Bacterial and microalgal communities in carp polyculture systems: Composition, affecting factors and further perspectives.

Ngoc Minh Ngan Bui[a,b,c,*], Jasmine Heyse[b], Jérôme Delamare-Debouttevillle[a], Tom Defoirdt[c], Ruben Props[b], Colin Shelley[a]

[a] WorldFish Headquarters, Jalan Batu Maung, Batu Maung, Bayan Lepas, Penang 11960, Malaysia

[b] Kytos BV, Technologiepark-Zwijnaarde 82, 9052 Ghent, Belgium

[c] Center for Microbial Ecology and Technology (CMET), Ghent University, Coupure Links 653, B-9000Gent, Belgium.

*Corresponding author: NgocMinhNgan.Bui@ugent.be

Abstract

Carp polyculture is the planet's most widely practiced fish production system, using multiple fish species living in diverse trophic and spatial niches of a pond to maximize productivity. Increases in farm productivity can be supported by using healthy stock, more effective use of inputs (e.g., feed, probiotics, fertilizers), and improved disease management. However, there is a lack of understanding on how microbial–host interactions can help avoid or manage dysbiosis in carp aquaculture systems to improve productivity. The availability of literature data derived from both traditional and new molecular techniques enables a comprehensive understanding of the diversity and functionality of the microbiota in carp polyculture systems. To support the development of improved best management practices for carp polyculture, we reviewed the current knowledge of microbiota in carp polyculture systems with a focus on bacteria and microalgae communities. This review highlights the link between the host microbiota and the rearing environment microbiota, thereby emphasizing its importance in steering the rearing water microbiota to reduce microbial dysbiosis in both the water and the gut. Strong evidence implies that factors such as probiotics, prebiotics, feed, fertilizers, and manipulation of environmental parameters have a significant effect on carp microbiota. Development of management strategies towards three key areas (microbiome health assessment, technological improvements, and product management) are essential for the health of carp polyculture and will likely be critical for the industry's expansion.

KEYWORDS: Microbiomes, microbial management, microbial regulation, dysbiosis, fish health.

1. Introduction

Carp is the most widely cultivated fish species in aquaculture worldwide (FAO, 2022). Growing different carp species with partially or completely different feed spectrums and feeding habits in the same pond helps to use the available resources more efficiently (Hao-Ren, 1982a; Kestemont, 1995). Carp polyculture began in China during the Tang dynasty (618-907 A.D.)(Hao-Ren, 1982b). It was dramatically improved in the 1960s when Chinese major carps (silver carp *Hypophthalmichthys molitrix* (Valenciennes, 1844), bighead carp *Aristichthys nobilis* (Richardson, 1845), grass carp *Ctenopharyngodon idella* (Valenciennes, 1844), and black carp *Mylopharyngodon piceus* (Richardson, 1846)) were widely introduced to most countries of Europe and Asia such as Poland (Opuszyński, 1981), Bulgaria (Dimitrov, 1987), and Hungary (Horvath et al., 1984), India and Israel (Milstein, 2005).

Carp farming practices are being intensified to meet the increasing demand for aquatic products, particularly in countries such as Bangladesh, where space for ponds is very limited. However, maintaining good water quality in intensive cultivation systems is challenging due to the high load of inorganic nutrients, fish feces, overfeeding, and the often limited opportunities for water exchange (Bentzon-Tilia et al., 2016a). The shifting from extensive to semi-intensive and intensive practices is often accompanied by an increase in the occurrence of infectious diseases, which poses one of the main impediments to the sustainable growth of the aquaculture industry (Shinn et al., 2018; Stentiford et al., 2017). Therefore, diseases in aquaculture have been widely studied, particularly in identifying causative agents and preventing disease outbreaks using risk assessments and biosecurity protocols (Bouwmeester et al., 2021).

Modifying fish microbial communities has the potential to significantly influence health and disease outcomes in farming operations (de Bruijn et al., 2018; Gilbert et al., 2016). However, disentangling interactions and identifying keystone species for specific functions in microbial communities has proven

difficult because of the complex structure of these communities, especially when environmental impacts on population dynamics and activities are considered (de Bruijn et al., 2018). Most of the existing investigations have focused on the gut microbiota because of its intricate role in maximizing feed conversion, growth, and overall aquaculture productivity (Perry et al., 2020). Nevertheless, microbiota on/in the skin, gills, and water is expected to be equally important in disease resistance and susceptibility (McMurtrie et al., 2022) (Figure 1). To completely comprehend the effect of microbiota on fish health, we must have a deeper understanding of the interactions between microbial diversity and community variation associated with organs, including the gills, skin, and gut, but also in the rearing water. In addition, nutrient enrichment in fishponds produced by fertilizer and supplemental feeding causes eutrophication, commonly resulting in heavy algal blooms. These blooms can cause poor growth and even mass fish mortality due to deteriorating water quality, mainly dissolved oxygen depletion (Padmavathi & Durga Prasad, 2017). A greater understanding of the relationship between bacteria, microalgae, and fish could prevent disease, improve yields, and create aquaculture expansion and improvement strategies (Bentzon-Tilia et al., 2016b; Dittmann et al., 2017). This review describes the current state-of-the-art research on carp microbial communities, particularly determining the dynamics of bacterial and microalgal populations in the different compartments of the aquaculture infrastructure of carp (polyculture) systems. In addition, the effects of inputs such as probiotics, antibiotics, fertilizer, feed, and water quality on microbial communities are also discussed. Finally, further perspectives will be indicated.

2. Bacteria in carp polyculture systems

2.1. Bacteria in rearing environments

Bacterial biomass is one of the most significant trophic levels in an aquatic environment. The organic matter in manure or fertilizers provides bacteria with dissolved and particulate substrates, and the bacteria-laden particles provide feed for filter-feeding and detritus-consuming carp (e.g., common carp Cyprinus carpio (Linnaeus, 1758) and mud carp Cirrhinus molitorella (Valenciennes, 1844)). Besides, the mineralized fraction of manure stimulates phytoplankton production, which can serve as feed for herbivorous carp (e.g., silver carp *Hypophthalmichthys molitrix*, grass carp *Ctenopharyngodon idella*) (Kalcheva et al., 2010).

In rearing water, the dominant bacterial phyla were Bacteroidetes, Actinobacteria, and Proteobacteria. However, the proportion of each bacterial taxon varied mainly depending on geography, system, and fish species composition (Table 1). Li et al. (2021) investigated the microbiological composition of water in black carp *(Mylopharyngodon piceus)* polyculture ponds using 16S rRNA gene amplicon sequencing. They found that bacterial diversity increased throughout the mid-culture phase and declined during the late culture period due to lesser nutrient availability in the late culture period and that Proteobacteria (43.7%), Actinobacteria (24.9%), and Bacteroidetes (12.1%) were the most abundant phyla in the water column. Similarly, in silver carp and bighead carp cultivations, Actinobacteria (32.04%), Cyanobacteria (27.65%), Proteobacteria (22.64%), and Bacteroidetes (16.2%) are the most abundant bacterial taxa (Meng et al., 2021). In freshwater ecosystems like carp polyculture systems, Actinobacteria have a beneficial effect and play an essential role in the recycling of organic matter (Ghai et al., 2014; Shijila Rani et al., 2022) and are well-known producers of bioactive products (e.g., novonestmycins A, 19-methoxybafilomycin C1 amide, 21-deoxybafilomycin A1,0) (Berna et al., 2015; Jose et al., 2021; van Keulen & Dyson, 2014). Flavobacterium can be associated with fish disease (e.g., koi, longfin eels, rainbow trout) (Loch & Faisal, 2015). It can show a high abundance following the senescence and decline of freshwater cyanobacterial bloom (Newton et al., 2011). Cyanobacteria in pond water can fix atmospheric nitrogen and produce dissolved organic compounds that heterotrophic bacteria can use as a nutrient source (Louati et al., 2015).

Limnohabitans transport carbon from primary producers to higher trophic levels (Wang et al., 2017). Proteobacteria have been shown to participate in various biochemical processes (e.g., carbon and nitrogen cycling) in aquatic environments (Klase et al., 2019).

In response to the severe effects produced by pathogens, recent studies have revealed the need for commensal microbiota for the normal functioning of organs in the vertebrate host (Castejón et al., 2021). Commensal microbes from the aquatic environment can trigger the hatching stage, thereby modulating the development of the immune system which may confer disease resistance. They can also stimulate the fish innate immunity by eliciting a temporary inflammatory response, which, combined with constitutively produced antimicrobial effectors, increases the resistance of fish larvae to an infectious disease after hatching (Villegas et al., 2012).

There is likely a large variation in the bacterial population amongst different carp polyculture systems due to several influencing factors. The microbiota in carp ponds is affected by nutrient availability (a bottom-up control) and predatory pressure (a top-down control) (Pace & Cole, 1994). Nutrient levels in pond water have been shown to correlate significantly with microbial populations. For instance, dominant pond water bacteria Betaproteobacteria, Alphaproteobacter, Cyanobacteria, Roseiflexaceae, Dinghuibacter, Cryomorphaceae, and Actinobacteria prefer nutrient-rich environments with a strong positive correlation with TN, NO_2^-, and NO_3^- (Dai et al., 2021a). In contrast, bacterial populations were found to have a negative correlation with NH4+ because it may inhibit on microorganisms when at high concentrations (Parker et al., 2012). High volumes of ammonia nitrogen are often enhanced in aquaculture ponds due to massive organic matter decomposition (Dai et al., 2021b). Kalcheva et al. (2010) determined bacterioplankton communities in seven carp polyculture ponds of common carp (*Cyprinus carpio*), bighead carp (*Aristichthys nobilis*) and grass carp (*Ctenopharyngodon idella*) in a two-year experiment in 2007-2008. The results showed that the total number and biomass of bacteria were twice higher in 2008 (2.93×10^5 cells/ml) than in 2007 (1.58×10^5 cells/ml) due to the richer organic manure applied in 2008. Using

Spearman correlation (Rs), they found that most abiotic factors negatively impacted bacterioplankton (e.g., transparency and pH). The highest negative correlation was found with the number of bacteria and NO_3-N (R_s =–0.64), while the relation with PO_4-P was positive (Rs =0.35). For top-down control, predators such as viruses (Middelboe et al., 2008), nano-flagellates (Jürgens & Matz, 2002), ciliates (Sherr & Sherr, 1987), rotifers (Bonecker & Aoyagui, 2006), and some Cladocera species, like Daphnia (Zöllner et al., 2003), can contribute to the grazing on bacteria in carp production systems.

2.2. Bacteria in/on carp organs

The mucosal tissues, which include the skin, gills, and gut, are in direct contact with the environment and serve as the initial interaction sites between bacteria and the host (de Bruijn et al., 2018). Understanding the dynamics of the microbial communities in these tissues is critical for health management. Comprehensive examinations of the bacterial load and species composition in healthy and diseased fish organs will be required to develop predictive tools for disease outbreaks and guide preventive measures. Several studies have been conducted on the bacterial composition in the intestine, gills, and skin of carp in polyculture systems (Table 2). Bacterial composition differs in distinct ecological niches (e.g., different parts of the gastrointestinal tract, gill, skin) and is influenced by fish species and rearing system. Previous research primarily relied on classic culture-based approaches to explore gut microbial diversity in carp species (Ichthyologica & Piscatoria, 2016; Mandal & Ghosh, 2013; Mukherjee et al., 2016; Ray et al., 2010; Uddin & Al-Harbi, 2012). However, recent advances in sequencing technology have made it simpler to examine the microbial diversity in fish (Foysal, Fotedar et al., 2019).

Bacterial communities in the carp gut

Bacteria in the digestive tracts of carp serve critical roles in maintaining normal gut functions, including digestion of complex molecules, production of secondary metabolites, and defense against pathogens (Bird et al., 2010; X. Li et al., 2018; H. Liu et al., 2016). The gut is the most extensively studied organ in

156 microbial ecology, especially with the advance of high-throughput sequencing (Foysal, Fotedar, et al., 2019;
157 Tyagi & Singh, 2017). Mukherjee et al. (2020) indicated that Proteobacteria (15-40%), Firmicutes (16-21%),
158 Actinobacteria (18-34%), and Bacteroidetes (6-19%) were the main bacterial phyla in the guts of three
159 Indian major carps (IMCs). However, the abundance of each phylum is different for each species of fish.
160 For example, Bacteroidetes and Actinobacteria were more abundant in mrigal *Cirrhinus cirrhosis* (Bloch
161 1795) and rohu *Labeo rohita* (Hamilton, 1822), whereas Proteobacteria and Firmicutes were more
162 abundant in catla *Catla catla* (Hamilton, 1822). Bacteroidetes and Actinobacteria might be associated with
163 the digestion of complex polysaccharides in the diets of rohu and mrigal, which consume phytoplankton,
164 additional feeds, and plant detritus (Thomas et al., 2011). Proteobacteria and Firmicutes in catla are
165 involved in fermentative peptide and carbohydrate metabolism and vitamin B12 production (Larsen et al.,
166 2014), reflecting the feeding behavior of catla, which includes consumption of zooplankton and
167 omnivorous feeding. Under a polyculture system, the composition of the intestinal microbiota may co-
168 evolve with its host in response to feeding habits. Indian major carp utilize different ecological niches due
169 to differences in their feeding habits and preferences, so their varied diets might influence the composition
170 of the fish's symbiotic gut microbiota. The difference in the gut microbiota composition across species may
171 also indicate that particular endogenous variables may interact with environmental factors and diet
172 composition to shape the gut microbiota composition (Li et al., 2015). In addition, it is believed that various
173 sections of the gastrointestinal tract harbor different microbiota (Ni et al., 2014) and that the genotype of
174 the host influences the microbiota of the gastrointestinal tract (Navarrete et al., 2012; L. Zhao et al., 2013).
175 We think that additional investigation is necessary to clarify this.

176 Furthermore, the prevalence of a particular bacterial composition in the core gut microbiota of carp may
177 be partly attributed to various selective pressures within the host gut habitat (for instance, the selection
178 of Actinobacteria) that occupy a specific ecological niche. However, it may also be related to Actinobacteria
179 in the surrounding freshwater habitat and is available to colonize carp hosts. We believe it is critical to

identify the selection pressures influencing the development of microbial communities in the intestinal tract of various carp species.

In general, the fish gut also acts as a reservoir for various opportunistic pathogens (Li et al., 2015; Wu et al., 2012a). Uddin & Al-Harbi (2012) found that *A. hydrophila* (25.7%), *S. putrefaciens* (21.43%), and *V. cholerae* (19.29%), which are known as opportunistic pathogens, were abundant bacterial species in common carp intestines. Mahmoud et al. (2004) found diverse bacteria in the intestines of common carp, with the most common ones being Vibrionaceae, Enterobacteriaceae, and Flavobacterium. In addition, *Aeromonas* has been found to be dominant in the intestine of grass and crucian carp in polyculture(Li et al., 2015), while *Klebsiella* has been found in IMCs (Foysal, Fotedar et al., 2019; Mukherjee et al., 2020). *Aeromonas* and *Klebsiella* are both involved in opportunistic infections of freshwater fish aquaculture (Austin & Austin, 2016).

In general, any dysbiosis event in gut microbiota may significantly affect local and general physiology and metabolism (Patterson et al., 2014). Therefore, a change in the microbial load of the host can cause problems at different levels, mainly in the immune system, which can lead to disease (Montalban-Arques et al., 2015). Understanding the drivers of disease caused by opportunistic pathogens is essential for preventing outbreaks. On a broader scale, it is crucial to comprehend host/microbiota/environment interactions in opportunistic infections of carp. Moreover, bacterial disease can be reduced by taking preventative steps to minimize host stress and by actively intervening to increase the protective impact of the microbiota (i.e., prebiotics, probiotics, and symbiotics) (Derome et al., 2016).

Bacterial communities on carp gills

Compared to fish guts, fish gills are in direct contact with the surrounding water and, therefore, subject to environmental changes (Croft et al., 2005; Tarnecki et al., 2019). A study in Saudi Arabia identified the bacterial composition in pond water, sediments, the gills, and the intestines of common carp (Al-Harbi &

Uddin, 2008). The authors found that aerobic heterotrophic bacteria colonized fish gills in lower numbers than those in the fish intestine, and the bacterial flora of pond water and sediment reflect the bacterial composition of the gills and intestine of carp. Zhou et al. (2022) revealed that the diversity of bacteria in the gills was greater than that in the guts, and there was more Actinobacteria and Bacteroidetes abundance in the gills than in the guts. These bacterial phyla are also abundant in the surrounding water. It could imply that these bacteria originated in water but did not enter the gut in large quantities. Similarly, Uddin & Al-Harbi (2012) found that pond water bacteria influence the bacterial composition of fish gills and intestines, and bacteria in the carp intestine have a lower species diversity than bacteria on the gills.

It should be noted that gill disease can be caused by opportunistic bacteria already present on the gill surface. Potential disease-causing bacteria include *A. hydrophila* and *Pseudomonas* spp. (Austin & Austin, 2016), *S. putrefaciens* (Koziñska & Pekala, 2004), and *Streptococcus* spp. (Al-Harbi, 1994). Zhou et al. (2022) discovered that the abundance of potentially pathogenic *Pseudomonas* bacteria was higher in the grass carp gills than in the guts. In addition, they utilized LEfSe analysis (Linear discriminant analysis effect size) to identify many conditional pathogen (Cheng K. et al., 2019; Dabadé et al., 2016) indicator genera in gill, including *Flavobacterium*, *Clostridium_sensu_stricto_1, Arcobacter, Neorickettsia*, and *Bacteroides*. The abundance of these pathogens in the gill suggests that this organ might be a barrier for pathogens and can protect the intestines from potential infections.

