonous and Allchtonous Microbiota. The microflora can be termed as autochthonous when microbes adheres to epithelia of fish's gut while allchtonous are unable to colonize on GI tract. Allchtonous these groups of microbes enter inside the gut for some time but rejected for their colonization inside the gut (Ringø & Birkbeck 1999; Ringø et al. 2003; Kim et al. 2007; Merrifield et al. 2011). In some reports, it recorded that these microbes can colonize in between the microvilli under stress or same sort of special conditions (Olsen et.al. 2005). Autochthony microflora can be identified with particular criteria such as a) colonize in healthy fishes, b) colonize during early stages of host and persist for long time, c) can be cultured in free-living and hatchery-culture, d) can survive in anaerobic conditions, and e) colonization can be observed near stomach, proximal or distal intestine on their epithelial mucosa. The microbial colonization inside the fish gut depends on gastric acidity, digestive enzymes, bile salts, peristalsis, immune response and natural inhibitory compounds present near the fishes (Ringø et al. 2003; Ray et.al. 2012).

III. COMPOSITION AND DIVERSITY OF THE GUT MICROBIOME

Diverse group of microbes survive inside the fish's gut in symbiotic fashion. These microbes belong to four major phyla such as Firmicutes, Bacteroidetes, Actinobacteria and Proteobacteria. The first group of microbes are Firmicutes (e.g. Clostridium, Lactobacillus, Faecalibacterium, etc.) involved in degradation of dietary fibers, produces short-chain fatty acids (SCFAs) and promotes gut health of fish (Jandhyala, 2015). The groups helps in maintenance of intestinal barrier and immune-modulations. The second group of microbes are Bacteroidetes, plays important role energy release by the breakdown of complex carbohydrates (Talapko et.al., 2022). Altogether in balanced ratio these two phyla Bacteroidetes and Firmicutes maintained healthy gut while in absence it will cause obesity or inflammatory bowel disease (Vishwakarma,et.al. 2025).

Because of the different environmental conditions, composition gut microbiota is different in Marine and freshwater fishes (Li et al. 2017). Major phyla observed in both habitat are Fusobacteria and Proteobacteria (Givens et al. 2015, Li et al. 2017, Deb et al. 2020). The most common Proteobacteria observed in freshwater fishes are Aeromonas, Pseudomonas, and Enterobacter. In case of marine fishes, common gut flora includes Vibrio, Photobacterium, and Shewanella, etc. The member Firmicutes include Lactobacillus and Streptococcus, Actinobacteria, including Micrococcus, and Bacteroidetes such as Flavobacterium and Chryseobacterium (Sullam et al. 2012, Wu et al. 2012, Llewellyn et al. 2014, Givens et al. 2015, Deb et al. 2020). Firmicutes in marine species contains Bacillus and Clostridium, and Bacteroidetes such as Cytophaga (Llewellyn et al. 2014, Givens et al. 2015, Egerton et al. 2018, Ou et al. 2021, Uniacke-Lowe et al. 2024; Singh et.al. 2025).



- **Factors Affecting Fish Gut Microbiome**

The factors responsible for colonization inside the gut can be summarized as, a) random dispersal of microbes at the intestinal community, b) selective microbe-microbe or microbe host interactions. Microbial seeding occurred during developing larvae from surrounding environment, persists until maturity reached through the non-neutral processes (Yan et.al. 2016; Burns et.al. 2016). The most phenomenal colonization inside the gut is deterministic cause of microbe-microbe or host-microbe specific interactions (Talwar et.al. 2018).

- **Gnotobiotic models of marine fish**

Gnotobiotic model, in which fishes reared in one type of microbial species or reared in axenic culture (Pham et.al. 2008). This sort of technique used to find out sensitivity of organs against diverse group of microbes and to find out benefit aspects of this microbiota. The fish used as the ideal gnotobiotic model is zebrafish as it has particular characters like 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 correlation of microflora of gut, environmental factor and health benefits of fish can be established using gnotobiotic model (Weihaio et.al. 2021).

- **Gut microbiota of freshwater fish**

Diversification in the gut microbiota of the freshwater and marine water fishes recorded by several authors (Izvekova et al. 2007). Because of different environmental conditions, gutflora also varies in composition from marine water e.g. Acinetobacter, Aeromonas, Flavobacterium, Lactococcus, Pseudomonas, obligate anaerobes (Bacteroides, Clostridium and Fusobacterium) and members of family Enterobacteriaceae (Gómez and Balcazar, 2008; Uma et.al. 2020).

- **Effects of the microbiota on fish health**

Pathogenic microbes as the fish microbiomes are not always cause diseases. Prevalence of pathogens are more in case of mammals and plants whenever balance commensal microbes of fishes is disturbed, this process is also known as dysbiosis. The dominance of pathogenic microbes is suppressed in case of healthy fishes as in case of largemouth bronze gudgeons (*Coreius guichenoti*) prevalence of *Aeromonas* is detected but its present is more dominated in case of furunculosis-infected fish (Kumari, 2020).

