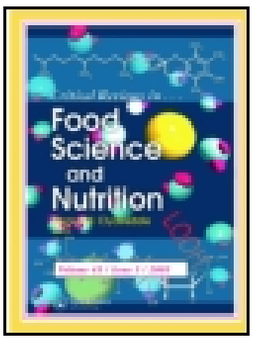

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REVIEW

Technological roles of microorganisms in fish fermentation: a review

Yanshun Xu[a,b], Jinhong Zang[a,b], Joe M. Regenstein[c], and Wenshui Xia[a,b]

[a]State Key Laboratory of Food Science and Technology, Jiangnan University, Wuxi, Jiangsu, China; [b]School of Food Science and Technology, Jiangnan University, Wuxi, Jiangsu, China; [c]Department of Food Science, Cornell University, Ithaca, New York, USA

ABSTRACT

Fermentation is an important way to process and preserve fish. It not only gives the product a unique flavor and texture, but it also contributes to increased nutritional value and better functional properties. The production of fermented fish relies on naturally occurring enzymes (in the muscle or the intestinal tract) as well as microbial metabolic activity. This review focuses on the role of microorganisms on texture change, flavor formation, and biogenic amines accumulation in fermented fish. In addition, the production conditions and the major biochemical changes in fermented fish products are also introduced to help understand the factors influencing the quality of fermented fish. Moreover, prospects for further research of fermented fish are discussed.

KEYWORDS

Fermented fish; microorganisms; texture; flavor; biogenic amines

Introduction

There has always been a close relationship between human beings, their food and the fermentative activities of microorganisms. Traditional fermented food is one of the intangibles of human history (Marco et al. 2017). Among them, fermented fish products have been part of different cultures for centuries. Fish fermentation first emerged as a means to preserve fresh fish, because they are extremely perishable, especially in hot and humid coastal areas (Tanasupawat and Visessanguan 2014).

Fermented fish products not only contribute significantly to the protein intake of a large number of people around the world, but are also an important source of minerals (mainly calcium and iron), and some B-group vitamins. During the fermentation process, the enzymatic activity of the raw material and the metabolic activity of microorganisms can change the nutritive and bioactive characteristics of fish matrices and produce beneficial effects on human health (Zang et al. 2019). For example, the beneficial aspects from the consumption of fermented fish products include antioxidant (Majumdar et al. 2016; Najafian and Babji 2018), antihypertensive (Fujita, Yamagami, and Ohshima 2001; Ichimura et al. 2003; Itou et al. 2004), antiproliferative (Martínez-Álvarez et al. 2016), anti-cancer (Koo et al. 2016; Lee et al. 2004) and anticoagulant (Singh et al. 2014) properties.

Due to the unique flavor, texture and preservation characteristics of fermented fish, the demand for fermented fish products continues to increase globally. However, the preservation role of fish fermentation is largely outdated due to the introduction of a cold chain and development of other preservation technology, especially in western countries. Today it is more a means of transformation and diversification of sensory demands (Waisundara, Jayawardena, and Watawana 2016). Fermented fish products are especially popular in Asia, Africa, and Europe. Many of these countries have their own unique types of fermented products based on differences in raw materials, environmental conditions, microorganisms and dietary traditions (Zang et al. 2019). Fermentation of fish has thrived in some regions of Europe as a local delicacy such as Hákarl in Iceland (Rajauria et al. 2016), Surströmming in Sweden (Miller et al. 2013) and Rakfisk in Norway (Amilien and Hegnes 2004). Fermented fish products are important in Africa. Examples of the most well-known fermented fish are Lanhouin, Momone and Feseekhin, which are sold as whole or sliced fish (El Sheikha and Montet 2014; Kindossi et al. 2016; Sanni, Asiedu, and Ayernor 2002). Asians were pioneers in the development of fermented fish products, which were exported from the Orient to Europe and North American. Various different types of fermented fish products including whole fish or fish pieces, sauces and pastes can be found in Asian markets (Daroonpunt et al. 2016; Ly, Mayrhofer, and Domig 2018; Zang, Xu, Xia, Jiang, et al. 2018).

Most fermented fish products are produced on a small scale according to family tradition and local geographic conditions with a specific microbiome at each stage of fermentation, resulting in a variety of product qualities. To standardize the final product, the use of the most dominant native microorganisms as selected starter cultures is receiving more attention. High quality fish products are obtained more reliably by controlling the growth of microorganisms and the conversion of enzymes. However, the role of microorganisms in the fish fermentation process has not been fully elucidated. This paper mainly focuses on reviewing the

CONTACT Yanshun Xu xuys@jiangnan.edu.cn; Jinhong Zang 15190273775@163.com State Key Laboratory of Food Science and Technology, Jiangnan University, 1800 Lihu Ave, Wuxi, Jiangsu 214122, China.

research on the roles of microorganisms in fish fermentations as well as the influence of fermentation conditions.