Bacterial communities on carp skin

In an aquatic environment, the external surfaces of fish are directly exposed to the surrounding bacteria. However, there is currently a dearth of interest in investigating the microbiota on fish skin, with only a few studies on different species being conducted (Kapetanović et al., 2006; Liu et al., 2008; Ringø & Holzapfel, 2000). The microbial population attached to the gills and skin of gibel carp *Carassius auratus gibelio* (Bloch,

1782) and bluntnose black bream *Megalobrama amblycephala* (Yih, 1955) in polyculture was analyzed by Wang et al. (2010) using PCR-denaturing gradient gel electrophoresis (DGGE). This study indicated that the bacterial, actinomycetal, and fungal diversities on fish skins were higher than those on the gills of the gibel carp.

The main interface between a fish and its environment is the mucosal surface of the skin. The mucus performs various functions, including ionic and osmotic control and defense against microbial diseases (Shephard, 1994). Mucus secretion is considered an essential factor in protecting against pathogen invasion. According to Marel et al. (2010), exposure to water with a high bacterial load did not cause clinical symptoms in carp. Still, the skin of exposed carp responded quickly with increased mucus production. Hypersecretion of mucus would wash adhering bacteria away, which helps fish defend against pathogens.

Furthermore, Chiarello et al. (2015) revealed that the bacteria on the skin of European seabass and gilthead seabream were more diverse than those in the aquatic environment. It might be related to the nutritional conditions present on the fish's surface. The mucus on the skin comprises a wide range of gel-forming glycoproteins, glycosaminoglycans, and proteins that can serve as food sources for epibiotic bacteria (Bordas et al., 1998; Shephard, 1994).

3. Microalgae in carp polyculture systems

3.1. The impact of microalgae on carp polyculture systems

Beneficial impact on carp polyculture systems

So far, studies on the diversity of microalgae in carp polyculture ponds are limited (Table 3). Microalgae are important primary producers in aquatic ecosystems (Nozaki, 1999). During the day, microalgae are a significant oxygen source in fishponds and consume nitrogenous waste products (Jia & Yuan, 2016). In addition to the bacteria consumed by carp, microalgae are also nutritious for the different carp species that grow together in polyculture (Hepher, 1988; Silva & Anderson, 1994). According to Wang et al. (2023),

249 the biofortified system with bacteria-microalgae associations in crucian carp *Carassius auratus gibelio*
250 (Bloch, 1782) ponds might promote intestinal health by enhancing digestive enzyme activity, villus length,
251 villus width, muscle thickness, and intestinal microbiota diversity.

252 The filtration physiology of carp is often described as follows: the water containing microalgal particles is
253 pushed into the oropharyngeal cavity by the rhythmic expansion and contraction of the opercula and
254 buccal chamber. Gill rakers filter suitable feed particles, with the filtered feed particles' size dependent
255 on the gill raker's gap size (Liu & Huang, 2008). While the water runs through the gill rakers, the filtered
256 feed particles are retained, reach the pharynx, and are ingested by the coordinated action of the filtering
257 organs (Sun & Meng, 1992; Zhao et al., 2014). Through this process, filtered feed particles are expected
258 to be larger than the gill raker gaps. However, microalgal particles smaller than the gill raker gaps were
259 regularly found in the foreguts of silver carp caught in lakes, rivers, reservoirs, and ponds (Ke et al., 2007;
260 Tucker, 2006; Xie & Liu, 2001; Yan et al., 2009), demonstrating that these tiny microalgal particles might
261 also be filtered. Thus, silver carp may have evolved additional feeding mechanisms to entrap microscopic
262 microalgal particles. It was discovered that there are large mucus cells in filter organs and adhered pollen
263 blocks in gill raker ditches and gill raker tubes of silver carp (Li & Dong, 1996). This mechanism is known
264 as the “food-sinking effect”. Therefore, when silver carp filter microalgal particles smaller than their gill
265 raker gaps, the “food sinking effect” may work as an additional feeding mechanism. It is supported by the
266 study of Görgényi et al. (2016) that found nanoplankton less than 10 μm in size in the foregut and hindgut
267 of Asian carp in Lake Balaton, Hungary.

268 *Harmful microalgal blooms (Cyanobacteria)*

269 It is widely known that the productivity of microalgae is determined by the ecological balance of several
270 physicochemical and biological parameters. The occurrence and abundance of microalgae in polyculture
271 ponds are influenced by various environmental parameters, including temperature, light, dissolved

oxygen, pH, nutrient composition, and soil condition. Certain microalgal blooms (cyanobacterial blooms) have been linked to water quality problems in aquaculture ponds and the enrichment of nutrients from unused feed and carp metabolic wastes. When cyanobacteria blooms occur, they can cause the death of fish (Carbis et al., 1995; Negri et al., 1995). Larger cyanobacteria, such as *Anabaena, Aphanizomenon, Microcystis, Oscillatoria,* can create off-flavor and form surface scum, which often causes algal die-off and water quality deterioration (Kim et al., 2018). Several cyanobacterial species from the *genera Anabaena, Oscillatoria, Lyngbya,* and *Phormidium* have been found to produce musty and earthy tastes in farmed fish (Tucker, 2000). In addition, cyanobacterial blooms can modify the composition of fish gut microbiota and holobiont functions, resulting in suboptimal states that could threaten host health (Gallet et al., 2023).

A study investigated the effect of blue-green algal blooms (*Microcystis, Oscillatoria*, and *Anabaena* blooms) on the nutritional composition of the water, the plankton diversity and density, and fish production of three carp polyculture ponds located in the West Godavari district, Andhra Pradesh, India (Padmavathi et al., 2017). The research showed that *M. aeruginosa* is the most harmful, causing the highest mortality in carp, followed by *Anabaena* and *Oscillatoria*. In addition, blue-green algae decreased the diversity and density of other plankton. Plankton diversity was lowest in the ponds with *Microcystis* bloom, followed by the ponds of *Anabaena* sp. and *Oscillatoria* sp. It indicates that *Microcystis* has the most potent inhibitory effect on other algae. Blue-green algal species grow out to become dominant, eliminating most other species in the ecosystem via excretions until they are only found sporadically (hetero-antagonism). As a result, the phytoplankton during blue-green algal blooms is abundant but not diverse (Lefèvre et al., 1952). Additionally, nitrogen-deficient waters are more favorable for *Anabaena* bloom formation than *Microcystis* and *Oscillatoria* blooms.

3.2. The impact of carp species on microalgal abundance

Many carp species, each with their own eating habits, can control the algal density in pond water. Silver carp have even been demonstrated to efficiently minimize the development of harmful algae and excessive blooms of other species (Zhang et al., 2006). In Shanghai, Tang et al. (2021) assessed the ability of carp to control cyanobacterial blooms in polycultures of silver carp and bighead carp with the freshwater pearl mussel *Hyriopsis cumingii* (I.Lea, 1852). They found that cyanobacterial blooms occurred in all ponds without silver and bighead carps but not in the ponds with the two carps, demonstrating that silver and bighead carps could suppress the occurrence of cyanobacterial blooms. Moreover, combining silver and bighead carp polycultures could increase microalgal diversity.

An enclosure experiment carried out in the Three Gorges Reservoir in China discovered that decreasing the level of certain zooplankton species, such as rotifers and copepods, results in a trophic cascade, releasing phytoplankton from herbivory and enabling it to develop (Zhou et al., 2011). Similarly, Ke et al. (2008) conducted an experiment in a Chinese lake by stocking bighead carp and silver carp. They found that silver and bighead carp shift to feeding mainly on zooplankton at low stocking densities, which may decrease the efficiency of controlling cyanobacterial blooms. According to Xie & Liu (2001) density of silver and bighead carps should be kept at or above 50g/m^3 for effective biomanipulation of Microcystis colonies in Lake Donghu, China. Therefore, a suitably high density of filter-feeding fish like silver and bighead carp is critical for effectively managing toxic algae blooms. In addition, Wang et al. (2008) studied 45 shallow lakes in China and found that lakes with higher bighead carp and silver carp yields had higher chlorophyll-a concentrations. It could be because smaller phytoplankton species that bigheaded carp do not consume have increased in abundance or because bighead carp feeding, and excretion boosted nutrient cycling and the development of phytoplankton.

4. Factors affecting the microbiota in carp systems.

4.1. Probiotics and prebiotics

Interest in applying probiotics to improve the survival, growth, and feed utilization of stocked animals and improve water quality has been growing in aquaculture (Farzanfar, 2006; Gatesoupe, 1999; Qi et al., 2009). Table 4 summarizes studies on the effects of probiotics on carp microbiota. Probiotics have been associated with the benefits of decreased intestinal pathogens (Abid et al., 2013) by colonizing the gastrointestinal mucosal epithelium in the digestive tracts of several fish species (Merrifield et al., 2010; Nakandakare et al., 2013; Sharifuzzaman & Austin, 2010) and may inhibit pathogens by producing inhibitory molecules and/or directly competing for space, nutrients, and oxygen (Addo et al., 2017; Chen et al., 2010; Nandi et al., 2017). However, to our knowledge, little research has been conducted on the impact of supplemental probiotics on the microbiota community in freshwater polyculture systems. Adding probiotics may not significantly impact water quality and the microbial community of polyculture systems because fish with various feeding behaviors may increase the system's stability to prevent bacterial colonization (Zhou et al., 2017). One study has shown that adding probiotics to carp polyculture systems has no significant impact on the bacterial community in the rearing water (Zhou et al., 2017). Recent interest has increased in producing live microalgae with probiotics because interactions between species may increase the value of the end product. Several studies have demonstrated that introducing algae and probiotics may impact the microbiota and boost gut health and total production in fish, shrimp, and mussel aquaculture (Perković et al., 2022). Therefore, more research is needed on using a combination of bacterial and algal species that may enhance the beneficial effect on microbiota in carp polyculture systems.

It is crucial to understand which factors influence the impacts of probiotics on microbiota in carp polyculture. There are two main factors: the ability of the probiotic to colonize the system and its relative dominant relationship with the existing bacterial community in the pond under cultivation (Zhou et al.,

2017). The availability of ecological niches also plays a vital role in adapting introduced microorganisms to an environment (Kassen & Rainey, 2004). Tang et al. (2016) examined the effects of three commercial microbial products (Novozymes pond plus, Zhongshui BIO-AQUA, and Effective Microorganisms) on production performance and water quality in a polyculture system of grass carp, gibel carp, and silver carp with low nutrient loading in a short-term experiment. The findings revealed that adding the three commercial microbial products did not substantially enhance production performance or water quality. Thus, long-term experiments should be conducted to investigate the function of microbial products in freshwater polyculture systems with different nutrient loadings and species compositions.

The effectiveness of probiotic supplementation has been demonstrated to be higher in Biofloc technology (BFT) aquaculture systems compared to conventional systems. According to Haraz et al. (2023), the BFT system, probiotic enrichment, and symbiosis efficiently increase the overall bacterial count and enhance the water quality conditions for hazardous nitrogen species. It has been found that a number of Bacillus and Lactobacillus strains greatly accelerate the removal of TAN, NO_2, and NO_3 (Bahnasawy et al., 2020). This may be because fish with probiotic supplementation have better rates of protein assimilation and digestion, which means that less ammonia or nitrogen from feces enters the water (Green et al., 2019). Similarity, Mohammadi et al. (2021) found that beneficial bacteria reduced toxic inorganic nitrogen compound concentrations and increased electrical conductivity in water, showing improving water quality and mineralization.

Besides probiotics, prebiotics are also a dietary supplement that may help with growth, digestive enzyme activity, immune response, stress resistance, and improving water quality (Dawood & Koshio, 2015). Common prebiotics used in carp culture are Mannanoligosaccharide, β-Glucan, Xylooligosaccharide, Inulin, and Chitosan (Dawood & Koshio, 2015). Prebiotics are non-digestible materials for fish that can be metabolized by gut microbiota (Ringø et al., 2014). Dietary prebiotic supplementation can change or alter gut morphology and enhance commensal microbiota growth, thereby affecting diversity and density

(Hoseinifar et al., 2016a; Jung-Schroers et al., 2016a; Kühlwein et al., 2013). However, to our knowledge, there is little study on the impact of prebiotics on carp polyculture systems.

4.2. Antibiotics

Antibiotics can act as an ecological factor that drives the evolution of community structure (Aminov & Mackie, 2007). In the micro-ecosystem, the impacts of antibiotics include phylogenetic structure change and resistance acquisition (Ding & He, 2010).

Antibiotics have the potential to alter the composition of bacterial communities. Each bacterial taxon has a particular sensitivity to each antibiotic. It implies that at any given antibiotic concentration, the community's most vulnerable members will be suppressed while the rest will increase in relative abundance, and as such may result in dysbiosis in the aquaculture system (Martínez, 2017). According to a study by Sun et al. (2021), an antibiotic cocktail (vancomycin, enrofloxacin, florfenicol, and metronidazole) altered the microbial community structure within the intestinal mucosal and luminal niches in grass carp.

In addition, antibiotics have been shown to select for antibiotic-resistant microbes. The ability of bacteria to spread antibiotic resistance via mobile genetic agents (plasmids, transposons, insertion sequence elements, gene cassettes, and class 1 integrons) is responsible for the rapid increase in the number of resistant and multiresistant bacteria (Patil et al., 2016; Piotrowska et al., 2017). The fish gut environment favors horizontal gene transfer and is a significant reservoir for antimicrobial resistance genes (Yuan et al., 2019). In a study by Yuan et al. (2019), the abundance of antimicrobial resistance genes in the guts of Chinese freshwater carp collected from four retail marketplaces in Hefei, China, was quantified. The findings suggested that the relative abundances of ARGs (*sulI*, *sulII*, *blaTEM*-1, *tetA*, *tetO*, *tetQ*, and *tetW*) were quantified in the range of 10−6 - 10−1 gene copies per 16S rRNA gene, suggesting potential risks to human health. Besides, Zdanowicz et al. (2020) found that planktonic *Aeromonas* in three carp ponds in

Poland differed in their resistance to antibiotics, with 96–99% *Aeromonas* strains being resistant to amoxicillin, ampicillin, clindamycin, and penicillin, 60% of isolates being resistant to erythromycin and only 5–6% being resistant to chloramphenicol and ciprofloxacin. However, all *Aeromonas* isolates were susceptible to gentamycin and streptomycin. Therefore, there is an urgent need for increased antimicrobial consumption surveillance and a better understanding of the risk of antimicrobial resistance transmission across the microbiome-aquatic animal-human interface.

Nowadays, there is a growing interest in utilizing plants or their metabolites as antibiotic alternatives. For example, mint acts as an antibacterial agent and stress alleviator to the immune system of fish (Kate et al., 2023), demonstrating potential applications in environmental and health management.

4.3. Fertilization

Fertilization is a cost-effective and ecologically friendly approach to increasing fish production by stimulating the trophic chain components from the bottom (Woynarovich et al., 2010). The precise application of inorganic and organic fertilizers can increase fish production in a carp polyculture system.

Fresh manure (a type of organic fertilizer) can provide fishponds with some of the necessary mineral nutrients and carbon for the growth of heterotrophic bacteria. They also stimulate the microbiota in carp polyculture systems by providing organic matter, macronutrients, and micronutrients (Minich et al., 2018). The oxygen demand, total nitrogen and phosphorus content, and freshness of manure are essential nutrients for phytoplankton production (including autotrophic and heterotrophic microorganisms) (Wohlfarth & Schroeder, 1979). Also, manure and the bacteria that grow on it are good microscopic food sources for zooplankton due to their high protein content (Woynarovich et al., 2010).

Numerous types of manure have been used in carp polyculture, where cow, poultry, and semi-liquid pig manure are of the highest interest (Wohlfarth & Schroeder, 1979). Jha et al. (2008) compared four fishpond management regimes: poultry manure, live zooplankton, cow dung, and a commercial pellet

diet. They discovered that the average numbers of heterotrophic bacteria in pond water receiving poultry manure or cow dung were substantially higher than in other treatments. The composition of the livestock manure microbiota and its effect on the water microbiota varied depending on the producing species. However, the presence of pathogens in manure is considered one of the most critical factors in disease transmission. Pathogens in manure have been reported to survive for up to four months in aquatic environments, depending on the type of manure, temperature, pH, oxygen level, ammonia concentration, and competing organisms (Guan & Holley, 2003).

Inorganic fertilizers may supply additional carbon sources (Cole, 1999) and boost the availability of mineral nutrients in the rearing environment (Jana et al., 2001). Dissolved organic carbon is an essential source of nutrients for bacteria (Kosolapov et al., 2017). On the other hand, mineral nutrients (phosphorus) are often the growth-limiting factors for bacteria (Matz & Jürgens, 2003). Excessive nutrient loading when using inorganic fertilizer may result in a decrease in gross primary productivity as a result of algae shading the pond surface. On the contrary, nutrients in organic manure are released more gradually and consistently. The more regulated the nutrition release rate, the more efficiently phytoplankton consumes nutrients and the higher the fish output. Furthermore, the excreta of grass carp can be utilized to fertilize the water and produce plankton for filter-feeding fish to consume (Kumar et al., 2005). The use of a combination of grass carp and organic fertilizer resulted in the highest net fish yield, followed by using only organic fertilizers and then inorganic fertilizers (Kumar et al., 2005).