The development effect such as life span and shape the body are the resultant of interaction between host and microbiota, leads to popularization of term holobiont and the hologenome (Bordenstein and Theis, 2015; Foster et.al. 2017; McFall-Ngai et.al., 2013). The mechanism involved in the host-microbiome interactions plays pivotal role in the functions of holobionts (Simon et al., 2019; Diwan et.al. 2013). Recent years, the microbiome concept is getting more attention as the healthy gut is maintained by the altered microbes through the prevention and treatment of the disease, an important advantage governed by holobiont. Healthy microbiota of fish's gut maintained by probiotics, prebiotics, and synbiotics. It is also recommended by the many author to use biofloc system for checking disease spreads among cultivable organisms and promotes healthy conditions during the aquaculture farming (Diwan et.al., 2021; Rajeev et.al., 2020; Van Doan et.al., 2020; Wang et.al., 2019).

Gut microbiome plays important role in development and physiological functions of the host. The host-microbiome interactions controls growth, breeding and immune system. The surrounding environment is the major factor which can be responsible for the any sort disease outbreak in aquatic environment (Diwan et.al., 2021; Sun et.al. 2019).

- **Development of gut microbiota in fish**

The first feed to growing larvae responsible for microbial colonizations. The dominant microbiota reported in the fish eggs most often are Cytophaga, Flavobacterium, and Pseudomonas (Austin, 1982; Yoshimizu et al., 1986), variation among the species observed (Hansen and Olafsen, 1989; Romero and Navarrete, 2006; McIntosh et al., 2008). The most prevalent microbes in the primary developmental stages are species-specific because of variation in binding glycoproteins



on the egg surface (Larsen, 2014). The population of eggs controlled by the influence of surrounding environment. The freshly hatched larvae possess the first colonisers as the chorion-associated microbes, which colonize at the developing GI tract. Once the larvae begin to eat and drink, the microbial composition becomes diversified (Hansen and Olafsen, 1989; Korsnes et al., 2006; Reid et al., 2009; Lauzon et al., 2010).

Diversification in microbiota of captive state of fishes observed in freshwater samples (Bucio et al., 2006) and marine fishes (Nelson et al., 2013). In case of captured fishes, the microbiota influenced by the climate and diets. The microbiota manipulated in captive fish breeding and rearing. Antibiotics at industry levels during the farming controls the microbial diversity in aquaculture systems (Navarrete et al., 2008; Lozano et al., 2018).

- **Gut microbiota in fresh water, brackish water and marine fish**

The most dominant colonisers in the Gut of fishes are fungi, protists, viruses, and bacteria. Bacteria (Rombout et al., 2011) dominate the intestinal regime. Microbiota among the different trophic level from same sources are restricted to distinguish. Trophic level has great influence on microbial composition. In an investigation from the same water sample diverse group of microbes were recorded in different trophic levels such as herbivorous (e.g. *Megalobrama amblycephala* and *Ctenopharyngodon idellus*), carnivorous (e.g. *Siniperca chuatsi* and *Culteral burnus*) and omnivorous (e.g. *Cyprinus carpio* and *Carassius auratus* and filter-feeder *Hypophthalmichthys molitrix* and *H. nobil*) (Liu et al., 2016). Microbiota associated with herbivorous fishes involved in fermentative digestions e.g. marine fishes, such as flatfish (Liston, 1956), salmon (Yoshimizu and Kimura, 1976), and sea chub (Rimmer and Wiebe, 2006). Very rate information is available on microbiota associated with brackishwater fishes. Brackishwater fishes possesses the microbiota, which belongs to both sort of sources like freshwater as well as marine water. This microbiota having potential cellulolytic and amylolytic activity (Rani et.al. 2012).

- **Factors affecting fish gut microbiome (FGM)**

The Fish Gut Microbiome depends on two factors such as intrinsic and extrinsic factors. The intrinsic factors contains gender, immunity and genetics while extrinsic factor composed of water quality, feed and antibiotics (Figure 1).

The environmental factor as if salinity, climate and geographical location have great impact on the bacterial communities (e.g free living and symbiotic bacteria) (Ray, 2016; Zhang et al., 2016). The most factor influence microbial composition is diet of the fishes. Microbiome composition can change along with alteration of diet in controlled environmental conditions (Desai et al., 2012; Ingerslev et al., 2014a,b; Estruch et al., 2015; Schmidt et al., 2017). Habitat and microbial composition is significant but reason behind still not clear. With respect to diverse environmental conditions like freshwater and marine water, the microbial composition in the fish's gut shown great variations (Herlemann et al., 2011; Ghanbari et al., 2015). In comparison to diet, the environmental factors responsible contaminants in food and dietary elements often neglected.

The composition of microbes in FGM have shown taxonomical and regional differences. The animal health affected by stress. The exposure of stress to the fishes most probably caused by water quality, high pollutants content, inadequate photoperiod, oxygen levels, temperature, dense population, under-nourishment, storage and handling (Cantas et al., 2012). Several authors investigated the microbial composition during ontogenetic growth (Romero and Navarrete, 2006; Ingerslev et al., 2014a,b; Bledsoe et al., 2016; Stephens et al., 2016).



