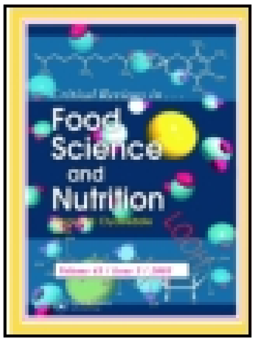

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REVIEW

Quality, functionality, and microbiology of fermented fish: a review

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ABSTRACT
Fermentation is a traditional food preservation method and is widely used for improving food safety, shelf life, and organoleptic and nutritional attributes. Fermented fish are produced and consumed in different parts of the world and are an integral part of many food cultures. Furthermore, fermented fish are a source of interesting microbes and are an important industry in many countries. This review tries to update the types and manufacturing processes for fermented fish around the world. The emphasis is on this work related to fermented fish and their health benefits, as well as the contribution of microorganisms to their fermentation. A variety of different approaches have been used to determine and understand microbial composition and functionality. Moreover, some challenges and future research directions regarding fermented fish are also discussed in this review. Further research into fermented fish products is of crucial importance not only for the food industry but also for human health. However, extensive in vivo and toxicological studies are essential before the application of bioactive-rich fermented fish products for human health benefits.

KEYWORDS
Fermentation; fish; microbiology; quality attributes

Introduction

Fish and fish products are good sources of polyunsaturated fatty acids, essential minerals and vitamins, and represent an important component of the human diet, providing almost 20% of the average daily animal protein intake for about 3.1 billion people (Tacon and Metian 2017; Zang et al. 2018). Numerous studies have found a beneficial association between fish product consumption and human health. For example, reduction of metabolic syndrome and the prevention of cardiovascular diseases (Baik et al. 2010; Siscovick et al. 2017). Moreover, higher life expectancy and the lower incidence of obesity in Japan than in the US has been repeatedly reported in previous studies, which is attributed to the higher per capita fish intake (Tacon and Metian 2013). Research has also shown that fish product consumption not only has protective associations with dementia but also has a significant inverse correlation with the annual prevalence of major depression (Fotuhi, Mohassel, and Yaffe 2009; Morris et al. 2016; Tanskanen et al. 2001).

Despite increased global demand for fish and fish-based products, several challenges such as the vulnerability to corruption, susceptibility to oxidation, and seasonal availability have resulted in the development of preservation methods (Yu, Regenstein, and Xia 2018; Zang et al. 2016). Of all the preservation methods such as freezing, salting and smoking, fermentation, in particular, has been the most widely used method (Panda et al. 2011). It is a low-cost, convenient and energy-efficient preservation method of fish muscle.

Fermented fish are products of historical, regional and cultural significance. Fermentation of fish is an ancient technology and there is evidence that suggests that fermented fish were widespread during the Yayoi period in Japan (300 BCE to 300 CE) (Beddows 1998). Fermented fish products have been a staple part of the diets in a number of countries. However, fermented fish prepared in the different countries are unique in their organoleptic properties because of the difference of the geographical location, environmental factors, food preference, and the availability of fish sources (Tamang and Samuel 2010; Waisundara, Jayawardena, and Watawana 2016). Moreover, fermented fish products are strongly connected with the food cultures of different countries, especially in many Southeast Asian countries, where they are part of the culture of many different ethnic groups.

All these fermented fish products have traditionally been prepared on the basis of empirical knowledge without any knowledge of the microbes involved in the process until the development of modern microbiology. Generally, fermented fish are defined in modern terms as fresh fish that have undergone a series of desirable biochemical changes through the action of microorganisms or enzymes. These changes include acidification (carbohydrate catabolism), gelation of myofibrillar and sarcoplasmic proteins of muscle, and degradation of proteins and lipids. In many cases, acidification also produces some antimicrobial substances, resulting in the reduction of the risk of contamination and the extension of shelf life. Gelation of proteins of muscle changes the elasticity, cohesion and hardness of end-products. Degradation

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of proteins and lipids releases a bounty of flavorful taste compounds and nutrients that are more easily digestible and absorbable (Mouritsen et al. 2017).

Current research on fermented fish and other food products has begun to focus on the role of microbes in the fermentation process. It has been determined that the primary and secondary microbial metabolism produced during fermentation are the key steps responsible for much of the final product quality of wine and meat such as taste, texture and nutritional value (Fadda, Lopez, and Vignolo 2010; Styger, Prior, and Bauer 2011). Furthermore, there is a growing interest in developing techniques to examine microbial succession during fermentation. However, no review has systematically and comprehensively focused on fermented fish. This review will focus on current work on fermented fish around the world with an emphasis on the effect of microbes on fermented fish quality. Future prospects and trends will also be discussed.

Types of traditional fermented fish products

There are different types of fermented fish products. As shown in Figure 1, according to the final product appearance, fermented fish can be divided into three groups: Fermented whole or in pieces such that the fish retains as much as possible of its original structure (Zeng et al. 2013a). Fermented fish pastes where the fish are converted into paste-like products (Giri et al. 2010) and fermented fish sauce where the fish is completely converted into a liquid form (Lopetcharat et al. 2001).

Fermented fish products can also be divided into two classification based on processing methods: Spontaneous fermentations and fermentations using starter culture. Spontaneous fermentation occurs using the microorganisms that were already on the raw materials or in the air, and is guided by the experience of the processor (Devi, Deka, and Jeyaram 2015). It is difficult to control the environmental parameters and sometimes metabolites produced by undesirable strains can lead to an abnormal fermentation and poor quality products (Capozzi et al. 2017). Spontaneous fermentation was optimized through back-slopping where a small quantity of a previously performed successful fermentation was retained and added to the new batch resulting in the introduction of a substantial inoculum (Leroy and De Vuyst 2004). Hwanhlem et al. (2011) reported that the application of back-slopping technique in the fermentation of Plasom shortened the fermentation process and reduced the risk of fermentation failure.