Fermentation conditions

Fermented fish products are often produced according to family tradition and geographic preferences and large differences exist in production methods. In general, most of the traditional fermented products involve salting, drying and occasionally smoking, and marinating. There are several factors, such as raw materials, fermentation temperature, time, humidity, salt concentrations and other conditions, that affect the fermentation efficiency. Among them, controlling fermentation temperature has been shown to be the simplest and most effective method to affect microbial growth and reduce the production of biogenic amines (BA) (Ormanci and Colakoglu 2017). Natural fermentation has been reported to be best controlled at low temperatures (3–7 °C), or ambient temperature (28–38 °C) (Anihouvi et al. 2007; Paludan-Müller et al. 2002; Skåra et al. 2015). In addition, the temperature is commonly controlled according to the optimum growth temperature of the starter cultures. For example, lactic acid bacteria (LAB), including *Lactobacillus plantarum* CCRC10069, *Lactococcus lactis subsp. lactis* CCRC 12315 and *Lactobacillus helveticus* CCRC 14092 have been used for the production of fermented mackerel mince at 37 °C (Yin, Pan, and Jiang 2002). Silver carp sausages fermented with *Pediococcus pentosaceus* at 23–30 °C showed the greatest consumer acceptance (Xu et al. 2010c). Furthermore, fermentation using mixed starter cultures has mostly been done at 25 °C (Zang, Xu, Xia, Jiang, et al. 2018). Because different microorganisms have different optimal growth temperature and generation temperature of metabolites, a two-stage temperature control strategy has sometimes been used to improve quality and safety of fermented fish (Xu et al. 2019). The salt concentration may range from 0 to 30% (w/w) in different types of fermented fish. For fermentation time, several weeks to several months have been reported depending on the salt concentration and fermentation temperature (Yi 1993). In addition, it is better to control the moisture of fermented fish at 50–70% (Zeng et al. 2013a), which can provide a longer shelf life. Furthermore, the addition of carbohydrate in the fermentation system can provide an extra energy source to accelerate the growth of microbes. Fermentation may be carried out under either aerobic or anaerobic conditions, depending on the microbial species involved.

Biochemical characteristics during fermentation of fish

Complex biochemical reactions take place during fish fermentation, which significantly change the initial characteristics of the fish tissue. Proteolysis or proteins degradation is one of the most important biochemical changes. A large number of peptides and amino acids are produced during fermentation due to the cleavage of proteins by microbial or indigenous proteases. Xu et al. (2010a) found that the content of salt-soluble and water-soluble proteins in fermented silver carp sausage decreased gradually, while the content of free amino acids and non-protein nitrogen increased gradually during fermentation. These results are consistent with that reported by Nie, Lin, and Zhang (2014) that as fermentation progressed, salt-soluble and water-soluble proteins in grass carp sausages inoculated with *Lactobacillus plantarum* ZY40 and *Pediococcus pentosaceus* GY23 were degraded, while α-amino nitrogen, trichloroacetic acid (TCA)-soluble peptides and free amino acids increased.

Myosin heavy chains (MHCs) were more susceptible to proteolysis than actin, which had also been previously observed (Riebroy et al. 2004; Zeng et al. 2013b).

Lipolysis and lipid oxidation are also two other important biochemical reactions during fermentation. The total concentration of free amino acids, conjugated dienes (CD) and thiobarbituric acid reactive substances (TBARS) increased during fish fermentation (Gao, Wang, Jiang, et al. 2016). There were slight changes in neutral lipids (NL) in low-salt fermented fish while a decrease was observed in a Ghanaian fermented fish product (Yankah, Ohshima, and Koizumi 1993). The small differences in lipolysis were presumed to be due to the different fermentation procedures and the different raw materials. Furthermore, the proportion of phospholipids (PL) decreased significantly with a concomitant increase in free fatty acids (FFA) during low-salt fermentation of fish. Similarly, a depletion in phosphatidyl inositol (PI), phosphatidyl choline (PC), sphingomyelin (SL) and phosphatidyl ethanolamine (PE) and increased phosphatidic acid (PA) and lysophosphatidyl choline (LPC) were observed in salted fermented Bouri fish muscle (El-Sebaiy and Metwalli 1989). Higher proportions of monounsaturated fatty acids and polyunsaturated fatty acids (PUFA) were liberated than saturated fatty acids after fish fermentation which improved the free docosahexaenoic acid (DHA) in fish and shrimp pastes (Montaño, Gavino, and Gavino 2001). The addition of starter cultures could also decrease the loss of the PUFA during fermentation. More PE and phosphatidylserine (PS) as well as polyene phospholipids were also detected in the Suan yu (a traditional Chinese fermented fish) inoculated with *Saccharomyces cerevisiae* 31 and mixed starter cultures (Zang, Xu, Xia, Jiang, et al. 2018).

In addition, free amino acids, especially Asp/Asn, Glu/Gln, Met, Phe, Leu, Val, and Ile increased during fermentation (Wang, et al., 2017). Lactic acid was the major organic acid, and small amounts of other organic acids such as acetic, citric, succinic, and formic acids were also detected (Zhao et al. 2017). The contents of amino acids and organic acids are significantly affected by different salt concentrations, because different enzymes are activated and the type and activity of microbes changed at different salt levels, resulting in different end products (Lopetcharat et al. 2001).