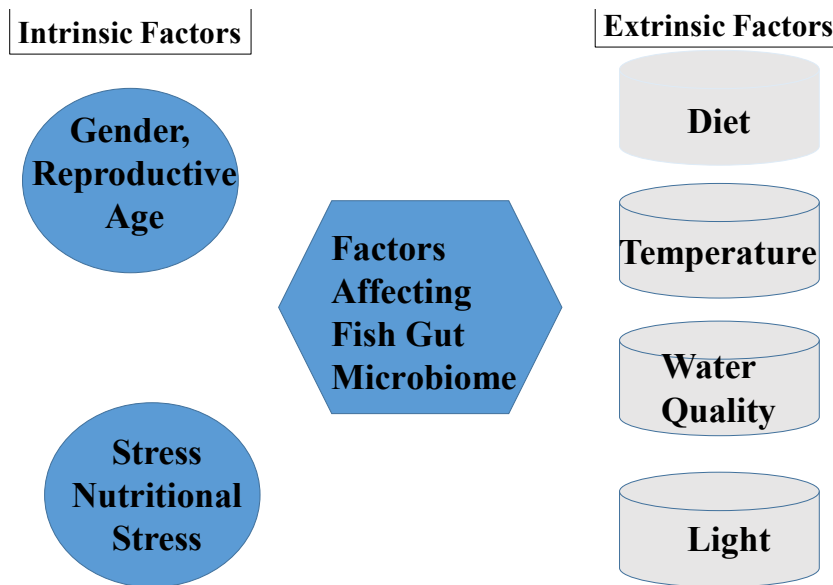


Figure 1: Factors affecting the fish gut microbiome (Intrinsic and Extrinsic factors)

• **Fishmeal in Aquaculture Farming**

The FGM are colonize together with other microbes in symbiotic or endosymbiosis fashion (e.g. Escherichia coli, Salmonella, Listeria inhabiting the GI tract) (Vine et al., 2006). The aquatic feed formulations provides enriched diet to the fishes containing protein-rich components with balanced amino acids and high palatability. Often shortage of fishmeal suggests that the fishmeal cannot compete with the current demand of the aquaculture market. The major component of fishmeal is soybean meal obtained as the byproduct during soybean oil extraction. The nutritional value of soybean meal constrained by some unnecessary factors like phytate, tannins, and soybean lectins (Francis et al., 2001), responsible for poor feed intake and palatability (Zhang et al., 2013) and reduction in the growth performance (Kumar et al., 2012; Xinru et al., 2026).

The portion of FM can be replace by animal-byproduct and make it cheaper (Forster et al., 2003; Hernandez ´ et al., 2008; Davis et al., 2002). The regular use of animal byproduct is restricted because of lower protein digestion and utilization level, lack of balanced amino acids (deficiency in methionine) (Tan et al., 2005). The enzymatic hydrolysis can convert large complex protein molecules into good amino acid balance and bioactive peptides (antioxidant, anti-hypertensive, immunomodulatory, and antimicrobial peptides (Chalamaiah et al., 2012, Javaherdoust et al., 2020b). The Hydrolyzed porcine mucosa (HPM) and enzymatic chicken liver powder (ECLM) are rich source of protein containing small peptides and free amino acids. The HPM more often used in case of piglets (Cho et al., 2010; Figueroa et al., 2016; Myers et al., 2014). HPM helps in the improment meat quality (Yang et al., 2022). The growth performance of tilapia affected by the replacement of FM with chicken liver meal and dried porcine solubles (Wu et al. 2021a; Hongjie et al. 2023. Diverse microbes with good enzymatic activities detected in GI tract of rohu, catla, mrigal, bata, murrel, orange-fin labeo, Nile tilapia, and climbing perch (Mondal et al., 2010).

IV. CONCLUSION

The microbiota resides in GI tract influence the growth and development of host. The enzymatic secretions helps in the digestion of complex food molecules for the easily available food molecules. The prevalence of microbiota during the early stages of ontogenic development shown species-specific. Later on after the maturity, the prevalence of microbes increase and diversified with the intake of water and food molecules. The understanding of fish microbiota helps in the



understanding of sensitivity and growth effects. This portion reveals the feed controls can manipulate microbiota and alter physiological effects.