Fermentations using starter cultures that are added directly to the raw materials allows the fermentation process to be better controlled so that the quality characteristics can be, hopefully, standardized (Yongsawatdigul, Rodtong, and Raksakulthai 2007). Production still requires careful attention to details. The selection of starter cultures is crucial when using this method. The selected microorganisms should be well adapted to the fermentation environment and must have technologically-compliant characteristics and have only nonpathogenic microorganisms, preferably ones that are probiotic and can produce bacteriocins or other antimicrobials again undesirable organisms (Johansen 2018).

Starter cultures are made using different types of microorganisms including bacteria and fungi. For fungi-based fermentation, several species of *Aspergillus genus* and *Actinomucor genus* have been used to ferment surimi (Zhao et al. 2017; Zhou et al. 2014) and fermented silver carp fish paste (Kasankala, Xiong, and Chen 2012). Fermentations inoculated with fungi not only successfully reduced the number of pathogenic microorganisms, but also increases the production of taste- and flavor-inducing compounds. Moreover, the beneficial effects of four commercially available mold starters on fermented fish pastes have been documented in terms of nutritional and sensory characteristics (Giri, Osako, and Ohshima 2009). However, the use of commercial starter cultures is still a matter of debate and not widely used, as the lack of adaptability to the fermentation

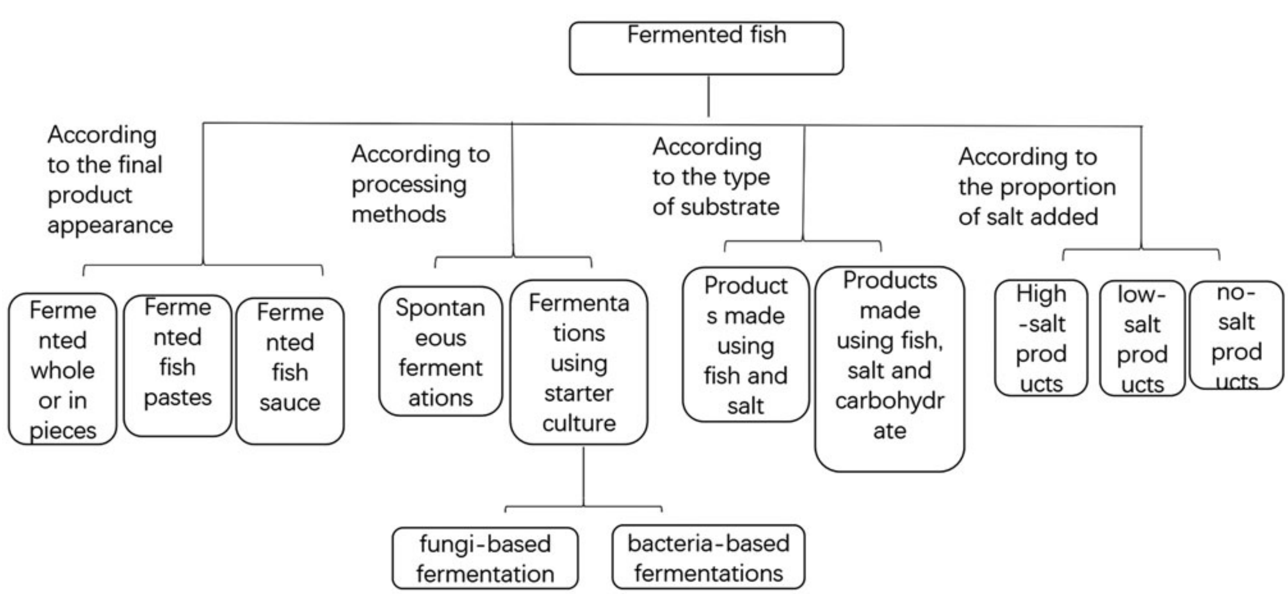

Figure 1. Types of traditional fermented fish products.

environment with different raw materials and the lack of flexibility in adjusting the fermentation to obtain the desired properties of the end product. For bacteria-based fermentations, lactic acid bacteria (LAB) have traditionally been the dominant microorganisms in many fermented fish products and different lactic acid bacteria starters have been used to produce fermented fish (Kose and Hall 2011; Nie, Lin, and Meng 2016; Riebroy, Benjakul, and Visessanguan 2008; Semjonovs et al. 2015; Speranza et al. 2017). For example, Som-fug, a Thai fermented fish, is made by adding the *Lactobacillus plantarum*, *Pediococcus acidilactici*, and *P. pentosaceus* (Riebroy, Benjakul, and Visessanguan 2008). *L. plantarum*, *Lactococcus lactis subsp. lactis* and *L. helveticus* have been used for the production of ferment mackerel mince at 37 °C (Yin, Pan, and Jiang 2002). In addition, a mixed-strain culture (*L. plantarum* 120, *L. plantarum* 145, and *P. pentosaceus* 220) has been used to prepare Suan yu, a traditional China fermented fish, reducing fermentation time and improving the quality of the whole carp-based product (Zeng et al. 2015). Similar to fermentation with fungi, fermentation with LAB has been reported to suppress the growth of spoilage microflora and improve the organoleptic qualities. Furthermore, LAB convert peptides and/or oligopeptides to amino acids, improving the aroma characteristics (Yin, Pan, and Jiang 2002).

In addition, depending on the type of substrate used in the fermentation processes, the traditional fermented fish products can be divided into two other classifications: (1) Products made using fish and salt. (2) Products made using fish, salt and carbohydrate.

Carbohydrate sources generally include rice, millet, flour, and even sirup or sugar. Millet is used as the major carbohydrate source in Northeastern Asian countries, whereas in Southeastern Asian countries, rice is commonly used as a carbohydrate source (Lee 1997). The addition of carbohydrates to a mixture of fish and salt not only provide an energy source to accelerate the fermentation, but the added carbohydrates help absorb excess moisture and impart a distinctive flavor to the final product (Paludan-Müller et al. 2002).

Furthermore, fermented fish can be classified into three classes based on the proportion of salt added: High-salt (more than 20% of the total weight), low-salt (3–8%), and no-salt products. The addition of salt will lead to the reduction of water activity. Salt is also believed to have a strong influence on the microbial flora in two ways: the high concentration of salt prevents the growth of spoilage microorganisms due to its intrinsic antibacterial properties. On the other hand, it is conducive to the growth of halophilic and salt-tolerant microorganisms (Lopetcharat et al. 2001). Salt also helps to enhance flavor by activating some of the enzymes inherent in the fish flesh or in the microorganisms (Mariutti and Bragagnolo 2017). It is therefore of interest to determine the optimal salt concentration for each type of fermentation.

