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Fermented fish and fermented fish-based products, an ever-growing source of microbial diversity: A literature review



Luca Belleggia^a, Andrea Osimani^{a,*}

^a Dipartimento di Scienze Agrarie, Alimentari ed Ambientali, Università Politecnica delle Marche, via Brecce Bianche, Ancona, Italy

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ABSTRACT

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Fermented fish and fermented fish-based products are part of the diet of many countries all over the world. Their popularity is not only due to the unique flavor, the distinct texture, and the good nutritional quality, but also to the easiness of the production process, that is commonly based on empirical traditional methods. Fish fermentation techniques usually rely on the combination of some key steps, including salting, addition of spices or additives, and maintenance of anaerobic conditions, thus selecting for the multiplication of some protechnological microorganisms. The objective of the present review was to provide an overview of the current knowledge of the microbial communities occurring in fermented fish and fish-based products. Specific information was collected from scientific publications published from 2000 to 2022 with the aim of generating a comprehensive database. The production of fermented fish and fish-based foods was mostly localized in West African countries, Northern European countries, and Southeast Asian countries. Based on the available literature, the microbial composition of fermented fish and fish-based products was delineated by using viable counting combined with identification of isolates, and culture-independent techniques. The data obtained from viable counting highlighted the occurrence of microbial groups usually associated with food fermentation, namely lactic acid bacteria, staphylococci, Bacillus spp., and yeasts. The identification of isolates combined with cultureindependent methods showed that the fermentative process of fish-based products was generally guided by lactobacilli (Lactiplantibacillus plantarum, Latilactobacillus sakei, and Latilactobacillus curvatus) or Tetragenococcus spp. depending on the salt concentration. Among lactic acid bacteria populations, Lactococcus spp., Pediococcus spp., Leuconostoc spp., Weissella spp., Enterococcus spp., Streptococcus spp., and Vagococcus spp. were frequently identified. Staphylococcus spp. and Bacillus spp. confirmed a great adaptation to fermented fish-based products. Other noteworthy bacterial taxa included Micrococcus spp., Pseudomonas spp., Psychrobacter spp., Halanaerobium spp., and Halomonas spp. Among human pathogenic bacteria, the occurrence of Clostridium spp. and Vibrio spp. was documented. As for yeast populations, the predominance of Candida spp., Debaryomyces spp., and Saccharomyces spp. was evidenced. The present literature review could serve as comprehensive database for the scientific community, and as a reference for the food industry in order to formulate tailored starter or adjunctive cultures for product improvement.

1. Introduction

Fish and fish products represent staple foods that are included in the dominant portion of a standard diet due to the availability of key macronutrients and micronutrients. Nutrients provided by fish include: i) high-quality protein that contains essential amino acids for human nutrition; ii) long-chain omega-3 fatty acids, whose function is to improve the visual and cognitive human development; iii) minerals, such as calcium, phosphorus, zinc, iron, selenium, and iodine; and iv) vitamins A, B, and D (FAO, 2022). In the last decades these nutritional features have attracted consumers of both middle-income and developed countries in order to prevent malnutrition and non-communicable diseases (FAO, 2022). In fact, the global apparent aquatic food consumption is constantly growing from 9.0 kg per capita in 1961 to estimated 21.4 kg in 2030, at an average increase rate of 3.0 percent per year (FAO, 2022). The increasing fish consumption is not only attributable to its massive farming, but also to a refined use of the raw material, improved distribution channels, and reduction of wastes (FAO, 2022).

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^{*} Corresponding author at: Dipartimento di Scienze Agrarie, Alimentari ed Ambientali, Università Politecnica delle Marche, via Brecce Bianche, 60131 Ancona, Italy.

E-mail address: a.osimani@univpm.it (A. Osimani).

Due to its high perishability, fish is available on the market as fresh food for a limited period of time, especially in developing countries. Therefore, numerous strategies to increase the shelf-life of such perishable food, and thus curbing post-harvest losses, were developed; among these, freezing, drying, smoking, salting, and fermentation.

Fermentation is a method used for the preservation of food since the Neolithic period, around 10,000 years B. C. The continued use of this practice to the present day is given not only by the extended shelf-life of the obtained end products, but also for their enhanced sensory and nutritional characteristics (Bourdichon et al., 2012). During fermentation, numerous metabolic activities are exerted by microorganisms to obtain energy from organic substrates that are demolished into simpler components through the use of microbial enzymes (Marti-Quijal et al., 2020). Fermented foods are beneficial to human health, since they are rich in bioactive compounds and potentially probiotic microorganisms, moreover, fermentation leads to the biochemical degradation of antinutrients and to an improved digestibility of the end product (Singh, De Mandal, Mathipi, Ghatak, & Kumar, 2018; Marti-Quijal et al., 2020). Currently, almost any type of food can be processed using a fermentation process, including food of vegetable origin, such as olive, cabbage, and cereal flours, and food of animal origin, such as milk, meat, and fish.

Fermented fish and fermented fish-based products are part of the diet of many countries all over the world. According to tradition, they can be consumed either as the main dish, as side dish, or as a condiment. Their popularity is not only due to the unique flavour, the distinct texture, and the good nutritional quality, but even to the easiness of the production process, that differs from one country to another. It is noteworthy that, along years, fermented fish and fermented fish-based products were traditionally manufactured following empirical traditional and ancient methods. Indeed, these artisanal processes were usually developed in the absence of scientific knowledge and technological means, according to a few variations of process or ingredients. Hence, the sensory improvements were mainly based on colour, odour, and taste changes, caused by microbiological, chemical, and physical modifications that were unknown at that time (Anihouvi, Kindossi, & Hounhouigan, 2012).

Fish is so perishable because, after the harvesting, there is a rapid deterioration of the flesh caused by autolytic enzymes and microbial activity. The spoilage process speed depends on environment conditions, in fact with a tropical climate it starts within only 12 h after fish catchment. First, muscle tissues become stiff due to the rigor mortis, characterized by the action of autolytic enzymes, such as ATPase and ADPase. Afterwards, the decomposition and lysis of muscle cells follow, during which blood and exudates, containing both oil and protein, drain out. These processes result in tissue unstiffening, production of peptides and amino acids, and lipid oxidation and hydrolysis (Prabhakar, Vatsa, Srivastav, & Pathak, 2020). During the decay of fish flesh, the proliferation of spoilage microorganisms, mainly belonging to the genera Pseudomonas, Vibrio, Photobacterium, Serratia, Shewanella, and Aeromonas, and to the family of Enterobacteriaceae, is generally observed. The uncontrolled microbial growth leads to the synthesis of several alcohols, organic acids, amines, sulphides, aldehydes, and ketones, that are responsible for typical off-flavours of rotten fish (Prabhakar et al., 2020). Furthermore, the decarboxylation of free amino acids mediated by microbial enzymes could cause the production of biogenic amines (BAs) that are non-volatile low-molecular weight nitrogenous organic bases. If consumed at high levels, BAs are hazardous for the human health, as they can produce several adverse physiological effects such as hypotension, hypertension, nausea, headache, rash, dizziness, cardiac palpitation, intracerebral haemorrhage, and even death (Zeng, Xia, Jiang, & Yang, 2013a). The physico-chemical characteristics and the natural microbiota of fish strictly influence the type and quantity of BAs formed. Moreover, the process conditions during the whole production chain could exert a significant role, since they can modulate the metabolic activity of some undesired microbial groups (Kongkiattikajorn, 2015).

some key steps, including salting, addition of spices or additives, and maintenance of anaerobic conditions, thus selecting for the multiplication of some beneficial microorganisms. In more detail, before fermentation, the fish can be mechanically treated, through cutting, pressing, and gutting (the presence of viscera is of critical concern, since their microbiota could influence the ripening process), moreover, fish can be subjected to drying and smoking (Oetterer et al., 2003; Kakati, & Goswami, 2013a). The use of salt represents one of the oldest and most effective methods of fish preservation, thus leading to the selection of a salt-adapted microbiota. In more detail, after the addition of salt, some physico-chemical changes in the fish tissues are induced, including i) the reduction of moisture content and water activity caused by the diffusion of salt into the fish flesh, and ii) the increased solubility of proteins that tend to be denatured, this latter phenomenon known as salting-in (Erkan, Tosun, Alakavuk, & Ulusoy, 2009; Hernandez-Herrero, Roig-Sagués, López-Sabater, Rodríguez-Jerez, & Mora-Ventura, 2002; Nahar, Zakaria, Hashim, & Bari, 2017). Therefore, microbial and enzymatic activities generally decrease; in addition, the chloride ions cause the death of non-halotolerant microorganisms (Wheaton, & Lawson, 1985). Hence, the microbiota evolution is mainly driven by the capability of microorganisms to survive and grow under a hypersaline environment. Indeed, the salt concentration allows the selection of microorganisms that are moderately halophiles (0.9-3.4 M NaCl), extremely halophiles (3.4-5.1 M NaCl), or halotolerant (able to grow both in the presence of relatively high levels and absence of salt) (Perez et al., 2018). Hence, the optimal choice of salt rate is pivotal to promote the growth of suitable fermenting microbial groups as well as to obtain final products with pleasant sensory traits (Paludan-Müller, Madsen, Sophanodora, Gram, & Møller, 2002). The establishment of anaerobiosis during fish fermentation could also select for microbial taxa that are well adapted to this specific environmental condition. The anaerobic condition is usually achieved through filling with brine or oil the dedicated sealed fermentation containers (Skåra, Axelsson, Stefánsson, Ekstrand, & Hagen, 2015; Majumdar, Roy, Bejjanki, & Bhaskar, 2016a).