REFERENCES

1. Agbabiaka, L.A. 2012. Food and feeding habits of *Tilapia zilli* (Pisces: Chichlidae) in river Otamiri South Eastern Nigeria. *Bio. Sc. Disc.* 3(2): 146-148.
2. Austin, B. 2002. The Bacterial Microflora of Fish, *The Scientific World Journal* (2002) 2: 558-572. DOI 10.1100/tsw.2002.137.
3. Austin, B. and Austin, D.A. (1987) *Bacterial Fish Pathogens, Disease of Farmed and Wild Fish*. Ellis Horwood, Chichester.
4. Austin, B., 1982. Taxonomy of bacteria isolated from a coastal, marine fish-rearing unit. *Journal of Applied Microbiology*, 53(2):253-268.
5. Bairagi, A., Sarkar Ghosh, K., Sen, S.K. and Ray, A.K., 2004. Evaluation of the nutritive value of *Leucaena leucocephala* leaf meal, inoculated with fish intestinal bacteria *Bacillus subtilis* and *Bacillus circulans* in formulated diets for rohu, *Labeo rohita* (Hamilton) fingerlings. *Aquaculture Research*, 35(5):436-446.
6. Barry, T., Powell, R. and Gannon, F., 1990. A general method to generate DNA probes for microorganisms. *Biotechnology*, 8(3):233-236.
7. Bhat, R.A., Dhillon, O., Hoque, F. and Sundaray, J.K. 2024. Insights on fish gut microbiome-A review. *Journal of Aquaculture*, 32: 1-33. <https://doi.org/10.61885/joa.v32.2023.294>.
8. Bledsoe, J.W., Peterson, B.C., Swanson, K.S. and Small, B.C., 2016. Ontogenetic characterization of the intestinal microbiota of channel catfish through 16S rRNA gene sequencing reveals insights on temporal shifts and the influence of environmental microbes. *PloS one*, 11(11):p.e0166379.
9. Bordenstein, S.R., Theis, K.R. 2015. Host biology in light of the microbiome: ten principles of holobionts and hologenomes, *PLoS Biol.* 13 (8): e1002226.
10. Burns AR, Stephens WZ, Stagaman K, Wong S, Rawls JF, Guillemin K, Bohannan BJ (2016) Contribution of neutral processes to the assembly of gut microbial communities in the zebrafish over host development. *ISME J* 10:655–664. <https://doi.org/10.1038/ismej.2015.142>.
11. Cantas, L., Sørby, J.R.T., Aleström, P. and Sørum, H., 2012. Culturable gut microbiota diversity in zebrafish. *Zebrafish*, 9(1):26-37.
12. Chalamaiah, M., Hemalatha, R., Jyothirmayi, T., 2012. Fish protein hydrolysates: proximate composition, amino acid composition, antioxidant activities and applications: a review. *Food Chem.* 135, 3020–3038.
13. Chipps, S.R. and Garvey, J.E. 2007. Assessment of food habits and feeding patterns, In; Guy, C.S. and Brown, M.L. (eds.). *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda. pp. 473-514.
14. Cho, J., Lindemann, M., Monegue, H., Cromwell, G., 2010. Feeding value of dried porcine solubles for weanling pigs. *Prof. Anim. Sci.* 26, 425–434.
15. Davis, D., Arnold, C., McCallum, I., 2002. Nutritional value of feed peas (*Pisum sativum*) in practical diet formulations for *Litopenaeus vannamei*. *Aquac. Nutr.* 8, 87–94.
16. Deb S, Das L, Das SK. Composition and functional characterization of the gut microbiome of freshwater pufferfish (*Tetraodon cutcutia*). *Arch Microbiol* 2020;202:2761–70.
17. Desai, A.R., Links, M.G., Collins, S.A., Mansfield, G.S., Drew, M.D., Van Kessel, A.G. and Hill, J.E., 2012. Effects of plant-based diets on the distal gut microbiome of rainbow trout (*Oncorhynchus mykiss*). *Aquaculture*, 350:134-142.
18. Diwan, A.D. Harke, S.N., Panche G., Archana, N. 2021. Aquaculture industry prospective from gut microbiome of fish and shellfish: an overview, *J. Anim. Physiol. Anim. Nutr.* 106 :441–469, <https://doi.org/10.1111/jpn.13619>.