Microorganisms and microbial enzymes in fermented fish

Various authors have reported a large range of microorganisms involved in fish fermentation (Zhang et al. 2015).

Table 1. Microbial enzymes isolated from fermented fish.

Enzyme	Source microorganism	References
Protease	*Bacillus megaterium*; *Bacillus subtilis* CN2; *Bacillus subtilis* JM-3; *Bacillus subtilis* A26; *Staphylococcus*; *Micrococcus spp*	Thapa, Pal, and Tamang (2004); Uchida et al. (2004); Yossan, Reungsang, and Yasuda (2006); Kim and Kim 2005; Jemil et al. (2014); Anihouvi et al. (2007)
Amine oxidase	*Bacillus amyloliquefaciens* FS05; *Bacillus polymyxa*; *Staphylococcus*	Lee, Kim, et al. (2015); Zaman et al. (2011); Anihouvi et al. (2007); Mah and Hwang (2009b)
Lipase	*Bacillus spp*; *Staphylococcus spp*; *Staphylococcus warneri*; *Proteus*; *Klebsiella*	Kanlayakrit and Boonpan (2007); Anihouvi et al. (2007); Tanasupawat, Phoottosavako, and Keeratipibul (2016); Pochanart and Phat (2020)
Esterase	*Lactobacillus plantarum 120*; *Staphylococcus xylosus 135*; *Saccharomyces cerevisiae 31*	Gao et al. (2017)
Amylolytic enzyme	*Lactobacillus plantarum*	Olympia et al. (1995)
Fibrinolytic enzyme	*Virgibacillus sp.*	Montriwong et al. (2012); Sinsuwan, Rodtong, and Yongsawatdigul (2007); Sinsuwan, Rodtong, and Yongsawatdigul (2008)
β-glucosidases	*Bacillus sp. SJ-10*	Lee, Kim, et al. (2015)
Glutamic acid decarboxylase	*Lactobacillus brevis RK03*	Wu et al. (2018)
Amino acid lyase	yeast; *micrococcus*; *bacillus brevis*	Yvon and Rijnen (2001)
Aminotransferases	*Saccharomyces cerevisiae 152*; *Lactobacillus plantarum 120*; *Lactobacillus pentococcus 220*	Liu et al. (2008); Smit, Smit, and Engels (2005)
Amino acid decarboxylase	*Bacillus coagulans*; *Bacillus megaterium*; *S. epidermidis*; *S. xylosus*; *K. oxytoca*; *E. cloacae*; *Pseudomonas cepaciae*; *Tetragenococcus muriaticus*; *Morganella morganii*; *Proteus vulgaris*; *Enterobacter aerogenes*	Rodtong, Nawong, and Yongsawatdigul (2005); Tsai et al. (2005); Kimura, Konagaya, and Fujii (2001)
Amine dehydrogenases	*Alcaligenes xylosoxidans*	Kondo et al. (2004); Tapingkae et al. (2010)

These microorganisms may vary depending on the type of fish, the salt concentration, and the fermentation stage. Therefore, a detailed understanding of the microflora of fermented fish products and their impact on fermentation are crucial to the selection and determination of functional starter cultures and the improvement of product quality and safety.

Lactic acid bacteria (LAB) and yeasts are found as the dominant microorganisms in many fermented fish products (Paludan-Müller et al. 2002; Thapa, Pal, and Tamang 2004). Major genera of the LAB such as acid- and bile-resistant *Lactobacillus* (Kuda et al. 2013), *Leuconostoc* (Gelman, Drabkin, and Glatman 2000), *Streptococcus* (Hwanhlem et al. 2011), *Lactococcus*, *Weissella* (Bao et al. 2018; Srionnual et al. 2007), *Pediococcus* (Siddegowda, Bhaskar, and Gopal 2017), halophilic lactococci, such as *Tetragenococcus* (Kuda et al. 2014; Udomsil et al. 2016) and *Vagococcus* (Dai et al. 2013) have been isolated from various fermented fish. Furthermore, several LAB genera, such as *Lactobacillus*, *Leuconostoc*, *Lactococcus*, have been shown to have probiotic activity (Kuda et al. 2016; Lee et al. 2007). Some of the isolated strains have shown antioxidant, antagonistic activity and anti-inflammatory properties (Aarti et al. 2016; Hwanhlem et al. 2011). For example, *Lactobacillus brevis* strain LAP2 showed significant DPPH scavenging and hydrogen peroxide resistant properties (Aarti et al. 2017). Similarly, lipid oxidation of grass carp sausage was prevented using *L. plantarum* ZY-40 (Nie, Lin, and Meng 2016).