Fermented fish products around the world

Europe and North America are major producers of fermented foods. Significant fermented products include fermented dairy products, beverages and meat products. Fermented beverages and dairy products are also common in South America (Marsh et al. 2014). However, only minor quantities of fermented legumes, starch crops and fish products are produced in North America. Therefore, little scientific research has been carried out on fermented fish (Waisundara, Jayawardena, and Watawana 2016). At present, fermented fish products are especially popular in Asia, Africa, and Northern Europe, where many nations have their own unique types of fermented products (Table 1). This uniqueness reflects the special combination of raw materials, ambient conditions, microorganisms and dietary traditions in each region.

Fermented fish in Northern Europe

Fermented fish as a traditional staple food is popular in European countries. However, only a few traditional fermented fish products are still produced. For instance, garum is a famous fermented fish sauce from the ancient Greeks and Romans (Aquerreta, Astiasarán, and Bello 2002). Mackerel and herring are considered the best ingredients to make garum. The fermentation was carried out over several months, at least nine months. Many small Italian and Spanish companies are still producing fish sauces based on the recipe for garum production (Mouritsen et al. 2017; Smriga et al. 2010).

Hákarl, an Icelandic delicacy, is fermented shark meat and can be stored for long periods (up to several years) (Rajauria et al. 2016). It must be obtained through two processes, fermentation and drying. The fermentation of shark may take 3–6 weeks and drying varies from several weeks to months depending on the temperature and the fishing season. Urea in the hákarl was converted into ammonia by bacterial ureases and trimethylamine (TMA) N-oxide was also decomposed into TMA by the bacteria during fermentation. However, the level of ammonia and TMA diminished somewhat during the drying period (Skåra et al. 2015). Moreover, this potentially harmful raw material, fresh shark meat, which is considered poisonous, can be made into a nutritious food product (Rögnvaldardóttir and Leaman 2012). The fermented Hákarl had an important role in providing energy and nutrition to Icelanders in earlier times and today is very popular among the older population.

Surströmming made from herring is a fermented fish product and is known for its unique smell in the northern parts of Sweden. The herring is first pre-salted in saturated salt solution and then the herring with head and gut removed is fermented in barrels at 15–18 °C for 3–4 weeks. After fermenting, the fermented product is transferred to cans along with the brine. Fermentation continues in the can for about half a year. During this fermentation process, the anaerobic halophile bacteria, *Haloanaerobium*, are responsible for the properties of Surströmming (Kobayashi, Kimura, and Fujii 2000). It is reported that Surströmming typically contains 11.8% protein, 8.8% salt, and 3.8% fat and the pH value is 7.1–7.4. However, pregnant women and women hoping to become pregnant are recommended to

Table 1. Different examples of fermented fish products around the world.

Name	Type	Raw Material	Salt:Fish	Fermentation time	Microbe	Country
Garum	Sauce	*Tunnus thynnus, Scomber scombrus*	25%	9 months	None reported	Roman
Hákarl	Whole (slices)	Greenland Shark (*Somniosus microcephalus*), salt	0	3–6 weeks	*Moraxella, Acinetobacter, Lactobacillus sp.*	Iceland
Surströmming	Whole (slices)	Baltic herring, salt	17%	3–4 weeks	*Halanaerobium*	Sweden
Rakfisk	Whole (slices)	Salmonid freshwater fish, salt	>5%	9–10 weeks	*Lactobacilli*	Norway
Lanhouin	Whole (slices)	Cassava fish (*Pseudotolithus sp.*), Spanish mackerel (*Scomberomorus tritor*), salt	15–35%	3–8 days	*Bacillus, Staphylococcus, Corynebacterium, Pseudomonas, Micrococcus, Streptococcus, Achromobacter, Alcaligenes*	Benin, Togo, Ghana
Momoni	Whole (slices)	Snakehead fish, salt, palm sirup, roasted rice	15–40%	2–3 days	*Micrococcus, Staphylococcus aureus, Staphylococcus sp., Bacillus sp., Lactobacillus sp., Pseudomonas, Pediococcus, Klebsiella, Debaryomyces, Hansenula, Aspergillus.*	Ghana
Feseekh	Whole (slices)	*Alestes baremose, Hydrocynus sp.*, salt	20–30%	60 days	None reported	Egypt
Nam-pla	Sauce	*Stolephorus spp. Ristrelliger spp. Cirrhinus spp.*, salt	>20%	5–12 months	Homofermentative tetrad-forming lactic acid bacteria	Thailand
Budu	Sauce	Raw anchovies (Stolephorus spp.) and salt	20–30%	3–12 months	*Micrococcus luteus, Staphylococcus arlettae*	Malaysia
Patis	Sauce	*Clupea spp. Decapterus spp. Leionathus spp.*, salt	22–26%	3–12 months	None reported	Philippine
Bakasang	Sauce	Sardines (*Engraulis japonicus*), salt, glucose	10–20%	40 days	*Micrococcus, Streptococcus, Pediococcus sp.*	Indonesia
Yu-lu	Sauce	Anchovies (*Engraulis japonicus*), snakehead fish (*Channa asiatica*)	33%	6 months	*Halotolerant*, LAB and Yeast	China
Plaa-som	Whole (slices)	*Puntius sophore*, salt, palm sirup, roasted rice	6–11%	8–12 days	*Pediococcus pentosaceus, Lactobacillus alimentarius, Weissella, L. planetarium, Lactococcus garvieae, Zygosaccharomyces rouxii*	Thailand
Suan yu	Whole (slices)	Fresh-water fish (*Cyprinus carpio* L.), roasted rice, salt and sugar	3%	30–60 days	*L. plantarum, Pediococcus pentosaceus, Leuconostoc, Paralimentarius, Saccharomyces cerevisiae, Hansenula anomala*	China
Pekasam	Whole	lampam java (*Pontius goniotus*), black tilapia (*Oreochromis mossambicus*), uncooked rice, salt	>10%	2–3 weeks or 12 months	None reported	Malaysia
Shidal	Whole	Punti fish (*Puntius sophore*), phasa fish (*Setipinna phasa*)	0	3–5 months	*Staphylococcus; Micrococcus, Bacillus*	India
Hukuti maas	Whole (slices)	Puthy maas (*Ticto barb*), roasted green chilies, tomatoes, ginger, rice, salt	None reported	12 months	*Lactococcus lactis ssp. lactis*	India
Ngari	Whole (slices)	*Puntius sophore*	0	4–6 months	*Lactococcus lactis subsp. cremoris, L. plantarum, Bacillus subtilis, Candida, Saccharomycopsis.*	India
Jeotgal	Whole (slices)	Shrimp, shellfish, fish, salt	5–30%	2 months or a few years	*Achromobacter, Bacillus, Brevibacterium, Flavobacterium, Halobacterium, Leuconostoc, Micrococcus, Pseudomonas, Staphylococcus, Sarcina, Saccharomyces, Torulopsis*	Korean
Katsuobushi	Whole (slices)	Skipjack (*Euthynnus pelamis* or *Katsuwonus pelamis*), eastern little tuna (*E. affinis*), frigate mackerel (Auxis rochei), frigate tuna (*A. thazard*), oriental bonito (*Sarda orientalis*)	10–15%	3–4 months	*Aspergillus, Eurotium*	Japan
Narezushi	Whole (slices)	Crucian carp, horse mackerel, chub mackerel, salt, cooked rice	20–30%	2–3 months	*Lactobacillus acidipiscis, Lactobacillus versmoldensis*	Japan
Fish-nukazuke	Whole (slices)	Mackerel, sardine, salt, cooked rice	10–15%	12 months	*Tetragenococcus muriaticus, Tetragenococcus halophilus*	Japan