In general, the fermentation process could be carried out by microorganisms naturally contaminating the raw materials, thus leading to a spontaneous fermentation. Moreover, selected and artificially inoculated microorganisms (starter cultures) could be used to guide the fermentation process. It is noteworthy that, regarding fermented fish and fish-based products, selected starter cultures are generally used only in a few industrial-scale productions, where reliable, predictable, and fast fermentation processes are desired (Saithong, Panthavee, Boonyaratanakornkit, & Sikkhamondhol, 2010). Moreover, the guided fermentation assures the safety of the final product, as the growth of pathogenic microbial groups and the synthesis of potentially harmful compounds, such as BAs, can be avoided.

The objective of the present review is to provide an overview of the current knowledge of the microbial communities naturally occurring in fermented fish and fish-based products. The information gathered could be used by scientific community and food industry to select the predominant microorganisms implied in the spontaneous fermentation of fish and construct *ad hoc* starter or adjunctive cultures for quality and safety enhancement of the product. To reach this aim, a description of the main features of the most relevant traditional fermented fish and fish-based products manufactured worldwide was reported. Then, based on the available scientific literature, a comprehensive database including microbiological data on ready-to-eat fermented fish and fish-based products was generated. The main microbial groups detected in the same products were finally described and discussed, considering their potential role during fermentation of fish and fish-based products.

2. Methodology

2.1. Search approach

Fish fermentation techniques generally rely on the combination of

The literature search focused on scientific publications concerning

the microbiota of fermented fish-based products and its dynamics during production processes. The search engines used for such purpose comprised ScienceDirect (https://www.sciencedirect.com/) and PubMed (https://pubmed.ncbi.nlm.nih.gov/). The selection of studies included articles published from 2000 to 2022 in peer-reviewed journals written in English and was based on the use of the following keywords: "fermented fish", "fermented fish-based product", "fermented fish byproduct", "fermented fish microbiota", "fermented fish microbial quality", "fish fermentation", "fermented fish microorganism", "fermented fish microbiology". To identify suitable publications, titles and abstracts were checked first, then, a thorough reading of each selected paper was performed. A cross-check based on the names of popular and traditional fermented fish-based products was then carried out. Ready-to-eat foods both from small-scale and large-scale productions, and laboratory-scale preparations were also included. A cross-refencing approach was applied to acquire other related scientific studies. The following types of publication were excluded: books, thesis, project documents, proceedings, papers that did not include microbiological analyses on fermented fish-based products, papers related to microbiological aspects of crustaceans and molluscs, and papers dealing with the microbiological characterization of fermented fish-based products added with starter cultures (Garofalo et al., 2019). A total of 191 publications were finally selected, counting 168 research articles and 23 review papers.

2.2. Database generation

The following information was obtained from each of the 168 research articles: i) the authors and year of publication; ii) the fish species object of the study; iii) the local name of the fermented fishbased product; iv) the country of origin of the product; v) the collection and production point of the product (collected from market, ecommerce, or nature; processed by food industry, research laboratory, or local producer); vi) the analytical methods used, whether culturedependent (viable counts combined with phenotypical, physiological and/or culture-independent identification and characterization of isolates) or culture-independent; vii) the viable count results of bacteria and eumycetes; viii) the identified genera and/or species of bacteria and eumycetes both from phenotypical, physiological, and molecular methods. The extracted information was used to generate a database table showing data of each research article listed in alphabetical order and sorted according to the continent of origin.

3. Occurrence of fermented fish-based products in world continents

The most relevant traditional fermented fish and fish-based products manufactured worldwide are summarized in Table 1. For each traditional product, fish species, other ingredients, key production steps, and processing time traditionally applied were listed with no further mention on the text.

3.1. Africa

In African countries, seafood products represent an important food supply source, as in Gambia, Ghana, and Sierra Leone, where they reach more than 50% of the total animal protein source of the human diet. It is noteworthy that, in the African continent, an extreme perishability of fish and cold storage limits could lead to post-harvest losses of fresh fish up to 25% (FAO, 2022). Indeed, in regions of West Africa and in tropical countries, difficulties in maintaining refrigerated conditions and shortage of ice constitute the main problems for fresh fish storage and consumption (Anihouvi, Sakyi-Dawson, Ayernor, & Hounhouigan, 2007). To overcome this issue, treatments as drying, smoking, salting, grilling, frying, and fermentation, or a combination of these processes, are usually applied to fresh fish, thus leading to the production of many fish-based foods (Anihouvi et al., 2006; Koffi-Nevry, & Koussémon,

2012).

Among fermented fish-based products manufactured in countries of West Africa, Lanhouin, originated in the coastal regions of the Gulf of Benin, is commonly used as a condiment in urban and rural areas in Southern Benin and in Togo and Ghana (Anihouvi et al., 2006; Anihouvi, Kindossi, et al., 2012). Moreover, in Ghana, the so-called Momone, or Momoni, is popularly used as condiment for the consumption of yam, cocovam and others unripe plantain, and flavouring stews and soups (Sanni et al., 2002; Adadi et al., 2019). Feseekh, also called Fesick or Fesikh, is usually consumed as the main dish in celebratory Egyptian feasts (Amin et al., 2020). Marine fishery products constitute an important animal protein source also in Senegal, where the total of seafood production is mainly realized by artisanal fisheries. In such a country, the most common traditional fermented fish product is represented by Guedi, particularly appreciated by the local populations for its remarkable flavour and taste (Diop et al., 2009; Anihouvi, Kindossi, et al., 2012). Adjuevan is an Ivorian fermented fish product commonly consumed as condiment because of its strong smell (Koffi-Nevry, & Koussémon, 2012; Anihouvi, Kindossi, et al., 2012).

3.2. America

To the authors' knowledge, few scientific studies focused on the microbiota of fermented fish or fermented fish-based products manufactured in the American continent. The available studies were related to a few products obtained from the fermentation of anchovies and sardines.

Anchovies (*Engraulis* spp.) are frequently used in Argentina, Uruguay, and Peru. Such a small pelagic fish could deteriorate as soon as harvested, due to the presence of highly active enzymes with proteolytic and lipolytic action. To overcome this concern, salting and fermentation guarantee the increase of the shelf-life of the product as well as the formation of pleasant sensory traits. The final product is marketed as "canned anchovies". Sardines (*Sardinella brasiliensis*) were highly consumed in Brazil for decades and, to date, they have a steady consumption market. The final product is commercialized in the form of canned sardines or salted-pressed sardines (Perez et al., 2018; Oetterer et al., 2003; Hernandez-Herrero et al., 2002).

3.3. Asia

Asia certainly represents the most heterogeneous and rich continent in terms of fermented fish products, especially in the Southeast Asian countries, where they are widely distributed in rural and urban markets (Arcales, & Alolod, 2018). The different varieties of fermented fish products were named in accordance with local traditions, hence, sometimes, the same food products have different terms.

Among the abovementioned delicatessen, fish sauce is a clear reddish-golden or brown liquid largely used as condiment and characterized by a strong umami taste. Its name varies depending on the country of origin, with more than eight different variants of Asian fish sauces. The distinctive flavour of such food preparation is obtained through a spontaneous long-term fermentation that determines a proper protein hydrolysis induced by endogenous proteinases of fish and microbial proteinases, and the development of typical flavour and colour characteristics (Dissaraphong, Benjakul, Visessanguan, & Kishimura, 2006; Wang et al., 2018; Ohshima et al., 2019).

Thailand is included in the lower Mekong subregion of Southeast Asia, along with Cambodia, Myanmar, Vietnam, and Laos. The tropical monsoonal climate of this subregion is typically warm and highly humid, so food preservation becomes pivotal to maintain the edibility and safety of food supplies, especially in rural areas. *Plaa-som*, also called *Pa-som* in Laos, is a Thai fermented fish whose production varies depending on family or local preferences (Saithong et al., 2010; Kopermsub, & Yunchalard, 2010; Marui et al., 2014). *Som-fug*, similarly to *Som-fak*, is served as a main dish or as an accompaniment with

Table 1

Most relevant traditional fermented fish-based products realized worldwide.

