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Tilapia aquaculture, emerging diseases, and the roles of the skin microbiomes in health and disease

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Abstract

Aquaculture is playing an increasingly important role in global food security, especially for low-income and food-deficit countries. The majority of aquaculture production occurs in freshwater earthen ponds and tilapia has quickly become one of the most widely adopted culture species in these systems. Tilapia are now farmed in over 140 countries facilitated by their ease of production, adaptability to a wide range of environmental conditions, fast growth, and high nutritional value. Typically, tilapia have been considered a hardy, disease resilient species; however, the disease is increasing with subsequent threats to the industry as their production is intensified. In this review, we discuss tilapia production, with a focus on Bangladesh as one of the top producing countries, and highlight the problems associated with disease and treatment approaches for them, including the misuse of antimicrobials. We address a key missing component in understanding health and disease processes for sustainable production in aquaculture, specifically the role played by the microbiome. Here we examine the importance of the microbiome in supporting health, focused on the symbiotic microbial community of the fish skin mucosal surface, the abiotic and biotic factors that influence the microbiome, and the shifts that are associated with diseased states. We also identify conserved taxa of skin microbiomes that may be used as indicators of health status for tilapia offering new opportunities to mitigate and manage the disease and optimize environmental growing conditions and farming practices.

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The rise of aquaculture and tilapia production

Aquaculture is one of the fastest-growing food-producing sectors (Anderson et al. 2017; Barría et al. 2021) and is playing a central role in meeting the demand for nutritious and affordable food for billions of people globally (Lynch and MacMillan 2017; Tigchelaar et al. 2022). Currently, aquatic foods contribute around 17% of the global animal protein, 7% of all protein sources (FAO 2022; Obiero et al. 2019) and provide at least 20% of the per capita intake of animal protein for 3.3 billion people (FAO 2022). In many low-income and developing countries, including Bangladesh, aquatic food provides more than half of their total animal protein intake (Arthur et al. 2022; FAO 2022). Fish furthermore contain long-chained poly-unsaturated fatty acids, together with many micronutrients (e.g. calcium, iron, zinc), vitamins, and minerals, which are dietary elements especially important for nutritionally vulnerable people (Ahern et al. 2021; Arthur et al. 2022; Béné et al. 2016, 2015; HLPE 2014). Recognizing the health potential of fish, many countries, including India, Brazil, Chile, and sub-Saharan African countries, have incorporated fish into their national school-feeding programmes (Ahern et al. 2021; Béné et al. 2016; Wineman et al. 2022).

The demand for fisheries products is increasing dramatically. Illustrating this, between 1961 and 2019, global aquatic food consumption increased by 3% annually, almost twice that of the annual global population growth rate (1.6%) (FAO 2020, 2022). In line with the global demand, fisheries and aquaculture production have increased (reaching 214 million tonnes in 2020) and it is predicted that aquaculture will contribute to over half of the global fish consumption by 2030 (FAO 2020). Aquaculture now delivers 49.2% of the worldwide supply of aquatic products, most of which are used for human consumption and has a total value of US$ 281.5 billion (FAO 2022).

In Bangladesh, one of the most densely populated countries (nearly 170 million people living in an area of 148,460 km^2) and poorest nations in the world (Lauria et al. 2018), fish represents about 60% of animal protein intake in the national diet (DoF 2020; Lauria et al. 2018; Shamsuzzaman et al. 2017) with an average consumption of approximately 23 kg/year per person (DoF 2020). Bangladesh now ranks third globally for inland open water capture and fifth in aquaculture production (DoF 2020; FAO 2020). More than 12% (over 20 million) of the total human population of Bangladesh depends directly or indirectly, on the fisheries sector for their livelihood (DoF 2020). In 2019–2020, aquaculture contributed 3.52% of the gross domestic product in Bangladesh and aquatic animal products (including crustaceans, fish, and molluscs) are Bangladesh's most valuable export after textiles and footwear (OEC 2020).

Among the 87.5 million tonnes of aquatic animals produced by global aquaculture, 57.5 million tonnes of this is finfish (FAO 2022). A diverse range of fish species are cultured in different aquaculture systems across freshwater, brackish water, inland saline water, and marine waters; however, in 2020, only 28 finfish species groups made up 79% (45.4 million tonnes) of the total finfish aquaculture production (FAO 2022). Of these species, Nile tilapia (*Oreochromis niloticus*) is ranked third, representing 7.9% (4.5 million tonnes) of the total finfish production with other tilapias accounting for an additional 1.9% (around 1.1 million tonnes) (Fig. 1a). Only grass carp (*Ctenopharyngodon idellus*) and silver carp (*Hypophthalmichthys molitrix*) are higher produced finfish species farmed globally than tilapia (FAO 2022). Among the various species of tilapia, Nile tilapia is the most widely distributed and preferred species for aquaculture; over 90% of all commercially produced tilapia farmed outside of Africa are Nile tilapia (Prabu et al. 2019; Wang and Lu 2016).
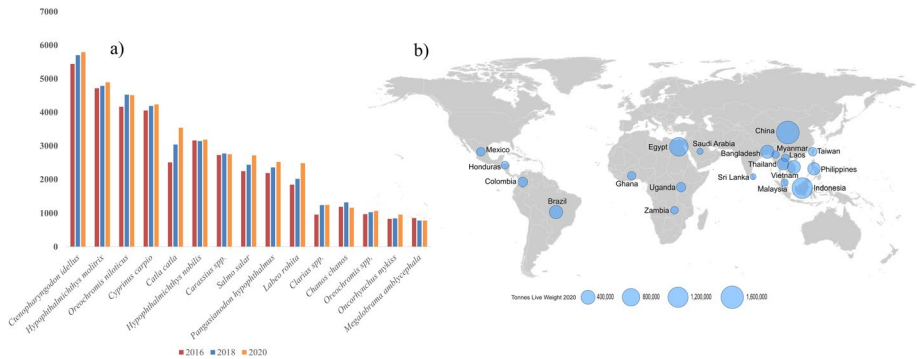
Fig. 1 **a** The top 15 finfish species and species groups in global aquaculture (data for 2016 to 2022 (FAO 2020, 2022)). Production units are in thousands of tonnes (live weight). **b** Top 20 countries producing tilapia (in tonnes live weight; Data from FAO FishStatJ, May 2022)

Monosex tilapia are favoured due to their fast growth and high production potential (Prabu et al. 2019), and the fact that generally they do not breed well in the natural environment, thus reducing the risk of them becoming an invasive species. Other commercially important common tilapia species include the Mozambique tilapia (*O. mossambicus*), blue tilapia (*O. aureus*), the Zanzibar tilapia (*O. hornorum*), and various hybrid tilapia species (Machimbirike et al. 2019; Prabu et al. 2019).

With their relative ease of farming, good market demand, and stable market price, the farming and production of tilapia have increased considerably over the last few decades (Wang and Lu 2016). They are also reasonably fast-growing, reaching around 400 g in 6/7 months (Baqui and Bhujel 2011), allowing farmers to harvest two or more crops each year depending on the harvesting size. They can also tolerate a wide range of environmental conditions and they grow well even in poor water quality conditions with low oxygen levels (Li et al. 2017a; Rebouças et al. 2015; Yu et al. 2021a). Some tilapia can also live in brackish water and can even adapt to full-strength seawater (Rahman et al. 2021; Rengmark et al. 2007), widening the areas across which they can be cultured. Tilapia are furthermore benthopelagic omnivorous fish that feeds on algae, plankton, detritus, small invertebrates, and bacterial films. This relatively low trophic need lends them well to highly sustainable forms of aquaculture practice (Tesfahun and Temesgen 2018; Wang and Lu 2016), including biofloc systems (Khanjani et al. 2022). This is reflected by the fact that 140 countries in the world have introduced at least one species of tilapia into their fish farming systems (Barroso et al. 2019; Deines et al. 2016; Fitzsimmons 2015). Tilapia farming has grown exceptionally fast compared with the aquaculture of other species, with production growing by 11% per annum for the last three decades (from 0.3 million tonnes in 1987 to 5.9 million tonnes in 2017, with a value of approximately US$11 billion (Barroso et al. 2019)). In terms of quantity, the share of tilapia in global aquaculture has increased from 1.9% in 1987 to 5.3% in 2017 and in terms of value, from 1.5% to 4.4% (Barroso et al. 2019), emphasizing its importance to global food security. Asian countries produce most of the world's tilapia and are the major consumers of this fish species (Fig. 1b).