4.4. Feeding

In semi-intensive systems, supplemental feeding benefits the fish both directly as feed and indirectly as fertilizer (Milstein, 1992). When carp are fed only cereals, the proportion of nutritional supply driving the bacterial–detrital food chain may reach over 95%, with just 5% being used directly for fish biomass growth (Olah, 1986). Natural feeds (phytoplankton and zooplankton) can still contribute up to 40–68% of the output in ponds when supplemental feeding is used (Burford et al., 2002, 2004; Cam et al., 1991; Porchas-

Cornejo et al., 2012). Energy for natural feed production is often provided through carbohydrate administration in dry feed to increase the C:N ratio to 15–20 (Asaduzzaman et al., 2008; Avnimelech & Kochba, 2009; Crab et al., 2007). When the C:N ratio of nutrient input exceeds 10, significant quantities of bacterial biomass are found in the food web, in which heterotrophic bacteria become dominant (Boyd, 1990; Lancelot & Billen, 1985). Organic and inorganic nitrogen is taken up by heterotrophic bacteria, which keep ammonia and nitrite levels in the pond low (Avnimelech, 1999; Hari et al., 2004, 2006). Heterotrophic bacteria also provide a protein source, promoting nutrient flow through the food web and producing fish graze on natural feeds (Asaduzzaman et al., 2008). An increase in stocking density and dry feed use is believed to decrease the relative contribution of natural feed to carp production (Kabir et al., 2019). In addition, the increase in supplementary feed and unconsumed feed increases ammonia concentration, which is expected to be critical in determining the structure of the ammonia-oxidizer community in the rearing environment (Koops et al., 2003).

When selecting dietary ingredients for artificial diets, it is vital to consider the response of the bacterial population in the rearing environment. Some ingredients may promote the growth of bacteria that are harmful to fish health, while others may inhibit the growth of bacteria that are beneficial to fish health (Rimoldi et al., 2018). For example, the gut microbiota and fish health are negatively impacted by soybean meal (the main fish meal substitute in aquafeeds) as it contains anti-nutritional factors that can cause intestinal damage. On the other hand, ingredients like fructooligosaccharides, mannan-oligosaccharide, and sodium butyrate benefit the related bacterial microbiota (Infante-Villamil et al., 2021a). In the gibel carp, growth and survival rates were unaffected by a commercial feed mixed with terrestrial plants used in Chinese medicine (*Pastinaca sativa, Astragalus membranaceus*, and *Atractylodes macrocephala Koidz*). However, bacterial (alpha-)diversity measures in the fish gut were improved, and the abundance of potential fish pathogens such as *Aeromonas* spp., *Acinetobacter* spp., and *Shewanella* spp. subsequently decreased (Wu et al., 2018). Therefore, diet selection is important for animal performance and bacterial

community in carp ponds. Future microbiota research should focus on establishing methods for determining whether or not a specific diet is appropriate to elicit beneficial changes in bacterial communities that may impact carp's health and production.

Live feed, like zooplankton, is rich in protein but poor in carbohydrates (Ruttkay, 1975). The major zooplankton groups in earthen carp ponds are protozoans, rotifers, and two crustacean groups, copepods, and cladocerans (Anton-Pardo & Adámek, 2015). As a live feed, zooplankton is a protein source and is essential as a natural feed for juveniles, adults, and marketable-sized carp. However, live feed consumed by carp may contain diverse bacteria, including pathogens like *Flavobacterium* (Skjermo & Vadstein, 1993). Therefore, live feed ingestion is one of the possible mechanisms of pathogen acquisition by carp (Snoussi et al., 2006). Until now, there have been few studies on the effects of dry and live feed on the microbiota of carp polyculture systems. From our literature review, we can conclude that more studies need to be conducted to assess the mechanisms through which dry feed and live feed modulate the microbiota and productivity in the rearing system in its broadest sense (e.g., water, gut, skin, etc.).

4.5. Abiotic parameters of the rearing environment

Pathogens such as bacteria, viruses, protozoans, and other biotic stressors, when combine with abiotic stressors, worsen aquaculture activity (Abisha et al., 2022). The abiotic environment influences the structure and dynamics of communities via the networks of species interacting in a carp polyculture pond. Dissolved oxygen and temperature were shown to be strongly linked with changes in microbial community composition, and they are also claimed to have an impact on bacterial growth (Guan et al., 2020).

Dissolved oxygen (DO) levels in non-aerated carp ponds are mainly determined by the relative magnitudes of photosynthetic oxygen production and total plankton respiration (Steel, 1980). Fishponds with low levels of DO may promote the growth of waterborne microorganisms by encouraging nutrient regeneration from anoxic sediments (Testa & Michael Kemp, 2012). Dissolved oxygen depletion inhibits

nitrification and the coupled nitrification–denitrification process (Kemp et al., 1990), lowering inorganic nitrogen removal and increasing the buildup of ammoniacal nitrogen. In freshwater fishponds in India, nitrifier abundance was highest during the rainy season, followed by winter, and was lowest during the summer, when oxygen levels were lowest (Kumari et al., 2011). In other words, during the summer, heterotrophic bacteria compete more for oxygen with other microorganisms (autotrophic bacteria, zooplankton, protozoa) than during the rainy and winter seasons (Donderski & Kalwasinska, 2003). Furthermore, hydrogen sulfide gases, which are considered toxic, can formed during anaerobic decomposition and cause severe mortalities in aquaculture ponds (Chien, 1992). Sulfur oxidizing bacteria (SOB) can, under aerobic conditions, metabolize sulfide to nontoxic sulfate. SOB can be detected and characterized by using molecular techniques based on the soxB functional gene (Krishnani, Gopikrishna, et al., 2010; Krishnani, Kathiravan, et al., 2010).

Several studies have shown that the abundance of species in the core microbiota of pond sediments is highly correlated with water temperature (Hu et al., 2022; Tas et al., 2009; Tian et al., 2009; Z. Zhao et al., 2020). Li et al. (2021) demonstrated that temperature is the primary environmental factor shaping the dominant microbial genera, including *Prochlorococcus, Chryseobacterium, Acinetobacter, Rheinheimera, Polynucleobacter*, and *Janthinobacterium* in the water column. Jana et al. (2019) discovered that a 5°C increase in water temperature during winter resulted in a 36% yield increase for tropical fishes in polyculture (rohu, mrigal, bata, Japanese punti, grass carp, common carp, magur, and freshwater prawn) through microbial-driven augmented manure mineralization. In addition, carp gut microbial composition is also influenced by temperature variations (Nayak, 2010; Ringø et al., 2016). Changes in the overall bacterial abundance (high in the summer and low in the winter) have been reported between the summer and fall seasons (Al-Harbi & Uddin, 2004). Elevated temperatures may also harm the culture system by promoting harmful algal blooms and altering the structure of the plankton community (Abisha et al., 2022).

The optimum temperature for the growth of nitrifying bacteria is between 20°C to 28°C (Verstraete & Focht, 1977). During the summer, carp ponds' nitrification rate typically decreases due to increased respiration of heterotrophic bacteria in both soil and water, leading to lower dissolved oxygen levels (Kumari et al., 2011). This explains the decrease in the nitrifying bacterial population in sediment and water throughout the summer (Gundersen & Mountain, 1973). Carlucci & Strickland (1968) discovered that when ammonia concentrations rose, the ammonia-oxidizer activity increased. During the summer, the nitrification potential rate and number of nitrifiers were lowest in the bottom and surface water of the carp pond because heterotrophic bacteria and autotrophic algae are more successful at competing for ammonia than nitrifiers. Rising temperatures in summer also accelerate the mineralization of organic waste (feeds and feces), which increases the concentration of inorganic nitrogen compounds and decreases dissolved oxygen and pH in the water. These environmental changes influence bacterial communities in the rearing system, such as increasing the abundance of Cyanobacteria in the water and potential pathogens (e.g., the genera *Vibrio, Aeromonas*, and *Shewanella*) in fish guts, which may result in the occurrence of red-operculum disease in crucian carp (Infante-Villamil et al., 2021b; Li et al., 2017). During the rainy and winter seasons, nitrifying bacteria may be able to utilize ammonia even at low concentrations due to decreased competition (Yoshifumi et al., 2009). The presence of nitrifying and denitrifying organisms can be quantified by the abundance of functional marker genes such as ammonia monooxygenase (*amoA*), nitrite-oxido-reductase (*norB*), nitrite reductase (*nirS*) and nitrous oxide reductase (*nosZ*) (Kathiravan & Krishnani, 2014; Krishnani, 2010; Krishnani et al., 2009; Krishnani & Kathiravan, 2010; Velusamy & Krishnani, 2013).

5. Conclusion and further perspectives

Studies on bacterial and microalgal communities in carp polyculture systems have shown a link between the host microbiota and the rearing environment microbiota, illustrating the importance of steering this rearing water microbiota to reduce the emergence of diseases and improve carp health.

Microbial diversity was significantly higher in water than in the fish gill and gut and was significantly higher in the gills than in the gut (Kuang et al., 2020). The dominant bacterial phyla in rearing water and carp organs are Firmicutes, Bacteroidetes, Actinobacteria, Proteobacteria, and Fusobacteria. However, fish microbiota diversity varies even in the same fish species when reared in different environments. It is influenced by many, not independent, factors. The dominant microbial taxa are formed by the composition of the microbial community in the rearing environment and by selective feeding by carp species affecting the internal and external microbiota. The microbial composition also depends on diets, fish species, rearing conditions, and geography (Tran et al., 2018). At the organ level, distinct ecological niches (e.g., different parts of the gastrointestinal tract, gill, and skin) harbor diverse microbiota, and the microbial community is influenced by the host's genetics.

Moreover, many species in carp polyculture systems, each with their own eating habits, can control the microalgal size and composition in the pond. The variation in microalgal populations might be caused by variations in mixing conditions, carp species composition, and nutrition availability. The farming of carp polyculture can be hampered by the formation of microalgal blooms owing to water quality problems and the enrichment of nutrients caused by the microbial decomposition of unused feed and fish metabolic wastes. Elevated N:P ratios can induce the P-limitation of bacteria in eutrophic environments because phytoplankton is a better competitor for P than bacteria (Heath et al., 2003). Moreover, the increased bacterial biomass produces carbon dioxide via respiration, which increases the amount of dissolved inorganic carbon available to phytoplankton (Green, 2015).

In general, *Vibrio, Enterobacter, Aeromonas,* and *Flavobacterium* are the main genera involved in opportunistic carp infections. Besides, Cyanobacteria *Microcystis, Oscillatoria,* and *Anabaena* blooms are commonly found in carp polyculture. Understanding the drivers of disease/bloom caused by these species is essential for preventing outbreaks. Additionally, strong evidence suggests that factors such as

551 probiotics, prebiotics, feed, fertilizers, and manipulation of environmental parameters can strongly
552 influence carp microbiota.

553 The microbial composition differences between studies with the same fish species could be due to the
554 animal life stage, sample size, and techniques, such as differences in the analyzed genome region and the
555 sequencing platform used (Foysal, Fotedar et al., 2019). A significant problem with the available carp
556 microbiota data is the large differences in findings from different laboratories using different experimental
557 designs and methodologies.

558 We have identified three areas that show promise to impact carp polyculture management:

559 **Microbiome health assessment**. It is critical to examine the external and internal microbiota of more
560 species in the carp polyculture systems to understand microbiome-associated host species in conjunction
561 with the characterization of metabolic specialization and disease resistance. More research into the
562 composition, diversity, and manipulation of carp polyculture microbiota will assist farmers in steering the
563 system, leading to more resilient farming systems and enhanced fish health. It will also be extremely
564 useful to get insights into the microbiota of broodstock, eggs, larvae, and water microbiota in
565 hatchery/nursery systems and their relationship with fish health. This knowledge is essential for shaping
566 the rearing water microbiota of a system and understanding its influences on the fish microbiota.

567 **Technological improvements**. Notably, most microbiota research in carp polyculture systems has relied
568 on data from older, less precise techniques (e.g., DGGE, plate counting) or, more recently, semi-
569 quantitative next-generation sequencing techniques. In recent years, it has been shown that combining
570 data from this technology with quantitative methods can yield surprisingly different insights into the
571 compositional dynamics occurring in microbial ecosystems (Props et al., 2016). In the next years, using
572 new tools (such as single-cell technologies) to conduct extensive high-resolution sampling campaigns will

result in a better knowledge of the microbial community and the interactions between species and their environments.

Product management. Little research has been done on the impact of probiotics and prebiotics on the microbiota composition and diversity in carp polyculture systems. The low inoculation rate of exogenous bacteria derived from microbial products may limit their dominance in competition with native bacteria. Therefore, more research is needed to evaluate the effect of commercial probiotics and prebiotic products in improving beneficial bacteria in carp polyculture and their appropriate dosage. Besides, the use of antibiotics nowadays is driven by the pressure exerted on farms by disease outbreaks due to microbes. Thus, it is crucial to understand how they affect the overall physiology and composition of the microbiome by selecting a particular set of microbes and genes.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest with regard to this review.

References

Abid, A., Davies, S. J., Waines, P., Emery, M., Castex, M., Gioacchini, G., Carnevali, O., Bickerdike, R., Romero, J., & Merrifield, D. L. (2013). Dietary synbiotic application modulates Atlantic salmon (Salmo salar) intestinal microbial communities and intestinal immunity. *Fish & Shellfish Immunology*, *35*(6), 1948–1956. https://doi.org/10.1016/J.FSI.2013.09.039

Abisha, R., Krishnani, K. K., Sukhdhane, K., Verma, A. K., Brahmane, M., & Chadha, N. K. (2022). Sustainable development of climate-resilient aquaculture and culture-based fisheries through adaptation of abiotic stresses: a review. *Journal of Water and Climate Change*, *13*, 2671. https://doi.org/10.2166/wcc.2022.045

Addo, S., Carrias, A. A., Williams, M. A., Liles, M. R., Terhune, J. S., & Davis, D. A. (2017). Effects of Bacillus subtilis Strains on Growth, Immune Parameters, and Streptococcus iniae Susceptibility in Nile Tilapia, Oreochromis niloticus. *Journal of the World Aquaculture Society*, *48*(2), 257–267. https://doi.org/10.1111/JWAS.12380

Ahmadifar, E., Moghadam, M. S., Dawood, M. A. O., & Hoseinifar, S. H. (2019). Lactobacillus fermentum and/or ferulic acid improved the immune responses, antioxidative defence and resistance against Aeromonas hydrophila in common carp (Cyprinus carpio) fingerlings. *Fish and Shellfish Immunology*, *94*, 916–923. https://doi.org/10.1016/J.FSI.2019.10.019

Al-Harbi, A. H. (1994). First isolation of Streptococcus sp. from hybrid tilapia (Oreochromis niloticus × O. aureus) in Saudi Arabia. *Aquaculture*, *128*(3–4), 195–201. https://doi.org/10.1016/0044-8486(94)90308-5

Al-Harbi, A. H., & Uddin, M. N. (2004). Seasonal variation in the intestinal bacterial flora of hybrid tilapia (Oreochromis niloticus×Oreochromis aureus) cultured in earthen ponds in Saudi Arabia. *Aquaculture*, *229*(1–4), 37–44. https://doi.org/10.1016/S0044-8486(03)00388-0

Al-Harbi, A., & Uddin, M. N. (2008). Aerobic bacterial flora of common carp (Cyprinus carpio L.) cultured in earthen ponds in Saudi Arabia. *Journal of Applied Aquaculture*, *20*(2), 108–119. https://doi.org/10.1080/10454430802197292

Allameh, S. K., Ringø, E., Yusoff, F. M., Daud, H. M., & Ideris, A. (2017). Dietary supplement of Enterococcus faecalis on digestive enzyme activities, short-chain fatty acid production, immune system response and disease resistance of Javanese carp (Puntius gonionotus, Bleeker 1850). *Aquaculture Nutrition*, *23*(2), 331–338. https://doi.org/10.1111/ANU.12397

Allameh, S. K., Yusoff, F. M., Ringø, E., Daud, H. M., Saad, C. R., & Ideris, A. (2016). Effects of dietary mono- and multiprobiotic strains on growth performance, gut bacteria and body composition of Javanese carp (Puntius gonionotus, Bleeker 1850). *Aquaculture Nutrition*, *22*(2), 367–373. https://doi.org/10.1111/ANU.12265

Aminov, R. I., & Mackie, R. I. (2007). Evolution and ecology of antibiotic resistance genes. *FEMS Microbiology Letters*, *271*(2), 147–161. https://doi.org/10.1111/J.1574-6968.2007.00757.X

Anton-Pardo, M., & Adámek, Z. (2015). The role of zooplankton as food in carp pond farming: A review. *Journal of Applied Ichthyology*, *31*, 7–14. https://doi.org/10.1111/JAI.12852

Asaduzzaman, M., Wahab, M. A., Verdegem, M. C. J., Huque, S., Salam, M. A., & Azim, M. E. (2008). C/N ratio control and substrate addition for periphyton development jointly enhance freshwater prawn Macrobrachium rosenbergii production in ponds. *Aquaculture*, *280*(1–4), 117–123. https://doi.org/10.1016/J.AQUACULTURE.2008.04.019

Austin, B., & Austin, D. A. (2016). Bacterial Fish Pathogens: Disease of Farmed and Wild Fish. *Bacterial Fish Pathogens: Disease of Farmed and Wild Fish, Sixth Edition*, 1–732. https://doi.org/10.1007/978-3-319-32674-0