Country	Product name	Fish species	Other ingredients	Production steps	Treatment times	References
AFRICA Benin, Togo, Ghana	Lanhouin	Pseudotolithus spp. Scomberomorus tritor	Salt (5–30%)	Scaling, gutting and washing. Curing step overnight. Salting and fermentation. Washing by water added	Fermentation: 3–8 days Drying: 2–4 days	Anihouvi, Ayernor, Hounhouigan, & Sakyi-Dawsor (2006), Anihouvi, Kindossi, and Hounhouigan (2012)
Ghana	Momone Momoni	Caranx hippos	Salt (30%)	with fuel. Sun-drying. Scaling, gutting, and washing. Salting and fermentation. Washing in brine, rubbing with salt and cutting into small pieces.	Fermentation: 7 days Drying: few hours	Sanni, Asiedu, & Ayernor (2002)Adadi, Barakova, & Krivoshapkina (2019)
Egypt	Feseekh Fesick	Mugil cephalus	Salt	Sun-drying. Cleaning and resting step. Salting by layers and	Resting: n.s. Fermentation: 15	Amin, Ahmed, & Attia (2020) Mohamed, Livia, Hassan, Soher
Senegal	Fesikh Guedj	Podamasys jubelini Arius heudelotii	Salt (30-40%)	fermentation in jars. Scaling, salting and fermentation. Sun-drying. Fermentation overnight. Salting and sun-drying.	days to 3 months Fermentation: 2–3 days or 1 day Drying: 3–5 days	& Ahmed-Adel (2009) Diop, Dubois-Dauphin, Destain Tine, & Thonart (2009), Anihouvi, Kindossi, and Hounhouigan (2012)
Ivory Coast	Adjuevan	Chloroscombrus chrysurus	Salt	Scaling, cutting and salting (exudates are retained in a vat). Fermentation in resulting percolate. Sun-drying.	Fermentation: 12–48 h Drying: 2–7 days	Anihouvi, Kindossi, and Hounhouigan (2012)
AMERICA Argentina, Uruguay, Peru, Brazil	Canned anchovies or sardines	Engraulis spp. Sardinella brasiliensis	Salt (20%)	Washing and pre-salting. Beheading, gutting and fermentation. Desalting, filleting and packing into cans under brine or oil.	Pre-salting: minimum 24 h Fermentation: some weeks to 1 year	Kim et al. (2004)Oetterer et al. (2003)Perez et al. (2018)
ASIA						
Thailand	<i>Nam-Pla</i> (fish sauce)	Stolephorus spp.	Salt (30%)	Washing and salting. Fermentation in tank.	Fermentation: 15 months	Ohshima et al. (2019)
Korea	<i>Aekjeot</i> (fish sauce)	Engraulis japonicus	Salt (25%)	Salting (addition of solar salt solution). Fermentation in tank.	Fermentation: 6–7 months	Lee, Jung, & Jeon (2015)Koo et al. (2016)
Malaysia	<i>Budu</i> (fish sauce)	Stolephorus spp.	Salt (15–25%) TamarindCoconut sugar	Salting (immersion in brine). Fermentation in earthen containers.	Fermentation: 6–12 months	Zoqratt, & Gan (2021)Liasi et al (2009)
China	<i>Yu-Lu</i> (fish sauce)	Stolephorus spp.	Salt (20-30%)	Salting and fermentation in tank.	Fermentation: 12–18 months	Jiang, Zeng, Zhu, & Zhang (2007)Wang et al. (2018)
Iran	<i>Mahyaveh</i> (fish sauce)	Sardinella spp. Stelophorus spp.	SaltMustard (Brassica juncea)	Beheading and washing. Salting (immersion in brine) and fermentation in earthenware or glass jars. Mashing and filtering.	Fermentation: 25–30 days	Zarei et al. (2012)
Vietnam	<i>Nuoc Mam</i> (fish sauce)	Engraulis spp.	Salt (25–33%)	Salting and fermentation in wood, ceramic or cement vessel. Draining and filtering to obtain a transparent liquid.	Fermentation: 12–18 months	Anh (2015)
Indonesia	<i>Kecap Ikan</i> (fish sauce)	Stolephorus spp. Clupea spp. Leiognathus spp. Sardinella spp. Caranx spp. Puntius spp. Osteochilus spp.	Salt (20–30%) Brown sugar Spices	Gutting, washing and mincing. Salting and fermentation in tank. Filtering and addition other ingredients.	Fermentation: 4–12 months	Huda (2012)
Cambodia	Toeuk Trey (fish sauce)	n.s.	Salt (30%)	Salting and fermentation in tank. Collection of supernatant	Fermentation: maximum 1 year Drying: 1–4 months	Chuon et al. (2013)
Philippines	Patis	Clupeidae spp., Engraulidae spp., Leiognathidae spp.,	Salt (25–30%)	and sun-drying. Washing and salting. Fermentation until liquid forms on the top of	months Fermentation: 1–2 years	Olympia (1992)

Table 1 (continued)

Country	Product name	Fish species	Other ingredients	Production steps	Treatment times	References
mi i i	DI G			mixture. Draining and filtering.	D	
Thailand	Plaa-Som Pla-Som Pa-Som	n.s.	Salt Sugar Cooked or steamed sticky rice Garlic	Scaling, gutting and washing. Salting and resting step. Washing and addition of salt, sugar and rice. Fermentation in wrapped package.	Resting: 1–3 h Fermentation: 3–5 days	Saithong et al. (2010) Kopermsub, & Yunchalard (2010)Marui et al. (2014) Hwanhlem et al. (2011)
Thailand	Som-Fug Som-Fak	Cirrhinus microlepis	Salt Garlic Boiled rice	Frying or roasting. Addition of garlic, salt and rice to minced fish. Fermentation in wrapped package (banana leaves or plostic hogo)	Fermentation: 2–5 days.	Kongkiattikajorn (2015), Paludan-Müller, Valyasevi, et al. (2002)
Thailand, Laos	Pla-Ra Pa-Daek	n.s.	Salt Rice bran or roasted rice powder	plastic bags). Scaling, gutting and washing. Addition of salt and rice bran or roasted rice powder. Fermentation.	Fermentation: 6–12 months	Marui et al. (2015)Rodpai et al. (2021)
India	Shidal Shidol Seedal Ngari Telesech	Puntius sophore Setipinna phasa Gudusia chapra	Fish oil (extracted from the entrails of fresh fish) or vegetable oil	Washing and sun-drying. Rapid soaking and drying steps. Fermentation in earthen pots saturated with fish oil.	Drying: 4–5 days Fermentation: 3–6 months	Kakati, & Goswami (2013a)
India	Lonailish	Tenualosa ilisha	Salt	Washing, scaling and beheading. Cutting into diagonal steaks and salting. Drying in bamboo basket. Fermentation in tin filled with boiled and cooled brine.	Drying: 1–2 days Fermentation: 4–6 months	Kakati, & Goswami (2013a)
India	Tungtap	Puntius spp. Danio spp.	Salt (10%) Fish fat	Washing and sun-drying. Addition of fish fat and fermentation in earthen pot.	Drying: 3–4 days Fermentation: 3–6 months	Kakati, & Goswami (2013a)
India	Hentak	Esomus danricus Puntius sophore	Alocasia macrorhiza Onion	Sun-drying. Crushing of dried fish into powder. Addition of aroid plant and onion. Fermentation in earthen pot.	Drying: n.s. Fermentation: 15–20 days	Singh, De Mandal, Lalnunmawii, et al. (2018)
India	Utonga-Kupsu	Esomus danricus Puntius sophore Amblypharyngodon mola Channa punctata Mystus vittatus	Alocasia macrorhiza Mustard oil	Sun-drying. Crushing of ingredients into paste. Fermentation in earthen pot.	Drying: n.s. Fermentation: 1 month	Singh, De Mandal, Lalnunmawii, et al. (2018)
Japan	Narezushi	Carassius carassius (Funazushi) Trachurus japonicas (Aji- Narezushi) Scomber japonicus (Saba- Narezushi) Cololabis saira (Samma- Narezushi) Seriola quinqueradiata (Kaburazushi)	Salt Cooked rice Pepper leaves Red pepperFermented rice or barley (only for <i>Kaburazushi</i>)	Gutting and placing in a barrel. Covering with ingredients and fermentation.	Fermentation: 5 days to 2 months	Koyanagi et al. (2011)Doi et al. (2021)Kuda, Kaneko, Yano, & Mori (2010)
Japan	Kusaya	Decapterus spp.	Salt	Fermentation in tank containing brine stored underground. Drying.	Fermentation: n.s. Drying: n.s.	Fujii et al. (2016)
Japan	Nukazuke	Sardinops melanosticus (Iwahi-Nukazuke) Scomber japonicas (Saba- Nukazuke)	Salt Rice bran	n.s.	Fermentation: n.s.	Kuda et al. (2012)
Korea	Myeolchi-Jeot	Engraulidae spp.	Salt (20–30%)	Washing and draining. Salting by layers and fermentation.	Fermentation: 2–3 months	Koo et al. (2016)
Korea	Hongeo	Raja kenojei		Fermentation in ceramic jar.	Fermentation: 7–14 days	Zhao, Kim, & Eun (2019)Zhao, & Eun (2020)

Table 1 (continued)