In Bangladesh, Mozambique tilapia (*O. mossambicus*) was first introduced in the 1950s but the species only got wide acceptance through the introduction of the GIFT tilapia by the Bangladesh Fisheries Research Institute in partnership with WorldFish in the 1990s (Hussain 2004; Ponzoni et al. 2010). It is generally grown in polyculture systems with carp

species such as catla (*Catla catla*), rohu (*Labeo rohita*), common carp (*Cyprinus carpio*), silver carp (*H. molitrix*), and grass carp (*C. idella*) or catfish such as pangas (*Pangasius pangasius*), pabda (*Ompok pabda*), and shing (*Gagata youssoufi*), although monoculture of tilapia also occurs (Rahman et al. 2021). Bangladesh is now the third highest producer of tilapia in Asia and the fourth highest globally (DoF 2020; see Fig. 1b). Currently, in Bangladesh, tilapia is the third most farmed fish after pangas (*P. pangasius*) and rohu (*Labeo rohita*) (Fig. 2; DoF 2020). In 2019–2020, around 371,263 tonnes of tilapia were produced making up 9.69% of the annual fish production of inland water bodies (DoF 2020). The most popular method for culturing tilapia is in earthen, shallow depth (1–2 m) ponds that range from small-scale to large intensive commercial systems (DoF 2020). Almost all the produced tilapia is used for domestic consumption (Ahmed et al. 2012).

Diseases and their treatments in tilapia farming

To fulfil global demand, the aquaculture industry has expanded, primarily through the intensification of culture systems (Assefa and Abunna 2018). This, however, in many instances has resulted in overstocking, reduced water quality, and increased stress of the cultured fish that in turn renders the fish more susceptible to various infectious diseases. Disease is in fact now one of the major limiting factors to the growth of the aquaculture industry (Assefa and Abunna 2018). Globally, losses in the aquaculture sector due to diseases are estimated to exceed US$ 6 billion annually (Assefa and Abunna 2018; Stentiford et al. 2017; WorldBank 2014) but estimates vary, and according to Shinn et al. (2015), the global economic losses in finfish aquaculture range between US$ 1.05 to US$ 9.58 billion per year.

Tilapia are thought to be relatively disease-resistant to many common pathogens (Ferguson et al. 2014), but increasingly farmed tilapia are being shown to succumb to various disease causing organisms (Machimbirike et al. 2019; Surachetpong et al. 2020; see Table 1). Tilapia are particularly susceptible to infection by *Streptococcus* sp. including *Streptococcus dysgalactiae*, *S. iniae*, and *S. agalactiae* that are now among the most important bacterial pathogens, causing considerable economic losses throughout the world (Zamri-Saad et al. 2014). In China, for example, a large-scale outbreak of *Streptococcus* spp. in 2012,

Fig. 2 Production (tonnes) of the top ten fish species from pond aquaculture in Bangladesh for the years 2018–2019 and 2019–2020 (DoF 2020)
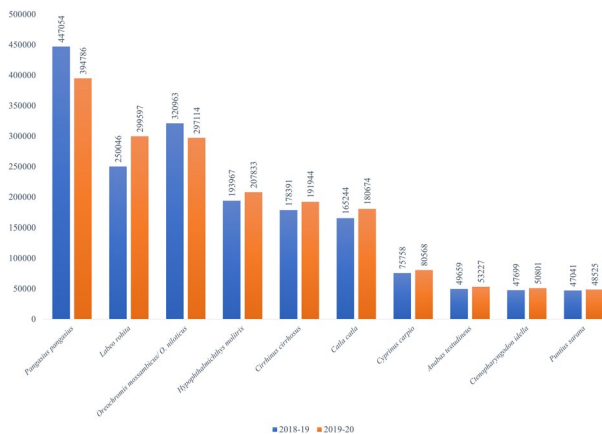
Table 1 The major bacterial, fungal, and parasitic diseases in tilapia and their common treatments

Disease	Causative agent(s)	Agent(s) Type	Clinical signs	Stressors contributing to disease	Common treatments	References
Streptococcosis	*Streptococcus* spp. including *S. agalactiae*, *S. iniae*, *S. dysgalactiae* and *Enterococcus* spp.	Bacteria	Red discolouration of the skin; lethargic; erratic swimming; exophthalmia with corneal opacity and haemorrhage in eyes; abdominal distension; skin haemorrhaging around the anus, the base of fins and anus, around the mouth, and in operculum; enlarged and nearly black spleen; and high mortality	Introduction of contaminated water and/or fry, high stocking density, high water temperature, high ammonia, low dissolved oxygen, unsuitable pH, poor husbandry management	Antibiotic in feed: Erythromycin at 50 mg/kg fish/d for 12 d; Oxytetracycline at 75–100 mg/kg fish/d for 14 days. Various commercial vaccines	Prabu et al. (2019); Rizkiantino et al. (2021); Zamri-Saad et al. (2014)
Motile *Aeromonas* septicaemia (MAS)	*Aeromonas hydrophila* and other related *Aeromonas* species	Bacteria	Loss of body balance; lethargic swimming; gasping at the water surface; external haemorrhage; exophthalmia; swollen abdomen; frequent high mortalities	Stress caused by high water temperature, water pH changes, low dissolved oxygen, high levels of ammonia and nitrites, high stocking density, parasitic infections, rough handling and transportation	Disinfectants (KMnO$_4$ at 4–10 mg/L for 1 h or 2–4 mg/L indefinite immersion), Antibiotics (Oxytetracycline as feed additive at 50 mg/kg fish/d for 12–14 d, 21 d withdrawal, probiotics (*Enterococcus faecium* at 8 g/kg feed for 45 d, *Saccharomyces cerevisiae* at 5 g/kg feed for 12 weeks), and various vaccines	Monir et al. (2020); Prabu et al. (2019); Stratev and Odeyemi (2017)

Table 1 (continued)

Disease	Causative agent(s)	Agent(s) Type	Clinical signs	Stressors contributing to disease	Common treatments	References
Columnaris	*Flavobacterium columnare*	Bacterium	Fin rot; necrotic lesions on skin and gills; irregular whitish to grey patches on the skin and/or fins; high mortality rates	Poor environmental conditions, high stocking densities, high organic load, and high-water temperature	$KMnO_4$ to the water at 2 mg/L; 20 min bath in $CuSO_4$ at 37 mg/L or depending on alkalinity, indefinite immersion with $CuSO_4$ at 0.5–3 mg/L	Declercq et al. (2013); Dong et al. (2015a); Figueiredo et al. (2005); Prabu et al. (2019)
Vibriosis	*Vibrio* spp.	Bacteria	Septicaemia; lethargy; anorexia; haemorrhages along the external body surface and the base of the fins; and high mortality	Caused by stress, poor water quality, low water temperature, and bad management practices	Antibiotic in feed	Elgendy et al. (2015); Elgendy et al. (2022); Prabu et al. (2019)
Edwardsiellosis	*Edwardsiella ictaluri, E. tarda*	Bacteria	Abnormal swimming; haemorrhages at the base of fins, operculum, belly, mouth, and vent; exophthalmia; bloody fluid in body cavity; swollen, dark red spleen; pale, mottled liver; and swollen, soft kidney	Imbalanced environmental conditions, such as high temperature, high organic load, and poor water quality	Antibiotic in feed	El-Yazeed and Ibrahem (2009); Nhinh et al. (2022); Park et al. (2012); Soto et al. (2012); Xu and Zhang (2014)