Avnimelech, Y. (1999). Carbon/nitrogen ratio as a control element in aquaculture systems. *Aquaculture*, *176*(3–4), 227–235. https://doi.org/10.1016/S0044-8486(99)00085-X

Avnimelech, Y., & Kochba, M. (2009). Evaluation of nitrogen uptake and excretion by tilapia in bio floc tanks, using 15N tracing. *Aquaculture*, *287*(1–2), 163–168. https://doi.org/10.1016/J.AQUACULTURE.2008.10.009

Bahnasawy, M. H., El-Ebiary, E.-S. H., El-Ghobashy, A. E., Helal, A. M., & El-Sisy, D. M. (2020). Effect of probiotic on water quality, growth performance and body composition of Nile tilapia (Oreochromis niloticus). *International Journal of Fisheries and Aquatic Studies*, *8*(1), 86–91. http://www.fisheriesjournal.com

Bentzon-Tilia, M., Sonnenschein, E. C., & Gram, L. (2016a). Monitoring and managing microbes in aquaculture – Towards a sustainable industry. *Microbial Biotechnology*, *9*(5), 576–584. https://doi.org/10.1111/1751-7915.12392

Bentzon-Tilia, M., Sonnenschein, E. C., & Gram, L. (2016b). Monitoring and managing microbes in aquaculture - Towards a sustainable industry. *Microbial Biotechnology*, *9*(5), 576–584. https://doi.org/10.1111/1751-7915.12392

Berna, M. G., Campa-Córdova, A. I., Saucedo, P. E., González, M. C., Marrero, R. M., & Mazón-Suástegui, J. M. (2015). Isolation and in vitro selection of actinomycetes strains as potential probiotics for aquaculture. *Veterinary World*, *8*(2), 170. https://doi.org/10.14202/VETWORLD.2015.170-176

Bird, A. R., Conlon, M. A., Christophersen, C. T., & Topping, D. L. (2010). Resistant starch, large bowel fermentation and a broader perspective of prebiotics and probiotics. *Beneficial Microbes*, *1*(4), 423–431. https://doi.org/10.3920/BM2010.0041

Bonecker, C. C., & Aoyagui, A. S. M. (2006). Relationships between rotifers, phytoplankton and bacterioplankton in the Corumbá reservoir, Goiás State, Brazil. *Rotifera X*, 415–421. https://doi.org/10.1007/1-4020-4408-9_43

Bordas, M. A., Balebona, M. C., Rodriguez-Maroto, J. M., Borrego, J. J., & Moriñigo, M. A. (1998). Chemotaxis of Pathogenic Vibrio Strains towards Mucus Surfaces of Gilt-Head Sea Bream (Sparus aurataL.). *Applied and Environmental Microbiology*, *64*(4), 1573–1575. https://doi.org/10.1128/AEM.64.4.1573-1575.1998

Bouwmeester, M. M., Goedknegt, M. A., Poulin, R., & Thieltges, D. W. (2021). Collateral diseases: Aquaculture impacts on wildlife infections. *Journal of Applied Ecology*, *58*(3), 453–464. https://doi.org/10.1111/1365-2664.13775

Boyd, C. E. (1990). *Water quality in ponds for aquaculture.* Agriculture Experiment Station, Auburn University, Alabama. https://doi.org/10.3/JQUERY-UI.JS

Burford, M. A., Preston, N. P., Glibert, P. M., & Dennison, W. C. (2002). Tracing the fate of 15N-enriched feed in an intensive shrimp system. *Aquaculture*, *206*(3–4), 199–216. https://doi.org/10.1016/S0044-8486(01)00720-7

Burford, M. A., Smith, D. M., Tabrett, S. J., Coman, F. E., Thompson, P. J., Barclay, M. C., & Toscas, P. J. (2004). The effect of dietary protein on the growth and survival of the shrimp, Penaeus monodon in outdoor tanks. *Aquaculture Nutrition*, *10*(1), 15–23. https://doi.org/10.1046/J.1365-2095.2003.00274.X

Cam, D., Rollet, P. É., Mariotti, A., & Guillaume, J. (1991). Contribution relative de la productivité naturelle et de l'aliment composé dans la nutrition de Penaeus japonicus élevé en conditions semi-intensives. *Aquatic Living Resources*, *4*(3), 175–180. https://doi.org/10.1051/ALR:1991019

Carbis, C. R., Waldron, D. L., Mitchell, G. F., Anderson, J. W., & McCauley, I. (1995). Recovery of hepatic function and latent mortalities in sheep exposed to the blue-green alga Microcystis aeruginosa. *The Veterinary Record*, *137*(1), 12–15. https://doi.org/10.1136/VR.137.1.12

Carlucci, A. F., & Strickland, J. D. H. (1968). The isolation, purification and some kinetic studies of marine nitrifying bacteria. *Journal of Experimental Marine Biology and Ecology*, *2*(2), 156–166. https://doi.org/10.1016/0022-0981(68)90006-3

Castejón, P., Cabas, I., Gómez, V., Chaves-Pozo, E., Cerezo-Ortega, I., Moriñigo, M. Á., Martínez-Manzanares, E., Galindo-Villegas, J., & García-Ayala, A. (2021). Vaccination of Gilthead Seabream After Continuous Xenoestrogen Oral Exposure Enhances the Gut Endobolome and Immune Status via GPER1. *Frontiers in Immunology*, *12*. https://doi.org/10.3389/fimmu.2021.742827

Chen, R., Zhou, Z., Cao, Y., Bai, Y., & Yao, B. (2010). High yield expression of an AHL-lactonase from Bacillus sp. B546 in Pichia pastoris and its application to reduce Aeromonas hydrophila mortality in aquaculture. *Microbial Cell Factories*, *9*. https://doi.org/10.1186/1475-2859-9-39

Chen, Y., Zhu, X., Yang, Y., Han, D., Jin, J., & Xie, S. (2014). Effect of dietary chitosan on growth performance, haematology, immune response, intestine morphology, intestine microbiota and disease resistance in gibel carp (Carassius auratus gibelio). *Aquaculture Nutrition*, *20*(5), 532–546. https://doi.org/10.1111/ANU.12106

Cheng K., Renyuan G., Xuebing Y., Linsheng H., & Huanlong Q. (2019). Probiotics improve gut microbiota dysbiosis in obese mice fed a high-fat or high-sucrose diet. *Nutrition*, *60*, 175–184. https://doi.org/10.1016/j.nut.2018.10.002

Chiarello, M., Villéger, S., Bouvier, C., Bettarel, Y., & Bouvier, T. (2015). High diversity of skin-associated bacterial communities of marine fishes is promoted by their high variability among body parts, individuals and species. *FEMS Microbiology Ecology*, *91*(7). https://doi.org/10.1093/FEMSEC/FIV061

Chien, Y. H. (1992). Water quality requirements and management for marine shrimp culture. *Proceedings of the Special Session on Shrimp Farming* , 144–156.

Cole, J. J. (1999). Aquatic Microbiology for Ecosystem Scientists: New and Recycled Paradigms in Ecological Microbiology. *Ecosystems* , *2*(3), 215–225. https://doi.org/10.1007/S100219900069

Crab, R., Avnimelech, Y., Defoirdt, T., Bossier, P., & Verstraete, W. (2007). Nitrogen removal techniques in aquaculture for a sustainable production. *Aquaculture*, *270*(1–4), 1–14. https://doi.org/10.1016/J.AQUACULTURE.2007.05.006

Croft, M. T., Lawrence, A. D., Raux-Deery, E., Warren, M. J., & Smith, A. G. (2005). Algae acquire vitamin B12 through a symbiotic relationship with bacteria. *Nature*, *438*(7064), 90–93. https://doi.org/10.1038/nature04056

Dabadé, D. S., Wolkers-Rooijackers, J. C. M., Azokpota, P., Hounhouigan, D. J., Zwietering, M. H., Nout, M. J. R., & den Besten, H. M. W. (2016). Bacterial concentration and diversity in fresh tropical shrimps (Penaeus notialis) and the surrounding brackish waters and sediment. *International Journal of Food Microbiology*, *218*, 96–104. https://doi.org/10.1016/J.IJFOODMICRO.2015.11.013

Dai, L., Liu, C., Peng, L., Song, C., Li, X., Tao, L., & Li, G. (2021a). Different distribution patterns of microorganisms between aquaculture pond sediment and water. *Journal of Microbiology*, *59*(4), 376–388. https://doi.org/10.1007/S12275-021-0635-5

Dai, L., Liu, C., Peng, L., Song, C., Li, X., Tao, L., & Li, G. (2021b). Different distribution patterns of microorganisms between aquaculture pond sediment and water. *Journal of Microbiology*, *59*(4), 376–388. https://doi.org/10.1007/s12275-021-0635-5

Das, A., Nakhro, K., Chowdhury, S., & Kamilya, D. (2013). Effects of potential probiotic Bacillus amyloliquifaciens FPTB16 on systemic and cutaneous mucosal immune responses and disease resistance of catla (Catla catla). *Fish and Shellfish Immunology*, *5*(35), 1547–1553. https://doi.org/10.1016/J.FSI.2013.08.022

Dawood, M. A. O., & Koshio, S. (2015). Recent advances in the role of probiotics and prebiotics in carp aquaculture: A review. *Aquaculture*, *454*, 243–251. https://doi.org/10.1016/J.AQUACULTURE.2015.12.033

de Bruijn, I., Liu, Y., Wiegertjes, G. F., & Raaijmakers, J. M. (2018). Exploring fish microbial communities to mitigate emerging diseases in aquaculture. *FEMS Microbiology Ecology*, *94*(1), 161. https://doi.org/10.1093/FEMSEC/FIX161

Derome, N., Gauthier, J., Boutin, S., & Llewellyn, M. (2016). Bacterial opportunistic pathogens of fish. In *The Rasputin effect: When commensals and symbionts become parasitic* (Vol. 3, pp. 81–108). https://doi.org/10.1007/978-3-319-28170-4_4

738 Dimitrov, M. (1987). Intensive polyculture of common carp, Cyprinus carpio L., silver carp,
739 Hypophthalmichthys molitrix (Val.) and black buffalo, Ictiobus niger (Raf.). *Aquaculture*
740 *(Netherlands)*, *65*(2), 119–125. https://doi.org/10.1016/0044-8486(87)90256-0

741 Ding, C., & He, J. (2010). Effect of antibiotics in the environment on microbial populations. *Applied*
742 *Microbiology and Biotechnology*, *87*(3), 925–941. https://doi.org/10.1007/S00253-010-2649-
743 5/TABLES/2

744 Dittmann, K. K., Rasmussen, B. B., Castex, M., Gram, L., & Bentzon-Tilia, M. (2017). The aquaculture
745 microbiome at the centre of business creation. *Microbial Biotechnology*, *10*(6), 1279–1282.
746 https://doi.org/10.1111/1751-7915.12877

747 Dochin, K. (2020). Phytoplankton species composition in seven fish ponds with a grass carp
748 polyculture (2018-2019). In *Annual of Sofia University "St. Kliment Ohridski"* (Vol. 104, p. 58).

749 Donderski, W., & Kalwasinska, A. (2003). Occurrence and Physiological Properties of
750 Bacterioplankton of Lake Chełmżyńskie (Poland). *Polish Journal of Environmental Studies*,
751 *12*(3), 287–295.

752 FAO. (2022). *The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation.*
753 *Rome, FAO*. FAO. https://doi.org/10.4060/CC0461EN

754 Farzanfar, A. (2006). The use of probiotics in shrimp aquaculture. *FEMS Immunology and Medical*
755 *Microbiology*, *48*(2), 149–158. https://doi.org/10.1111/J.1574-695X.2006.00116.X

756 Foysal, M. J., Fotedar, R., Gupta, S. K., Chaklader, M. R., & Foysal, J. (2019). Biological ball filters
757 regulate bacterial communities in marron (Cherax cainii) culture system. *Letters in Applied*
758 *Microbiology*, *68*(5), 455–463. https://doi.org/10.1111/lam.13125

759 Foysal, M. J., Momtaz, F., Kawsar, A. Q. M. R., Rahman, M. M., Gupta, S. K., & Tay, A. C. Y. (2019).
760 Next-generation sequencing reveals significant variations in bacterial compositions across the
761 gastrointestinal tracts of the Indian major carps, rohu (Labeo rohita), catla (Catla catla) and
762 mrigal (Cirrhinus cirrhosis). *Letters in Applied Microbiology*, *70*(3), 173–180.
763 https://doi.org/10.1111/LAM.13256

764 Galindo-Villegas, J., Garciá-Moreno, D., De Oliveira, S., Meseguer, J., & Mulero, V. (2012).
765 Regulation of immunity and disease resistance by commensal microbes and chromatin
766 modifications during zebrafish development. *Proceedings of the National Academy of*
767 *Sciences of the United States of America*, *109*(39). https://doi.org/10.1073/pnas.1209920109

768 Gallet, A., Halary, S., Duval, C., Huet, H., Duperron, S., & Marie, B. (2023). Disruption of fish gut
769 microbiota composition and holobiont's metabolome during a simulated Microcystis
770 aeruginosa (Cyanobacteria) bloom. *Microbiome*, *11*(1), 108. https://doi.org/10.1186/s40168-
771 023-01558-2

772 Gatesoupe, F. J. (1999). The use of probiotics in aquaculture. *Aquaculture*, *180*(1–2), 147–165.
773 https://doi.org/10.1016/S0044-8486(99)00187-8

774 Ghai, R., Mizuno, C. M., Picazo, A., Camacho, A., & Rodriguez-Valera, F. (2014). Key roles for
775 freshwater Actinobacteria revealed by deep metagenomic sequencing. *Molecular Ecology*,
776 *23*(24), 6073–6090. https://doi.org/10.1111/MEC.12985

777 Gilbert, J. A., Quinn, R. A., Debelius, J., Xu, Z. Z., Morton, J., Garg, N., Jansson, J. K., Dorrestein, P. C.,
778 & Knight, R. (2016). Microbiome-wide association studies link dynamic microbial consortia to
779 disease. *Nature*, *535*(7610), 94–103. https://doi.org/10.1038/NATURE18850

780 Görgényi, J., Boros, G., Vitál, Z., Mozsár, A., Várbíró, G., Vasas, G., & Borics, G. (2016). The role of
781 filter-feeding Asian carps in algal dispersion. *Hydrobiologia*, *764*(1), 115–126.
782 https://doi.org/10.1007/S10750-015-2285-2/FIGURES/6

783 Green, B. W. (2015). Fertilizers in aquaculture. In *Feed and Feeding Practices in Aquaculture* (pp.
784 27–52). Woodhead Publishing. https://doi.org/10.1016/B978-0-08-100506-4.00002-7

785 Green, B. W., Rawles, S. D., Schrader, K. K., Gaylord, T. G., & McEntire, M. E. (2019). Effects of
786 dietary protein content on hybrid tilapia (Oreochromis aureus × O. niloticus) performance,
787 common microbial off-flavor compounds, and water quality dynamics in an outdoor biofloc
788 technology production system. *Aquaculture*, *503*, 571–582.
789 https://doi.org/10.1016/j.aquaculture.2019.01.034

790 Guan, T. T. Y., & Holley, R. A. (2003). Pathogen Survival in Swine Manure Environments and
791 Transmission of Human Enteric Illness—A Review. *Hog Manure Management, the*
792 *Environment and Human Health*, 51–71. https://doi.org/10.1007/978-1-4615-0031-5_2

793 Guan, X., Wang, B., Duan, P., Tian, J., Dong, Y., Jiang, J., Sun, B., & Zhou, Z. (2020). The dynamics of
794 bacterial community in a polyculture aquaculture system of Penaeus chinensis, Rhopilema
795 esculenta and Sinonovacula constricta. *Aquaculture Research*, *51*(5), 1789–1800.
796 https://doi.org/10.1111/ARE.14528

797 Gundersen, K., & Mountain, C. W. (1973). Oxygen utilization and pH change in the ocean resulting
798 from biological nitrate formation. In *Deep Sea Research and Oceanographic Abstracts* (Vol.
799 20, pp. 1083–1091). Elsevier.