In addition to the predominant LAB, yeast diversity was frequently investigated in which *Saccharomyces cerevisiae* (*S. cerevisiae)* seemed to be the predominant yeast (Gao, Wang, Jiang, et al. 2016). Apart from *S. cerevisiae*, there was a wide variation in the other yeasts species occurring in the different fermented fish products such as *Zygosaccharomyces rouxii* (Paludan-Müller et al. 2002), *Kluyveromyces marxianus*, *Hansenula anomala*, *Candida tropicalis*, *Candida zeylanoides*, *Pichia fermentans*, *Hanseniaspora osmophilic*, *Rhodotorula glutinis* (Clementine et al. 2012; Sulieman, Hassan, and Elkhalifa 2014) and *Debaromyces hansenii* (Kuda et al. 2009). In addition, a variety of enzymes that affect the final product can be produced by microbes during fermentation (Table 1). The most important enzymes associated with fish fermentation are proteases, which hydrolyze proteins into smaller peptides or free amino acids. Microorganisms with specific proteases have the ability to develop different fermentation outcomes, some of which improve the product, while others may not help and might even be detrimental.

It was reported that almost all isolates of LAB showed low protease activity, whereas isolates of *Bacillus* strains showed higher proteolytic activities (Thapa, Pal, and Tamang 2004). For example, *Bacillus* were isolated from fermented fish (Budu) (Southern Thailand) with high protease activities (Choorit and Prasertsan 1992). Alkaline protease can be produced by *Bacillus megaterium* isolated from a Thai fish sauce (Yossan, Reungsang, and Yasuda 2006) and *Bacillus subtilis CN2* isolated from a Vietnamese fish sauce, respectively (Uchida et al. 2004). The *Bacillus subtilis* JM-3 protease from anchovy sauce was classified as an acid protease and has been used in the food processing industry (Kim and Kim 2005). Jemil et al. (2014) reported that fish protein can be biotransformed using *Bacillus subtilis* A26 proteolytic enzymes, generating peptides with antioxidant and antibacterial activities. In addition, *Bacillus* species are able to produce a large number of other enzymes such as amine oxidases. For example, *Bacillus amyloliquefaciens* FS05 and *Bacillus polymyxa* with oxidative deamination activity inhibited biogenic amine accumulation during fish fermentation (Lee, Kim, et al. 2015; Zaman et al. 2011). Apart from

Bacillus, *Staphylococcus* are also able to produce proteases and amine oxidases (Anihouvi et al. 2007; Mah and Hwang 2009b).

The lipases secreted by microbes contribute to the development of flavor in the products due to the degradation of lipids to free fatty acids. Anihouvi et al. (2007) reported that *Bacillus spp*. as well as *Staphylococcus spp*. had moderate proteolytic and lipolytic activities. *Micrococcus spp*. showed weak proteolytic activity and no lipolytic activity. Similar results were found by Kanlayakrit and Boonpan (2007) who showed that *Staphylococcus warneri* could produce greater lipase activity. *Staphylococcus simulans* PMRS35 isolated from Budu with high lipase activity could be used as starter culture in food industry (Pochanart and Phat 2020). *Proteus* and *Klebsiella* isolated and screened from traditional fermented fish also showed good lipase activity (Tanasupawat, Phoottosavako, and Keeratipibul 2016). Moreover, *Lactobacillus plantarum* 120, *Staphylococcus xylosus* 135, and *Saccharomyces cerevisiae* 31, are commonly used as starter cultures due to their ability to produce esterase activities, which generally led to the formation of desirable flavor (Gao et al. 2017). *Lactobacillus plantarum* with amylolytic enzymes were isolated from burong isda, an indigenous Philippine fermented food made from fish and rice (Olympia et al. 1995). *Virgibacillus sp*. with high fibrinolytic activity has been found in fermented fish sauces, reducing fibrin clots and lowering the risk of cardiovascular disease (CVD) (Montriwong et al. 2012; Sinsuwan, Rodtong, and Yongsawatdigul 2007; Sinsuwan, Rodtong, and Yongsawatdigul 2008).

The β-glucosidases gene was cloned from *Bacillus sp*. SJ-10 isolated from a squid jeotgal. β-Glucosidases are active in many biological processes such as the release of aromatic compounds from flavorless precursors (Bhatia, Mishra, and Bisaria 2002; Lee, Kim, et al. 2015). *Lactobacillus brevis* RK03 was also found to produce glutamic acid decarboxylase (GAD), a pyridoxal-5′-phosphate-dependent enzyme, and to have the highest γ-aminobutyric acid biosynthetic activity against hypertension (Won et al. 2015; Wu et al. 2018).

Texture characteristics of fermented fish products

Texture characteristics are crucial quality attributes of fermented fish products, which are influenced by both enzymes and microorganisms. Silver carp sausages inoculated with the combinations of *Staphylococcus xylosus*-12 with *Lactobacillus plantarum*-15, *Pediococcus pentosaceus*-ATCC33316, and *Lactobacillus casei subsp. casei*-1.001, showed more favorable textural properties (hardness, gumminess, springiness, and chewiness) during fermentation (Hu, Xia, and Ge 2007). Som-fug, a Thai fermented fish mince, inoculated with LAB generally showed higher hardness and adhesiveness than the control (without inoculum) (Riebroy, Benjakula, & Visessanguan, 2008).