Table 1 (continued)

Disease	Causative agent(s)	Agent(s) Type	Clinical signs	Stressors contributing to disease	Common treatments	References
Saprolegniosis	*Saprolegnia parasitica*	Fungus	Erratic swimming; cotton-like white, grey, or brown growths on the skin and fins; open lesions in muscle	Stressors include handling, mechanical damage, temperature fluctuation, poor hygiene, sexual maturity	Disinfectants such as $KMnO_4$ or $CuSO_4$. Use 1 mg/L of $CuSO_4$ for every 100 mg/L alkalinity up to 3.0 mg/L $CuSO_4$; formalin at 25 mg/L indefinite immersion or 150 mg/L for 1 h	El-Sayed (2020); Prabu et al. (2019); Zahran et al. (2017)
Ciliates	*Ichthyophthirius multifiliis* (Ich)	Protozoan parasite	White spots on the skin, gills, or fins of the affected fish	Low water temperature, intensive culture, poor water quality, contaminated water input	A single dose of $KMnO_4$ at 0.5–1.0 mg/L	El-Sayed (2020); Nguyen et al. (2020)
	Trichodina spp.	Protozoan parasite	Occurs on the skin and/or gills, and causes epidermal injuries including abrasions, lesions, and ulcers	Low water temperature, intensive culture, poor water quality, contaminated water input	Formalin at 170–250 mg/L for 1 h as bath or in ponds at 15–25 mg/L indefinitely for 5–10 d; $KMnO_4$ at 5 mg/L for 10–15 min; NaCl at 0.5–1.0% for 15 min	Attia et al. (2021); El-Sayed (2020); Xu et al. (2015)
Monogenetic trematodes	*Dactylogyrus* spp.	Metazoan parasite	Occurs on the skin, fins, or gills. Rapid opercular movements, thickened edges of gills and destruction of branchial epithelium	Poor handling, high stocking density, bad water quality, poor management, etc	A single dose of formalin at 250 mg/L for 35–40 min or two repeated doses of $KMnO_4$ at 5 mg/L in static water with a 2-day interval	El-Sayed (2020)

Table 1 (continued)

Disease	Causative agent(s)	Agent(s) Type	Clinical signs	Stressors contributing to disease	Common treatments	References
	Gyrodactylus spp.	Metazoan parasite	Damages gills; haemorrhage; increased mucus secretion	Poor handling, high stocking density, bad water quality, poor management	A single dose of formalin at 250 mg/L for 35–40 min or two repeated doses of $KMnO_4$ at 5 mg/L in static water with a 2-day interval	El-Sayed (2020)

caused 30–80% mortality of tilapia (Chen et al. 2012; Sun et al. 2016; Zhang 2021), with a direct economic loss of approximately US$ 1.0–1.5 billion (Liu et al. 2019). Streptococcosis outbreaks can be treated with antibiotics if they are administered at the early stage of the disease, but their oral administration can be difficult as the infected fish lose appetite (Zamri-Saad et al. 2014). Barnes et al. (2022) recently reviewed the benefits of autogenous vaccination as a local solution to reduce antimicrobial resistance and protect farmed species against key pathogens. Several vaccines are available for the treatment of Streptococcosis including AQUAVAC® Strep Sa (Merck Animal Health Company, USA), AquavacTM GarvetilTM (Intervet/Schering-Plough Animal Health), and NORVAX® STREP Si (Merck Animal Health Company, USA) (Zamri-Saad et al. 2014).

Other key emerging infectious bacterial pathogens include *Francisella noatunensis* subsp. *orientalis* that causes francisellosis (Nguyen et al. 2016); *Flavobacterium columnare* that causes columnaris (Dong et al. 2015a; Figueiredo et al. 2005); *Aeromonas hydrophila* (Monir et al. 2020), *A. jandaei*, and *A. veronii* (Dong et al. 2017b) causing motile *Aeromonas* septicaemia (MAS); vibriosis by *Vibrio* spp. (Elgendy et al. 2022); and edwardsiellosis caused by *Edwardsiella ictaluri* and *E. tarda* (Dong et al. 2019; El-Yazeed and Ibrahem 2009; Nhinh et al. 2022; Park et al. 2012; Soto et al. 2012; Xu and Zhang 2014). Other opportunistic facultative fungal infections include *Saprolegnia* spp. (Ali et al. 2019; Zahran et al. 2017) and protozoans, including *Ichthyophthirius multifiliis*, *Trichodina* spp., and *Dactylogyrus* spp. (Attia et al. 2021; El-Sayed 2020; Nguyen et al. 2020; Prabu et al. 2019; Xu et al. 2015).

For the treatment of bacterial vibriosis, antibiotics are effective when supplied via medicated feed or mixed in water (El-Gohary et al. 2020). Gram-negative motile aeromonads may be treated with potassium permanganate ($KMnO_4$) and with antibiotics in the feed (Monir et al. 2020; Prabu et al. 2019; Stratev and Odeyemi 2017). A recent study reported immersion vaccination against columnaris disease induced a strong immune response and improved survival against experimental infection of *F. columnare* (Kitiyodom et al. 2021). This opportunistic pathogen, in addition to fungal diseases such as white spots, can also be effectively treated via exposure to $CuSO_4$, $KMnO_4$, or salt/sodium chloride (El-Sayed 2020; Prabu et al. 2019). The available common treatments for treating the major disease problems caused by bacteria, parasites, fungi, etc. affecting tilapia are summarized in Table 1.

To date, eight viral diseases (five DNA and three RNA viruses) have been reported in tilapia (Table 2) some of which are causing huge losses in tilapia aquaculture (Machimbirike et al. 2019). Viral diseases like Herpes-like virus, iridoviral disease (IVD), viral nervous necrosis (VNN), tilapia lake virus (TiLV), and infectious spleen and kidney necrosis virus (ISKNV) that affect Nile tilapia and red hybrid tilapia (Dong et al. 2015b; Suebsing et al. 2016) are the most limiting viral disease-causing agents in tilapia culture. In contrast with bacterial diseases, viral diseases are much more difficult to control not only because of the lack of therapeutics but also because of the lack of knowledge of the pathogenesis of viral infections (Kibenge et al. 2012). Some commercial vaccines and selective breeding programmes have been successful in reducing the severity of some viral diseases, for most; however, there are no effective treatments or cures (Jansen et al. 2019). Viruses, therefore, tend to be considered the most important potential threats in aquaculture, including tilapia. This is well illustrated in the case of the newly emerged tilapia lake virus (TiLV) (Jansen et al. 2019).