800 Gupta, A., Gupta, P., & Dhawan, A. (2016). Paenibacillus polymyxa as a water additive improved
801 immune response of Cyprinus carpio and disease resistance against Aeromonas hydrophila.
802 *Aquaculture Reports*, *4*, 86–92. https://doi.org/10.1016/J.AQREP.2016.07.002

803 Han, S., Liu, Y., Zhou, Z., He, S., Cao, Y., Shi, P., Yao, B., & Ringø, E. (2010). Analysis of bacterial
804 diversity in the intestine of grass carp (Ctenopharyngodon idellus) based on 16S rDNA gene
805 sequences. *Aquaculture Research*, *42*(1), 47–56. https://doi.org/10.1111/J.1365-
806 2109.2010.02543.X

807 Hao-Ren, L. (1982a). Polycultural System of Freshwater Fish in China. *Canadian Journal of Fisheries*
808 *and Aquatic Sciences*, *39*(1), 143–150. https://doi.org/10.1139/F82-015

809 Hao-Ren, L. (1982b). Polycultural system of freshwater fish in China. *Canadian Journal of Fisheries*
810 *and Aquatic Sciences*, *39*(1), 143–150. https://doi.org/10.1139/F82-015

Haraz, Y. G., Shourbela, R. M., El-Hawarry, W. N., Mansour, A. M., & Elblehi, S. S. (2023). Performance of juvenile Oreochromis niloticus (Nile tilapia) raised in conventional and biofloc technology systems as influenced by probiotic water supplementation. *Aquaculture*, *566*. https://doi.org/10.1016/j.aquaculture.2022.739180

Hari, B., Madhusoodana Kurup, B., Varghese, J. T., Schrama, J. W., & Verdegem, M. C. J. (2004). Effects of carbohydrate addition on production in extensive shrimp culture systems. *Aquaculture*, *241*(1–4), 179–194. https://doi.org/10.1016/J.AQUACULTURE.2004.07.002

Hari, B., Madhusoodana Kurup, B., Varghese, J. T., Schrama, J. W., & Verdegem, M. C. J. (2006). The effect of carbohydrate addition on water quality and the nitrogen budget in extensive shrimp culture systems. *Aquaculture*, *252*(2–4), 248–263. https://doi.org/10.1016/J.AQUACULTURE.2005.06.044

Harikrishnan, R., Balasundaram, C., & Heo, M. S. (2010). Potential use of probiotic- and triherbal extract-enriched diets to control Aeromonas hydrophila infection in carp. *Diseases of Aquatic Organisms*, *92*(1), 41–49. https://doi.org/10.3354/DAO02240

Heath, R. T., Hwang, S. J., & Munawar, M. (2003). A hypothesis for the assessment of the importance of microbial food web linkages in nearshore and offshore habitats of the Laurentian Great Lakes. *Aquatic Ecosystem Health and Management*, *6*(3), 231–239. https://doi.org/10.1080/14634980301495

Hepher, B. (1988). Nutrition of Pond Fishes. *Nutrition of Pond Fishes*. https://doi.org/10.1017/CBO9780511735455

Horvath, L., Tamas, G., & Tolg, I. (1984). *Special methods in pond fish husbandry* (J. E. Halver, Ed.). Halver Corporation. https://agris.fao.org/agris-search/search.do?recordID=HU8500498

Hoseinifar, S. H., Eshaghzadeh, H., Vahabzadeh, H., & Peykaran Mana, N. (2016a). Modulation of growth performances, survival, digestive enzyme activities and intestinal microbiota in common carp (Cyprinus carpio) larvae using short chain fructooligosaccharide. *Aquaculture Research*, *47*(10), 3246–3253. https://doi.org/10.1111/ARE.12777

Hoseinifar, S. H., Eshaghzadeh, H., Vahabzadeh, H., & Peykaran Mana, N. (2016b). Modulation of growth performances, survival, digestive enzyme activities and intestinal microbiota in common carp (Cyprinus carpio) larvae using short chain fructooligosaccharide. *Aquaculture Research*, *47*(10), 3246–3253. https://doi.org/10.1111/ARE.12777

Hoseinifar, S. H., Soleimani, N., & Ringø, E. (2014). Effects of dietary fructo-oligosaccharide supplementation on the growth performance, haemato-immunological parameters, gut microbiota and stress resistance of common carp (Cyprinus carpio) fry. *British Journal of Nutrition*, *112*(8), 1296–1302. https://doi.org/10.1017/S0007114514002037

Hossain, M. M., Khan, S., Sarker, M. R. U., & Haque, M. M. (2008). Microalgal ecology in experimental carp - pangas polyculture ponds. *Journal of the Bangladesh Agricultural University*, *6*(1), 119–130. https://doi.org/10.22004/AG.ECON.276671

Hu, D., Wang, L., Zhao, R., Zeng, J., & Shao, Z. (2022). Core microbiome involved in nitrite removal in shrimp culture ponds. *Aquaculture Research*, *53*(5), 1663–1675. https://doi.org/10.1111/ARE.15698

Huang, L., Ran, C., He, S., Ren, P., Hu, J., Zhao, X., & Zhou, Z. (2015). Effects of dietary Saccharomyces cerevisiae culture or live cells with Bacillus amyloliquefaciens spores on growth performance, gut mucosal morphology, hsp70 gene expression, and disease resistance of juvenile common carp (Cyprinus carpio). *Aquaculture*, *438*, 33–38. https://doi.org/10.1016/J.AQUACULTURE.2014.12.029

Ichthyologica, A., & Piscatoria, E. T. (2016). Extracellular tannase-producing bacteria detected in the digestive tracts of freshwater fishes (Actinopterygii: Cyprinidae and Cichlidae). *Acta Ichthyologica Et Piscatoria* , *46*(3), 201–210. https://doi.org/10.3750/AIP2016.46.3.04

Infante-Villamil, S., Huerlimann, R., & Jerry, D. R. (2021a). Microbiome diversity and dysbiosis in aquaculture. *Reviews in Aquaculture*, *13*(2), 1077–1096. https://doi.org/10.1111/RAQ.12513

Infante-Villamil, S., Huerlimann, R., & Jerry, D. R. (2021b). Microbiome diversity and dysbiosis in aquaculture. *Reviews in Aquaculture*, *13*(2), 1077–1096. https://doi.org/10.1111/RAQ.12513

Jana, B. B., Chakraborty, P., Biswas, J. K., & Ganguly, S. (2001). Biogeochemical cycling bacteria as indices of pond fertilization: Importance of CNP ratios of input fertilizers. *Journal of Applied Microbiology*, *90*(5), 733–740. https://doi.org/10.1046/J.1365-2672.2001.01299.X

Jana, B. B., Nandy, S., Lahiri, S., Bag, S. K., Ghosh, P., Bhakta, J. N., Ghosh, D., Biswas, J. K., Bhattacharjee, A., & Jana, S. (2019). Does solar heated structure mimicking greenhouse effective to impede winter growth reduction of some tropical fishes? *Aquaculture*, *499*, 51–60. https://doi.org/10.1016/J.AQUACULTURE.2018.09.017

Jha, P., Barat, S., & Nayak, C. R. (2008). Fish production, water quality and bacteriological parameters of Koi carp ponds under live-food and manure based management regimes. *Zoological Research*, *29*(2), 165. https://doi.org/10.3724/SP.J.1141.2008.00165

Jia, H., & Yuan, Q. (2016). Removal of nitrogen from wastewater using microalgae and microalgae–bacteria consortia. *Cogent Environmental Science*, *2*(1). https://doi.org/10.1080/23311843.2016.1275089

Jose, P. A., Maharshi, A., & Jha, B. (2021). Actinobacteria in natural products research: Progress and prospects. *Microbiological Research*, *246*, 126708. https://doi.org/10.1016/J.MICRES.2021.126708

Jung-Schroers, V., Adamek, M., Jung, A., Harris, S., Dóza, S., Baumer, A., & Steinhagen, D. (2016a). Feeding of β-1,3/1,6-glucan increases the diversity of the intestinal microflora of carp (Cyprinus carpio). *Aquaculture Nutrition*, *22*(5), 1026–1039. https://doi.org/10.1111/ANU.12320

Jung-Schroers, V., Adamek, M., Jung, A., Harris, S., Dóza, S., Baumer, A., & Steinhagen, D. (2016b). Feeding of β-1,3/1,6-glucan increases the diversity of the intestinal microflora of carp

(Cyprinus carpio). *Aquaculture Nutrition*, *22*(5), 1026–1039. https://doi.org/10.1111/ANU.12320

Jürgens, K., & Matz, C. (2002). Predation as a shaping force for the phenotypic and genotypic composition of planktonic bacteria. *Antonie van Leeuwenhoek, International Journal of General and Molecular Microbiology*, *81*(1–4), 413–434. https://doi.org/10.1023/A:1020505204959

Kabir, K. A., Verdegem, M. C. J., Verreth, J. A. J., Phillips, M. J., & Schrama, J. W. (2019). Effect of dietary protein to energy ratio, stocking density and feeding level on performance of Nile tilapia in pond aquaculture. *Aquaculture*, *511*, 634200. https://doi.org/10.1016/J.AQUACULTURE.2019.06.014

Kalcheva, H., Terziyski, D., Kalchev, R., Dochin, K., & Ivanova, A. (2010). Control of zoo plankton and nutrients on bacterioplankton in fish ponds with carp larvae. *Agrojournal.Org*, *16*(3), 284–297. http://www.agrojournal.org/16/03-05-10.pdf

Kapetanović, D., Kurtović, B., Vardić, I., Valić, D., Teskeredžić, Z., & Teskeredžić, E. (2006). Preliminary studies on bacterial diversity of cultured bluefin tuna Thunnus thynnus from the Adriatic Sea. *Aquaculture Research*, *37*(12), 1265–1266. https://doi.org/10.1111/J.1365-2109.2006.01550.X

Kassen, R., & Rainey, P. B. (2004). The ecology and genetics of microbial diversity. *Annual Review of Microbiology*, *58*, 207–231. https://doi.org/10.1146/ANNUREV.MICRO.58.030603.123654

Kate, G. U., Krishnani, K. K., Kumar, N., Sukhdhane, K., Verma, A. K., Brahmane, M. P., Chadha, N. K., & Kumar, J. (2023). Abiotic and biotic stress alleviating effects of the medicinal and aromatic plant-derived product on striped catfish Pangasianodon hypophthalmus. *Fish and Shellfish Immunology*, *135*, 1050–4648. https://doi.org/10.1016/j.fsi.2023.108625

Kathiravan, V., & Krishnani, K. K. (2014). Pseudomonas aeruginosa and Achromobacter sp.: Nitrifying aerobic denitrifiers have a plasmid encoding for denitrifying functional genes. *World Journal of Microbiology and Biotechnology*, *30*(4), 1187–1198. https://doi.org/10.1007/s11274-013-1543-6

Ke, Z., Xie, P., & Guo, L. (2008). In situ study on effect of food competition on diet shifts and growth of silver and bighead carps in large biomanipulation fish pens in Meiliang Bay, Lake Taihu. *Journal of Applied Ichthyology*, *24*(3), 263–268. https://doi.org/10.1111/J.1439-0426.2008.01060.X

Ke, Z., Xie, P., Guo, L., Liu, Y., & Yang, H. (2007). In situ study on the control of toxic Microcystis blooms using phytoplanktivorous fish in the subtropical Lake Taihu of China: A large fish pen experiment. *Aquaculture*, *265*(1–4), 127–138. https://doi.org/10.1016/J.AQUACULTURE.2007.01.049

Kemp, W. M., Sampou, P., Caffrey, J., Mayer, M., Henriksen, K., & Boynton, W. R. (1990). Ammonium recycling versus denitrification in Chesapeake Bay sediments. *Limnology and Oceanography*, *35*(7), 1545–1563. https://doi.org/10.4319/LO.1990.35.7.1545

Kestemont, P. (1995). Different systems of carp production and their impacts on the environment. *Aquaculture*, *129*(1–4), 347–372. https://doi.org/10.1016/0044-8486(94)00292-V

Kim, K., Park, C., Yoon, Y., & Hwang, S. J. (2018). Harmful Cyanobacterial Material Production in the North Han River (South Korea): Genetic Potential and Temperature-Dependent Properties. *International Journal of Environmental Research and Public Health*, *15*(3). https://doi.org/10.3390/IJERPH15030444

Klase, G., Lee, S., Liang, S., Kim, J., Zo, Y. G., & Lee, J. (2019). The microbiome and antibiotic resistance in integrated fishfarm water: Implications of environmental public health. *Science of The Total Environment*, *649*, 1491–1501. https://doi.org/10.1016/J.SCITOTENV.2018.08.288

Koops, HP., Purkhold, U., Pommerening-Röser, A., Timmermann, G., & Wagner, M. (2003). The lithoautotrophic ammonia oxidizers. In M. Dworkin & S. Falkow (Eds.), *The prokaryotes:an evolving electronic resource for the microbiological community.* (pp. 3–13).

Kosolapov, D. B., Kopylov, A. I., Kosolapova, N. G., & Mylnikova, Z. M. (2017). Structure and functioning of the microbial loop in a boreal reservoir. *Inland Water Biology* , *10*(1), 28–36. https://doi.org/10.1134/S1995082917010102

Koziñska, A., & Pekala, A. (2004). First isolation of Shewanella putrefaciens from freshwater fish-a potential new pathogen of the fish. *Bulletin of the European Association of Fish Pathologists*, *24*(4), 189. https://doi.org/10.13140/RG.2.1.2736.7282

Krishnani, K. K. (2010). Detection and diversity of nitrifying and denitrifying functional genes in coastal aquaculture. *Aquaculture*, *302*(1–2), 57–70. https://doi.org/10.1016/J.AQUACULTURE.2010.01.024

Krishnani, K. K., Gopikrishna, G., Pillai, S. M., & Gupta, B. P. (2010). Abundance of sulphur-oxidizing bacteria in coastal aquaculture using soxB gene analyses. *Aquaculture Research*, *41*(9), 1290–1301. https://doi.org/10.1111/J.1365-2109.2009.02415.X

Krishnani, K. K., & Kathiravan, V. (2010). A quantitativemethod for detecting ammonia-oxidizing bacteria in coastal aquaculture systems. *Aquaculture Research*, *41*(11), 1648–1657. https://doi.org/10.1111/J.1365-2109.2010.02535.X

Krishnani, K. K., Kathiravan, V., Natarajan, M., Kailasam, M., & Pillai, S. M. (2010). Diversity of Sulfur-Oxidizing Bacteria in Greenwater System of Coastal Aquaculture. *Applied Biochemistry and Biotechnology*, *162*(5), 1225–1237. https://doi.org/10.1007/s12010-009-8886-3

Krishnani, K. K., Shekhar, M. S., Gopikrishna, G., & Gupta, B. P. (2009). Molecular biological characterization and biostimulation of ammonia-oxidizing bacteria in brackishwater aquaculture. *Journal of Environmental Science and Health - Part A Toxic/Hazardous Substances and Environmental Engineering*, *44*(14), 1598–1608. https://doi.org/10.1080/10934520903263637

Kuang, T., He, A., Lin, Y., Huang, X., Liu, L., & Zhou, L. (2020). Comparative analysis of microbial communities associated with the gill, gut, and habitat of two filter-feeding fish. *Aquaculture Reports*, *18*. https://doi.org/10.1016/J.AQREP.2020.100501

Kühlwein, H., Emery, M. J., Rawling, M. D., Harper, G. M., Merrifield, D. L., & Davies, S. J. (2013). Effects of a dietary β-(1,3)(1,6)-D-glucan supplementation on intestinal microbial communities and intestinal ultrastructure of mirror carp (Cyprinus carpio L.). *Journal of Applied Microbiology*, *115*(5), 1091–1106. https://doi.org/10.1111/JAM.12313

Kumar, M. S., Binh, T. T., Luu, L. T., & Clarke, S. M. (2005). Evaluation of fish production using organic and inorganic fertilizer: Application to grass carp polyculture. *Journal of Applied Aquaculture*, *17*(1), 19–34. https://doi.org/10.1300/J028V17N01_02

Kumari, V., Rathore, G., Chauhan, U., & Pandey, A. (2011). Seasonal variations in abundance of nitrifying bacteria in fish pond ecosystem. *Journal of Environmental Biology*, *32*, 153–159. http://krishi.icar.gov.in/jspui/handle/123456789/4949

Lancelot, C., & Billen, G. (1985). Carbon- nitrogen relationships in nutrient metabolism of coastal marine ecosystems. *Advances in Aquatic Microbiology. Vol. 3*, 263–321.

Larsen, A. M., Mohammed, H. H., & Arias, C. R. (2014). Characterization of the gut microbiota of three commercially valuable warmwater fish species. *Journal of Applied Microbiology*, *116*(6), 1396–1404. https://doi.org/10.1111/JAM.12475

Lefèvre, M., Jakob, H., & Nisbet, M. (1952). Auto- et heteroantagonisme chez les algues d'EAU douce in vitro et dans les collections d'EAU naturelles. *Annales de La Station Centrale d'hydrobiologie Appliquée*, *4*, 5–198.

Li D.S., & Dong S.L. (1996). The study of structure and function of the filter organs in silver carp and bighead. *Acta Zoological Sinica*, *42*, 10–15.

Li, T., Li, H., Gatesoupe, F. J., She, R., Lin, Q., Yan, X., Li, J., & Li, X. (2017). Bacterial Signatures of "Red-Operculum" Disease in the Gut of Crucian Carp (Carassius auratus). *Microbial Ecology*, *74*(3), 510–521. https://doi.org/10.1007/S00248-017-0967-1

Li, T., Long, M., Gatesoupe, F. J., Zhang, Q., Li, A., & Gong, X. (2015). Comparative analysis of the intestinal bacterial communities in different species of carp by pyrosequencing. *Microbial Ecology*, *69*(1), 25–36. https://doi.org/10.1007/S00248-014-0480-8

Li, X., Liu, L., Zhu, Y., Zhu, T., Wu, X., & Yang, D. (2021). Microbial community structure and its driving environmental factors in black carp (Mylopharyngodon piceus) aquaculture pond. *Water (Switzerland)*, *13*(21). https://doi.org/10.3390/W13213089

Li, X., Ringø, E., Hoseinifar, S. H., Lauzon, H. L., Birkbeck, H., & Yang, D. (2018). The adherence and colonization of microorganisms in fish gastrointestinal tract. *Reviews in Aquaculture*, *11*(3), 603–618. https://doi.org/10.1111/RAQ.12248

Li, X., Yan, Q., Xie, S., Hu, W., Yu, Y., & Hu, Z. (2013). Gut microbiota contributes to the growth of fast-growing transgenic common carp (Cyprinus carpio L.). *PloS One*, *8*(5). https://doi.org/10.1371/JOURNAL.PONE.0064577

Li, Y., Hu, S., Gong, L., Pan, L., Li, D., Cao, L., Khan, T. A., Yang, Y., Peng, Y., Ding, X., Yi, G., Liu, S., & Xia, L. (2020). Isolating a new Streptomyces amritsarensis N1-32 against fish pathogens and determining its effects on disease resistance of grass carp. *Fish & Shellfish Immunology*, *98*, 632–640. https://doi.org/10.1016/J.FSI.2019.10.038

Liu, H., Guo, X., Gooneratne, R., Lai, R., Zeng, C., Zhan, F., & Wang, W. (2016). The gut microbiome and degradation enzyme activity of wild freshwater fishes influenced by their trophic levels. *Scientific Reports* , *6*(1), 1–12. https://doi.org/10.1038/srep24340

Liu H.L., & Haung Z.G. (2008). Aquaculture Science of China. *Science Press, Beijing*.