consume it no more than 2–3 times a year because the raw material, Baltic herring, may contain dioxins (Miller et al. 2013).

Rakfisk is a native fish dish of Norway. It was usually made from salmonid freshwater fishes (trout or char) and salted (salt concentration 4–6% w/w), perhaps with the addition of a little sugar and fermented at low temperatures (4–8 °C) for several months. Rakfisk was commonly eaten from late fall through the Christmas season owing to its characteristic taste and flavor (Amilien and Hegnes 2004). LAB tend to be the dominant bacteria in the Rakfisk process. Rakfisk is usually a homemade product, so its tastes and smells are different from place to place, but it is possible to find that local products seem to have some similarity. Furthermore, it has become one of the first "protected designation of origin" local brand products in Norway (Amilien and Hegnes 2004).

In general, fish fermentations usually last from a few days or weeks to 1–2 years in Europe and in some cases sugars and spices as additives are added to the brine. Fermented fish products in Europe are generally sold as either whole fish, or as a fish sauce. The fermentation process generally involves salting and drying, or drying without salting, or salting without drying. In fact, with the exception of Hákarl, all the northern European fermented fish products are salted.

Fermented fish in Africa

The fishing industry is vital to the national socio-economic status of many countries in Africa. Fermentation is the most important way of preserving fish and are indigenous to the many different African cultures. In Africa, fermentation of fish for preservation was also usually combined with salting or drying, mainly because of climate and the extreme perishability of fresh fish (El Sheikha et al. 2014). Examples of the most well-known fermented fish in Africa are Lanhouin, Momone and Feseekh.

Lanhouin is made from whole cassava fish (*Pseudotolithus senegalensis*), a traditional fermented salted fish condiment in West African countries, and is generally processed on a traditional small-scale basis (Oguntoyinbo 2014). During the preparation of Lanhouin, the fresh fish are scaled, gutted, and washed for ripening for 8–11 hours followed by adding salt and allowing the fish to spontaneously ferment for 3–9 days. The added salt varies between 20% and 35% of the weight of fresh fish. The fermented fish is then washed to remove excess salt and sundried for 2–4 days. The final products are all characterized as having a strong odor. They are widely used as flavor enhancers in many types of dishes (Kindossi et al. 2012; Kindossi et al. 2016).

Momoni is a fermented fish in Ghana. Different types of freshwater fish, such as catfish, barracuda, sea bream and African jack mackerel (*Caranx hippos*), are used. They are allowed to ferment for 1–5 days (El Sheikha et al. 2014). The production of Momoni is based on traditional knowledge of fermentation and practical experience. Before fermenting, the fresh fish can be scaled and gutted, and the gill and gut regions are heavily salted (~30%). After fermenting, the product is washed with brine and cut into pieces, followed by sun-dried for a few hours (Sanni, Asiedu, and Ayernor 2002). Like Lanhouin, Momone is also widely used for its flavor enhancing properties (Sanni, Asiedu, and Ayernor 2002).

Feseekh are salted fermented products made without drying in Egypt. About 80% of Fessiekh is made from *Alestes baremose* (pebbly fish) while *Hydrocynus* sp. (tiger fish) make up the balance. The ratio of salt used varies widely and salt concentrations range from about 20–30% (Rabie et al. 2009). The processing of Fessiekh is carried out at temperatures ranging from 18 to 20 °C. It can be stored for more than three months. Feseekh is popular not only as an appetizer, but also as the main dish at some feasts, such as the Sham El Nessim celebration in Egypt (El Sheikha and Montet 2014).

Fish fermentations in African generally use high concentration of salt, and the fermentation period is short (from a few days to several weeks) and that the product is either whole or in pieces. The lack of standardization of the processing methods and hygiene are the main factor affecting product quality and the safety.