19. Diwan, A.D., Harke, S.N., Panche, A.N. 2023. Host-microbiome interaction in fish and shellfish: An overview, *Fish and Shellfish Immunology Reports* 4: 100091.
20. Egerton S, Culloty S, Whooley J et al. The gut microbiota of marine fish. *Front Microbiol* 2018;9:873. <https://doi.org/10.3389/fmicb.2018.00873>.
21. Estruch, G., Collado, M.C., Peñaranda, D.S., Tomás Vidal, A., Jover Cerdá, M., Pérez Martín ez, G. and Martínez-Llorens, S., 2015. Impact of fishmeal replacement in diets for gilthead sea bream (*Sparus aurata*) on the gastrointestinal microbiota determined by pyrosequencing the 16S rRNA gene. *PloS one*, 10(8):p.e0136389.
22. F. Sun, et al. 2019. Insights into the intestinal microbiota of several aquatic organisms and association with the surrounding environment, *Aquaculture* 507 (2019) 196–202.
23. Figueroa, J., Sol'a-Oriol, D., Guzman-Pino, S., Chetrit, C., Borda, E., Pérez, J., 2016. The use of porcine digestible peptides and their continuity effect in nursery pigs. *J. Anim. Sci.* 94, 1531–1540.
24. Forster, I., Dominy, W., Obaldo, L., Tacon, A., 2003. Rendered meat and bone meals as ingredients of diets for shrimp *Litopenaeus vannamei* (Boone, 1931). *Aquaculture* 219, 655–670.
25. Foster, K.R., Schluter, J., Coyte, K.Z., Rakoff-Nahoum, S. 2017. The evolution of the host microbiome as an ecosystem on a leash, *Nature* 548: 43.
26. Francis, G., Makkar, H. P., & Becker, K. (2001). Antinutritional factors present in plant-derived alternate fish feed ingredients and their effects in fish. *Aquaculture*, 199, 197–227. [https://doi.org/10.1016/S0044-8486\(01\)00526-9](https://doi.org/10.1016/S0044-8486(01)00526-9).
27. Ghanbari, M., Kneifel, W. and Domig, K.J., 2015. A new view of the fish gut microbiome: advances from next-generation sequencing. *Aquaculture*, 448:464-475.
28. Givens CE, Ransom B, Bano N et al. Comparison of the gut microbiomes of 12 bony fish and 3 shark species. *Mar Ecol Prog Ser* 2015;518:209–23.
29. Gómez GD and Balcázar JL, 2008. A review on the interactions between gut microbiota and innate immunity of fish. *FEMS Immunol Med Microbiol*, 52(2): 145-154, doi: 10.1111/j.1574-695X.2007.00343.x.
30. Gomez-Gil, B., Roque, A. and Turnbull, J.F., 2000. The use and selection of probiotic bacteria for use in the culture of larval aquatic organisms. *Aquaculture*, 191(1-3):259-270.
31. Hansen, G.H. and Olafsen, J.A., 1989. Bacterial colonization of cod (*Gadus morhua* L.) and halibut (*Hippoglossus hippoglossus*) eggs in marine aquaculture. *Applied and environmental microbiology*, 55(6):1435-1446.
32. Herlemann, D.P., Labrenz, M., Jürgens, K., Bertilsson, S., Waniek, J.J. and Andersson, A.F., 2011. Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *The ISME journal*, 5(10):1571-1579.
33. Hernández, C., Olvera-Novoa, M.A., Aguilar-Vejar, K., Gonzalez-Rodríguez, B., La Parra, D.E., A, I., 2008. Partial replacement of fish meal by porcine meat meal in practical diets for Pacific white shrimp (*Litopenaeus vannamei*). *Aquaculture* 277, 244–250.
34. Holben, W.E., Williams, P., Saarinen, M., Särkilahti, L.K. and Apajalahti, J.H., 2002. Phylogenetic analysis of intestinal microflora indicates a novel *Mycoplasma* phylotype in farmed and wild salmon. *Microbial ecology*, 44:175-185.
35. Hongjie, W., Beiping, T., Qihui, Y., Mingling, M., Yi, L., Shuyan, C. 2023. Growth, nonspecific immunity, intestinal flora, hepatopancreas, and intestinal histological results for *Litopenaeus vannamei* fed with diets supplement with different animal by-products, *Aquaculture Reports* 29: 101521.
36. Ingerslev, H.C., Strube, M.L., von Gersdorff Jørgensen, L., Dalsgaard, I., Boye, M. and Madsen, L., 2014b. Diet type dictates the gut microbiota and the immune response against *Yersinia ruckeri* in rainbow trout (*Oncorhynchus mykiss*). *Fish & shellfish immunology*, 40(2):624-633.



37. Ingerslev, H.C., von Gersdorff Jørgensen, L., Strube, M.L., Larsen, N., Dalsgaard, I., Boye, M. and Madsen, L., 2014a. The development of the gut microbiota in rainbow trout (*Oncorhynchus mykiss*) is affected by first feeding and diet type. *Aquaculture*, 424:24-34.
38. Izvekova GI, Izvekov EI and Plotnikov AO, 2007. Symbiotic microflora in fishes of different ecological groups. *Biol Bull*, 34(6): 610-618, doi:10.1134/S106235900706012X.
39. Jandhyala, S. M. (2015). Role of the normal gut microbiota. *World Journal of Gastroenterology*, 21(29), 8787. <https://doi.org/10.3748/wjg.v21.i29.8787>.
40. Javaherdoust, Shaghayegh, Sakineh Yeganeh, Abdolsamad Keramat Amirkolaie, 2020. Effects of dietary visceral protein hydrolysate of rainbow trout on growth performance, carcass composition, digestibility and antioxidant enzyme in juvenile *oncorhynchus mykiss*. *Aquac. Nutr.* 26 (1), 134–144. <https://doi.org/10.1111/anu.12975>.
41. Kariman, A., Shalloof, Khalifa N. 2009. Stomach contents and feeding habits of *Oreochromis niloticus* (L) from Abu-Zabal, Egypt. *World Applied Journal*. 6(1): 1-5.
42. Kido, M.H. 1996. Morphological variation in feeding traits of native Hawaiian stream fishes. *Pac. Sci.*, 50 (2): 184-193.
43. Kim, D., Brunt, J. & Austin, B. (2007) Microbial diversity of intestinal contents and mucus in rainbow trout (*Oncorhynchus mykiss*). *J. Appl. Microbiol.*, 102, 1654–1664.
44. Kim, S.H., Han, S.K. and Shin, H.S., 2006. Effect of substrate concentration on hydrogen production and 16S rDNA-based analysis of the microbial community in a continuous fermenter. *Process Biochemistry*, 41(1):199-207.
45. Korsnes, K., Nicolaisen, O., Skår, C.K., Nerland, A.H. and Bergh, Ø., 2006. Bacteria in the gut of juvenile cod *Gadus morhua* fed live feed enriched with four different commercial diets. *ICES Journal of Marine Science*, 63(2):296-301.
46. Kumar, V., Sinha, A. K., Makkar, H. P., De, B. G., & Becker, K. (2012). Phytate and phytase in fish nutrition. *Journal of Animal Physiology, Nutrition Animal*, 96, 335–364. <https://doi.org/10.1111/j.1439-0396.2011.01169.x>.
47. Kumari, K. 2020. The fish gut microbiota, current approaches and perspectives: A review, *Journal of Advances in Microbiology Research* 1(1): 19-22.
48. Larsen, A.M., Mohammed, H.H. and Arias, C.R., 2014. Characterization of the gut microbiota
49. Lauzon, H.L., Gudmundsdottir, S., Steinarsson, A., Oddgeirsson, M., Petursdottir, S.K., Reynisson, E., Bjornsdottir, R. and Gudmundsdottir, B.K., 2010. Effects of bacterial treatment at early stages of Atlantic cod (*Gadus morhua* L.) on larval survival and development. *Journal of Applied Microbiology*, 108(2):624-632.
50. Leulier F, MacNeil LT, Lee W-j, Rawls JF, Cani PD, Schwarzer M, Zhao L, Simpson SJ (2017) Integrative physiology: at the crossroads of nutrition, microbiota, animal physiology, and human health. *Cell Metab* 25:522–534.
51. Li X, Zhou L, Yu Y et al. Composition of gut microbiota in the gibel carp (*Carassius auratus gibelio*) varies with host development. *Microb Ecol* 2017;74:239–49.
52. Liston, J., 1956. Quantitative variations in the bacterial flora of flatfish. *Microbiology*, 15(2):305-314.
53. Liu, Y., Yao, Y., Li, H., Qiao, F., Wu, J., Du, Z.Y. and Zhang, M., 2016. Influence of endogenous and exogenous estrogenic endocrine on intestinal microbiota in zebrafish. *PloSone*, 11(10):e0163895.
54. Llewellyn MS, Boutin S, Hoseinifar SH et al. Teleost microbiomes: the state of the art in their characterization, manipulation and importance in aquaculture and fisheries. *Front Microbiol* 2014a;5: 207.
55. McFall-Ngai, M., Hadfield, M.G., Bosch, T.C.G., Carey, H.V., Domazet-Lošo, T., Douglas, A.E., Dubilier, N., Eberl, G., Fukami, T., Gilbert, S.F. et al. 2013. Animals in a bacterial world, a new imperative for the life sciences, *Proc. Natl Acad. Sci.* 110 (9) : 3229–3236.