Generally, gelation is an important functional property of fish protein affecting the texture of fish products. Fish mince could undergo gelation during fermentation. Hardness resulted from denaturation and gelation of muscle proteins (Riebroy, Benjakula, & Visessanguan, 2008). Springiness and cohesiveness reflected the development of internal bonding in the gel network of muscle protein (Visessanguan et al. 2004). During fish fermentation, the gelation was mainly induced by mild acidic conditions produced by microbial fermentation. For example, fermented fish mince could undergo gelation in the presence of organic acids such as acetic acid or lactic acids (Riebroy et al. 2007; Xu et al. 2010a), because pH lowering produces enough protein conformational changes, mainly unfolding, along with charge changes to allow network formation (Riebroy et al. 2009). Xu et al. (2010b) reported that as fermentation progressed, hydrophobic interaction, disulfide bonds and non-disulfide covalent bonds were mainly responsible for the formation of the gel network of fermented silver carp mince, and hydrophobic interactions were particularly important during the initial stage of gel formation. Extensive formation of disulfide bonds occurred during the later stage of fermentation, intensifying the gel network (Xu, Xia, and Jiang 2012). Moreover, myosin heavy chains were the main protein constituents for the gelation of fermented fish mince, and actin and low molecular weight protein probably produced by proteolysis were also involved in the formation of the gel network (Weng and Zheng 2015). Further research found that the head-head interactions of silver carp actomyosin occurred first during acidification, followed by denaturation of tails and cross-linking through the tails of myosin, and at the same time the head-linked oligomers aggregated further, resulting in the formation of a sequence-directed gel network. In this process, the disintegration of α-helix structure, the decrease of hydrogen bonds, the exposure of aromatic amino acid residues, and the increase of hydrophobic interactions gradually formed the gel (Xu, Xia, and Jiang 2012). In addition, ionic strength had a significant influence on acid-induced structural changes, aggregation and gel properties of silver carp myofibrils. Increasing ionic strength could increase partial unfolding of protein, leading to more active groups on the protein surface (Sun and Holley 2011; Xu, Jiang, and Xia 2013). Such conformational changes promoted interactions of protein molecules during acidification. Moreover, acid-induced gelation of fermented fish was also affected by fish species (Riebroy et al. 2009).

The gel properties of fermented fish products are not only attributed to the acidic environment produced by microbial fermentation but also to the action of endogenous and microbial enzymes in fermented fish. Liu et al. (2011) found that high activity of endogenous transglutaminase (TGase) catalyzed the formation of ε-(γ-Gln)-Lys bonds. These non-disulfide covalent bonds are heat resistant and have an important role in the process of heat-induced gelation. However, endogenous TGase had no significant effect on protein crosslinking during fermentation because the endogenous TGase activity declined rapidly with acidic conditions without the ability to produce ε-(γ-Gln)-Lys bonds. Whereas, endogenous cysteine proteases such as cathepsin B, L, H and aspartic proteases such as cathepsin D had the greatest influence on the modori reaction (gelation at lower

temperatures), mainly in the last stage. Metalloproteinases and serine proteases such as calpains and collagenolytic proteases had a little influence but only at the initial stage of fermentation (Yang, Xia, Zhang, et al. 2016). Generally, endogenous proteases had negative effects on gel strength throughout gelation (Yang et al. 2015), owning to their ability to cleave hydrophobic amino residues, resulting in decreased hydrophobic interactions. The breakdown of the α-helices and β-sheets, and the formation of random coils due to endogenous proteases led to a decrease of gel strength (Yang, Xia, Zhang, et al. 2016). During fish fermentation, gel properties were mainly affected by endogenous proteolysis, while the main role of microorganisms seemed to be the secondary hydrolysis of small proteins and peptides, contributing to the production of free amino acids which may be related to flavor and taste (Nie, Lin, and Zhang 2014; Yang, Xia, Zhang, et al. 2016).

Flavor characteristics of fermented fish products

The unique flavor of fermented fish is one of their important quality attributes. The research on flavor formation of fermented fish products mainly focuses on the extraction, separation and analysis of volatile flavor substances and the pathways of flavor development. A number of methods are currently used to extract flavor substances from fish products including solid phase extraction (SPE), solid-phase microextraction (SPME) (Giri, Osako, and Ohshima 2010), headspace solid-phase microextraction (HS-SPME) (Fratini et al. 2012; Gao, Wang, Jiang, et al. 2016), and simultaneous steam distillation–extraction (SDE) (Cha and Cadwallader 1995). Common separation methods include chemical separation and chromatographic separation. The detection systems used to identify and quantify the volatile compounds after separation including mass spectrum, infrared spectrum, nuclear magnetic resonance and ultraviolet spectrum (Bertuzzi et al. 2018). Gas chromatography-mass spectrometry (GC-MS) has become the preferred method for volatile compounds analysis of fish products, because it can detect trace levels of volatile compounds that can then be identified (Fukami et al. 2006; Iglesias and Medina 2008; Mohamed et al. 2012).

Gas chromatography-olfactometry (GC-O) (Fukami et al. 2002; Jónsdóttir et al. 2008; Varlet et al. 2006), aroma extract dilution analysis (AEDA) (Cayhan and Selli 2011) and the electronic nose (Li et al. 2013) have been successfully used to analyze fish flavor.