TiLV, also known as *Tilapia tilapinevirus*, was first reported in farmed tilapia in Israel in 2014 (Eyngor et al. 2014). It is now listed as an emerging finfish disease by the World Organization for Animal Health (OIE) with a high likelihood of being included in the list

Table 2 List of viral diseases with clinical signs and life stages affected in tilapines (adopted from Machimbirike et al. (2019))

Agent	Taxonomy (genus)	Tilapines host	Clinical signs and affected stage	Recorded geographical distribution	References
Lymphocystis disease virus (LCDV)	*Lymphocystivirus*	*Tilapia amphimelas, T. esculenta, T. variabilis,* and *Haplochromis* sp.	Wart-like growths mainly on the tails of infected fish. Juvenile tilapia affected but no mortality was recorded	North Tanzania	Paperna (1973)
Infectious pancreatic necrosis virus (IPNV)	*Aquabirnavirus*	Mozambique tilapia (*O. mossambicus*), Nile tilapia (*O. niloticus*)	Darkening of skin, pale gills, distended abdomen, white faecal casts, and abnormal swimming	Taiwan, Kenya	Hedrick et al. (1983); Mulei et al. (2018)
Bohle iridovirus (BIV)	*Ranavirus*	Mozambique tilapia (*O. mossambicus*)	Corkscrew-like swimming, fry affected with up to 100% mortalities	Australia	(Ariel and Owens 1997)
Iridovirus-like agent	unknown	Nile tilapia (*O. niloticus*)	Lethargic, swimming slowly or resting on the tank bottom, exophthalmia, and gill pallor. Mortalities mostly in fry	Canada	(McGrogan et al. 1998)
Viral nervous necrosis (VNN)	*Betanodavirus*	Nile tilapia (*O. niloticus*)	Neurological disorders including erratic swimming, loss of balance, lethargic, anorexic, and dark in colour. Mortalities range from 20–100% in larvae and juveniles, in both bath challenges and during outbreaks	Europe, Thailand, and Indonesia	Bigarré et al. (2009); Keawcharoen et al. (2015); Prihartini et al. (2015)

Table 2 (continued)

Agent	Taxonomy (genus)	Tilapines host	Clinical signs and affected stage	Recorded geographical distribution	References
Tilapia larvae encephalitis virus (TLEV)	*Herpesvirus*-like virus	Blue tilapia (*O. aureus*)	Whirling or spiral swimming behaviour, high mortality (above 90%) in laboratory-reared tilapia larvae	Israel	Shlapobersky et al. (2010); Sinyakov et al. (2011)
Tilapia lake virus (TiLV)	*Tilapinevirus*, species *Tilapia tilapinevirus*	Mango tilapia (*Sarotherodon galilaeus*), redbelly tilapia (*Tilapia zillii*), blue tilapia (*O. aureus*), wild tilapia (*Tristamellasimonis intermedia*), Nile tilapia (*O. niloticus*), red tilapia (*Oreochromis* sp.), hybrid tilapia (*O. niloticus × O. aureus*), red hybrid tilapia (*O. niloticus × O. mossambicus*), Mozambique tilapia (*O. mossambicus*)	Lethargy, loss of appetite, ocular alterations and lesions, scale protrusion, darkening of the skin, skin erosions, gill pallor, exophthalmia, and abdominal distension. Affected almost all stages and mortalities can reach up to 90%	Israel, Ecuador, Colombia, Egypt, Philippines, Thailand, Chinese Taipei, India, Malaysia, Indonesia, Tanzania, Uganda, Peru, the USA, Mexico, Bangladesh	Debnath et al. (2022); Eyngor et al. (2014); Machimbirike et al. (2019); Surachetpong et al. (2020)
Infectious spleen and kidney necrosis virus (ISKNV)	*Megalocytivirus*	*O. niloticus* and red hybrid tilapia (*O. niloticus × O. mossambicus*), red tilapia (*Oreochromis* sp.)	Lethargy, gill pallor, distension of the coelomic cavity, and mortalities range from 50 to 75% and are detected in ovaries of the adult female, fertilized eggs, fry, and fingerlings	Thailand, USA, Ghana, and Brazil	Dong et al. (2015b); Figueiredo et al. (2022); Ramírez-Paredes et al. (2021); Subramaniam et al. (2016); Suebsing et al. (2016)

of reportable finfish diseases (Sood et al. 2021). An investigation of samples collected from Thai hatcheries from 2012 to 2017 found the presence of TiLV in the majority of tested samples (Dong et al. 2017a). Before its discovery, more than 40 countries had imported tilapia fry and fingerlings from Thailand. Recent studies have confirmed the presence of TiLV in 16 countries including some of those countries receiving tilapia from Thailand (Fig. 3). To date, TiLV has been reported from Israel (Eyngor et al. 2014), Ecuador (Bacharach et al. 2016; Ferguson et al. 2014), Colombia (Tsofack et al. 2017), Egypt (Fathi et al. 2017; Nicholson et al. 2017), Philippines (OIE 2017a), Thailand (Dong et al. 2017b; Surachetpong et al. 2017), Chinese Taipei (OIE 2017b), India (Behera et al. 2018), Malaysia (Amal et al. 2018), Indonesia (Koesharyani et al. 2018), Tanzania and Uganda (Mugimba et al. 2018), Mexico (OIE 2018), Peru (Jansen et al. 2019), the USA (Ahasan et al. 2020), and Bangladesh (Chaput et al. 2020; Debnath et al. 2020; Hossain et al. 2020) (Fig. 3). In tilapia farms affected by TiLV, mortality has been reported at rates up to 90% (Dong et al. 2017a, 2017b; Eyngor et al. 2014). In Egypt in 2015, TiLV caused a production loss of approximately 98,000 tonnes resulting in an economic loss of US$ 100 million (Fathi et al. 2017).

The TiLV isolated from Bangladesh was found phylogenetically closely related to the several isolates of Thailand (Chaput et al. 2020; Debnath et al. 2020). In Bangladesh, TiLV has now been reported from different farms and hatcheries of at least 13 districts (Bagerhat, Barguna, Comilla, Cox's Bazar, Faridpur, Gazipur, Jessore, Khulna, Magura, Mymensingh, Narail, Satkhira, Rajbari) of the 64 districts farming tilapia (Debnath et al. 2020; Hossain et al. 2020). In Bangladesh, mortalities in the TiLV positive farms have been estimated at 50–90% in 2017 and 25–40% in 2019 (Debnath et al. 2020).

For ISKNV, reported mortalities of Nile tilapia and red hybrid tilapia (fry and juvenile) are in the range of 50–75% (Dong et al. 2015b; Figueiredo et al. 2022; Subramaniam
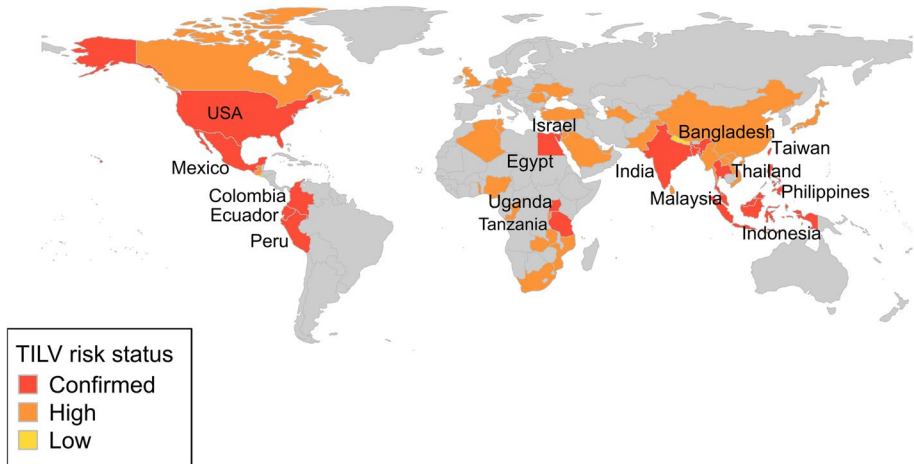

Fig. 3 Global distributions of reported TiLV. The red (16), orange (32), and yellow (2) colours indicate countries with confirmed TiLV, high and lower risk of TiLV infection, respectively, through tilapia fry and/or fingerlings imported from Thailand. Algeria, Bahrain, Belgium, Burundi, Canada, China, Congo, Germany, Guatemala, Japan, Jordan, Laos, Mozambique, Myanmar, Nigeria, Pakistan, Romania, Rwanda, Saudi Arabia, Singapore, South Africa, Sri Lanka, Switzerland, Togo, Tunisia, Turkey, Turkmenistan, Ukraine, United Arab Emirate, the UK, Vietnam, and Zambia are high-risk countries; El-Salvador and Nepal are lower risk countries (Dong et al. 2017a)

et al. 2016; Suebsing et al. 2016). During an ISKNV disease outbreak in tilapia in Ghana (September 2018 to March 2019), morbidity and mortality rates of 60–90% were recorded, with losses of more than 10 tonnes per day in many farms (Ramírez-Paredes et al. 2021). A similar outbreak of ISKNV in the cultured Nile tilapia fish farm was also reported in Brazil in 2020 (Figueiredo et al. 2022).