56. McIntosh, D., Ji, B., Forward, B.S., Puvanendran, V., Boyce, D. and Ritchie, R., 2008. Culture-independent characterization of the bacterial populations associated with cod (*Gadus morhua* L.) and live feed at an experimental hatchery facility using denaturing gradient gel electrophoresis. *Aquaculture*, 275(1-4):42-50.
57. Merrifield, D.L., Olsen, R.E., Myklebust, R. & Ringø, E. (2011) Dietary effect of soybean (*Glycine max*) products on gut histology and microbiota of fish. In: *Soybean and Nutrition* (El-Shemy, H. ed.), pp. 231–250. Intech, Rijeka, Croatia, ISBN 978-953-307-536-5.
58. Mishra, S.P. 2020. Observation and analysis of the gut contents of some common edible fresh water cat fishes of river Gomti at district Sultanpur, *Journal of Fisheries and Lifesciences* 5(2): 34-38.
59. Mishra, S.P. 2020a. Significance of fish nutrients for human health. *Int. J. Fish. Aquatic Research*. 5(3): 47-49.
60. Mishra, S.P. 2020b. Food and feeding habit of Indian major carp Bhakur (*Catla catla*) from Meeranpur Lake, Sultanpur, Uttar Pradesh. *Int. J. Fish. Aquatic Studies*. 8(4): 301-303.
61. Mishra, S.P. 2020c. Seasonal variation in gut contents of Indian major carp *Cirrhinus mrigala* from Meeranpur Lake, India. *International Journal of Biological Innovations*. 2(2): 202-208.
62. Mondal, S., Roy, T. and Ray, A.K., 2010. Characterization and identification of enzyme-producing bacteria isolated from the digestive tract of bata, *Labeo bata*. *Journal of the World Aquaculture Society*, 41(3):369-377.
63. Moriarty, D.J.W., 1996. Microbial biotechnology: a key ingredient for sustainable aquaculture. *Infotech Int.*, 4:29-33.
64. Myers, A., Goodband, R., Tokach, M., Dritz, S., Derouchey, J., Nelssen, J., 2014. The effects of porcine intestinal mucosa protein sources on nursery pig growth performance. *J. Anim. Sci.* 92, 783–792.
65. Nandi, A., Dan, S.K., Banerjee, G., Ghosh, P., Ghosh, K., Ringø, E. and Ray, A.K., 2017. Probiotic potential of autochthonous bacteria isolated from the gastrointestinal tract of four freshwater teleosts. *Probiotics and antimicrobial proteins*, 9:12-21.
66. Navarrete, P., Mardones, P., Opazo, R., Espejo, R. and Romero, J., 2008. Oxytetracycline treatment reduces bacterial diversity of intestinal microbiota of Atlantic salmon. *Journal of Aquatic Animal Health*, 20(3):177-183.
67. Nelson, T.M., Rogers, T.L., Carlini, A.R. and Brown, M.V., 2013. Diet and phylogeny shape the gut microbiota of Antarctic seals: a comparison of wild and captive animals. *Environmental microbiology*, 15(4):1132-1145.
68. of three commercially valuable warmwater fish species. *Journal of applied microbiology*, 116(6):1396-1404.
69. Olafsen, J.A. (2001) Interactions between fish larvae and bacteria in marine aquaculture. *Aquaculture* 200, 223–247.
70. Olsen, R.E., Sundell, K., Mayhew, T.M., Myklebust, R. & Ringø, E. (2005) Acute stress alters intestinal function of rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Aquaculture*, 250, 480–495.
71. Ou W, Yu G, Zhang Y et al. Recent progress in the understanding of the gut microbiota of marine fishes. *Mar Life Sci Technol* 2021;3:434–48.
72. Padmakumar, K.G., Bindhu, L., Sreerekha, P.S. and Joseph, N. 2009. Food and feeding behaviour of golden catfish, *Horabagrus brachysoma* (Gunther). *Ind. J. Fish.*, 56 (2): 139-142.
73. Pham LN, Kanther M, Semova I, Rawls JF (2008) Methods for generating and colonizing gnotobiotic zebrafish. *Nat Protoc* 3:1862–1875.
74. Rajeev, R., Adithya, K.K., Kiran, G.S., Joseph, S. 2020. Healthy microbiome: a key to successful and sustainable shrimp aquaculture, *Rev. Aquacult.* 13: 238–258, <https://doi.org/10.1111/raq.12471>.
75. Ray, A.K., Ghosh, K., Ringø, E. 2012. Enzyme-producing bacteria isolated from fish gut: a review, *Aquaculture Nutrition*, 18:465-492.