The main flavor compounds formed with fish fermentation process were detected using GC-MS, mainly acids, aldehydes, hydrocarbons, alcohols, ketones, esters, nitrogen-containing compounds and furans (Zeng, Zhang, and Zhu 2016). It was reported that microbial metabolism was crucial to the flavor formation of fermented fish products (Xu, Li, et al. 2018). Autochthonous microflora such as *Lactobacillus plantarum* 120, *Staphylococcus xylosus* 135 and *Saccharomyces cerevisiae* 31, isolated from Suan yu showed that the starter cultures improved the volatile composition (Gao, Wang, Jiang, et al. 2016). Higher levels of volatile compounds were detected in Suan yu inoculated with mixed starter cultures (Zeng et al. 2017). *Staphylococcus sp.* CMC5-3-1 and *Aspergillus oryzae* OAY1 were also used to improve the aroma of fish sauce (Natteewan Udomsil et al. 2015).

The characteristic flavor of fermented products is highly related to proteolysis and lipolysis. These hydrolysates are not only important taste substances, but also precursors of some important flavor substances of fermented products (Jokanovic et al. 2017). Most researchers believe that the protein degradation of fermented meat products is the result of the combined action of endogenous proteases and microbial enzymes. Endogenous proteases are mainly responsible for the hydrolysis of proteins into oligopeptides, while microbial enzymes contribute to the continuous degradation of oligopeptides into small peptides and free amino acids (Candogan and Acton 2004). Similar conclusions were also found for fermented seafood (Kasankala, Xiong, and Chen 2012; Yongsawatdigul, Rodtong, and Raksakulthai 2007). Muscle endogenous proteases, including cysteine and lysosomal enzymes, catalyze the degradation of myofibrillar proteins at the initial phase of fish fermentation (Chéret et al. 2007). However, endogenous enzymes activity was inhibited with high salt. Therefore, proteases released from halophilic bacteria have an important role at the initial stage of high salt fermentation of fish (Toyokawa et al. 2010; Udomsil et al. 2010).

In addition, microorganisms can further metabolize amino acids to produce flavor substances via two different pathways (Ardö 2006). The first pathway uses the side chains of some amino acids through an elimination reaction catalyzed by amino acid lyase, to release phenol, indole and methyl mercaptan. This pathway is found in yeast, *Micrococcus* and *Bacillus brevis* and mainly involves the metabolism of tyrosine, tryptophan and methionine (Yvon and Rijnen 2001). The second pathway is the main pathway of amino acid metabolism. It is initiated by aminotransferases that convert amino acids into their corresponding α-keto acids, and then the α-keto acids are further converted into aldehydes, alcohols, and esters. These reactions occur mainly with the aromatic amino acids (tyrosine, tryptophan, and phenylalanine), branched-chain amino acids (valine, leucine, and isoleucine), and methionine (Liu et al. 2008; Smit, Smit, and Engels 2005). Studies of fermented fish flavors found that branched chain amino acids (valine, leucine, and isoleucine) and the aromatic amino acid phenylalanine were degraded by *Saccharomyces cerevisiae* 152 to produce 3-methyl-1-butanol, 2-methyl-butanol, 2-methyl-propanol and phenyl-ethanol, respectively (Wang, et al., 2017). The degradation of leucine and phenylalanine resulted in the production of 3-methyl-1-butanol and phenylethanol, respectively, with *Lactobacillus plantarum* 120 and *Lactobacillus pentococcus* 220 (Wang, et al., 2017). However, the research on microbial metabolism of amino acids to produce flavor substances mainly focuses on dry-cured meat products, cheese, and fermented wine (Olesen and Stahnke 2003; Olesen and Stahnke 2004). The specific synthesis pathways of the important flavor substances produced using

amino acids metabolized by different microbial strains in fermented fish needs to be further clarified.

Lipid metabolism also has an important role in the formation of food flavor (Gilles 2009). Lipolysis of the triglycerides and phospholipids by microbial and indigenous enzymes results in the development of free fatty acids (FFA) including medium-chain (carbon chain lengths $\leq$10) FFA and long-chain (carbon chain lengths >10) FFA (Collins, McSweeney, & Wilkinson, 2003; Thierry et al. 2017). Lipolysis of phospholipids contributed largely to the release of FFA during fish fermentation (Xu, Li, et al. 2018). Furthermore, both microbial and endogenous lipases contributed to the FFA liberation in fermented fish while endogenous lipases also have a major role (Xu, Li, et al. 2018). FFA not only directly affect the formation of flavor compounds, but also are precursors of methyl ketones, secondary alcohols, esters and lactones (Smit, Smit, and Engels 2005). Flavor forming pathways originating from FFA includes the following: Saturated fatty acids were degraded by incomplete β-oxidation with thioesterase and decarboxylase to produce methyl ketones as a flavoring compound (Engelvin et al. 2000). Unsaturated fatty acids are converted into hydroperoxides by oxidation, which are further decomposed into small molecular flavor substances such as aldehydes (McSweeney and Sousa 2000). FFA are also combined with metabolite alcohols to produce ester flavor substances with esterase (Collins, McSweeney, & Wilkinson, 2003; Liu, Holland, and Crow 2004).