VNN, first reported in tilapia larvae in France (Bigarré et al. 2009), targets the central nervous system of fish including the brain, spinal cord, and retina, and leads to neuronal necrosis and is reported to affect more than 50 fish species (Machimbirike et al. 2019). During a VNN outbreak in Thailand of farm-raised tilapia larvae, the mortality rate was between 90 and 100% with the affected fish first showing clinical signs of neurological disorder (e.g. loss of balance, corkscrew-like swimming) (Keawcharoen et al. 2015). VNN has also been reported in tilapia fry in Indonesia, but here, no mortality was recorded (Prihartini et al. 2015). In the latest report of VNN from Egypt, mass mortalities (up to 70%) occurred in the hatchery-reared Nile tilapia fry (Taha et al. 2020). This section highlights the huge impacts associated with viral diseases that are now prevalent across major expanses of the world's most important tilapia aquaculture production sectors. Although there are many fish pathogens responsible for causing disease in aquaculture farms, there is little information available about viruses (except TiLV) causing disease in the aquaculture farms of Bangladesh. The possible reason for this is under-reporting, lack of diagnostic laboratories or support services, and training/costs of diagnostic methods, to do so.

Microbiomes of surface mucosa in tilapia

The fish skin and gills represent major pathways for pathogens to invade fish and thus act as a critical line of defence for maintaining host health by keeping microbes at bay (Glover et al. 2013; Lazado and Caipang 2014; Merrifield and Rodiles 2015). The fish skin and gill epithelial surfaces are coated in a mucus layer containing various immunogenic compounds, including antimicrobial peptides and enzymes, proteins such as immunoglobulins, defensins, lysozyme, proteases, esterase, and mucins (Gomez et al. 2013). Collectively these act as a critical component of the immune response which is active against invading microbes (Merrifield and Rodiles 2015). While it may sound like the defences of the fish's outer mucosal surfaces represent a hostile environment for microbial growth, they in fact offer an environment of mucin-associated glycans (Barr et al. 2013) that is nutrient-rich in contrast to the relatively sparse surrounding aquatic environment. Niche-adapted microbes that can resist the immunological components are therefore bountiful in the outer mucosal surfaces of fish and form an indigenous commensal microbiota (Legrand et al. 2018; Merrifield and Rodiles 2015). In turn, these commensals act as a further line of immune defence to obstruct pathogen colonization by antagonistic activity as well as competing for adhesion sites and/or nutrients (Legrand et al. 2018; Merrifield and Rodiles 2015). Disruption of the host-microbiome symbiotic relationship may lead to major changes in microbiota community structure in a process referred to as dysbiosis (Dillon and Charnley 2002). Stressful conditions often occur in aquaculture practices and can cause shifts in the microbiota to favour the propagation of opportunistic pathogens that are often ubiquitous, naturally present in the aquatic environment and/or form part of the fish microbiome (Boutin et al. 2013; Califano et al. 2017; Rud et al. 2017). The microbiome and immune system of fish show a direct and wide-ranging connection (Kelly and Salinas 2017; Yu et al. 2021b). For instance, microbiota colonization stimulates neutrophils granulocyte in gnotobiotic

zebrafish (Kanther et al. 2014). Meanwhile, in teleosts, secretory immunoglobulins (specifically IgT) are highly induced at mucosal surfaces to coat both pathobionts (potential pathological microorganisms which, under normal situations, live as non-harming symbionts) and commensals (Xu et al. 2013), preventing their intrusion into the blood. Where IgT is depleted, the microbiome becomes dysbiotic with concurrent depletion of IgT targeted microbial taxa, such as short-chain fatty acid-producing bacteria and proliferation of pathobionts associated with the disease. During disease challenges, IgT depletion also renders fish more susceptible to parasitic infection and associated mortality (Xu et al. 2020).

The advent of metabarcoding via next-generation sequencing of conserved ribosomal marker genes (16S for prokaryotes, 18S for eukaryotes, and internal transcribed spacer for fungi) has enabled the development of substantial knowledge of microbial communities comprising microbiomes in the health and disease of humans, and there is now an increasing focus on fish, albeit it much of this, research has focused on the gut microbiomes of high-value aquaculture species (i.e. Atlantic salmon and marine shrimp) due to their role in gut health, and through which feed conversion, growth, and overall productivity can be enhanced (Perry et al. 2020). Various studies however have now shown that the fish skin mucosal surface supports a unique microbial community that is discrete from communities supported by other body sites, such as the gut (Sylvain et al. 2020) and gill (Legrand et al. 2018; Minich et al. 2020b). Niche separation can be partially explained by the distinctive environment of the different mucosal surfaces. For instance, the gill supports specialist ammonia-oxidizing and denitrifying bacteria to clear these toxic metabolites excreted at the gill (van Kessel et al. 2016). The gut is typically associated with specialists such as obligate anaerobic bacteria (Sylvain et al. 2020) and those aiding digestion (Ray et al. 2012); however, the presence of niche-specialized taxa does not preclude the presence of other generalist aerobic taxa shared across body niche sites (de Bruijn et al. 2018). While the gut microbiota exists in a relatively stable and buffered environment, the outer mucosal surfaces of the skin (and gill) are in direct and continuous contact with the water of the culture environment. The microbiota of the skin niche must withstand fluctuating conditions, being largely comprised of generalist bacteria that are strongly influenced by the water microbiota and physicochemistry (Krotman et al. 2020; Sylvain et al. 2020). As such, the microbial communities of water and skin are closely interconnected, with bacterial taxa found in the surrounding water environment also forming a large composition of the skin microbiota. However, the skin microbiota is uniquely structured with specific taxa enrichment (Boutin et al. 2013; McMurtrie et al. 2022).

Environmental influences on the skin microbiome are reflected by inherent variability between fish cultured in different environments; however, conserved microbial hallmarks can be seen in skin microbiomes. Almost every published study, regardless of water salinity, has identified Proteobacteria (Pseudomonadota) as the dominant bacterial phyla of fish skin microbiomes, including tilapia (Boutin et al. 2013; Chiarello et al. 2015; Elsheshtawy et al. 2021; Krotman et al. 2020; Lokesh and Kiron 2016; McMurtrie et al. 2022; Rosado et al. 2019; Sultana et al. 2022); in particular, this comprises the Gammaproteobacteria class (Chiarello et al. 2019; Larsen et al. 2015; McMurtrie et al. 2022; Reinhart et al. 2019; Sylvain et al. 2020). Additionally, the phyla Actinobacteria (Actinomycetota) and Bacteroidetes (Bacteroidota) occur widely (Boutin et al. 2013; Chiarello et al. 2015; Lokesh and Kiron 2016; McMurtrie et al. 2022; Reinhart et al. 2019). Moving beyond coarse, taxonomic ranks can give insight into the occurrence and potential function of microbial taxa associated with specific host species. The biological significance of bacteria designated as core taxa remains unclear; however, their persistence across different environments may reflect functional importance. The two current studies of the tilapia skin microbiomes have identified core/enriched taxa including *Aeromonas*, *Cetobacterium*, Comamonadaceae, *Clostridium*, *LD29*, *Acinetobacter*, *Vibrio*, *Exiguobacterium*, *Plesiomonas*, *Sphingomonas*, *Pseudomonas*, and *Paucibacter* (Elsheshtawy et al. 2021;

McMurtrie et al. 2022) but their functional roles/importance are largely unknown. Changes in the abundance of members of the Comamonadaceae family (many are unclassified; there are 104 known species) in the tilapia gut microbiome have been associated with aluminium exposure (Yu et al. 2019) and immunostimulatory insulin exposure in Nile tilapia (Wang et al. 2021). Comamonadaceae have also been shown to be negatively correlated with ectoparasitism in the skin microbiome of Prussian carp *Carassius gibelio* (Kashinskaya et al. 2021).