Country	Product name	Fish species	Other ingredients	Production steps	Treatment times	References
Korea	Kajami-Sikhae Gajami-Sikhae	Verasper variegatus Glyptocephalus stelleri	Salt (5–10%) Cooked grain Red pepper powder White radish Garlic Ginger	Salting and resting step. Addition of other ingredients and fermentation.	Resting: 1 day Fermentation: 2 weeks	Koo et al. (2016)Kim, Won, Yang, Kim, & Kim (2022)Kim, Kim, Turner, Kim, et al. (2014) Kim, Kim, Turner, and Lee (2014)
ndonesia	Terasi	Stolephorus spp. Engraulis spp.	Green onionBoiled millet Salt (2–5%)	Washing, sun-drying and resting step overnight. Pounding, salting, repeated sun-drying and storage (twice)	Sun-drying: n.s. Storage: 2–3 days Fermentation: 1–2 weeks	Huda (2012)Rahayu (2003)
ndonesia	Peda	Rastrelliger neglectus	Salt (20–30%)	Grounding and fermentation. Salting.	Fermentation: 3	Rahayu (2003)
				Fermentation in sealed container. Washing and repeated salting.	days Repeated fermentation: 1–3 weeks	
ndonesia	Wadi	Anabas testudineus	Salt (10–20%) SugarCarbohydrate-based additive	Repeated fermentation. Salting and resting step. Addition of other ingredients and fermentation.	Resting: 1 day Fermentation: 7–14 days	Soemarie, Milanda, & Barliana (2022) Rahayu (2003)
Philippines	Bagoong	Clupeidae spp., Engraulidae spp., Leiognathidae spp., Sparidae spp.	Salt (25–30%)	Washing and salting. Fermentation until development of characteristic flavor.	Fermentation: several months	Olympia (1992)
Philippines	Burong Isda	Chanos chanos (Burong Bangus) Therapon plumbeus (Burong Ayungin) Osphronemus goramy (Burong Gurami) Tilapia nilotica (Burong Tilapia) Ophicephalus striatus (Burong Dalag) Clarias batrachus (Burong Hito) Arias manillensis (Burong Kanduli)	Salt Cooked rice	Washing, scaling, gutting and filleting. Salting and resting step overnight. Addition of cooked rice, packing in glass jar and fermentation.	Fermentation: 7–10 days	Olympia (1992)Arcales, & Alolod (2018)
China	Suan Yu Suanzhayu Suan Zuo Yu	Cyprinus carpio	Salt (3%) Sugar Cinnamon Star anise Wild pepper Ground roasted carbohydrate	Washing, scaling, gutting and filleting. Salting, addition of sungar and spices, and curing step. Drying of exudates. Addition of ground roasted carbohydrate and fermentation in tank.	Curing: 12–24 h Drying: n.s. Fermentation: 1–2 months	Sun, Liu, Wang, Sang, & Sun (2022),Meng, Yang, Wan, Zhu & Zeng (2022)Zeng, Xia, Jiang & Yang (2013b)
China	Chouguiyu	Siniperca chuatsi	Salt (6%) Fennel Cumin Star anise Chinese prickly ash Paprika Ginger Shallot Red pepper	Scaling, gutting and cleaning. Preparation of pickling solution with the other ingredients. Fermentation in jar filled with pickling solution.	Fermentation: 1–2 weeks	Xu et al. (2022)Yang et al. (2021)Yang, Li, et al. (2020) Dai, Wu, & Zhao (2013)
China	Zаоуи	Scomber japonicus Miichthys miiuy Trichiurus lepturus Muraenesox cinereus Pneumatophorus japonicus	Salt vinasse (fermented rice)	Filleting to collect dorsal muscle and washing. Salting, curing and draining. Addition of vinasse and fermentation.	Curing: 3 h Draining: 12 hFermentation: n. s.	Chen et al. (2022)Chen et al. (2021)
China	Yucha	n.s.	Salt Cooked rice Hot pepper	Cutting, salting and curing step. Draining, addition of other ingredients and fermentation in jars.	Curing: 1–2 h Fermentation: 3–5 weeks	Hu et al. (2016) Zhang et al. (2016)
Myanmar	Ngachin Pazun-Chin Ngagyin-Chin Ngaphae-Chin	Puntius schwanenfeldii Metapenaeus monoceros Cirrhinus mrigala Notopterus notopterus	Salt Boiled rice	n.s.	n.s.	Moe, Thwe, et al. (2015)

Table 1 (continued)

Country	Product name	Fish species	Other ingredients	Production steps	Treatment times	References
Myanmar	Ngapi Yegyo Ngapi	n.s.	Salt	Sun-drying and partial pounding. Salting and fermentation.	Drying: n.s. Fermentation: 4–6 months	Kobayashi et al. (2016)
Bangladesh	Chepa Shutki	Puntius stigma Puntius ticto Puntius sophore	Oil	Collection of fish abdominal oil. Washing and sun-drying. Soaking with water. Fermentation in oil- soaked vat.	Drying: 5 days Fermentation: 5 months	Nahar, Sayeed, et al. (2017)
Saudi Arabia	Hout-Kasef	Valamugil scheli	Salt	Cleaning, gutting and salting. Fermentation in wooden box.	Fermentation: minimum 1 month	Gassem (2019)
Cambodia	Prahok	Channa striata	Salt (15–20%)	Salting and pounding. Fermentation.	Fermentation: 20 days to 3 months	Chuon et al. (2013)
<i>EUROPE</i> Norway	Rakfisk	Salvelinus namaycush Salvelinus alpinus	Salt (4–7%)	Gutting and salting. Fermentation in container. Soaking with brine during fermentation.	Fermentation: 3–12 months	Bjerke et al. (2019)Skåra et al. (2015)
Iceland	Hákarl	Somniosus microcephalus		Cutting into chunks and washing. Fermentation in container. Cutting into small pieces and drying in shed.	Fermentation: 3–6 weeksDrying: n.s.	Skåra et al. (2015)Osimani et al (2019)
Sweden	Surströmming	Clupea harengus	Salt (17% in weaker brine)	Salting (immersion in saturated brine). Deheading, gutting (gonads and pyloric ceca are retained)	Salting: 1–2 days Fermentation: 3–12 weeks	Skåra et al. (2015)Belleggia et al. (2020)
Netherlands	Maatjes	Clupea harengus	Salt (2%)	Fermentation in barrel under weaker brine. Gutting and beheading. Salting (immersion in brine) and fermentation.	Fermentation: 1 day	Lyhs, Lahtinen, & Schelvis-Smi (2007)

vegetables (Kongkiattikajorn, 2015). Another popular Thai fermented fish is *Pla-ra*, also called *Pa-daek* in Laos, characterized by intense salty and sour flavours, depending on the amount of added salt and the fermentation time (Marui et al., 2015).

The use of preservation of fish through fermentation is an ancient practice also in Northeast India. Such a geographical area includes more than a hundred tribal groups, each with its own tradition and food culture. The production of these foods generally takes place in tribe households, following a process handed down from generation to generation. Hence, a fair variety of fermented fish products are realized, among these: i) *Shidal*, also called *Shidol*, *Seedal*, *Ngari*, or *Telesech*, ii) *Lonailish*, iii) *Tungtap*, iv) *Hentak*, and v) *Utonga-kupsu* (Kakati, & Goswami, 2013a; Singh, De Mandal, Lalnunmawii, et al.. 2018).

Sushi, the typical Japanese dish renowned worldwide, originates from a salted fermented fish, named *Narezushi*, that is popular in several areas of Japan. In ancient times, *Narezushi* was prepared using freshwater fish from inland rivers, but during the past half-century also marine fish was used due to increasing demand of the raw material. *Narezushi* is usually consumed for its beneficial effects on human health, as it is known to be an intestinal regulator, and its cultural significance, as it is eaten during local village festivals held with the arrival of autumn (Kuda et al., 2009; Matsui, Tsuchiya, Isobe, Maeda, & Narita, 2008; Koyanagi et al., 2011). Noteworthy, there are other fermented fishbased foods belonging to Japanese culture, including *Kusaya* and *Nukazuke* (Fujii et al., 2016; Kuda et al., 2012).

Doubtless, the most popular fermented fish food in Korea is *Jeotgal*, or *Jeot*. Of note, there are more than 160 different kinds of *Jeotgal*, of which about 30 are to date commercialized. Such a food preparation is frequently used as a side dish; in addition, it can also be used as ingredient or condiment for *kimchi* and other traditional Korean foods. Among all the variants, the most popular are *Myeolchi-Jeot*, *Hongeo*, and *Sikhae* (Koo et al., 2016).

In Indonesia, characterized by a high production of marine fish, different popular traditional fermented fish-based preparations were developed. Among them, *Terasi, Peda*, and *Wadi* represent the most popular products (Huda, 2012; Soemarie et al., 2022; Rahayu, 2003).

Based on the final concentration of salt, fermented fish products of the Philippines are distinguished into two groups. In more detail, the first group includes fermented fish containing from 15 to 20% of salt, such as *Bagoong* and *Patis* that are commonly used as condiments; the second group includes *Burong Isda* and its numerous variations (Olympia, 1992; Arcales, & Alolod, 2018).