76. Reid, H.I., Treasurer, J.W., Adam, B. and Birkbeck, T.H., 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(1-2):36-43.
77. Rengpipat, S., Rukpratanporn, S., Piyatiratitivorakul, S. and Menasaveta, P., 2000. Immunity enhancement in black tiger shrimp (*Penaeus monodon*) by a probiont bacterium (*Bacillus S11*). *Aquaculture*, 191(4):271-288.
78. Rimmer, D.W. and Wiebe, W.J., 1987. Fermentative microbial digestion in herbivorous fishes. *Journal of fish Biology*, 31(2):229-236.
79. Ringø, E. & Birkbeck, T.H. (1999) Intestinal microflora of fish larvae and fry. *Aquacult. Res.*, 30, 773–789.
80. Ringø, E. and Birkbeck, T.H., 1999. Intestinal microflora of fish larvae and fry. *Aquaculture research*, 30(2):73-93.
81. Ringø, E., Olsen, G.J., Mayhew, T.M. & Myklebust, R. (2003) Electron microscopy of the intestinal microflora of fish. *Aquaculture*, 227, 395–415.
82. Ringø, E., Schillinger, U. and Holzapfel, W., 2005. Antimicrobial activity of lactic acid bacteria isolated from aquatic animals and the use of lactic acid bacteria in aquaculture. In *Biology of growing animals*, 2:418-453.
83. Robertson, P.A.W., O-Dowd, C., Burrells, C., Williams, P., and Austin, B. (2000) Use of *Carnobacterium* sp. as a probiotic for Atlantic salmon (*Salmo salar* L.) and rainbow trout (*Oncorhynchus mykiss*, Walbaum). *Aquaculture* 185, 235-243.
84. Rombout, J.H., Abelli, L., Picchiatti, S., Scapigliati, G. and Kiron, V., 2011. Teleost intestinal immunology. *Fish & shellfish immunology*, 31(5):616-626.
85. Romero, J. and Navarrete, P., 2006. 16S rDNA-based analysis of dominant bacterial populations associated with early life stages of coho salmon (*Oncorhynchus kisutch*). *Microbial ecology*, 51:422-430.
86. Romero, J. and Navarrete, P., 2006. 16S rDNA-based analysis of dominant bacterial populations associated with early life stages of coho salmon (*Oncorhynchus kisutch*). *Microbial ecology*, 51:422-430.
87. Schmidt, V., Gomez-Chiarri, M., Roy, C., Smith, K. and Amaral-Zettler, L., 2017. Subtle microbiome manipulation using probiotics reduces antibiotic-associated mortality in fish. *Msystems*, 2(6):10-1128.
88. Simon, J.C., Julian, R.M., Christophe, M., Marc, A.S. 2019. Host-microbiota interactions: from holobiont theory to analysis, *Microbiome* 7: 5, <https://doi.org/10.1186/s40168-019-0619-4>.
89. Singh, B.K., Thakur, K., Kumari, H., Mahajan, D., Sharma, D., Sharma, A.K., Kumar, S., Singh, B., Pankaj, P.P., Kumar, R. 2025. A review on comparative analysis of marine and freshwater fish gut microbiomes: insights into environmental impact on gut microbiota, *FEMS Microbiology Ecology*, 101, fiae169. doi: 10.1093/femsec/fiae169.
90. Stephens, W.Z., Burns, A.R., Stagaman, K., Wong, S., Rawls, J.F., Guillemin, K. and Bohannan, B.J., 2016. The composition of the zebrafish intestinal microbial community varies across development. *The ISME journal*, 10(3):644-654.
91. Sullam KE, Essinger SD, Lozupone CA et al. Environmental and ecological factors that shape the gut bacterial communities of fish: a meta-analysis. *Mol Ecol* 2012;21:3363–78.
92. Syvokienė, J., Stankus, S. and Andreikėnaitė, L., 2011. Bacterioflora of digestive tract of fishes in vitro. *Veterinarija ir zootechnika*, 56(78): 213-233.
93. Talapko, J., Včev, A., Meštrović, T., Pustijanac, E., Jukić, M., & Škrlec, I. (2022). Homeostasis and dysbiosis of the intestinal microbiota: Comparing hallmarks of a healthy state with changes in inflammatory bowel disease. *Microorganisms*, 10(12), 2405. <https://doi.org/10.3390/microorganisms10122405>.
94. Talwar, C., Nagar, S., Lal, R., Negi, R.K. 2018. Fish Gut Microbiome: Current Approaches and Future Perspectives, *Indian J Microbiol* 58(4):397–414.
95. Tan, B., Mai, K., Zheng, S., Zhou, Q., Liu, L., Yu, Y., 2005. Replacement of fish meal by meat and bone meal in practical diets for the white shrimp *Litopenaeus vannamei* (Boone). *Aquac. Res.* 36, 439–444.