The genus *Cetobacterium*, more specifically *C. somerae*, remains one of the most frequently identified commensals of microbiomes in the skin (and gut and gill) of tilapia (Bereded et al. 2022; Elsaied et al. 2019; Elsheshtawy et al. 2021; McMurtrie et al. 2022). Isolates from freshwater fish guts have been shown to synthesize vitamin B12 (Sugita et al. 1991; Tsuchiya et al. 2008), which is speculated to promote fish health. Experimental monitoring studies suggest *Cetobacterium* is an essential component of healthy fish gut microbiomes as abundance was significantly depleted in spring viremia of carp virus (SVCV) infected common carp (*Cyprinus carpio*) (Meng et al. 2021) and in crucian Carp (*Carassius auratus*) suffering red-operculum disease (Li et al. 2017b). Additionally, the application of probiotics has been shown to increase the abundance of *Cetobacterium* in the skin and gill of Nile tilapia (Wang et al. 2020), while specific application of the *C. somerae* XMX-1 fermentation product resulted in improved gut health and disease resilience against *Aeromonas veronii/hydrophila* challenge (Zhou et al. 2022).

Numerous strains of *Aeromonas* and *Pseudomonas* found within tilapia skin microbiomes are widely recognized as opportunistic fish pathogens (Austin and Austin 2016; Crumlish and Austin 2020). Of these, the disease caused by *Aeromonas hydrophila* is particularly impactful for tilapia aquaculture (Nicholson et al. 2020). However, pathogenicity is strain-specific; therefore, microbiome surveys via metabarcoding using short hypervariable regions cannot assert pathogenic potential. Additionally, numerous *Pseudomonas* strains and species inhabiting fish-associated microbiomes are true commensals, protecting against invasive infections. For instance, *Pseudomonas fluorescens* is reported as a pathogen (Liu et al. 2015), yet selected strains have been shown to offer protection for rainbow trout (*Oncorhynchus* mykiss) against infection by the pathogenic oomycete *Saprolegnia parasitica* (González-Palacios et al. 2019) and *Vibrio anguillarum* (Gram et al. 1999). Similar probiotic effects of *P. fluorescens* have also been reported experimentally in Nile tilapia (Eissa et al. 2014). However, even for these species, the symbiotic function may change in response to host health, environmental conditions, and microbiome dysbiosis.

Given that the fish mucosal layer in the skin and gill surfaces provides the first line of defence against pathogens, characterizing shifts in the composition of these microbiomes can potentially provide insights into what changes are associated with/lead to disease outbreaks. However, the variable nature of the fish skin and gill microbiomes and the wide array of environmental and host factors that can alter them clearly complicates dissecting those key changes and shifts in the microbial assemblages that can be linked with disease onset for disease prediction.

Factors influencing microbiomes of mucosal surfaces in health and disease

Diseases are often context-dependent and "pathogens" may exist in the culture environment biomes (water, sediment, biofilms) and host-associated microbiomes without ever causing disease. Passage to a disease state is dependent on many biotic and abiotic factors

that influence the diversity and composition of fish mucosal microbiomes. Here, we review various factors known to influence the fish skin microbiome, as these factors contribute to the inherent variability of microbiome composition between individuals and may also prove influential for transitions to disease states.

Water quality The external surface of fish is continuously exposed to water which results in a dynamic relationship between planktonic and skin surface microbial communities. Intensive aquaculture practices in ponds can lead to poor water quality, including build-up of nutrients, organic matter, and toxic products (Avnimelech and Ritvo 2003) such as nitrite (Chen et al. 2017). Furthermore, water quality parameters of aquaculture ponds follow diurnal patterns (Shoko et al. 2014). Given that planktonic pond communities can be strongly influenced by water quality (Casé et al. 2008), it is not surprising that water quality also has a significant impact on the bacterial community of fish skin. For example, in brook trout (*Salvelinus fontinalis*) experimentally exposed to a mixture of 11 chemical compounds, representing typical hydraulic fracturing waste, after an exposure to an antibiotic (oxytetracycline), recovery varied according to the treatment group and resulted in a shifted microbial community composition, where in particular taxa belonging to *Flavobacterium* were subsequently more abundant in treatment groups than in the controls (Galbraith et al. 2018). Some of the tested chemicals in that study, such as NaCl and Mg_2Cl_2, are routinely applied in aquaculture practices. Various water physicochemistry parameters such as water temperature, salinity, pH, and dissolved oxygen are also reported to shape fish skin microbiomes (Krotman et al. 2020). The algal content of ponds, which varies widely in tilapia earthen pond systems is also associated with changes in skin microbiomes, but given its relationship with dissolved oxygen this may be related to changes in the pond physicochemistry more generally (Kunlasak et al. 2013). Nevertheless, a lower alpha diversity of the skin microbiome has been reported in Pacific chub mackerel (*Scomber japonicus*), under conditions of increasing chlorophyll *a* concentration with a shift also in skin microbiota community structure (beta diversity) (Minich et al. 2020a).

Geographical location and habitat Geographic location has widely been reported as one of the strongest predictors of microbial communities of fish skin; however, it is likely much of this may be related to the different environmental parameters of location (McMurtrie et al. 2022; Sylvain et al. 2020), and this, for example, can influence planktonic communities which have a close and dynamic relationship to the skin microbiome. Geographic location has been shown to be a significant and major predictor of skin microbiome structure in European catfish (*Silurus glanis*) (Chiarello et al. 2019); striped mullet (*Mugil cephalus*), red snapper (*Lutjanus campechanus*), spotted seatrout (*Cynoscion nebulosus*), sand seatrout (*Cynoscion arenarius*), pinfish (*Lagodon rhomboides*), and Atlantic croaker (*Micropogonias undulatus*) (Larsen et al. 2013); flag cichlid (*Mesonauta festivus*), pacu (*Mylossoma duriventre*), and black piranha (*Serrasalmus rhombeus*) (Sylvain et al. 2020); and redbreast tilapia (*Coptodon rendalli*) and shire tilapia (*Oreochromis shiranus*) (McMurtrie et al. 2022). Each geographical location is likely to vary in a multitude of environmental factors and habitat features that are influential to skin microbiome processes. As an extreme example of this, a comparison of Atlantic salmon (*Salmo salar)* from wild and hatchery-reared populations has shown that the skin microbiome of fish from an artificial environment had a lower alpha diversity and uniquely structured beta diversity and exhibited less interindividual variation (Webster et al. 2018). Among different aquaculture

systems, Atlantic salmon reared in recirculating aquaculture systems were found to have a greater skin microbiota richness compared to flow through systems (Minich et al. 2020b).