Regarding Chinese fermented fish products, the scientific literature reported some studies focusing on i) *Suan Yu*, a low-salted fermented whole fish snack, known for its non-fishy flavour, that maintains all the nutritional qualities of the raw material compared with other similar products; ii) *Chouguiyu*, also called stinky madarinfish, recognised for its unique firm but tender texture and singular strong odour; iii) *Zaoyu*, renowned for its pleasant aroma derived from the addition of the fermented steamed glutinous rice vinasse; iv) *Yucha*, the most popular supplementary food of the Li population in the Hainan province (Zeng et al., 2013b; Dai et al., 2013; Chen et al., 2021; Hu et al., 2020).

Finally, other fermented fish preparations from Myanmar (*Ngachin*, *Ngapi*, etc.), Cambodia (*Prahok*), Bangladesh (*Chepa Shutki*), and Saudi Arabia (*Hout-Kasef*) were studied, although limited information on these preparations is available in the scientific literature.

3.4. Europe

Salting represented an effective strategy for food preservation also in Northern European countries where such a technique was applied since the Viking Era (Belleggia et al., 2020). It is noteworthy that, due to the limited availability of salt in Scandinavian Peninsula and Iceland, new preservation methods based on empirical approaches were developed in those geographical areas (Skåra et al., 2015). Hence, the use of low quantity of salt, coupled with newly developed processes, have led to the production of unique fish-based delicacies characterized by peculiar sensory traits.

Rakfisk is a Norwegian fermented fish, traditionally eaten from late autumn and during Christmas season, whose production remains mostly localized in the inland area of the country. *Rakfisk* is characterized by peculiar taste, odour, and spreadable texture (Skåra et al., 2015; Bjerke et al., 2019).

During the fourteenth century, shark fishing became a common practice in Iceland. Fermented shark, also known as *Hákarl*, represented a key element of the Icelanders diet for centuries. *Hákarl* is characterized by a soft texture, a cheesy appearance, a pungent ammonia smell, and a firm fishy taste (Skåra et al., 2015; Osimani et al., 2019).

Baltic herring is among the most representative species of the Baltic Sea, due to its ubiquity and abundance. During the sixteenth century, on the Swedish coast of the Gulf of Bothnia, the art of herring preservation by local people gave birth to the so-called *Surströmming*. This latter preparation is a wine-coloured product with a notorious odour, as much that its consumption could represent a real challenge (Skåra et al., 2015; Belleggia et al., 2020).

Baltic herring is also used for the preparation of *Maatjes*, a low salted fish product popular in the Netherlands. The herring is typically caught between May and July, just before its spawning, as it contains the most suitable amount of subcutaneous fat, comprised between 16 and 20% (Lyhs et al., 2007).

4. The microbiota of fermented fish and fermented fish-based products

Microbiological data collected from 168 selected research papers regarding the microbiota composition of fermented fish-based products are summarized in Table 2.

In the reviewed literature, culture-dependent analyses mainly consisted of microbiological viable counts that allowed an imprint of the main microbial populations involved in the fermentative process to be obtained. The results emerged from viable counts highlighted the occurrence of several emblematic microbial groups typically associated with food fermentation, including lactic acid bacteria, Staphylococcus spp., Bacillus spp., and yeasts, albeit with highly heterogenous loads. First, the determination of total aerobic mesophilic bacteria was widely assessed in fermented fish-based products and confirmed an intense microbial activity with counts up to 9.3 Log colony forming units (cfu) g^{-1} . Of note, viable counts of total halophilic bacteria, extremely favoured by the common addition of salt in this kind of preparations, were frequently performed, with values up to 7.5 Log cfu g^{-1} . Significantly, the fermentation process of fish-based preparations was dominated by lactic acid bacteria irrespective of the type of fermented food, with counts up to 9.5 Log cfu g⁻¹. Moreover, species of Staphylococcus and Bacillus were commonly detected, with values up to 5.9 and 5 Log cfu g^{-1} , respectively. Lactic acid bacteria, *Staphylococcus* spp., and *Bacillus* spp. were strictly associated with the development of the sensory, nutritional, and hygienic quality of many fermented foods (Admassie, 2018; Heo, Lee, & Jeong, 2020; Kimura, & Yokoyama, 2019).

As for potentially pathogenic bacterial groups, viable counts were regularly carried out to evaluate safety risks associated with fermented fish-based products. In most of the cases, Enterobacteriaceae, coliforms, *Yersinia* spp., *Salmonella* spp., *Escherichia coli, Campylobacter* spp., *Listeria* spp., and *Clostridium perfringens* were not detected in the end products. The absence of pathogens was attributed to the addition of salt, confirmed as one of most efficient strategies to inhibit the growth and survival of undesired microorganisms. Noteworthy, at the beginning of the production process of fish-based products, the presence of Enterobacteriaceae was constantly documented, with viable counts up to 6 Log cfu g⁻¹ (Hua, Sun, Xu, Gao, & Xia, 2022; Hua et al., 2020; Liu et al., 2021; Zeng et al., 2013b; Hwanhlem, et al., 2011). Since

Enterobacteriaceae were reported as the main microbial group involved in BAs production in aquatic products (Visciano, Schirone, & Paparella, 2020), the use of selected pro-technological strains capable of rapidly guide the fermentation process and inhibit spoilage and pathogenic bacteria was suggested by many authors (Hua et al., 2022; Hua et al., 2020; Liu et al., 2021; Zeng et al., 2013b; Hwanhlem, et al., 2011). The detection of the foodborne pathogens *Staphylococcus aureus* and *Bacillus cereus* via viable counting was occasionally reported (Fall et al., 2017; Taorem, & Sarojnalini, 2012; Sarojnalini, & Suchitra, 2009; Pongsetkul, & Benjakul, 2021; Kakati, & Goswami, 2013b; Thapa et al., 2004). The presence of these pathogens in fermented fish-based products is related to the ability of both species to tolerate and grow under salt concentrations higher than 7% (Rajkowski, & Bennett, 2003; Schleifer, & Bell, 2015).

As for yeasts, counts up to 8.7 Log cfu g^{-1} were reported. Yeasts represent one of the predominant microbial populations in fermented foods and are usually implied in sensory quality enhancement through remarkable lipolytic and proteolytic actions (Hua et al., 2022).

Finally, the occurrence of moulds, that are commonly associated with food deterioration, discoloration, aroma and taste worsening, and shelf-life reduction, was generally not reported (Osimani et al., 2016).

The combination of culture-dependent and -independent methods, these latter based on the identification of microbial genomic conserved regions, usually offers more accurate results for the study of the microbiota of complex food matrices (Belleggia et al., 2020). Hence, a comprehensive description of the microbial taxa mainly detected via isolation or through metataxonomic analyses, together with their potential role during fermentation of fish and fish-based products, follows.

4.1. Lactic acid bacteria

Lactic acid bacteria comprise a group of Gram-positive microorganisms growing under microaerophilic to strictly anaerobic conditions with common metabolic and physiological characteristics. The scientific interest on these microorganisms was usually associated with their fermentative activity and probiotic potential, but also with the production of valuable metabolites used as nutraceuticals, pharmaceutics, commodity chemicals, and flavour or aroma compounds. Moreover, during the fermentative process, lactic acid bacteria can synthetize antimicrobial substances, including organic acids, hydrogen peroxide and bacteriocins, that inhibit the proliferation of spoilage and pathogenic bacteria (Sharma, Kaur, Lee, & Park, 2019; Putra et al., 2018). The metabolism of lactic acid bacteria allows a rapid conversion of sugars to lactic acid, acetic acid, acetaldehyde, ethanol, and diacetyl. However, in absence of a carbohydrate source, as in most of fermented fish and fishbased products, they can exploit an elaborate proteolytic system to completely break down proteins and peptides into free amino acids (Hugenholtz & Kleerebezem, 1999). The latter are then used through decarboxylase and deaminase enzymes for energy production, along with the formation of flavours components or biogenic amines (Zuljan et al., 2016).

The predominance of lactic acid bacteria in most of fermented fish and fish-based products suggested their occurrence in the raw materials and thus in the aquatic environment. Noteworthy, lactic acid bacteria considerably differ in morphology and tolerance to temperature, pH, and salt levels (George et al., 2018). The great heterogeneity of this microbial group was also reflected in the lactic acid bacteria populations present in fermented fish-based preparations. Among the predominant communities, lactobacilli (Zheng et al., 2020) and *Tetragenococcus* spp. were certainly the most represented. The parting line between the predominance of lactobacilli or *Tetragenococcus* spp. was presumably the salt concentration of approximately 10% (Marui et al., 2015). As confirmed in most of the scientific studies reported in Table 2, *Tetragenococcus* spp. were frequently detected as the main fermentative bacteria involved in fish sauces and other high-salt foods, whereas lactobacilli species dominated in low-salt fish-based foods such as the

Table 2

Microbiological data collected from 168 selected research papers regarding the microbiota composition of fermented fish-based products.