Fermented fish in Asian countries

Fermented fish have a long history in Europe and north Africa, but now Southeast and East Asian countries are the leaders in their production. Fermented fish found in Asia differ from the rest of the world and have been part of the culinary culture of Southeast Asian countries. Fish fermentation times in Southeast Asian are relatively longer (several months or even longer) compared with other countries. Various different types of fermented fish products including whole fish or fish pieces, sauces and pastes can be found in Asian markets. Fermented fish sauces are traditionally used throughout Asia and have annually expanded into international markets. These sauces are known by different names in different countries. In Thailand it is called Nam-pla (Daroonpunt et al. 2016); in Malaysia it is called Budu (Ahmad 2014); In the Philippines it is called Patis (Elegado et al. 2016); in Indonesia it is called Bakasang (Fatimah et al. 2017); and in China it is called Yu-lu (Wang et al. 2018). These products are made using similar raw materials, processing methods and have similar final compositions. Generally, fish and salt are the major ingredients usually in a ratio of 3-5:1 and some fish sauces also contain a variety of herbs and spices. These sauces are generally dependent on the development of halophilic bacteria cultures. Fish sauces generally contain all of the essential amino acids, vitamins and minerals, but its nutritional value might be questioned due to the high concentration of salt, especially when used with diets that are otherwise high in salt (Lopetcharat et al. 2001).

There are other types of fermented fish products in Southeast Asia besides fish sauces. For example, Plaa-som is a Thai fermented fish product for which whole fish or fish fillets are mixed with salt (8:1; fish:salt ratio, w/w), cooked rice and minced garlic. In some case, cooked rice and garlic are replaced by palm sirup and roasted rice (Kopermsub and Yunchalard 2010). *Pediococcus pentosaceus* and *Zygosaccharomyces rouxii* were the predominant species during fermentation of Plaa-som. It is normally suggested that the content of salt should not exceed 7% for high quality Plaa-som products (Paludan-Müller et al. 2002). Suan yu, a Chinese traditional low-salt fermented fish, is also produced by fermenting whole freshwater fish. The products are well accepted by consumers in China because they retain almost all the nutrition of fish and have a unique flavor. It has been reported that the fermentation time of Suan yu can be shortened and the quality improved with the use of a starter culture (Zeng et al. 2013b).

Pekasam is a Malaysia fermented whole fish product prepared by mixing freshwater fish with salt and ground, roasted, uncooked rice. The minimum amount of salt should be 10%. Different fermentation period (2–3 weeks or 12 months) have been used to make different products. The longer fermentation processes can produce better products (Ezzat et al. 2015).

Shidal is a fermented product from dried salt-free punti fish (*Puntius sophore*) and phasa fish (*Setipinna phasa*). It is very much popular in India. Fermentation is done for 3–5 months at ambient temperature. *Staphylococcus* was the dominant genus in punti shidal, whereas *Micrococcus* and *Bacillus* were the dominant genera in phasa shidal (Majumdar et al. 2016).

Hukuti maas is also a special fish dish in North-East India. It is prepared using salted small fish puthy maas (*Ticto barb*) and roasted green chilies, tomatoes, ginger and rice. Hukuti maas are traditionally fermented and preserved for about a year at low temperature (approximately <20 °C) (Kumar et al. 2014).

Ngari is a fermented fish product of Manipur in North-East India and is usually eaten as a side-dish with cooked rice. The fermentation process is usually combined with drying (3–4 days) (Thapa, Pal, and Tamang 2004).

Jeotgal is a traditional salted and fermented seafood in Korean cuisine. It is made by adding 5–30% (w/w) salt to raw materials such as shrimp, shellfish and fish. The fermentation period of jeotgal is usually determined by the concentration of salt and fermentation temperature. For example, two months for jeotgal with low-salt levels (6–18%), and a few years for jeotgal with a high-salt content (over 20%) have been used to allow the appropriate taste to develop (Guan, Cho, and Lee 2011).

Dried bonito products (Katsuobushi) are a traditional seasoning in Japan. They are manufactured by boiling, smoking, drying and fermenting. Skipjack (*Euthynnus pelamis* or *Katsuwonus pelamis*), eastern little tuna (*E. affinis*), frigate mackerel (*Auxis rochei*), frigate tuna (*A. thazard*), and oriental bonito (*Sarda orientalis*) can all be used as raw materials. It is reported that the taste of the fermented product is better when done with raw fish with higher fat content (Lin and Hwang 2008). The *Aspergillus* and *Eurotium* species participate in the fermentation process (Miyake et al. 2009).

Fish-nukazuke and Narezushi are also salted and fermented fish with rice-bran and are very popular in Japan, particularly in the Hokuriku area. Narezushi species are abundant and have been prepared using various freshwater fishes or marine fishes such as Crucian carp, horse mackerel, and chub mackerel (An et al. 2010; Kanno et al. 2012). Mackerel and sardines are the main raw materials for fish-nukazuke. In general, the treated fish have been scaled, gutted, headed, and are then stuffed and covered with cooked rice, mixed with different concentrations of salt and fermented at room temperature for several months (Kosaka et al. 2012). In addition, puffer fish ovaries can also be used as raw materials for fish-nukazuke. Their deadly tetrodotoxin disappears during the long-term salting (2 years) and fermentation (1–2 years) (Kuda, Mihara, and Yano 2007).

Fish paste is another form of fermented fish in Southeast Asia. They are staple foods in Southeast Asia such as Cambodia, Laos, Myanmar, Thailand, and Vietnam, with the highest consumption in Cambodia (5.1 kg per capita per year) (Ly, Mayrhofer, and Domig 2018). Fish pastes might also be significant dietary sources of micronutrients and protein.

Health benefits and safety of fermented fish

Fermentation has traditionally been used to preserve fresh fish, but nowadays in many cases it also produces many nutritional elements with higher bioavailability. These biologically active substances are mainly derived from the extensive degradation of protein during fermentation that have been linked with several beneficial biological properties (Elegado et al. 2016; Je et al. 2005).

Antioxidant activity

Recent studies have shown that uncontrolled free radicals including peroxyl radicals, hydroxyl radicals, superoxide anion radical, 1,1-diphenyl-2-picrylhydrazyl (DPPH) radical and peroxynitrite anions can attack various tissue components leading to a number of pathologies such as autoimmune diseases, neurodegenerative disorders, and cancers (Kehrer and Klotz 2015; Najafian and Babji 2014). Jemil et al. (2014) showed that fermented fish meat protein hydrolysates have hydrophobic amino acids that were produced during fermentation may have noticeable free radical-scavenging activity and can protect against oxidation by donating protons to the free radicals.