Host Host-specific factors also govern fish microbial assemblages. These are particularly important for the gastrointestinal microbiome, while environmental factors have greater relevance for the skin mucosal surface (Sylvain et al. 2020). Nevertheless, host-related factors do contribute to the skin microbiome, and in some cases, fish species have been reported as one of the most influential factors (Chiarello et al. 2018; Larsen et al. 2013). Fish skin microbiomes undoubtedly show a high degree of inter-individual variation, even amongst fish of the same species in the same environment (Berggren et al. 2022). Inter-individual variation of skin microbiomes was shown in a seminal study of artificially reared brook charr (*Salvelinus fontinalis*) (2nd-generation progeny following population cross) where the abundance of select commensals could be directly correlated with host genomic regions through genetic linkage analysis (Boutin et al. 2014). Genetics therefore evidently plays a complementary role, highlighting the breadth and complexity of host associated and environmental processes which govern fish microbiome composition.

Diseases/infections In stress-free conditions, the balance of microbes in fish microbiomes works to help prevent pathogen entry and causing disease. Indigenous bacteria contained in surface mucosal layers contribute to the host defence by colonization resistance (preventing pathogen growth) (Dillon and Charnley 2002), and via the production and secretion of friction preventing polymers and complex inhibitory antimicrobials (Austin 2006; Krotman et al. 2020; Takeuchi et al. 2021; Tiralongo et al. 2020). However, a change in the host-microbiome symbiotic relationship may lead to a major change/reduction in microbial diversity. A study on the yellowtail kingfish (*Seriola lalandi*), for example, illustrated an overall reduction of microbial diversity in the skin and gills at disease onset, and furthermore, the emergence of a specific community (pathogenic) was reflected by a change in immune states of the host (Legrand et al. 2018). Another study on Atlantic salmon (*Salmo salar* L.) challenged with salmonid alphavirus reported a decrease in abundance of proteobacterial taxa and an increase of opportunistic taxa, e.g. *Flavobacteriaceae*, *Streptococcaceae*, and *Tenacibaculum* sp. on the skin samples (Reid et al. 2017). A recent study on striped catfish (*Pangasianodon hypophthalmus*) challenged with *Aeromonas hydrophila* similarly showed that pathogen concentration stimulates the skin immune response by altering the mucosal microbiota and increasing the prevalence of opportunistic pathogens (Chen et al. 2022). Li et al. (2017b) reported that during "red-operculum" disease in crucian carp (*Carassius auratus*), genera belonging to *Aeromonas*, *Vibrio*, and *Shewanella* were dominant while in healthy fish genera from *Cetobacterium*, *Cyanobacterium* and *Clostridiaceae* were more abundant. They also reported that genera present in diseased fishes were absent or rarely present in the environmental samples. An imbalance in the microbial diversity can also allow for the invasion of a secondary pathogen (de Bruijn et al. 2018; Reid et al. 2017). For example, in Atlantic salmon infected with sea lice infection, higher levels of secondary pathogens belonging to *Vibrio*, *Flavobacterium*, *Tenacibaculum*, and *Pseudomonas* genera ensue (Llewellyn et al. 2017).

While microbial alterations of the fish skin are undoubtedly associated with disease, it is nevertheless often challenging to disentangle whether microbiota shifts are a contributing factor, causal, or a direct consequence of the disease as the plethora of biotic and abiotic factors known to influence fish microbiomes undoubtedly contribute to these disease processes. This indeed may well help to explain when and why disease states arise, in some

environments in the presence of a given pathogen, while in other environments, fish remain disease-free. It is furthermore worth emphasizing that there is increasing evidence that disease cannot be attributed to single aetiological agents, and disease progression is highly dependent on the collective community of microorganisms in a system (Bass et al. 2019). The one pathogen–one disease model is moving towards the pathobiome concept, where disease in the animal is now seen as the result of interactions between host-associated prokaryotes, eukaryotes, and viruses, their host, and the environment (Bass et al. 2019). Many multi-faceted diseases and syndromes are now emerging, for instance in shrimp (Kooloth Valappil et al. 2021), further emphasizing the importance of understanding the microbiomes of aquaculture species and their environment.

Effects of antibiotics on fish microbiomes

Antibiotics are used extensively to fight bacterial infections in humans or animal hosts. In aquaculture, their use is often indiscriminate, particularly in LMICs where there is very limited regulation (Thornber et al. 2020). In livestock/food-animal, an estimated 118,940 tonnes (95% confidence interval [CI] 91,455 to 172,811 tonnes) was consumed in 2013 and it is projected that around 181,650 tonnes (95% CI 136,847 to 269,465 tonnes) will be consumed by 2030 (Sriram et al. 2021; Van Boeckel et al. 2017). In 2018, the total global antibiotic consumption was 40.1 billion (95% uncertainty interval [UI] 37.2 to 43.7 billion) defined daily doses (DDD) and although the consumption rate between 2000 and 2018 remained relatively stable in high-income countries, there was a 76% increase in LMICs, South Asia (India, Pakistan, Nepal, Bangladesh, and Bhutan) where over a quarter (25·2%) of all antibiotics were consumed (Browne et al. 2021). Misuse of antibiotics has received a high profile due to the risk of antimicrobial resistance (AMR) which is estimated to result in the deaths of 0.7 million people each year (O'Neill 2016; Willyard 2017), but although the uncontrolled use of antibiotics in aquaculture (especially in LMICs) may spread AMR, this has not been well studied (Preena et al. 2020). Furthermore, beyond the long-term implications of AMR, misuse of antibiotics may have immediate implications for microbiomes associated with aquaculture as antibiotics can target commensal bacteria that support fish health, immune function, and disease resilience. Antibiotics may thus reduce the microbial community mass and/or diversity, alter community composition, and/or change the enzymatic functions (Carlson et al. 2017; Ferrer et al. 2017).

The most common ways for the administration of antibiotics in aquaculture in many countries, including Bangladesh, are by medicated feed and direct introduction into the pond water (Ali et al. 2016; Shah et al. 2014; Song et al. 2016). Antibiotics are often poorly absorbed into the body, highly water soluble, and resistant to degradation; therefore, antibiotic residues are widely detected in aquatic environments (Da Le et al. 2021; Fu et al. 2022; Hossain et al. 2017; Limbu et al. 2018; Liu et al. 2021; Sotto et al. 2017). Illustrating this, the widely used antibiotics oxytetracycline and sulfamethoxazole have been measured in rivers in China at concentrations between 174.9 ± 266.9 and 741.85 ng/L (Bai et al. 2014; Dong et al. 2016) and between 259.60 and 385.00 ng/L (Chen and Zhou 2014), respectively, and the antibiotic ciprofloxacin has been recorded in the surface water in India up to 635 ng/L (Singh et al. 2019). In a recent study of surface waters from urban and rural areas of Bangladesh, eight antibiotics were detected with the highest concentration of 1407 ng/L (ciprofloxacin), 909 ng/L (azithromycin), 728 ng/L (SMX), 205 ng/L (clarithromycin),

153 ng/L (trimethoprim), 138 ng/L (acetyl sulfamethoxazole), 77 ng/L (anhydroerythromycin), and 22 ng/L (sulfadiazine) (Angeles et al. 2020). Many aquaculture farms are located in areas adjacent to rivers that are also often used as water sources for aquaculture activities (Hossain et al. 2018). Similarly, in the surface water of the old Brahmaputra River, which is widely used for open-water-fed aquaculture, a wide range of antibiotics have been measured at a concentration of up to 13.51 ng/L for metronidazole, 17.20 ng/L for trimethoprim, 11.35 ng/L for sulfonamides, 16.68 ng/L for macrolides, and 8.80 ng/L for carbamazepine (Hossain et al. 2018). Within finfish aquaculture ponds in Bangladesh sulfamethoxazole, trimethoprim, tylosin, sulfadiazine, sulfamethazine, sulfamethizole and penicillin G have been reported at a concentration of up to 20.02 ng/L, 41.67 ng/L, 39.34 ng/L, 17.97 ng/L, 11.71 ng/L, 10.81 ng/L, 7.83 ng/L, respectively (Hossain et al. 2017). Specifically, in tilapia farms in Bangladesh, sulfadiazine, sulfamethoxazole, tylosin, and trimethoprim have been reported at concentrations of up to 17.97 ng/L, 14.46 ng/L, 4.87 ng/L, and 1.57 ng/L, respectively (Hossain et al. 2017). During monsoon periods, in many of the major freshwater finfish aquaculture areas in Asia, fish pond waters mix with river water and this may further increase the spread of antibiotic-resistance genes to and from aquaculture systems. Importantly, some antibiotics can bioaccumulate in animal tissues (Carnevali et al. 2017), exacerbating the likely development of antibiotic-resistant bacteria that can pass into the food chain (Banerjee and Ray 2017; Fu et al. 2017). It is estimated that 75% of the antibiotics administrated through feed in aquaculture enter the aquatic environment through leaching from the uneaten food and excretion of the cultured species (Hossain et al. 2017; Lalumera et al. 2004).