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
AFRICA Benin	Pseudotolithus spp. Scomberomorus tritor	Lanhouin	Collected from market and processing plant (end products)	Viable counts		Total aerobic mesophilic bacteria (6.0–7.0). Total halophilic bacteria (5.0–5.8). <i>Micrococcus</i> spp. (5.0–5.4). <i>Bacillus</i> spp. (3.7–4.1). Coliforms (<1). <i>Escherichia coli</i> (<1). <i>Clostridium</i> spp. (1.6–1.8). <i>Salmonella</i> spp. (abs.). <i>Staphylococcus aureus</i> (abs.). Malda			Anihouvi et al. (2006
3enin	Pseudotolithus spp.	Lanhouin	Processed by scientific laboratory	Viable counts. Phenotypical and physiological characterization of isolates		(abs.). Molds (<1) Total aerobic mesophilic bacteria (4.9). Total halophilic bacteria (4.7). <i>Micrococcus</i> spp. (4.0). <i>Bacillus</i> spp. (5.0). Bacterial endospores (2.0–3.0). Enterobacteriaceae (<1). Yeast	Bacillus spp., Bacillus subtilis, Bacillus licheniformis, Bacillus megaterium, Bacillus mycoides, Bacillus cereus, Corynebacterium spp., Micrococcus spp., Micrococcus luteus, Staphylococcus spp., Staphylococcus spp., Staphylococcus syp., Staphylococcus syp.		Anihouvi et al. (200'
Egypt	Chelon ramada	Fesikh	Collected from market (raw materials) Processed by scientific laboratory	Viable counts		 (<1). Total aerobic mesophilic bacteria (<1). Lactic acid bacteria (<1–5.5). 			Amin et al. (2020)
Ghana	Caranx hippos	Momoni	Collected from market (end products)	Viable counts. Phenotypical characterization of isolates		Total aerobic mesophilic bacteria (8.4). Non-fastidious bacteria (6.1). Lactic acid bacteria (4.7). Enterobacteriaceae (2.8). Yeasts (2.8). Molds	Bacillus megaterium, Bacillus subtilis, Bacillus polymyxa, Bacillus licheniformis, Lactobacillus brevis, Lactobacillus plantarum, Pseudomonas fluorescens, Pediococcus acidilactici, Staphylococcus spp., Klebsiella spp.	Debaryomyces hansenii, Hansenula anomala, Aspergillus flavus	Sanni et al. (2002)
Ivory Coast	Galeoides decadactylus	Adjuevan	Collected from producer (end products)	Viable counts	PCR-DGGE	(1.8). Yeasts (2.8–6.3).		Debaryomyces spp., Debaryomyces hansenii, Hansenula anomala,	Clementine et al. (2012)

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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
								Saccharomyces cerevisiae, Candida tropicalis, Candida zeylanoides, Pichia fermentans, Kluyveromyces spp., Kluyveromyces marxianus, Hanseniaspora osmophila, Rhodotorula glutinis	
Ivory Coast	Chloroscombrus chrysurus	Adjuevan	Collected from producer (end products)	Viable counts. Phenotypical and physiological characterization of Gram-negative bacteria isolates		Total aerobic mesophilic bacteria (5.9). Lactic acid bacteria (4.0). Coliforms (2.0). Enterobacteriaceae (2.7). Eumycetes (1.5).	Escherichia coli, Enterobacter spp., Proteus spp., Klebsiella spp., Serratia marcescens, Salmonella spp., Salmonella arizonae, Pseudomonas spp., Pseudomonas fluorescens		Koffi-Nevry, & Koussémon (2012)
vory Coast	Chloroscombrus chrysurus	Adjuevan	Collected from producer (end products)	Viable counts. Phenotypical characterization of isolates		Lactic acid bacteria (5.1).	Leuconostoc lactis, Lactobacillus fermentum, Pediococcus spp., Streptococcus spp.		Koffi-Nevry, Ouina, Koussémon, & Brou (2011)
Nigeria	Sardinella sp.		Collected from market (raw materials) Processed by scientific laboratory	Viable counts		Total aerobic mesophilic bacteria (2.3–2.5).			Achinewhu, & Oboh (2002)
Vigeria	Sardinella sp.		Collected from market (raw materials). Processed by scientific laboratory	Viable counts. Phenotypical and physiological characterization of isolates		Non-fastidious bacteria (4.7–5.8). Gram-negative bacteria (4.6–5.8)	Staphylococcus epidermidis, Bacillus licheniformis		Achinewhu, Amadi, Barimalaa, & Eke (2004)
Nigeria	Chrysichthys nigrodigitatus		Collected from natureProcessed by scientific laboratory	Viable counts		Total aerobic mesophilic bacteria (5.0–5.9).			Oyelese, Sao, Adeuya & Oyeleye (2013)
Senegal	Arius latisculatus Pseudotolithus brachygnatus Pomadasys jubelini	Guedj	Collected from processing plants and laboratory (end products)	Viable counts		Total aerobic mesophilic bacteria (3.5–7.5). Lactic acid bacteria (<1–5.7). Coliforms (<1–4.7). <i>Staphylococcus aureus</i> (<2–2). Sulphite- reducing cancerbia			Fall et al. (2017)

reducing anaerobic bacteria (<1–3.1). *Salmonella* spp. (abs.). Eumycetes

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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
						(<1–2.4). Vibrio pathaemolyticus			
AMERICA						(abs.).			
Argentina	Engraulis anchoita		Collected from nature. Processed by scientific laboratory	Viable counts Phenotypical and physiological characterization of isolates		Total halophilic bacteria (~4). <i>Staphylococcus</i> spp. (~4).	Salinicoccus spp., Micrococcus spp., Mesophilobacter spp., Paracoccus spp., Marinobacter spp.		Czerner, & Yeannes (2014)
Argentina	Engraulis anchoita		Collected from factories (end products)	Phenotypical and physiological characterization of isolates			Halococcus spp.		Felix, Czerner, Ameztoy, Ramirez, Yeannes (2016)
Argentina	Engraulis anchoita		Collected from processing plant (end products)	Viable counts		Total halophilic bacteria (4.4).			Perez et al. (2018)
Argentina	Engraulis anchoita		Collected from industry (end products)	Phenotypical and physiological characterization of isolates. Sequencing of 16S rRNA regions of isolates			Halobacterium spp., Halomonas spp., Halovibrio spp.		Perez, Murialdo, Ameztoy, Zaritzky, Yeannes (2020)
Brasil	Sardinella brasiliensis		Collected from nature. Processed by scientific laboratory	Viable counts		Total aerobic mesophilic bacteria (~3). Total halophilic bacteria (~3). Coliforms (<1). Escherichia coli (abs.). Staphylococcus aures (abs.). Salmonella spp.			Oetterer et al. (200
Oregon	Merluccius productus		Collected from processing plant. Processed by scientific laboratory	Viable counts. Phenotypical and physiological characterization of isolates		(abs.). Total halophilic bacteria (<1).	Micrococcus kritinae, Staphylococcus xylosus, Staphylococcus equorum, Bacillus spp.		Lopetcharat & Park (2002)
ASIA Bangladesh	Puntius sophore	Chepa shutki	Collected from producer and retailer (end products) Processed by scientific laboratory	Viable counts		Total aerobic mesophilic bacteria (6.0–8.1).			Nahar, Sayeed, et a (2017)
Cambodia		Prahok Toeuk Trey	Collected from plants and factories	Viable counts. Phenotypical and physiological characterization of isolates. Sequencing		Total aerobic mesophilic bacteria (2.0-7.0). Total halophilic bacteria (<1-6.0). Yeasts (<1-2.0).	Tetragenococcus spp., Clostridium spp., Staphylococcus spp., Bacillus spp., Virgibacillus spp., Lysinibacillus spp., Psychrobacter spp.,	Rhodotorula spp., Candida spp.	Chuon et al. (2013)