Esters are important flavor compounds in fermentation of Suan yu which are involved indirectly in the metabolism of FFA, whereby the esterification and alcoholysis reactions lead to the biosynthesis of esters (Liu, Holland, and Crow 2004). It was found that LAB can promote the production of acetate compounds, while *Staphylococcus* and yeast can promote the production of ethyl compounds (Andrade et al. 2010; Cano-García et al. 2014; Sidira et al. 2015). Furthermore, the biosynthesis of esters in fermented fish is mainly influenced by the pH. For example, the biosynthesis pathway of *L. plantarum* 120 was esterification and alcoholysis. Lp-120 preferentially produced esters via alcoholysis at high pH, while *S. xylosus* 135 and *S. cerevisiae* 31 preferentially formed esters at low pH (Gao, et al., 2018). In addition, chain length of alcohols positively affected biosynthesis of acetate esters. With carbon number from 2 to 6, microbial ester-synthesis activity increased with the increase of aliphatic alcohol carbon number, whilst microbial ester-synthesis activity decreased with the increase of fatty acid carbon number ($C > 8$) (Gao et al. 2018). Lipolysis in fish fermentations is well understood, however, the elucidation of enzymes and metabolic pathways converting FFA to flavor compounds during fermentation needs further work.

As stated above, metabolic activity by microflora can generate a series of volatiles through the metabolism of amino acid and fatty acid, eventually contributing to flavor and quality development. Therefore, the incorporation of metabolic versatility and microbial diversity may offer the potential for new and improved products.

Safety characteristics of fermented fish products

Although fermented fish products contain large amounts of amino acids, which can produce good flavor substances, they may be potential precursors of biogenic amines (BA). BA are low molecular weight compounds that are formed by microbial decarboxylation of the corresponding amino acids or by transamination of aldehydes and ketones, including aromatic (tyramine and 2-phenylethylamine), aliphatic (putrescine, cadaverine, spermine and spermidine) and heterocyclic (histamine and tryptamine) compounds (Zarei et al. 2011; Zhai et al. 2012).

Excessive intake of biogenic amines, especially histamine, can result in toxicological effects to consumers such as hypertension, headache, diarrhea, rash, and localized inflammation. Putrescine and cadaverine have been suggested to be able to potentiate histamine toxicity (Lehane and Olley 2000). High levels of biogenic amines have been found in fermented fish products owing to the availability of their precursors (amino acids) and the presence of microorganisms with amino acid decarboxylases and favorable conditions for their growth and decarboxylation activity (Tsai et al. 2006). For example, Naila et al. (2011) found high levels of histamine (5490 mg/kg) in the fish paste Rihaakuru, which is an important condiment in the Maldives, whereas tryptamine was not detected and phenylethylamine only occurred at low levels (<25 mg/kg). Similarly, Huang et al. (2010) studied histamine in dried fish products within the range of 63.1–479 mg/kg. Large amounts of histamine (155–579 mg/kg) were also detected in fermented fish products made from anchovies (Mah et al. 2002). In fact, the production of biogenic amines can also be influenced by raw materials (Brillantes, Paknoi, and Totakien 2002). Yongsawatdigul, Choi, and Udomporn (2004) reported the subtle changes of histamine during Indian anchovy fish sauce fermentation, indicating that high levels of histamine may be associated with the histamine content of the raw material.

Furthermore, a variety of bacterial species were identified as histamine-producing including *Bacillus coagulans* and *Bacillus megaterium* from fermented fish products in Taiwan (Tsai et al. 2006); *S. epidermidis*, *S. xylosus*, *K. oxytoca*, *E. cloacae*, *Pseudomonas cepaciae*, and *Bacillus spp*. from salted Spanish anchovies (Rodriguez-Jerez et al. 1994); *Pantoea spp*. and *E. cloacae* from salted mackerel in Taiwan (Tsai et al. 2005); halophilic bacteria, such as *Tetragenococcus muriaticus* from fish sauce (Kimura, Konagaya, and Fujii 2001); *Morganella morganii*, *Proteus vulgaris*, and *Enterobacter aerogenes* from Indian anchovy (*Stolephorus indicus*) (Rodtong, Nawong, and Yongsawatdigul 2005); halotolerant *Staphylococcus spp*., *Vibrio spp*., and *Pseudomonas* III/IV-NH from fermented salted sardine and fish products (Yatsunami and Echigo 1993). In addition, low pH (4.0–5.5), which can be achieved in salted anchovies, for example, is favorable for enhancing amino acid decarboxylase activity (Kimura, Konagaya, and Fujii 2001). It has been shown that transcription of many decarboxylase genes is induced at low pH and that BA accumulation can represent a cellular defense mechanism against acid stress, improving cell performance with acid conditions (Barbieri et al. 2019). Furthermore, accumulation of histamine in salted and

fermented fish products may also be affected by the distribution of halophilic histamine-related bacterial flora (Kuda, Mihara, and Yano 2007).