96. Uma, A., Subash, P., Abraham, T.J. 2020. Importance of Gut Microbiota in Fish – A Review, *Indian J. Anim. Hlth.* 59(2)-Special Issue: 181-194. DOI: 10.36062/ijah.59.2SPL.2020.181-194.
97. Uniacke-Lowe S, Stanton C, Hill C et al. The marine fish gut microbiome as a source of novel bacteriocins. *Microorganisms* 2024;12:1346.
98. Van Doan, H., Hoseinifar, S.H., Ringø, E., Angeles Esteban, M., Dadar, M., Dawood, M.A. et al. 2020. Host-associated probiotics: a key factor in sustainable aquaculture, *Rev. Fish. Sci. Aquacult.* 28 (1): 16–42.
99. Vine, N.G., Leukes, W.D. and Kaiser, H., 2006. Probiotics in marine larviculture. *FEMS microbiologyreviews*, 30(3):404-427.
100. Vishwakarma, B., Sawant, M.S., Amberkar, D. 2025. The Gut Microbiome: A Comprehensive Review of its Role in Human Health and Disease, *International Journal of Research Studies in Microbiology and Biotechnology (IJRSMB)* 10(2): 7-25.
101. Wang, Y.C., Hu, S.Y., Chiu, C.S., Liu, C.H. 2019. Multiple-strain probiotics appear to be more effective in improving the growth performance and health status of white shrimp, *Litopenaeus vannamei*, than single probiotic strains, *Fish Shellfish Immunol.* 84: 1050–1058.
102. Weihao, O., Guijuan, Y., Yanjiao, Z., Kangsen, M. 2021. Recent progress in the understanding of the gut microbiota of marine fishes, *Marine Life Science & Technology* 3:434–448. <https://doi.org/10.1007/s42995-021-00094-y>.
103. Wu S, Wang G, Angert ER et al. Composition, diversity, and origin of the bacterial community in grass carp intestine. *PLoS One* 2012;7:e30440.
104. Wu, J.P., Liu, W., Wen, H., Zhou, Y., Wu, J.J., 2021a. Animal by-products with or without enzymatic hydrolysis completely replacement of fish meal in genetically improved farmed tilapia diets (*Oreochromis niloticus*). *Aquac. Res.* 52, 291–301.
105. Xinru, L., Lingling, H., Yuanyuan, W., Qi, Z., Xiaoqin L., Xiangjun, L. 2026. *Aquaculture and Fisheries*, <https://doi.org/10.1016/j.aaf.2026.02.002>.
106. Yan Q, Li J, Yu Y, Wang J, He Z, Van Nostrand JD, Kempfer 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* 18:4739–4754. <https://doi.org/10.1111/1462-2920.13365>
107. Yang, X., Zhi, X., Song, Z., Wang, G., Zhao, X., Chi, S., Tan, B., 2022. Flesh quality of hybrid grouper (*Epinephelus fuscoguttatus* G., ZHAO, X., CHI, S. & TAN, B. 2022. Flesh quality of hybrid nal bacterial communities are clo *Animal. Nutrition* 8, 114–124.
108. Yoshimizu, M. and Kimura, T., 1976. Study on the intestinal microflora of salmonids. *Fish pathology*, 10(2):243-259.
109. Yoshimizu, M., Takizawa, H., Kamei, Y. And Kimura, T., 1986. Interaction between fish pathogenic viruses and microorganisms in fish rearing water: survival and inactivation of infectious pancreatic necrosis virus, infectious hematopoietic necrosis virus and *Oncorhynchus masou* virus in rearing water. *Fish Pathology*, 21(4):223-231.
110. Zhang, J., Guo, L., Feng, L., Jiang, W., Kuang, S., Liu, Y., Hu, K., Jiang, J., Li, S., & Tang, L. (2013). Soybean β -conglycinin induces inflammation and oxidation and causes dysfunction of intestinal digestion and absorption in fish. *PLoS One*, 8, Article e58115. <https://doi.org/10.1371/journal.pone.0058115>.
111. Zhang, M., Sun, Y., Liu, Y., Qiao, F., Chen, L., Liu, W.T., Du, Z. and Li, E., 2016. Response of gut microbiota to salinity change in two euryhaline aquatic animals with reverse salinity preference. *Aquaculture*, 454:72-80.