Table 2	l (contin	ued)
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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
				of 16S rDNA regions of isolates			Halobacillus spp., Alkalibacterium spp., Kocuria spp., Lentibacillus spp., Micrococcus spp.		
China	Scomber japonicus	Ζаоуи	Collected from market (raw materials). Processed by scientific laboratory	Viable counts	High-throughput sequencing of 16S rRNA regions of samples	Total aerobic mesophilic bacteria (6.7).	Lactobacillus spp.		Chen et al. (2022)
China	Synchiropus splendidus	Chouguiyu	Collected from factory (end products)	Viable counts Phenotypical characterization of lactic acid bacteria isolates Sequencing of 16S rRNA regions of lactic acid bacteria isolatesARDRA		Lactic acid bacteria (6.2).	Lactobacillus sakei, Lactococcus lactis, Lactococcus raffinolactis, Lactococcus garvieae, Macrococcus caseolyticus, Vagococcus spp., Enterococcus hermenniensis, Streptococcus parauberis		Dai et al. (2013)
China	Engraulidae spp.		Collected from factory (end products)		High-throughput sequencing of 16S rRNA regions of samples		Tetragenococcus spp., Pseudomonas spp., Psychrobacter spp., Tissierella spp., Carnobacterium spp., Gallicola spp. Vibrio spp., Pseudoalteromonas spp., Halomonas spp.		Du, Zhang, Gu, Song & Gao (2019)
China		Yucha	Collected from producer (end products)	Viable counts	High-throughput sequencing of 16S rRNA regions of samples	Lactic acid bacteria (7.9).	Lactobacillus spp., Lactococcus spp., Enterococcus spp., Vibrio spp., Acinetobacter spp.		Hu et al. (2020)
China		Yu-Lu	Collected from natureProcessed by scientific laboratory	Viable counts	r. r	Total aerobic mesophilic bacteria (~6).			Jiang et al. (2007)
China		Suanyu	Collected from producer (end products)	Phenotypical and physiological characterization of lactic acid bacteria isolates. Sequencing of 16S rDNA regions of lactic acid bacteria isolates	High-throughput sequencing of 16S rRNA regions of samples		Lactobacillus spp., Lactobacillus plantarum, Lactobacillus brevis, Lactobacillus alimentarius, Lactobacillus farciminis, Lactobacillus acidipiscis, Tetragenococcus spp., Weissella spp., Staphylococcus spp.		Liu et al. (2021)
China			Collected from factory (end products)	Sequencing of 16S rRNA regions of isolates	High-throughput sequencing of 16S rRNA regions of samples		Tetragenococcus spp. Tetragenococcus spp., Halomonas spp., Staphylococcus epidermidis, Staphylococcus captis, Staphylococcus lentus, Acinetobacter spp., Bacillus spp., Halobacillus spp., Jeotgalicoccus spp.,		Ma et al. (2021)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
							Lactobacillus spp., Oceanobacillus spp., Sporosarcina spp., Virgibacillus spp.		
China	Cyprinus carpio L.	Suan Yu	Collected from supermarket (raw materials). Processed by scientific laboratory	Physiological characterization of amine-producing bacteria isolates. Sequencing of 16S rDNA regions of amine-producing bacteria isolates			Enterobacter spp., Enterobacter asburiae, Enterobacter cloacae, Enterobacter ludwigii, Enterobacter hormaechei, Klebsiella aerogenes, Klebsiella aerogenes, Klebsiella pneumoniae, Klebsiella oxytoca, Klebsiella variicola, Morganella morganii, Citrobacter youngae, Citrobacter freundii, Pantoea aggiomerans		Meng et al. (2022)
China	Lateolabrax japonicas		Collected from fish farm (end products)		High-throughput sequencing of 16S and 18S rRNA regions of samples		Clostridiaceae spp., Clostridium spp., Alkalibacillus spp., Hathewaya spp., Lentibacillus spp.	Aspergillus spp.,	Nie et al. (2022)
China	Trachinotus ovatus		Collected from fish farm (raw materials). Processed by scientific laboratory		High-throughput sequencing of 16S rRNA regions of samples		Halobacterium spp., Clostridium spp., Natrinema spp., Alkalibacillus spp., Natrialba spp.,		Qiu et al. (2022)
China	Siniperca chuatsi		Collected from processing plant (raw materials). Processed by scientific laboratory		High-throughput sequencing of 16S rRNA regions of samples		Fusobacterium spp., Psychrilyobacter spp., Psychromonas spp., Arcobacter spp., Acidaminococcus spp., Shewanella spp., Bacteroides spp.		Shen et al. (2021)
China		Suanyu	Collected from farmer (end products)		High-throughput sequencing of ITS regions of samples			Kodamaea spp., Debaryomyces spp., Wallemia spp., Zygosaccharomyces spp., Dipodascaceae spp., Fusarium spp., Alternaria spp., Hyphopichia spp., Lasiosphaeriaceae spp.	Sun, Liu, et al. (202
China	Parabramis pekinensis		Collected from supermarket (raw materials) Processed by scientific laboratory	Viable counts		Total aerobic mesophilic bacteria (\sim 4–9.2), Lactic acid bacteria (\sim 5–9). Pseudomonadaceae (\sim 3–8.1). Coliforms (\sim 3–8.4).			Tian, Gao, Xu, Xia, Jiang (2021)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
China		Yu-Lu	Collected from factory (end products)		High-throughput sequencing of 16S rRNA regions of samples		Halanaerobium spp., Halomonas spp., Fusobacterium spp., Photobacterium spp., Tetragenococcus spp., Halanaerobacter spp., Vibrio spp., Salinivibrio spp.		Wang et al. (2018)
China		Yu-Lu	Collected from factory (end products)		High-throughput sequencing of genomic DNA fragments of samples		Halococcus spp., Halanaerobium spp., Halomonas spp., Tetragenococcus spp., Candidatus Frackibacter		Wang, Li, et al. (2020
China	Cyprinus carpio	Suan Zuo Yu	Collected from market (raw materials). Processed by scientific laboratory		High-throughput sequencing of 16S rRNA regions of samples		spp. Staphylococcus spp., Macrococcus spp., Weissella spp., Lactobacillus spp., Alcanivorax spp.		Wang, Xu, et al. (2020)
China	Siniperca chuatsi		Collected from market (end products)		High-throughput sequencing of 16S rRNA regions of samples		Vibrio spp., Psychrilyobacter spp., Shewanella spp., Fusobacterium spp., Vagococcus spp., Plesiomonas spp., Psychromonas spp., Arcobacter spp., Carnobacterium spp., Citrobacter spp., Acidaminococcus spp., Acinetobacter spp., Streptococcus spp., Lactococcus spp.		Wang et al. (2021)
China	Engraulidae spp.	Yu-Lu	Collected from factory (end products)		High-throughput sequencing of genomic DNA fragments of samples		Halanaerobium spp., Psychrobacter spp., Photobacterium spp., Tetragenococcus spp., Photobacterium spp., Pseudomonas spp., Vibrio spp., Shewanella spp., Halobacterium spp.		Wang et al. (2022)
China			Collected from company (end products)	Sequencing of 16S rDNA regions of protease-producing isolates Real-time PCR			Flatobacterium spp. Bacillus subtilis, Bacillus amyloliquefaciens, Virgibacillus halodenitrificans, Bacillus aryabhattai, Bacillus vallismortis, Bacillus cereus, Bacillus megaterium, Bacillus tequilensis, Bacillus		Xiao et al. (2014)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
							marisflavi, Bacillus methylotrophicus, Bacillus vietnamensis		
China	Siniperca chuatsi	Chouguiyu	Collected from market (raw materials). Processed by scientific laboratory		High-throughput sequencing of 16S rRNA regions of samples		Vibrio spp., Pseudoalteromonas spp., Marinomonas spp., Serratia spp., Shewanella spp., Lactobacillales spp.		Xu et al. (2022)
China	Synchiropus splendidus	Chouguiyu	Collected from market Processed by scientific laboratory		High-throughput sequencing of 16S rRNA regions of samples		Vibrio spp., Fusobacterium spp., Psychrobacter spp., Pseudoalteromonas spp., Psychrilyobacter spp., Arcobacter spp., Oceanisphaera spp.		Yang, Li, et al. (2020
China	Cyprinus carpio L.	Suanzhayu	Collected from market (raw materials). Processed by scientific laboratory		High-throughput sequencing of 16S rRNA and ITS regions of samples		Lactobacillus spp., Staphylococcus spp., Vagococcus spp., Morganella spp., Vibrio spp., Streptococcus spp., Lactococcus spp., Enterococcus spp., Weissella spp., Macrococcus spp., Proteus spp., Peptostreptococcus spp.	Saccharomyces spp., Candida spp., Apiotrichum spp., Trichosporon spp., Debaryomyces spp., Colletotrichum spp., Cryptococcus spp., Verticillium spp., Waitea spp.	Yang, Jiang, et al. (2020)
China	Cyprinus carpio L.	Suan Yu	Collected from market (raw materials)	Sequencing of 16S rDNA regions of amine-producing isolates			Enterobacter spp., Enterobacter asburiae, Enterobacter hormaechei, Enterobacter ludwigii, Enterobacter cloacae, Klebsiella aerogenes, Klebsiella oxytoca, Klebsiella pneumoniae, Morganella morganii, Citrobacter youngae		Yang, Meng et al. (2020)
China	Siniperca chuatsi	Chouguiyu	Collected from ecommerce (end products)		High-throughput sequencing of 16S rRNA and ITS regions of samples		Vagococcus spp., Fusobacterium spp., Psychrobacter spp., Hafnia- Obesumbacterium spp., Lactobacillus spp., Psychrilyobacter spp., Vibrio spp., Shewanella spp., Sedimentibacter spp., Salinivibrio spp., Lactococcus spp.	Mortierella spp., Chaetomium spp., Cladosporium spp., Gibberella spp., Penicillium spp., Aspergillus spp., Wallemia spp., Staphylotrichum spp., Alternaria spp., Plectosphaerella spp.	Yang et al. (2021)
China		Suan Yu	Collected from shops (end products)	Viable counts		Lactic acid bacteria (5.5–7.9)t. <i>Micrococcus</i> spp. (4.1–5.3). Enterobacteriaceae (<1). Pseudomonadaceae			Zeng et al. (2013a)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
China		Suan Yu	Collected from processing plants (end products)	Viable counts Phenotypical and physiological characterization of isolates. Sequencing of 16S and 26S rRNA regions of isolates		 (<1). Yeasts (<1). Yeasts (5.1–6.7). Total aerobic mesophilic bacteria (6.0–6.2). Lactic acid bacteria (~9). Bacillus spp. (<1). Staphylococcus spp. (4.1). Eumycetes (~6). Enterobacteriaceae (<1). Pseudomonadaceae (<1). Enterococcus spp. (<1). Salmonella spp. 	Lactobacillus spp., Lactobacillus plantarum, Pediococcus pentosaceus, Staphylococcus xylosus, Staphylococcus saprophyticus	Saccharomyces cerevisiae, Hansenula anomala	Zeng, Chen, & Zhanş (2016)
China	Pseudosciaena crocea		Collected from factory (raw materials) Processed by scientific laboratory	Viable counts Sequencing of 16S rDNA regions of isolates RFLP analysis		(abs.). Listeria monocytogenes (abs.). Total aerobic mesophilic bacteria (2.7). Lactic acid bacteria (<1). Enterobacteriaceae (<1). Staphylococcus spp. (2.1).	Staphylococcus vitulinus, Staphylococcus aureus, Staphylococcus xylosus, Staphylococcus saprophyticus, Staphylococcus nepalensis, Staphylococcus sciuri, Staphylococcus succinus, Staphylococcus succinus, Staphylococcus succinus, Staphylococcus succinus, Staphylococcus succinus, Pseudomonas putida, Pseudomonas fulva, Proteus		Zhang, Li, Xu, Wu, & Dai (2015)
China		Yucha	Collected from settlement families (end products)	Sequencing of 16S rRNA regions of isolates	High-throughput sequencing of 16S rRNA regions of samples Real-time PCR		penneri, Proteus vulgaris, Bacillus subtilis Lactobacillus spp., Lactobacillus pentosus, Lactobacillus fancirmins, Lactobacillus farciminis, Lactobacillus farciminis, Lactobacillus rhamnosus, Lactobacillus casei, Lactobacillus casei, Lactobacillus senioris, Lactobacillus pentoris, Lactobacillus fermentum, Lactobacillus buchneri, Lactobacillus buchneri, Lactobacillus rustorum, Lactobacillus rustorum, Lactobacillus penson, Enterocaccus spp., Enterocacus spp., Enterobacter spp.,		Zhang et al. (2016)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
China	Oreochromis niloticus		Collected from market (raw materials)	Viable counts	High-throughput sequencing of 16S rRNA regions of samples	Total aerobic mesophilic bacteria (8.4).	Salinivibrio spp., Acinetobacter spp., Macrococcus spp., Kluyvera spp., Clostridium spp. Lactococcus spp., Pediococcus spp., Enterobacter spp., Citrobacter spp., Streptococcus spp.,		Zhao et al. (2021)
China	Ctenopharyngodon idellus		Collected from supermarket (raw materials). Processed by scientific		High-throughput sequencing of 16S rRNA and ITS regions of samples		Enterococcus spp., Enterococcus spp., Lactobacillus spp. Cobetia spp., Staphylococcus spp., Ralstonia spp., Acinetobacter spp., Vibrio spp.		Zhao, Hu, & Chen (2022)
India	Puntius spp.	Shidal	laboratory Collected from market (end products)	Viable counts		Total aerobic mesophilic bacteria (6.4-7.3). Lactic acid bacteria (4.4-4.7). <i>Bacillus</i> spp. (2.1-2.4). <i>Micrococcus</i> spp. (1.9-2.0). <i>Staphylococcus</i> spp. (2.7-3.2). Coliforms (<1). <i>Escherichia coli</i> (<1) . <i>Salmonella</i> spp. (abs.). Yeasts (2.5-2.8)			Ahmed, Dora, Sarkar Chowdhury, & Ganguly (2013)
India	Tenualosa ilisha Pangasius pangasius Rastrelliger kanagurta Stolephorus indicus Cypselurus spp. Scomberomorus commerson Pampus argenteus Eleutheronema tetradactylum Caranx spp. Etroplus suratensis Parastromateus niger Pangasius hypopthalmus		Collected from market (end products)	Viable counts Sequencing of 16S rRNA regions of isolates		Total halophilic microbes (3.9–8.8).			Das, Kumar, & Naya (2020)
India	hypopthalmus Puntius sophore	Ngari	Collected from artisanal	Viable counts Sequencing of 16S	PCR-DGGE	Total aerobic mesophilic bacteria (7.7). Lactobacilli	Staphylococcus cohnii, Staphylococcus carnosus, Staphylococcus		Devi, Deka, & Jeyaram (2015)