Liu, Y., Lv, H., Xu, L., Zhang, K., Mei, Y., Chen, J., Wang, M., Guan, Y., Pang, H., Wang, Y., & Tan, Z. (2022). The Effect of Dietary Lactic Acid Bacteria on Intestinal Microbiota and Immune Responses of Crucian Carp (Carassius auratus) Under Water Temperature Decrease. *Frontiers in Microbiology*, *13*. https://doi.org/10.3389/FMICB.2022.847167

Liu Y., Zhou, Z., Shi, P., He, S., & Yao, B. (2008). The comparative analysis of the attached bacterial flora in the gill and body surface of Epinephelus awoara in cages by PCR-DGGE. *Journal of Agricultural Science and Technology*, *10*, 81–86. https://en.cnki.com.cn/Article_en/CJFDTotal-NKDB200801016.htm

Loch, T. P., & Faisal, M. (2015). Emerging flavobacterial infections in fish: A review. *Journal of Advanced Research*, *6*(3), 283–300. https://doi.org/10.1016/J.JARE.2014.10.009

Luo, M., An, R., Fu, J., Wan, S., Zhu, W., Wang, L., & Dong, Z. (2022). Comparative analysis of the gut microbiota in bighead carp under different culture patterns. *Journal of Applied Microbiology*, *132*(2), 1357–1369. https://doi.org/10.1111/JAM.15248

Mahmoud, B. S. M., Yamazaki, K., Miyashita, K., Il-Shik, S., Dong-Suk, C., & Suzuki, T. (2004). Bacterial microflora of carp (Cyprinus carpio) and its shelf-life extension by essential oil compounds. *Food Microbiology*, *21*(6), 657–666. https://doi.org/10.1016/J.FM.2004.03.001

Maji, U. J., Mohanty, S., Pradhan, A., & Maiti, N. K. (2017). Immune modulation, disease resistance and growth performance of Indian farmed carp, Labeo rohita (Hamilton), in response to dietary consortium of putative lactic acid bacteria. *Aquaculture International*, *25*(4), 1391–1407. https://doi.org/10.1007/S10499-017-0122-5/FIGURES/3

Mandal, S., & Ghosh, K. (2013). Isolation of tannase-producing microbiota from the gastrointestinal tracts of some freshwater fish. *Journal of Applied Ichthyology*, *29*(1), 145–153. https://doi.org/10.1111/J.1439-0426.2012.02054.X

Marel, M., Caspari, N., Neuhaus, H., Meyer, W., Enss, M. L., & Steinhagen, D. (2010). Changes in skin mucus of common carp, Cyprinus carpio L., after exposure to water with a high bacterial load. *Journal of Fish Diseases*, *33*(5), 431–439. https://doi.org/10.1111/J.1365-2761.2010.01140.X

Martínez, J. L. (2017). Effect of antibiotics on bacterial populations: a multi-hierachical selection process. *F1000Research*, *6*. https://doi.org/10.12688/F1000RESEARCH.9685.1

Matz, C., & Jürgens, K. (2003). Interaction of Nutrient Limitation and Protozoan Grazing Determines the Phenotypic Structure of a Bacterial Community. *Microbial Ecology*, *45*(4), 384–398. https://doi.org/10.1007/S00248-003-2000-0

McMurtrie, J., Alathari, S., Chaput, D. L., Bass, D., Ghambi, C., Nagoli, J., Delamare-Deboutteville, J., Mohan, C. V., Cable, J., Temperton, B., & Tyler, C. R. (2022). Relationships between pond water and tilapia skin microbiomes in aquaculture ponds in Malawi. *Aquaculture*, *558*, 738367. https://doi.org/10.1016/J.AQUACULTURE.2022.738367

Meng, L. J., Zhang, Y., Li, X. X., Liu, J. H., Wen, B., Gao, J. Z., & Chen, Z. Z. (2021). Comparative analysis of bacterial communities of water and intestines of silver carp (Hypophthalmichthys molitrix) and bighead carp (H. nobilis) reared in aquaculture pond systems. *Aquaculture*, *534*, 736334. https://doi.org/10.1016/J.AQUACULTURE.2020.736334

Merrifield, D. L., Bradley, G., Baker, R. T. M., & Davies, S. J. (2010). Probiotic applications for rainbow trout (Oncorhynchus mykiss Walbaum) II. Effects on growth performance, feed utilization, intestinal microbiota and related health criteria postantibiotic treatment. *Aquaculture Nutrition*, *16*(5), 496–503. https://doi.org/10.1111/J.1365-2095.2009.00688.X

Middelboe, M., Jacquet, S., & Weinbauer M. (2008). Viruses in freshwater ecosystems: an introduction to the exploration of viruses in new aquatic habitats. *Freshwater Biology*, *53*(6), 1069–1075. https://doi.org/10.1111/j.1365-2427.2008.02014.x

Milstein, A. (1992). Ecological aspects of fish species interactions in polyculture ponds. *Hydrobiologia*, *231*(3), 177–186. https://doi.org/10.1007/BF00018201

Milstein, A. (2005). Polyculture in aquaculture. *Animal Breeding Abstracts*, *73*(12), 15–41. https://doi.org/10.1079/cabireviews20053207372

Minich, J. J., Zhu, Q., Xu, Z. Z., Amir, A., Ngochera, M., Simwaka, M., Allen, E. E., Zidana, H., & Knight, R. (2018). Microbial effects of livestock manure fertilization on freshwater aquaculture ponds rearing tilapia (Oreochromis shiranus) and North African catfish (Clarias gariepinus). *MicrobiologyOpen*, *7*(6), e00716. https://doi.org/10.1002/MBO3.716

Mohammadi, G., Rafiee, G., Tavabe, K. R., Abdel-Latif, H. M. R., & Dawood, M. A. O. (2021). The enrichment of diet with beneficial bacteria (single- or multi- strain) in biofloc system enhanced the water quality, growth performance, immune responses, and disease resistance of Nile tilapia (Oreochromis niloticus). *Aquaculture*, *539*. https://doi.org/10.1016/j.aquaculture.2021.736640

Mohapatra, S., Chakraborty, T., Prusty, A. K., Das, P., Paniprasad, K., & Mohanta, K. N. (2012). Use of different microbial probiotics in the diet of rohu, Labeo rohita fingerlings: effects on growth, nutrient digestibility and retention, digestive enzyme activities and intestinal microflora. *Aquaculture Nutrition*, *18*(1), 1–11. https://doi.org/10.1111/J.1365-2095.2011.00866.X

Montalban-Arques, A., De Schryver, P., Bossier, P., Gorkiewicz, G., Mulero, V., Gatlin, D. M., & Galindo-Villegas, J. (2015). Selective manipulation of the gut microbiota improves immune

status in vertebrates. In *Frontiers in Immunology* (Vol. 6, Issue 512). Frontiers Media S.A. https://doi.org/10.3389/fimmu.2015.00512

Mukherjee, A., Dutta, D., Banerjee, S., Ringø, E., Breines, E. M., Hareide, E., Chandra, G., & Ghosh, K. (2016). Potential probiotics from Indian major carp, Cirrhinus mrigala. Characterization, pathogen inhibitory activity, partial characterization of bacteriocin and production of exoenzymes. *Research in Veterinary Science*, *108*, 76–84. https://doi.org/10.1016/J.RVSC.2016.08.011

Mukherjee, A., Rodiles, A., Merrifield, D. L., Chandra, G., & Ghosh, K. (2020). Exploring intestinal microbiome composition in three Indian major carps under polyculture system: A high-throughput sequencing based approach. *Aquaculture*, *524*, 735206. https://doi.org/10.1016/J.AQUACULTURE.2020.735206

Mulyani, Y., Aryantha, I. N. P., Suhandono, S., & Pancoro, A. (2018). Intestinal bacteria of common carp (Cyprinus carpio L.) as a biological control agent for aeromonas. *Journal of Pure and Applied Microbiology*, *12*(2), 601–610. https://doi.org/10.22207/JPAM.12.2.18

Nakandakare, I. B., Iwashita, M. K. P., Dias, DdeC., Tachibana, L., Ranzani-Paiva, M. J. T., & Romagosa, E. (2013). Incorporation of probiotics in the diet for juvenile Nile tilapias: hematological, immunological and microbiological parameters. *Boletim Do Instituto de Pesca*, *39*(2), 121–135.

Nandi, A., Banerjee, G., Dan, S., Ghosh, P., Ghosh, K., & Ray, A. (2017). Screening of autochthonous intestinal microbiota as candidate probiotics isolated from four freshwater teleosts. *Current Science*, *113*(4), 767–773. https://doi.org/10.18520/CS/V113/I04/767-773

Nandi, A., Banerjee, G., Dan, S., Ghosh, P., Ghosh, K., Ray, A., & Ringø, E. (2017). Probiotic Potential of Autochthonous Bacteria Isolated from the Gastrointestinal Tract of Four Freshwater Teleosts. *Probiotics and Antimicrobial Proteins*, *9*(1), 12–21. https://doi.org/10.1007/S12602-016-9228-8

Navarrete, P., Magne, F., Araneda, C., Fuentes, P., Barros, L., Opazo, R., Espejo, R., & Romero, J. (2012). PCR-TTGE analysis of 16S rRNA from rainbow trout (oncorhynchus mykiss) gut microbiota reveals host-specific communities of active bacteria. *PLoS ONE*, *7*(2). https://doi.org/10.1371/JOURNAL.PONE.0031335

Nayak, S. K. (2010). Role of gastrointestinal microbiota in fish. *Aquaculture Research*, *41*(11), 1553–1573. https://doi.org/10.1111/J.1365-2109.2010.02546.X

Negri, A. P., Jones, G. J., & Hindmarsh, M. (1995). Sheep mortality associated with paralytic shellfish poisons from the cyanobacterium Anabaena circinalis. *Toxicon : Official Journal of the International Society on Toxinology*, *33*(10), 1321–1329. https://doi.org/10.1016/0041-0101(95)00068-W

Newton, R. J., Jones, S. E., Eiler, A., McMahon, K. D., & Bertilsson, S. (2011). A Guide to the Natural History of Freshwater Lake Bacteria. *Microbiology and Molecular Biology Reviews*, *75*(1), 14–49. https://doi.org/10.1128/MMBR.00028-10/SUPPL_FILE/SUPPLEMENTAL_TABLE_2.ZIP

Nozaki, K. (1999). Algal community structure in a littoral zone in the north basin of Lake Biwa. *Japanese Journal of Limnology*, *60*(2), 139–157. https://doi.org/10.3739/RIKUSUI.60.139

Olah, J. (1986). Carp production in manured ponds. In *Aquaculture of cyprinids*. INRA.

Opuszyński, K. (1981). Comparison of the usefulness of the silver carp and the bighead carp as additional fish in carp ponds. *Aquaculture*, *25*(2–3), 223–233. https://doi.org/10.1016/0044-8486(81)90184-8

Pace, M. L., & Cole, J. J. (1994). Comparative and experimental approaches to top-down and bottom-up regulation of bacteria. *Microbial Ecology*, *28*(2), 181–193. https://doi.org/10.1007/BF00166807

Padmavathi, P., & Durga Prasad, M. K. (2017). Studies on algal bloom disasters in carp culture ponds. *Journal of Morphological Sciences*, *24*(2).

Padmavathi, P., Prasad, M. K. D., Padmavathi, P., & Prasad, M. K. D. (2017). Studies on algal bloom disasters in carp culture ponds. *Journal of Morphological Sciences*, *24*(2), 32–43.

Parker, A. E., Dugdale, R. C., & Wilkerson, F. P. (2012). Elevated ammonium concentrations from wastewater discharge depress primary productivity in the Sacramento River and the Northern San Francisco Estuary. *Marine Pollution Bulletin*, *64*(3), 574–586. https://doi.org/10.1016/j.marpolbul.2011.12.016

Patil, H. J., Benet-Perelberg, A., Naor, A., Smirnov, M., Ofek, T., Nasser, A., Minz, D., & Cytryn, E. (2016). Evidence of increased antibiotic resistance in phylogenetically-diverse aeromonas isolates from semi-intensive fish ponds treated with antibiotics. *Frontiers in Microbiology*, *7*(NOV), 1875. https://doi.org/10.3389/FMICB.2016.01875/BIBTEX

Patterson, E., Cryan, J. F., Fitzgerald, G. F., Ross, R. P., Dinan, T. G., & Stanton, C. (2014). Gut microbiota, the pharmabiotics they produce and host health. *Proceedings of the Nutrition Society*, *760*, 477–489. https://doi.org/10.1017/S0029665114001426

Perković, L., Djedović, E., Vujović, T., Baković, M., Paradžik, T., & Čož-Rakovac, R. (2022). Biotechnological Enhancement of Probiotics through Co-Cultivation with Algae: Future or a Trend? *Marine Drugs 2022, Vol. 20, Page 142*, *20*(2), 142. https://doi.org/10.3390/MD20020142

Perry, W. B., Lindsay, E., Payne, C. J., Brodie, C., & Kazlauskaite, R. (2020). The role of the gut microbiome in sustainable teleost aquaculture. *Proceedings of the Royal Society B*, *287*(1926). https://doi.org/10.1098/RSPB.2020.0184

Piotrowska, M., Rzeczycka, M., Ostrowski, R., & Popowska, M. (2017). Diversity of Antibiotic Resistance Among Bacteria Isolated from Sediments and Water of Carp Farms Located in a Polish Nature Reserve. *Polish Journal of Environmental Studies*, *26*(1), 239–252. https://doi.org/10.15244/PJOES/64910

Porchas-Cornejo, M. A., Martinez-Porchas, M., Rafael Martinez-Cordova, L., & Ramos, L. (2012). Consumption of Natural and Artificial Foods by Shrimp (Litopenaeus vannamei) Reared in

Ponds with and without Enhancement of Natural Productivity. *The Israeli Journal of Aquaculture*, *59*(4), 1–7. https://www.researchgate.net/publication/237153343

Props, R., Monsieurs, P., Mysara, M., Clement, L., & Boon, N. (2016). Measuring the biodiversity of microbial communities by flow cytometry. *Methods in Ecology and Evolution*, *7*(11), 1376–1385. https://doi.org/10.1111/2041-210X.12607

Qi, Z., Zhang, X. H., Boon, N., & Bossier, P. (2009). Probiotics in aquaculture of China — Current state, problems and prospect. *Aquaculture*, *290*(1–2), 15–21. https://doi.org/10.1016/J.AQUACULTURE.2009.02.012

Qin, Y., Hou, J., Deng, M., Liu, Q., Wu, C., Ji, Y., & He, X. (2016). Bacterial abundance and diversity in pond water supplied with different feeds. *Scientific Reports*, *6*(1), 35232. https://doi.org/10.1038/srep35232

Ray, A. K., Roy, T., Mondal, S., & Ringø, E. (2010). Identification of gut-associated amylase, cellulase and protease-producing bacteria in three species of Indian major carps. *Aquaculture Research*, *41*(10), 1462–1469. https://doi.org/10.1111/J.1365-2109.2009.02437.X

Rimoldi, S., Terova, G., Ascione, C., Giannico, R., & Brambilla, F. (2018). Next generation sequencing for gut microbiome characterization in rainbow trout (Oncorhynchus mykiss) fed animal by-product meals as an alternative to fishmeal protein sources. *PloS One*, *13*(3). https://doi.org/10.1371/JOURNAL.PONE.0193652

Ringø, E., Dimitroglou, A., Hoseinifar, S. H., & Davies, S. J. (2014). Prebiotics in Finfish: An Update. *Aquaculture Nutrition: Gut Health, Probiotics and Prebiotics*, 360–400. https://doi.org/10.1002/9781118897263.CH14

Ringø, E., & Holzapfel, W. (2000). Identification and Characterization of Carnobacteria Associated with the Gills of Atlantic Salmon (Salmo salar L.). *Systematic and Applied Microbiology*, *23*(4), 523–527. https://doi.org/10.1016/S0723-2020(00)80026-0

Ringø, E., Zhou, Z., Vecino, J. L. G., Wadsworth, S., Romero, J., Krogdahl, Olsen, R. E., Dimitroglou, A., Foey, A., Davies, S., Owen, M., Lauzon, H. L., Martinsen, L. L., De Schryver, P., Bossier, P., Sperstad, S., & Merrifield, D. L. (2016). Effect of dietary components on the gut microbiota of aquatic animals. A never-ending story? *Aquaculture Nutrition*, *22*(2), 219–282. https://doi.org/10.1111/ANU.12346

Ruttkay, A. (1975). Ecological study of carp nutrition. *Kísérletügyi Közlemények*, *67*, 133–156.