The control of BA formation mainly focused on controlling the growth of biogenic amine producing bacteria. It was also found that many microorganisms are capable of producing amine-degrading enzymes either amine oxidases or amine dehydrogenases (Bakke et al. 2005; Kondo et al. 2004; Lee, Kim, et al. 2015; Siddiqui et al. 2000; Tapingkae et al. 2010). Decarboxylation in microorganisms can be reversed by the action of amine oxidases, resulting in their detoxification and the production of aldehydes, hydrogen peroxide, and ammonia (Tittarelli et al. 2019). The application of starter strains having histamine-degrading activity is an effective way to decrease the amount of histamine produced during fermentation. Zaman et al. (2014) investigated the ability of halotolerant *Staphylococcus carnosus* FS19 to inhibit histamine formation in fish sauce. They observed that *Staphylococcus carnosus* FS19 could reduce histamine production by ~15% as compared to the control. In addition, a huge reduction of histamine, putrescine, cadaverine, and tyramine during salted fish fermentation was achieved when *Bacillus polymyxa* was used as the starter culture (Lee et al. 2016). Inoculation of *Staphylococcus xylosus* No. 0538 in salted and fermented anchovy effectively suppressed the production of biogenic amine (Mah and Hwang 2009b).

Other parameters such as salt concentration, spices and food additives may also influence the variation of microbiota composition, resulting in differences in BA content. The use of salt concentration >17% in fermented tuna (*Thunnus albacares*) viscera (*dayok*) can minimize the formation of histamine (Besas and Dizon 2012). Furthermore, an extract of garlic and glycine also had a positive effect in reducing BA (Mah and Hwang 2009a; Mah, Kim, and Hwang 2009). In addition, modified atmosphere packaging and vacuum packaging are currently popular preservation methods, which may inhibit the growth of microorganisms with amino acid decarboxylase activity (Chong et al. 2011).

A large amount of BA and nitrite also make it possible to have the risk of nitrosamines contamination in fermented fish products. Nitrosamines are potent carcinogens, and high-dose or long-term intake can both cause various kinds of cancers (De Mey et al. 2014). It has been found that three autochthonous strains isolated from Chinese traditional fermented fish could degrade N-nitrosodimethylamine (NDMA) directly and the levels of the precursors of NDMA were also inhibited (Liao et al. 2019). However, the mechanism of nitrosamine formation needs additional work. Therefore, further understanding the relationships between BA and the formation of nitrosamines as well as the role of microflora could help assure the safety of fermented fish products.

Future prospects of microflora functions in fermented fish

The influence of microbial diversity and related metabolites on the final flavor, texture and safety of fermentation fish products is attracting increasing attention. However, the mysterious relationship between microbial diversity and the relevant metabolome as well as their influence on the quality development of fermented fish remains unclear despite the multiple microbiology methods that have been used to determine the microbial composition in some fermented fish. The identification of the entire microbial community of fermented fish can be obtained using next-generation sequencing (NGS) or high-throughput sequencing (HTS) techniques (Van Dijk et al. 2014). These techniques are based primarily on the analysis of microbial nucleic acid sequences and comparison with sequence data in databases to provide information regarding the identity and potential functions of many more microorganisms (Rastogi and Sani 2011). Having established most of the taxonomy, the current research shifted to function. Information about the different strains within a species as well as the proteins expressed are being used to better understand the roles of the microbiota in fermented fish. For example, a shotgun metaproteomic method was used to identify and annotate 2175 proteins from the traditional Chinese fermented fish *Siniperca chuatsi* and they found that *Streptococcus sp.*, *Bacillus sp.*, *Escherichia sp.*, and *Pseudoalteromonas sp.*, were involved in amino acid metabolism (Ji et al. 2017).

The gene expression and the active populations during fermentation were also observed. The findings provide useful insights into identifying the major bacterial metabolic activities and the metabolically active bacteria at the flavor-forming stage of fermentation (Duan et al. 2016). Many studies of microbial function have focused on commercially important fermented products, such as cheese, wine, bread and beer (Bokulich, Bamforth, and Mills 2012; Liu et al. 2017; Pétel, Onno, and Prost 2017; Zheng et al. 2018), while studies of fermented fish microorganisms are still very limited. The information obtain above can be combined with other 'Omics'-based approaches, such as proteomics and metabolomics. The combinational analysis of the microbiota and metabolites should enable a better understanding of the relationship between the food matrix and its microflora.

Conclusions

Fermentation is an important processing technology in many parts of the world for the production of fish products. Besides preserving fish, organoleptic, textural and flavor properties are enhanced through the fermentation process. However, the production of traditional fermented fish still mainly relies on long-term fermentation of autochthonous microflora, and the extent of industrial processing is still limited. Microbial metabolic activity has an important role in the formation of fermented fish quality, but the knowledge of the pathways used by the microbes in quality development of fermented fish is still limited. Detailed information of the fermentation conditions, biochemistry and microbiology of traditional fermented fish products is essential for improving organoleptic properties, safety, nutritional and health benefits. The structure and function of complex microbial communities during fish fermentation as well as their relationship with the quality development of

fermented fish still needs further study. In addition, the development of new aquatic products with different textural and flavor attributes using microbial fermentation technology offers the potential to expand the market for these products.

Disclosure statement

The authors attested that there were no conflicts of interest with respect to this paper.

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