Aluko (2012) reported that the large number of small peptides released during fermentation also had hydroxyl and DPPH radical scavenging capacities. In addition, Loma fermented fish (Pekasam) with high antioxidant activity has the potential to be a natural functional ingredient to prevent ROS-related chronic diseases (Najafian and Babji 2018). The fermented fish product, Shidal, could be used as a potential source of nutrients and natural antioxidants (Majumdar et al. 2016).

High coenzyme Q10 (CoQ10)-content (291 mg/g) has been found in Jeotgal, a fermented product from Korea (Pyo and Oh 2011). CoQ10 is an essential cofactor for energy production and an immune system enhancer. It is also a powerful antioxidant (Kaikkonen et al. 2002). A CoQ10 deficiency may cause several clinical disorders, including chronic heart failure (Mortensen et al. 2014), hypertension (Kumar et al. 2009), Parkinson's disease (Shults, Haas, and Beal 1999) and malignancy (Portakal et al. 2000). Fermented Jeotgal is used as an exogenous CoQ10 supplement (Martínez-Álvarez et al. 2016).

Antihypertensive activity

Fermented fish can also be a source of antihypertensive peptides. Generally, hypertension is related to the angiotensin I-converting enzyme (ACE). Large amounts of peptides showing ACE inhibitory activity may be formed during the processing of fermented fish (Sørensen et al. 2004; Itou and Akahane 2004, 2009; Itou et al. 2006) and hence have potential antihypertensive effects. There is evidence showing that katsuobushi oligopeptides, which were derived from the traditional Japanese food "Katsuobushi," or dried bonito, can effectively control blood pressure without any adverse side effects on human health (Fujita, Yamagami, and Ohshima 2001). Furthermore, dried bonito is considered a nutritional supplement that can promote the recovery from fatigue (Kuroda et al. 2007). In addition, Narezushi produced from salted mackerel by fermentation with boiled rice also has antihypertensive effects (Ichimura et al. 2003; Itou et al. 2007)

Anti-cancer activity

Lee et al. (2004) reported that peptide fractions isolated from anchovy sauce had anticarcinogenic activity through the induction of apoptosis in a human lymphoma cell line, which is a model system to show the potential to prevent that type of cancer. It has been reported that somatic mutations can be prevented using several fermented fish products such as kajami-sikhae (flat fish), chuneobamjeot (shad gizzard), the main types of Jeotgals, which due to their strong antiproliferative effects against the liver hepatocellular carcinoma cell HepG2 (Koo et al. 2016; Lim et al. 2001) can be considered as potential anti-carcinogens. Additionally, immunomodulatory bioactive substance including high concentration of glutamine, dipeptides and tripeptides containing glutamic acid, and several fatty acids, derived from fermented fish sauce made from Pacific whiting, used as commercial dietary supplement (Duarte et al. 2006).

Anticoagulant and fibrinolytic activity

Anticoagulant and antiplatelet drugs are historically used to prevent the formation of thrombus. Some seafood sauces contain several active substances that can be considered as stable fibrin-clotting inhibitors (Martínez-Álvarez et al. 2016). The active substances prevent the formation of a thrombus by protecting fibrinogen from the action of thrombin. They may be useful taken orally for the prevention of thrombotic diseases with molecular weights between 1 and 5 kDa (Kim, Chae, and In 2004). Fibrinolytic enzymes have been also reported in fermented small cyprinid fish (*Puntius sophore*), which were specific to breaking down fibrin and fibrinogen (Singh et al. 2014). Although beneficial effects of fermented fish have been proposed, further investigation still need to be done, particularly clinical studies.

Safety issues with fermented fish

Fermented fish have some negative effects on human health in addition to providing health benefits. For example, the high amounts of salt added to ferment fish may be a problem and with some circumstances, there may be the generation of biogenic amines (BA) during the fermentation process. It is known that the presence of BA may have adverse effects on humans if the levels of biogenic amines in foods exceed the recommended limits. In addition, they may be potential precursors of carcinogenic nitrosamines (Biji et al. 2016).

Excessive intake of sodium chloride is associated with hypertension and consequently increases the risk of cardiovascular disease (MacGregor and De Wardener 2002). How to reduce the content of BA and salts has become the focus of some fish fermentation research. Many researchers have shown that the use of microorganisms that are able to degrade BA is a potentially effective method to deal with this problem (Álvarez and Moreno-Arribas 2014). The degradation pathway of biogenic amines needs to be further clarified and it remains to be determined whether it is applicable to specific fermentation products.

There are a number of other approaches in addition to adding less salt to deal with this problem (Yu et al. 2014). One alternative is the partial replacement of salt, in particular, with potassium chloride (KCl) in combination with masking agents and flavor enhancers or the use of electrodialysis or other techniques including soaking prior to consumption to desalt fermented fish products (Chindapan, Devahastin, and Chiewchan 2009; Sanceda, Suzuki, and Kurata 2003).

Role of microorganisms in fermentation of fish

Microorganisms have an important role in producing better and safer fermented fish products due to their unique metabolic characteristics. The microorganisms referred to include those added as starter agents and those found during fermentation.

Stability and keeping quality

Fermented fish stability and quality not only rely on raw material characteristics, but also are attributed to the action of a series of antimicrobial compounds produced by microorganisms during fermentation. These compounds include many organic acids, ethanol, hydrogen peroxide and bacteriocins, which inhibit the growth of or inactivate spoilage and pathogenic microorganisms (O'Bryan et al. 2015).

Organic acids such as lactic, acetic and propionic acids, are generally considered to provide an acidic environment and inhibit the growth of acid sensitive spoilage microorganisms. Furthermore, acids can directly act upon the cell wall of Gram-negative bacteria and cause the failure of proton motive forces, reducing the colonization of pathogenic bacteria (Dittoe, Ricke, and Kiess 2018). Acetic acid is more inhibitory than lactic acid and can inhibit yeasts, molds and bacteria (Ross, Morgan, and Hill 2002).