Sharifuzzaman, S. M., & Austin, B. (2010). Kocuria SM1 controls vibriosis in rainbow trout (Oncorhynchus mykiss, Walbaum). *Journal of Applied Microbiology*, *108*(6), 2162–2170. https://doi.org/10.1111/J.1365-2672.2009.04618.X

Shephard, K. L. (1994). Functions for fish mucus. *Reviews in Fish Biology and Fisheries* , *4*(4), 401–429. https://doi.org/10.1007/BF00042888

Sherr, E. B., & Sherr, B. F. (1987). High rates of consumption of bacteria by pelagic ciliates. *Nature* , *325*(6106), 710–711. https://doi.org/10.1038/325710a0

Shijila Rani, A. S., Babu, S., Anbukumaran, A., Prakash, P., Veeramani, S., & Ambikapathy, V. (2022). Isolation of Actinobacteria from Shrimp. In D. Dharumadurai (Ed.), *Methods in Actinobacteriology* (pp. 27–30). Springer Protocols Handbooks. Humana, New York, NY. https://doi.org/10.1007/978-1-0716-1728-1_6

Shinn, A. P., Pratoomyot, J., Griffiths, D., Trong, T. Q., Vu, N. T., Jiravanichpaisal, P., & Briggs, M. (2018). Asian shrimp production and the economic costs of disease. *Asian Fisheries Science*, *31*, 29–58. https://doi.org/10.33997/J.AFS.2018.31.S1.003

Silva, S. de, & Anderson, T. (1994). *Fish nutrition in aquaculture* (S. de Silva & T. Anderson, Eds.). Chapman & Hall.

Skjermo, J., & Vadstein, O. (1993). Characterization of the bacterial flora of mass cultivated Brachionus plicatilis. *Hydrobiologia*, *255–256*(1), 185–191. https://doi.org/10.1007/BF00025838

Snoussi, M., Chaieb, K., Mahmoud, R., & Bakhrouf, A. (2006). Quantitative study, identification and antibiotics sensitivity of someVibrionaceae associated to a marine fish hatchery. *Annals of Microbiology 2006 56:4*, *56*(4), 289–293. https://doi.org/10.1007/BF03175020

Steel, J. A. (1980). Phytoplankton models. In E. D. LeCren & R. H. Lowe-McConnell (Eds.), *Functioning of Freshwater Ecosystems* (pp. 220–227). Cambridge University Press, Cambridge.

Stentiford, G. D., Sritunyalucksana, K., Flegel, T. W., Williams, B. A. P., Withyachumnarnkul, B., Itsathitphaisarn, O., & Bass, D. (2017). New Paradigms to Help Solve the Global Aquaculture Disease Crisis. *PLoS Pathogens*, *13*(2), 1–6. https://doi.org/10.1371/JOURNAL.PPAT.1006160

Sun, B. Y., Yang, H. X., He, W., Tian, D. Y., Kou, H. Y., Wu, K., Yang, C. G., Cheng, Z. Q., & Song, X. H. (2021). A grass carp model with an antibiotic-disrupted intestinal microbiota. *Aquaculture*, *541*, 736790. https://doi.org/10.1016/J.AQUACULTURE.2021.736790

Sun, X. M., & Meng, Q. W. (1992). Development and structure of the filter and digestive organs and their relations with the food habits in silver carp and bighead. *Journal of Fisheries of China*, *16*, 202–212.

Tang, J. Y., Dai, Y. X., Li, Y. M., Qin, J. G., & Wang, Y. (2016). Can Application of Commercial Microbial Products Improve Fish Growth and Water Quality in Freshwater Polyculture? *North American Journal of Aquaculture*, *78*(2), 154–160. https://doi.org/10.1080/15222055.2015.1116474

Tang, Y., Zhao, L., Cheng, Y., Yang, Y., Sun, Y., & Liu, Q. (2021). Control of cyanobacterial blooms in different polyculture patterns of filter feeders and effects of these patterns on water quality and microbial community in aquacultural ponds. *Aquaculture*, *542*, 736913. https://doi.org/10.1016/J.AQUACULTURE.2021.736913

Tarnecki, A. M., Brennan, N. P., Schloesser, R. W., & Rhody, N. R. (2019). Shifts in the Skin-Associated Microbiota of Hatchery-Reared Common Snook Centropomus undecimalis During Acclimation to the Wild. *Microbial Ecology*, *77*(3), 770–781. https://doi.org/10.1007/s00248-018-1252-7

Tas, S., Yilmaz, I. N., & Okus, E. (2009). Phytoplankton as an indicator of improving water quality in the Golden Horn Estuary. *Estuaries and Coasts*, *32*(6), 1205–1224. https://doi.org/10.1007/S12237-009-9207-3/TABLES/5

Testa, J. M., & Michael Kemp, W. (2012). Hypoxia-induced shifts in nitrogen and phosphorus cycling in Chesapeake Bay. *Limnology and Oceanography*, *57*(3), 835–850. https://doi.org/10.4319/LO.2012.57.3.0835

Thomas, F., Hehemann, J. H., Rebuffet, E., Czjzek, M., & Michel, G. (2011). Environmental and gut Bacteroidetes: The food connection. *Frontiers in Microbiology*, *2*(MAY), 93. https://doi.org/10.3389/FMICB.2011.00093/BIBTEX

Tian, C., Tan, J., Wu, X., Ye, W., Liu, X., Li, D., & Yang, H. (2009). Spatiotemporal transition of bacterioplankton diversity in a large shallow hypertrophic freshwater lake, as determined by denaturing gradient gel electrophoresis. *Journal of Plankton Research*, *31*(8), 885–897. https://doi.org/10.1093/PLANKT/FBP028

Tran, N. T., Xiong, F., Hao, Y. T., Zhang, J., Wu, S. G., & Wang, G. T. (2018). Starvation influences the microbiota assembly and expression of immunity-related genes in the intestine of grass carp (Ctenopharyngodon idellus). *Aquaculture*, *489*, 121–129. https://doi.org/10.1016/J.AQUACULTURE.2018.02.016

Tucker, C. S. (2000). Off-Flavor Problems in Aquaculture. *Reviews in Fisheries Science*, *8*(1), 45–88. https://doi.org/10.1080/10641260091129170

Tucker, C. S. (2006). Low-density silver carp Hypophthalmichthys molitrix (Valenciennes) polyculture does not prevent cyanobacterial off-flavours in channel catfish Ictalurus punctatus (Rafinesque). *Aquaculture Research*, *37*(3), 209–214. https://doi.org/10.1111/J.1365-2109.2005.01417.X

Tyagi, A., & Singh, B. (2017). Microbial diversity in Rohu fish gut and inland saline aquaculture sediment and variations associated with next-generation sequencing of 16S rRNA gene. *Journal of Fisheries and Life Sciences*, *2*(1), 1–8.

Uddin, N., & Al-Harbi, A. H. (2012). Bacterial flora of polycultured common carp (Cyprinus carpio) and African catfish (Clarias gariepinus). *International Aquatic Research*, *4*(1), 1–9. https://doi.org/10.1186/2008-6970-4-10/TABLES/2

van Keulen, G., & Dyson, P. J. (2014). Production of specialized metabolites by Streptomyces coelicolor A3(2). *Advances in Applied Microbiology*, *89*, 217–266. https://doi.org/10.1016/B978-0-12-800259-9.00006-8

Velusamy, K., & Krishnani, K. K. (2013). Heterotrophic nitrifying and oxygen tolerant denitrifying bacteria from greenwater system of coastal aquaculture. *Applied Biochemistry and Biotechnology*, *169*(6), 1978–1992. https://doi.org/10.1007/s12010-013-0109-2

Verstraete, W., & Focht, D. D. (1977). Biochemical Ecology of Nitrification and Denitrification. *Advances in Microbial Ecology*, *1*, 135–214. https://doi.org/10.1007/978-1-4615-8219-9_4

Wang, C., Xu, S., Jiang, C., Peng, X., Zhou, X., Sun, Q., Zhu, L., Xie, X., & Zhuang, X. (2023). Improvement of the growth performance, intestinal health, and water quality in juvenile crucian carp (Carassius auratus gibelio) biofortified system with the bacteria-microalgae association. *Aquaculture*, *562*, 738848. https://doi.org/10.1016/J.AQUACULTURE.2022.738848

Wang, W., Zhou, Z., He, S., Liu, Y., Cao, Y., Shi, P., Yao, B., & Ringø, E. (2010). Identification of the adherent microbiota on the gills and skin of poly-cultured gibel carp (Carassius auratus gibelio) and bluntnose black bream (Megalobrama amblycephala Yih). *Aquaculture Research*, *41*(9), e72–e83. https://doi.org/10.1111/J.1365-2109.2009.02459.X

Wang, Y., Hatt, J. K., Tsementzi, D., Rodriguez-R, L. M., Ruiz-Pérez, C. A., Weigand, M. R., Kizer, H., Maresca, G., Krishnan, R., Poretsky, R., Spain, J. C., & Konstantinidis, K. T. (2017). Quantifying the importance of the rare biosphere for microbial community response to organic pollutants in a freshwater ecosystem. *Applied and Environmental Microbiology*, *83*(8). https://doi.org/10.1128/AEM.03321-16/SUPPL_FILE/ZAM999117774S1.PDF

Wohlfarth, G. W., & Schroeder, G. L. (1979). Use of manure in fish farming—A review. *Agricultural Wastes*, *1*(4), 279–299. https://doi.org/10.1016/0141-4607(79)90012-X

Woynarovich, A., Moth-Poulsen, T., & Péteri, A. (2010). Carp polyculture in Central and Eastern Europe, the Caucasus and Central Asia. In *FAO Fisheries and Aquaculture*. Food and Agriculture Organization of the United Nations. JP 00590

Wu, S., Wang, G., Angert, E. R., Wang, W., Li, W., & Zou, H. (2012a). Composition, diversity, and origin of the bacterial community in grass carp intestine. *PLoS ONE*, *7*(2). https://doi.org/10.1371/JOURNAL.PONE.0030440

Wu, S., Wang, G., Angert, E. R., Wang, W., Li, W., & Zou, H. (2012b). Composition, diversity, and origin of the bacterial community in grass carp intestine. *PLoS ONE*, *7*(2). https://doi.org/10.1371/JOURNAL.PONE.0030440

Wu, Z. B., Gatesoupe, F. J., Li, T. T., Wang, X. H., Zhang, Q. Q., Feng, D. Y., Feng, Y. Q., Chen, H., & Li, A. H. (2018). Significant improvement of intestinal microbiota of gibel carp (Carassius auratus gibelio) after traditional Chinese medicine feeding. *Journal of Applied Microbiology*, *124*(3), 829–841. https://doi.org/10.1111/JAM.13674

Wu, Z. X., Feng, X., Xie, L. L., Peng, X. Y., Yuan, J., & Chen, X. X. (2012). Effect of probiotic Bacillus subtilis Ch9 for grass carp, Ctenopharyngodon idella (Valenciennes, 1844), on growth performance, digestive enzyme activities and intestinal microflora. *Journal of Applied Ichthyology*, *28*(5), 721–727. https://doi.org/10.1111/J.1439-0426.2012.01968.X

Xie, P., & Liu, J. (2001). Practical Success of Biomanipulation using Filter-Feeding Fish to Control Cyanobacteria Blooms: A Synthesis of Decades of Research and Application in a Subtropical Hypereutrophic Lake. *The Scientific World Journal*, *1*, 337–356. https://doi.org/10.1100/TSW.2001.67

Yan, L., Zhang, G., Liu, Q., & Li, J. (2009). Optimization of culturing the freshwater pearl mussels, Hyriopsis cumingii with filter feeding Chinese carps (bighead carp and silver carp) by

orthogonal array design. *Aquaculture*, *292*(1–2), 60–66. https://doi.org/10.1016/J.AQUACULTURE.2009.03.037

Yogesh, C. R., Ritu, A., Malobica, D. T., & Hema, T. (2014). Qualitative and quantitative study on bacterial flora of farm raised common carp, Cyprinus carpio in India. *African Journal of Microbiology Research*, *8*(11), 1125–1129. https://doi.org/10.5897/AJMR2013.6330

Yoshifumi, A., Tatsunori, N., Reiji, T., Kiyoshi, Y., & Tatsuaki, T. (2009). Seasonal changes in abundance of ammonia-oxidizing archaea and ammonia-oxidizing bacteria and their nitrification in sand of an eelgrass zone. *Microbes and Environments*, *24*(1), 21–27. https://doi.org/10.1264/JSME2.ME08536

Yuan, L., Wang, L., Li, Z. H., Zhang, M. Q., Shao, W., & Sheng, G. P. (2019). Antibiotic resistance and microbiota in the gut of Chinese four major freshwater carp from retail markets. *Environmental Pollution*, *255*, 113327. https://doi.org/10.1016/J.ENVPOL.2019.113327

Zdanowicz, M., Mudryk, Z. J., & Perliński, P. (2020). Abundance and antibiotic resistance of Aeromonas isolated from the water of three carp ponds. *Veterinary Research Communications*, *44*(1), 9–18. https://doi.org/10.1007/S11259-020-09768-X/TABLES/5

Zhang, H., Dong, W., Chen, L., Wang, Y., Muhammad, L., Ju, A., Shan, X., Ma, H., & Kong, L. (2020). Effects of dietary Lactobacillus plantarum C20015 on growth, immunity, and disease resistance in koi carp. *Aquaculture International*, *28*(5), 1797–1809. https://doi.org/10.1007/S10499-020-00558-5

Zhang, X., Xie, P., Hao, L., Guo, N., Gong, Y., Hu, X., Chen, J., & Liang, G. (2006). Effects of the phytoplanktivorous silver carp (Hypophthalmichthys molitrixon) on plankton and the hepatotoxic microcystins in an enclosure experiment in a eutrophic lake, Lake Shichahai in Beijing. *Aquaculture*, *257*(1–4), 173–186. https://doi.org/10.1016/J.AQUACULTURE.2006.03.018

Zhao, L., Wang, G., Siegel, P., He, C., Wang, H., Zhao, W., Zhai, Z., Tian, F., Zhao, J., Zhang, H., Sun, Z., Chen, W., Zhang, Y., & Meng, H. (2013). Quantitative Genetic Background of the Host Influences Gut Microbiomes in Chickens. *Scientific Reports*, *3*(1), 1–6. https://doi.org/10.1038/srep01163

Zhao, Z., Dong, S., Wang, F., Tian, X., & Gao, Q. (2014). Effect of algae density on breathing and feeding of filter-feeding silver carp (Hypophthalmichthys molitrix Val.). *Aquaculture*, *433*, 133–136. https://doi.org/10.1016/J.AQUACULTURE.2014.05.043

Zhao, Z., Jiang, J., Pan, Y., Dong, Y., Chen, Z., Zhang, G., Gao, S., Sun, H., Guan, X., Wang, B., Xiao, Y., & Zhou, Z. (2020). Temporal dynamics of bacterial communities in the water and sediments of sea cucumber (Apostichopus japonicus) culture ponds. *Aquaculture*, *528*, 735498. https://doi.org/10.1016/J.AQUACULTURE.2020.735498

Zhou, D., Zhang, T., Ren, L., Fang, D. A., & Xu, D. P. (2022). Differential Study of Microbiota in the Gill and Intestine of Silver Carp (Hypophthalmichthys molitrix) from the Algae-Dominated and Hydrophyte-Dominated Areas of Taihu Lake, China. *Fishes*, *7*(6), 304. https://doi.org/10.3390/FISHES7060304/S1

Zhou, G., Zhao, X., Bi, Y., & Hu, Z. (2011). Effects of silver carp (Hypophthalmichthys molitrix) on spring phytoplankton community structure of Three-Gorges Reservoir (China): Results from an enclosure experiment. *Journal of Limnology*, *70*(1), 26–32. https://doi.org/10.3274/JL11-70-1-05

Zhou, P., Chen, W., Zhu, Z., Zhou, K., Luo, S., Hu, S., Xia, L., & Ding, X. (2022). Comparative Study of Bacillus amyloliquefaciens X030 on the Intestinal Flora and Antibacterial Activity Against Aeromonas of Grass Carp. *Frontiers in Cellular and Infection Microbiology*, *12*, 2. https://doi.org/10.3389/FCIMB.2022.815436/BIBTEX

Zhou, T., Zheng, X., Tang, J., Qin, J., & Wang, Y. (2017). Effect of three commercial microbial products on bacterial community in a freshwater fish polyculture system. *Aquaculture Research*, *48*(8), 4449–4460. https://doi.org/10.1111/ARE.13270

Zöllner, E., Santer, B., Boersma, M., Hoppe, H. G., & Jürgens, K. (2003). Cascading predation effects of Daphnia and copepods on microbial food web components. *Freshwater Biology*, *48*(12), 2174–2193. https://doi.org/10.1046/J.1365-2426.2003.01158.X

Tables

Table 1. Some studies on bacterial microbiota in rearing water of carp polyculture systems

County	Culture system	Bacterial identification technology	Dominant bacterial taxa in pond rearing water	Ref.
India	Indian major carps (rohu, catla and mrigal) polyculture ponds	16S rRNA gene amplicon sequencing	*G*enera: *Actinomyces, Pseudonocardia, Sediminibacterium, Bacteroides, Exiguobacterium, Brochothrix Macrococcus, Alkalibacterium, Leuconostoc, Lactococcus, Shewanella, Trabulsiella, Acinetobacter, Psychrobacter, Luteolibacter* Families: *Coriobacteriaceae, Planococcaceae, Planococcaceae, Halomonadaceae*	(Mukherjee et al., 2020)
	Indian major carps (rohu, catla and mrigal), Silver carp ,	Morphological tests, staining procedures and bio-chemical and physiological tests.	Species: *Corynebacterium* spp., *Pseudomonas aeruginosa*, *P. fluorescens, P. aureofasciens, Aeromonas hydrophila, Flavobacter devorans, Proteus* sp., *Micrococcus* sp.,	(Yogesh et al., 2014)