Total global antibiotic use in aquaculture in 2017 was estimated at 9307 tonnes (95% uncertainty interval [UI] 2869 to 40,576 tonnes) and this is predicted to rise to 11,793 tonnes (UI 3804 to 53,792 tonnes) in 2030 (Schar et al. 2020; Sriram et al. 2021). Antibiotic use in aquaculture varies depending on fish species, geographics, type of infection, and country-specific legal requirements. Suggested doses, when mixed with food for oxytetracycline and sulfamethoxazole in aquaculture, are 50–250 mg/kg of fish body weight per day for 3 to 21 days (Enis Yonar et al. 2011; Limbu et al. 2018) and 100–200 mg/kg of fish body weight per day for 5 days (Liu et al. 2017), respectively. Disease conditions, however, often cause a loss of appetite in fish (Miranda et al. 2018); therefore, much of the antibiotic dose is released directly into the aquaculture pond. Furthermore, antibiotic administration is not targeted, resulting in animals of mixed health status (diseased and non-diseased fish) being treated with antibiotics, giving rise to potential microbial dysbiosis which may render the culture organism more susceptible to disease. Experimental studies have confirmed this theory, with grass carp (*Ctenopharyngodon idella*) subjected to antibiotic-induced intestinal dysbiosis more susceptible to disease after challenge with *Aeromonas hydrophila* (Sun et al. 2022).

In fish, antibiotic exposure has also been experimentally shown to exert selective pressures on skin, gill, and gut microbiomes. Dietary doses of oxytetracycline (100 mg/kg) (Payne et al. 2021) and sulfamonomethoxine (200 and 300 mg/kg) (Ming et al. 2020) given to Nile tilapia were found to cause minimal changes to alpha and beta diversity metrics of gut microbial communities; however, these exposures were not found to cause altered abundance in taxa for genera containing reputed pathogens. Further experimental evidence, however, has shown perturbation of skin and gut microbiomes, with enrichment of potentially opportunistic pathogens, following oral exposure of yellowtail kingfish *Seriola lalandi* to an antibiotic cocktail of oxytetracycline (200 mg/kg), erythromycin (50 mg/kg), and metronidazole (50 mg/kg). Interestingly, this study also suggests that the skin microbiome of fish is more resilient to antibiotic exposure than the gut microbiome, with a faster

return to a "normal" microbial community assemblage (Legrand et al. 2020). Long-term exposure to oxytetracycline and sulfamethoxazole has been shown to adversely affect the growth, metabolism, immunity, and intestinal morphology of Nile tilapia (Limbu et al. 2018), although it is unclear to what degree these health impacts are mediated by changes via the microbiome.

Antibiotic exposure in farmed fish also poses the risk of antimicrobial resistant gene (ARGs) selection in the resistome of fish microbiomes (Sáenz et al. 2019), fish faeces (Muziasari et al. 2017), sediment (Muziasari et al. 2016), and water (Patil et al. 2020). Controlled antibiotic exposure of *Piaractus mesopotamicus* to florfenicol (9.7 mg/kg) led to an increased abundance and diversity of ARGs in the fish gut microbiome, together with enrichment of *Enterobacteriaceae* whose genomes were associated with ARGs, including reputed nosocomial infection causing genera *Citrobacter*, *Klebsiella*, and *Plesiomonas*. Interestingly, antibiotic exposure also increased the co-occurrence of ARGs with mobile genetic elements, particularly transposases and phage integrases, whose abundances increased and were found to flank several ARGs (Sáenz et al. 2019). Furthermore, the sediment below the European aquaculture cage culture with a history of antibiotic use was found to be enriched in mobile genetic elements, including transposons and integrons (Muziasari et al. 2016). Together this highlights the potential for ARG spread in fish microbiomes and the wider aquaculture environment, raising the risk of AMR dissemination.

Final considerations and future research needs

Aquaculture will inevitably play a very major role in future global food security and not least for LIFD countries. Low trophic feeding finfish such as tilapia will feature strongly in the future expansion/intensification of freshwater aquaculture not least for their ability to tolerate less favourable water conditions, adaptability more generally, good nutritious qualities, and overall robustness against pathogens. However, the emergence and increasing prevalence of a wide range of diseases are limiting the future growth of the aquaculture industry with major economic consequences. This is especially the case in countries such as Bangladesh, where most production occurs in open earthen ponds in rural communities with minimal biosecurity. Research and support are urgently required to combat emerging diseases, and this requires more fundamental knowledge of disease prevalence, propagation, and pathogenesis to support the development of specific treatments and vaccines. Fundamentally it also requires the adoption of effective management and biosecurity plans, which included increasing farmer education around the management of diseases and misuse of antimicrobials.

Pertinent to these outlined action areas for aquaculture security is a need to holistically understand the functional microbial systems that interface between the pond environment and cultured fish. This in turn can help in optimizing conditions for fish growth, health, and disease avoidance. Understanding microbiomes and how they can be augmented for host protection against disease could play a very significant role in the further development of aquaculture, especially as production is intensified. Healthy skin and gill mucosal surfaces in fish are naturally colonized by pathogens (Rosado et al. 2019) that form an important part of a host's microbiome (Califano et al. 2017; Rud et al. 2017). Generally, however, the skin microbiome in unstressed fish is dominated by taxa with probiotic and antimicrobial activity (Rosado et al. 2019), and therefore, they often do not cause disease (de Bruijn et al. 2018). In order to develop a deep and meaningful understanding of microbiomes in the

mucosal surfaces of fish and how they function to prevent disease, we need to better understand the microbial assemblages of these mucosal surfaces and how they function. Next-generation sequencing has allowed for high throughput analysis of the bacterial community structure and dynamics, but less attention has been applied to assessing the functions of the microbiomes and very little attention has been directed to the viruses and bacteriophages in these mucosal communities that are likely to play a crucial rule. Given the important roles played by environmental and host-related factors in influencing mucosal microbiomes of fish, these factors too also need to be more thoroughly considered for understanding the passage of fish from healthy to diseased states.

A deeper understanding of mucosal microbiomes associated with health and disease should furthermore allow for the development and application of more effective probiotics for finfish aquaculture. Probiotics offer the opportunity to optimize health, in turn reducing the reliance on antibiotics. A combined approach to investigating the role of the microbiome during probiotic (or prebiotic) application might help improve their efficacy. Finally, a critical need in the development of microbiome research is in the identification of conserved biomarkers of the mucosal surface that can act as signals for changing health status to help in our understanding relating to disease prevention in tilapia and other fish culture practices.

Declarations

Ethical approval Not applicable.

Competing interests The authors declare no competing interests.

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