Moreover, most *Lactobacilli* species are able to form hydrogen peroxide which inhibits the growth of psychrotrophic and pathogenic microorganisms. In particular, inhibition by hydrogen peroxide may be due to the strong oxidizing effects on membrane lipids and cellular proteins (Rattanachaikunsopon and Phumkhachorn 2010). The bactericidal effect of hydrogen peroxide depends on the concentrations used and environmental factors such as pH and temperature (Reis et al. 2012).

Bacteriocins refer to a range of antimicrobial peptides and proteins. The production of bacteriocin is a dynamic process and is regulated by quorum-sensing mechanisms depending on cell density and concentration of the inducer (Galvez et al. 2008; Turovskiy et al. 2007). There are many examples that show that almost all LAB species have the ability to produce bacteriocins (Pringsulaka et al. 2012) including *L. plantarum* isolated from Suan-yu; *L. paracasei* isolated from Budu (Abbasiliasi et al. 2014) and *Lactococcus lactis* isolated from Hukuti maas (Kumar et al. 2014). They have a wide antibacterial spectrum and most food-borne pathogens including but not limited to *Staphylococcus aureus, Salmonella enterica, Enterococcus faecalis, Clostridium botulinum,* and *Listeria monocytogenes* were inhibited (Reis et al. 2012).

Organoleptic and nutritional characteristics

The diversity of the microbial community and endogenous enzymes are able to provide fermented fish with desired properties such as extended shelf life and good organoleptic properties. Flavor is the main determinant of fermented fish quality and is one of the principle factors involved in consumer purchasing decisions. Previous studies have shown that proteins, lipids and carbohydrates as substrates are broken down by microbial communities to alcohols, aldehydes, volatile fatty acids and amino acids during fermentation. The formation of the characteristic flavor of fermented fish is mainly because of the balance of microbial metabolites (Gowda, Narayan, and Gopal 2016; Jeong et al. 2013). Xu et al. (2018) suggested that autochthonous (indigenous) microflora dominated the generation of volatile flavor compounds in fermented fish. *Staphylococcus sp*. CMC5-3-1, contributing to the generation of a desirable dark chocolate note, could be used as a starter culture to improve the freshness and aroma of fish sauce (Udomsil et al. 2017).

There is evidence that bacteria involved in the development of flavor can be attributed to their ability to secrete enzymes such as amylases, proteases and lipases. For example, the strains of *Virgibacillus sp*. SK 33 and SK37 and *Staphylococcus sp*. SK1-1-5 as started cultures produced proteinases that increased the desirable volatile compounds of fish sauce (Yongsawatdigul, Rodtong, and Raksakulthai 2007). Udomsil et al. (2010) also reported that LAB can convert peptides and/or oligopeptides to precursors of volatile compounds through high intracellular aminopeptidase activities. In addition, *Tetragenococcus halophilus* has an important role in improving the flavor characteristic of fish sauce as reported by Thongsanit et al. (2002), because they can produce numerous volatile compounds, such as 2-methylpropanal, 2-methylbutanal, 3-methylbutanal and benzaldehyde. The contribution of yeasts to flavor development also is attributed to their powerful lipolytic and proteolytic activities. It is reported that *Aspergillus luchuensis* showed a proteolytic activity that when used as a starter culture resulted in a low-salt fish sauce with better flavor (Kim et al. 2016).

The formation mechanism of flavor compounds has been studied in other fermented foods such as wine and dairy products. The major pathways include lipolysis or oxidation of fatty acids and amino acid metabolism. However, at present, the research on the flavor of fermented fish is limited to the identification of the main flavor substances in the fermentation process and the enhancement of the overall flavor by adding microorganisms that have affect flavor formation. Although the principal components contributing to flavor, such as proteases, peptidases and lipases may be known, lack of knowledge of the exact mechanism of the generation of specific flavor limits the understanding of the nuances of flavor development. Therefore, the volatile flavor release mechanisms, the relationship between flavor and microbes, and the synergistic effects of flavor compounds still need to be systematically investigated.

In addition, some microorganisms present in fermented fish may degrade toxic or antinutritive factors, produce bacteriocins and nutraceuticals. For example, *Tetragenococcus halophilus* isolates from fish Nukazuke suppressed histamine production and enhance product safety. Isolated *Weissella* strains from Thai fermented fish (Plaa som) were able to produce antibacterial compounds and folate. Therefore, fermented products produced using these strains might be promoted for their functional properties (Deatraksa et al. 2018; Kuda et al. 2012; Nakamura et al. 2012).

Approaches used for characterizing the microbiota in fermented fish

The microbial community of fermented fish has an important role in product safety, flavor, texture, and health aspects. Analysis of the microbial community structure during fermentation is a prerequisite for better understanding of fermented fish. Numerous and different techniques are available to do microbial analysis and are mainly grouped into two categories: culture-dependent methods and molecular methods (Temmerman, Huys, and Swings 2004).

Culture-based methods are routinely applied to enumerate microbe and observe the phenotypic characteristics (such as colony morphology), microscopic details (such as Gram stain reaction and cell morphology), and isolate or identify a certain number of colonies (Davis 2014). Microbe quantitation is done by counting the total number of colony-forming units (CFU) grown on an agar plate or broth with different chemical compositions from serial dilutions. The media for the identification and enumeration of strains based on the characteristics of the microbe are limited and no one single medium can be suitable for all strains (Davis 2014). Moreover, the approach may be particularly useful for estimating those microbes that are capable of replicating under experimental conditions. It is estimated that traditional culture-based techniques are only capable of culturing less than 1% of the microbiota of high-diversity environments (Giraffa and Neviani 2001).

Traditional, culture-based techniques require a large amount of time and material cost and fail to provide an accurate and complete enumeration of the microbial community present, but food-associated microorganisms and their dynamics have been studied using this method for a long time (Justé, Thomma, and Lievens 2008).

Paludan-Müller et al. (2002) identified 350 yeast strains from Plaa-som, a Thai fermented fish product, using phenotypic characteristics, rDNA intergenic spacer (ITS) PCR and carbohydrate assimilation. The results showed that problems and shortcomings of culturing methods involve low taxonomic resolution and even failed to detect some species or genera.