	Grass carp and Common carp			
China	Black carp polyculture ponds	16S rRNA gene amplicon sequencing.	Major phyla: Proteobacteria, Actinobacteria, Bacteroidetes. Genera: *Prochlorococcus, Bacillus, Polynucleobacter, Chryseobacterium, Novosphingobium, Acinetobacter, Flavobacterium, Oscillospira, Ruminococcaceae, Agrobacterium, Comamonas, Janthinobacterium, Rheinheimera*	(Li et al., 2021)
	Grass carp, Crucian carp and bighead carp polyculture		Major phyla: Bacteroidetes, Proteobacteria, Actinobacteria, Fusobacteria and Verrucomicrobia	(Li et al., 2015)
	Silver, bighead carp polyculture ponds	16S rRNA gene amplicon sequencing	Major phyla: *Beta* Proteobacteria, *Alpha* Proteobacteria, *Gamma* Proteobacteria, Acidobacteria, Planctomycetes	(Tang et al., 2021)

	Grass carp, gibel carp and bluntnose black bream	16S rDNA gene sequences	Major phyla: Proteobacteria, Bacteroidetes, Firmicutes,	(Han et al., 2010)
	Silver carp and bighead carp pond	16S rRNA gene amplicon sequencing	Major phyla: Actinobacteria, Cyanobacteria , Proteobacteria and Bacteroidetes	(Meng et al., 2021)
	Polyculture with grass carp as the main species	16S rRNA gene amplicon sequencing	Major phyla: Actinobacteria, Cyanobacteria , Proteobacteria and Bacteroidetes	(Qin et al., 2016)
Saudi Arabia	Common carp	Morphological observation, Gram staining, biochemical testing	Species*: Aeromonas hydrophila, Bacillus* sp*., Corynebacterium urealyticum, Edwardsiella* sp*., Micrococcus* sp*., Pseudomonas* sp*., Shewanella putrefaciens, Staphylococcus* sp*., Streptococcus* sp*., Vibrio* sp*.,* Unidentified Gram-negative rods*, Cellulomonas cellulans, Gordona* sp*.*	(Al-Harbi & Uddin, 2008)

Common carp and African catfish polyculture	Morphological observation, Gram staining, biochemical testing	Species: *A. hydrophila, Corynebacterium* sp*., C. Urealyticum,* *Edwardsiella* sp*., Micrococcus* sp*., S. putrefaciens, Staphylococcus* sp*.,* *Streptococcus* sp*., Vibrio* sp*.,* Unidentified Gram−negative rods	(Uddin & Al-Harbi, 2012)

Table 2. Bacterial diversity in/on carp organs.

Carp species	Organ	System	Bacterial identification technology	Bacterial diversity	Ref.
Common carp (*Cyprinus carpio*)	Gills	Common carp monoculture	Aerobic plate counts, Gram's stain, motility, morphology, biochemical tests, thiosulphate-citrate-bile sucrose (TCBS) agar, vibriostatic agent, commercial API 20E, API 20 STREP (bioMerieux,	Species*: A. hydrophila, C. urealyticum, Micrococcus sp., S. putrefaciens, Staphylococcus* sp*., Vibrio* sp*.,* Unidentified Gram-negative rods	(Al-Harbi & Uddin, 2008)
	Gut	Common carp monoculture		Species*: A. hydrophila, Bacillus* sp*., C. urealyticum, Edwardsiella* sp*., Micrococcus* sp*., Pseudomonas* sp*., S. putrefaciens, Staphylococcus* sp*., Streptococcus* sp*., Vibrio* sp*.,* Unidentified Gram-negative rods	(Al-Harbi & Uddin, 2008)
	Gills	Common carp -African catfish polyculture		Species: *A. hydrophila, Corynebacterium* sp*., Micrococcus* sp*., Staphylococcus* sp*., S. putrefaciens., Vibrio alginolyticus, V. cholerae, Vibrio* sp*., V. vulnificus,* Unidentified Gram-negative rods	(Uddin & Al-Harbi, 2012)

Gut	Common carp -African catfish polyculture	Marcy l'Etoile, France), and BIOLOG (BIOLOG, Inc., Hayward, California) methods	Species: *A. hydrophila, Corynebacterium* sp*., Micrococcus* sp*., Bacillus* sp*., Edwardsiella* sp*., Pantoea* sp*., S. putrefaciens, Staphylococcus* sp*., Pseudomonas* sp*., Streptococcus* sp*., V. alginolyticus, V. cholerae, Vibrio* sp*., V. vulnificus,* Unidentified Gram-negative rods	(Uddin & Al-Harbi, 2012)
Gut	Indian major carps (rohu, catla and mrigal), Silver carp, Grass carp and Common carp	Morphological test, staining procedures and bio-chemical and physiological tests.	Species: *Corynebacterium* spp*., Aeromonas hydrophila, Flavobacter devorans, Pseudomonas aeruginosa, Vibrio* sp*., Achromobacter* sp*.*	(Yogesh et al., 2014)
Skin	Indian major carps (rohu, catla and mrigal), Silver carp, Grass carp and Common carp	Morphological test, staining procedures and bio-chemical and physiological tests.	Species: *Corynebacterium* spp., *Aeromonas hydrophila*, *Flavobacter devorans*, *Achromobacter* sp., *Pseudomonas aeruginosa*, *Vibrio* sp., *Proteus* sp.	(Yogesh et al., 2014)

	Gut	Common carp from Floating nets cage	16S rRNA gene amplicon sequencing	Major phyla: Proteobacteria and Firmicutes	(Mulyani et al., 2018)
Transgenic common carp (*Cyprinus carpio*)	Gut	Monoculture	16S rRNA gene amplicon sequencing	Major phyla: Proteobacteria, Fusobacteria, Bacteroidetes and Firmicutes	(Li et al., 2013)
Indian major carps - rohu (*Labeo rohita*), catla (*Labeo catla*) and mrigal (*Cirrhinus cirrhosus*)	Gut	Indian major carp polyculture	High-throughput sequencing of 16S rRNA gene	Major phyla: Proteobacteria, Firmicutes, Actinobacteria and Bacteroidetes	(Mukherje e et al., 2020)
	Gut	Indian major carp polyculture	16S rRNA gene amplicon sequencing	Major phyla: (Proteobacteria and Fusobacteria are the most abundant), 51 classes, and 374 genera (*Aeromonas* and *Cetobacterium* are the most abundance)	(Foysal, Momtaz, et al., 2019)

Grass carp (*Ctenophary ngodon idella*)	Gut	Grass carp, Gibel carp and bluntnose black bream polyculture	16S rRNA gene amplicon sequencing	Major phyla: Proteobacteria, Firmicutes and Actinobacteria	(Han et al., 2010)
	Gut	Grass carp monoculture	16S rRNA gene amplicon sequencing	Major phyla: Proteobacteria, Firmicutes, Cyanobacteria, and Actinobacteria.	(Wu et al., 2012b)
	Gut	Grass carp, Crucian carp and bighead carp polyculture	16S rRNA gene amplicon sequencing	Major phyla: Fusobacteria, Firmicutes, Proteobacteria, and Bacteroidetes	(Li et al., 2015)
Bighead carp *(Hypophthal michthys nobilis)*	Gut	Bighead carp - tilapia polyculture Bighead carp- common carp polyculture	16S rRNA gene amplicon sequencing	Major phyla: Proteobacteria, Firmicutes, Fusobacteria *and* Cyanobacteria	(Luo et al., 2022)
	Gut	Grass carp, Crucian carp and bighead carp polyculture	16S rRNA gene amplicon sequencing	Major phyla: Fusobacteria, Firmicutes, Proteobacteria, and Bacteroidetes	(Li et al., 2015)

	Gut	Silver carp and bighead carp pond	16S rRNA gene amplicon sequencing	Major phyla: Proteobacteria, Actinobacteria , Firmicutes and Bacteroidetes	(Meng et al., 2021)
Crucian carp (*Carassius carassius*)	Gut	Grass carp, Crucian carp and bighead carp polyculture	16S rRNA gene amplicon sequencing	Major genera: *Cetobacterium* and *Aeromonas*	(Li et al., 2015)
Gibel carp (*Carassius gibelio*)	Gill and Skin	Gibel carp and bluntnose black bream polyculture	16S rRNA gene amplicon sequencing	Major phyla: Proteobacteria*,* Firmicutes	(Wang et al., 2010)
Silver carp (*Hypophthalmichthys molitrix*)	Gut	Silver carp and bighead carp pond	16S rRNA gene amplicon sequencing	Major phyla: Proteobacteria and Chloroflexi	(Meng et al., 2021)

Table 3. Summarized diversity of microalgae in the rearing water and the carp gut in polyculture systems

Polyculture systems	Microalgae diversity	Notes	Ref.
Carp - pangasius polyculture ponds	Chlorophyceae, Cyanophyceae, Bacillariophyceae and Euglenophyceae	- The highest microalgal cell density corresponded with high nutrient concentrations (NO_3-N and PO_4-P). - Chlorophyceae was the most dominant group followed by Cyanophyceae, Bacillariophyceae and Euglenophyceae.	(Hossain et al., 2008)
Common carp, hybrid bighead carp and grass carp polyculture	Total 259 taxa of planktonic algae were identified during a two-year study (2018-2019) First year: 216 taxa Second year (reduce stocking density of grass carp twice): 150 taxa	- High stocking density of grass carp can disturb the functioning of the aquatic ecosystem. - Cyanoprokaryotes from genera *Aphanizomenon, Dolichospermum*, and *Microcystis*, which are potent cyanotoxin producers affecting the ecosystem and human health, were found in the system.	(Dochin, 2020)
Filter-feeding Asian carps (hybrids of silver carp and	In water: A total of 100 phytoplankton species with *Cyclotella ocellata* had the highest relative abundance.	- There are viable cells of several phytoplankton taxa (e.g., diatoms, blue-greens, desmids, volvocalean and	(Görgényi et

bighead carp) polyculture	In foregut fish: 138 phytoplankton species with the most frequent was *Cyclotella ocellata.* In hindgut fish: 149 viable phytoplankton species.	- chlorococcalean green algae), which managed to survive the physical and chemical digestion. - Cryptophytes, dinoflagellates, and euglenophytes were observed in both the lake water and foregut samples but were absent in the hindgut samples.	al., 2016)

Table 4. Examples of studies investigating the effects of probiotics and prebiotics on carp microbiota

Probiotic/prebiotic	Fish species	Effects	Ref.
Probiotics			
Paenibacillus polymyxa, Lactobacillus fermentum, ferulic acid, Lactobacillus, *Saccharomyces cerevisiae, Bacillus amyloliquefaciens*	Common carp (*Cyprinus carpio*)	Improved fish survival after *A. hydrophila* challenge	(Ahmadifar et al., 2019; Gupta et al., 2016; Harikrishnan et al., 2010; Huang et al., 2015)
Bacillus amyloliquefaciens BaX030	Grass carp (*Ctenopharyngodon idella*)	Increased abundance of beneficial bacteria (Fusobacterium, Proteobacteria, Gemmobacter) in the intestine Decreased abundance of potential pathogenic bacteria (*Planctomycetes, Aeromonas*)	(Zhou et al., 2022)

Bacillus subtilis Ch9	Grass carp (*Ctenopharyngodon idella*)	Increased abundance of total aerobic and facultative anaerobic bacteria Increased abundance of *Bifidobacterium* and *Lactobacillus*	(Wu et al., 2012)
Streptomyces amritsarensis N1-32	Grass carp (*Ctenopharyngodon idella*)	Improved fish survival after *Aeromonas veronii* challenge	(Li et al., 2020)
Enterococcus faecalis	Javanese carp (*Puntius gonionotus*)	Improved fish survival after *A. hydrophila* challenge	(Allameh et al., 2017)
Enterococcus faecalis, Lactobacillus fermentum and *Leuconostoc mesenteroides*	Javanese carp (*Puntius gonionotus*)	Increased abundance of lactic acid bacteria in gut Decreased abundance of Gram -negative bacteria in gut	(Allameh et al., 2016)
Bacillus amyloliquefaciens	Catla (*Catla catla*)	Inhibited *A. hydrophila, Edwardsiella tarda, Vibrio harveyi* and *Vibrio parahaemolyticus*	(Das et al., 2013)

Lactic acid bacteria	Rohu (*Labeo rohita*)	Increased survival of fish challenged with *A. hydrophila*	(Maji et al., 2017)
B. subtilis, Lactococcus lactis and *S. cerevisiae*	Rohu (*Labeo rohita*)	Increased abundance of total heterotrophic bacterial population	(Mohapatra et al., 2012)
Lactic acid bacteria	Crucian carp (*Carassius carassius*)	Increased abundance of Firmicutes and Proteobacteria in gut Decreased abundance of Actinobacteria in gut	(Liu et al., 2022)
Lactobacillus plantarum C20015	Koi carp (*Cyprinus carpio*)	Increase in survival of fish challenged with *A. veronii*	(Zhang et al., 2020)
Prebiotics			
β-1,3/1,6-glucan	Common carp (*Cyprinus carpio*)	Higher number of bacterial operational taxonomic units (OTUs) in gut carp	(Jung-Schroers et al., 2016b)

		Decreased abundance of *S. putrefaciens* and *Vibrio* sp. in gut	
Short chain fructo-oligosaccharide	Common carp (*Cyprinus carpio*)	No effect on total viable counts of heterotrophic aerobic bacteria in gut Increased abundance of lactic acid bacteria	(Hoseinifar et al., 2016b)
Fructo-oligosaccharide (FOS)	Common carp (*Cyprinus carpio*)	Increased abundance of total heterotrophic bacterial population and lactic acid bacteria	(Hoseinifar et al., 2014)
Chitosan	Gibel carp (*Carassius gibelio*)	Decreased abundance of pathogen bacteria *A. veronii* Improved *Cellulomonas hominis, Bacillus oceanisediminis* and two uncultured bacterium species	(Chen et al., 2014)

Figure

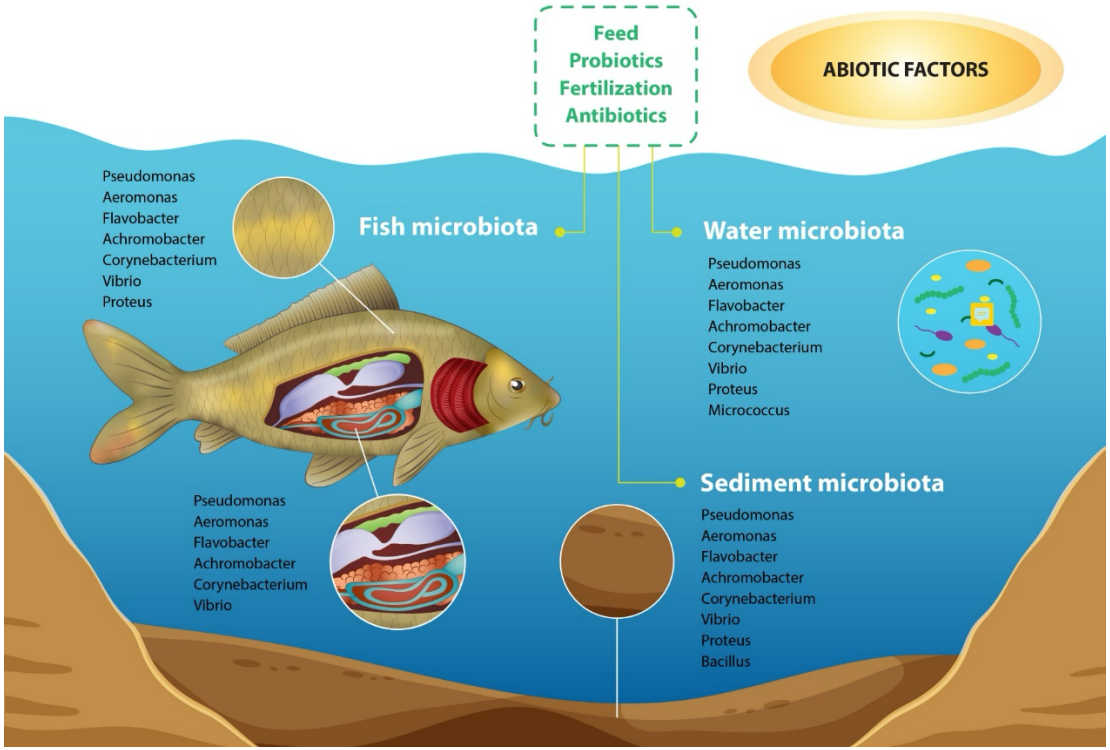

Figure 1. Illustration of bacterial composition of pond water and sediment as well as skin and intestine of common carp, cultured under polyculture (consisting of Catla (*Catla catla*), Rohu (*Labeo rohita*), Mrigal (*Cirrhinus mrigala*), Silver carp (*Hypophthalmichthys molitrix*), Grass carp (*Ctenopharyngodon idella*) and Common carp (*Cyprinus carpio*)) and factors affecting them.