To solve the problem of time, specificity, resolution and culturability with traditional methods, many molecular methods have been developed. These molecular ecological methods include denaturing gradient gel electrophoresis (DGGE) (Lv et al. 2017), quantitative (q)PCR, and new generation sequencing technologies (Frickmann et al. 2017).

Of the methods currently available, most of the techniques are based on PCR. DGGE is a method to detect community profiling by separating the PCR amplicons of the same size but different sequences (Ercolini 2004). This method can be used to detect heterogeneity among DNA sequences, and screening and grouping the isolates and following their dynamics over time but not always suitable for the identification of all species and it is not quantitative. It also does not distinguish between living and dead bacteria. The bacterial dynamics during fermentation of Ngari were monitored by Devi, Deka, and Jeyaram (2015) using PCR-DGGE and the drastic change of bacterial community structural was confirmed. Thongruck et al. (2017) used PCR-DGGE coupled with traditional isolation procedures and viable staining counts to monitor the changes of LAB. The results showed that the method provide better resolution of several species when the difference in sequences are wide enough. However, DGGE is poorly adapted to industrial applications due to its time and expense.

"Real-time" qPCR is considered as a method for the detection and quantification of specific microbial taxa in a given sample (Juvonen, Partanen, and Koivula 2010). This method relies on nucleic acid sequence amplification using PCR and reporter molecule detection, and does not require post-PCR sample handling, resulting in much faster assays. Thus, qPCR can be applied to precisely quantitate specific species or for the detection of potential targeted spoilage markers (e.g., amino acid-decarboxylase genes for biogenic amine production) (Álvarez and Moreno-Arribas 2014). It can also be used for specific population growth tracking or for microbial stability testing (Juvonen and Haikara 2009; Juvonen, Koivula, and Haikara 2008; Ladero et al. 2011; Lucas, Claisse, and Lonvaud-Funel 2008). In fermented fish products, qPCR is considered to be the most commonly used method to estimate bacterial population abundance (Jeong et al. 2013). qPCR, however, is not a community profiling technique and is less efficient when used to comprehensively characterize mixed microbiota or other samples containing a diverse, unknown microbial community.

The Illumina (San Diego, CA, USA) and the 454 Life Sciences Platform (Branford, CT, USA) sequencing technologies are community profiling methods and have recently been applied with complex microbial systems. The Illumina system is a sequencing by-synthesis method based on the fluorescent of reversible terminator nucleotides detection and pyrosequencing is used to detect the incorporation of nucleotide bases using pyrophosphate release and luciferase activity. The Illumina sequencing system seems to be more suitable than the 454 Life Science Platform to study fermentation systems, owing to its lower cost and greater sequence coverage. Pyrosequencing has also been commercially available for a longer time (Van Dijk et al. 2014). Compared with DGGE, pyrosequencing and the use of the Illumina system provide more comprehensive sensitivity and relative quantification. Furthermore, these methods provided unprecedented opportunities for sequencing the complete genome of every community member present. They offer new ways to show holistically the metabolic capacity of the system at the molecular level (Simon and Daniel 2011; Warnecke and Hess 2009). At present, new generation sequencing technologies have been used to show the dynamics and diversity of microbial community succession of some whole fermented fish environments (Lee, Jung, and Jeon 2015; Roh et al. 2010). Furthermore, metaproteomic analysis has been successfully applied to fermented fish, making it possible to study the microflora from taxonomy to function (Ji et al. 2017).

In general, the new generation of sequencing technologies are promising methods for analyzing microbial ecosystems. However, each approach has its own advantages and limitations (Table 2). These methods should be carefully used with full consideration of their limitations.

Future prospects and challenge

The demand for fermented fish is increasing worldwide. Attention has been given to the role of microbes during fermentation and different new techniques have been developed to better understand microbial ecological communities. However, to date, most of research work on microbe has been descriptive, i.e., only involved in the preliminary identification of microflora. The relationship between the

Table 2. Selected numerous and different techniques for microbial community analysis in fermented fish.

Method	Theory	Advantages	Disadvantages	References in fermented fish
Culture-dependent methods	Plate-based counting	Microscopic characterization of the cell morphology of the isolates	Time-consuming; only for culturable microorganisms	Perez et al. (2018); Kopermsub and Yunchalard (2010); Saithong et al. (2010)
Denaturing gradient gel electrophoresis	Separation of heterologous DNA sequences by the denaturant concentration gradient	Separation of amplicons single base-pair differences	Technically difficult; expensive and time-consuming;	An et al. (2010); Fujiiet al. (2011); Yoshikawa et al. (2010); Clementine et al. (2012)
Quantitative PCR	Fluorescent reporter dyes to combine the amplification and detection steps of the PCR reaction	Allows microbial populations to be quantified; accurate	Targeted primers for specific populations; special instruments are needed	Clementine et al. (2012); Xiao et al. (2014)
Illumina Sequencing	Sequencing-by-synthesis; determination of DNA sequence based on captured markers at the newly synthesized fluorescence ends	High-resolution; less expensive than pyrosequencing;	Expensive; lower resolution than pyrosequencing	Lee, Jung, and Jeon (2015)
454 Life Sciences Pyrosequencin	Sequencing-by-synthesis; enzyme cascade chemiluminescence in the same reaction system catalyzed by 4 enzymes	High-resolution; higher resolution than Illumina sequencing	Expensive; lower coverage than Illumina sequencing	Lee, Jung, and Jeon (2015); Roh et al. (2010)

regulation of flavor production and microbial metabolites remains to be understood. Moreover, the production of traditional fermented fish products is a longstanding industry in the world but only a few production approaches have been commercialized. Future research studies are needed to explore the detailed mechanisms of microbial influence on the quality of fermented fish. Another research area that needs to be addressed is the nutritional value and safety of fermented fish products. These should to be better understood because of the increasing demand of fermentation products in both domestic and international markets.

Conclusion

Fermented fish processes are increasingly attractive research topics. Fermented fish are produced in different ways around the world. A wide range of beneficial biological activities and substances have been found. The fermented fish and fish products have a great potential in the development of novel fish products with improved sensory attributes, nutritive value, and health benefits.

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