Table 2	(continued)
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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
			production centres (end products)	rRNA regions of isolatesARDRA		 (8.0). Lactococci (8.0). Staphylococcus spp. (3.5). Enterobacteriaceae (<3). Yeast (5.5). Molds (<3) 	saprophyticus, Tetragenococcus halophilus, Lactobacillus pobuzihii, Enterococcus faecium, Bacillus indicus, Kocuria halotolerans, Clostridium irregulare, Azorhizobium caulinodans, Macrococcus caseolyticus		
ndia	Puntius spp. Setipinna phasa	Shidal	Collected from market (end products)	Viable counts Physiological characterization of lactic acid bacteria isolates. Sequencing of 16S rRNA regions of lactic acid bacteria isolates		Total aerobic mesophilic bacteria (7.1).	Lactobacillus plantarum, Pediococcus pentosaceus, Pediococcus acidilactici, Pediococcus lolii, Enterococcus lactis, Enterococcus faecalis		Gupta, Mohanty, & Majumdar (2021)
India	Puntius sophore Setipinna phasa	Phayssa Shidol Puthi Shidol	Collected from market (end products)	Viable counts		Total aerobic mesophilic bacteria (5.1–5.4). Staphylococcus aureus (1.8–2.4). Streptococcus spp. (1.0–1.1). Escherichia coli (<1). Salmonella spp. (abs.). Eumycetes (1.2–1.7).			Kakati, & Goswami (2013b)
ndia	Puntius spp.	Shidal	Collected from production centre (end products)	Viable counts		Total aerobic mesophilic bacteria (7.1). Eumycetes (<1).			Mahanta, & Muzaddadi (2012)
ndia	Tenualosa ilisha	Lona Ilish	Collected from market (end products)	Viable counts. Phenotypical and physiological characterization of isolates		Total aerobic mesophilic bacteria (2.3).	Micrococcus spp., Bacillus spp.		Majumdar, Basu, & Anandan (2005)
india	Puntius sophore Puntius spp.	Ngari Hentaak	Collected from market (end products)	Viable counts Phenotypical and physiological characterization of isolates		Total aerobic mesophilic bacteria (6.7–7.8). Lactic acid bacteria (4.9–6.2).	Micrococcus spp., Staphylococcus spp.		Majumdar et al. (2015)
ndia	Puntius sophore Setipinna phasa	Puti Shidal Phasa Shidal	Collected from market (end products)	Viable counts. Physiological characterization of isolates		Total aerobic mesophilic bacteria (6.4–6.9). Lactic acid bacteria (4.5–4.8).	Staphylococcus spp., Micrococcus spp., Bacillus spp.		Majumdar, Roy, Bejjanki, & Bhaska (2016b)
India	Tenualosa ilisha	Lona Ilish	Collected from market (end products)	Viable counts. Physiological characterization of isolates		Total aerobic mesophilic bacteria (2.3).	<i>Micrococcus</i> spp., <i>Bacillus</i> spp.		Majumdar, & Basu (2010)

Table	2	(continued)
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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
India	Puntius spp.	Sheedal	Collected from market (end products)	Physiological characterization of <i>Staphylococcus</i> spp. Isolates Sequencing of <i>rpoB</i> regions of <i>Staphylococcus</i> spp. isolates		Total aerobic mesophilic bacteria (7.1).	Staphylococcus piscifermentans, Staphylococcus warneri, Staphylococcus hominis, Staphylococcus condimenti, Staphylococcus arlettae, Staphylococcus sciuri, Staphylococcus nepalensis		Majumdar, & Gupta (2020)
India	Puntius spp.	Shidal	Collected from production plants (end products)	Viable counts		Total aerobic mesophilic bacteria (6.0). Eumycetes (2.4)t.			Muzaddadi (2015)
India	Puntius spp.	Tungtap	Collected from market (end products)	Sequencing of 16S rRNA regions of isolates			Lactobacillus pobuzihii		Rapsang, Kumar, & Joshi (2011)
India	Puntius spp. Danio spp.	Tungtap	Collected from market (end products)	Viable counts. Physiological characterization of isolates		Total aerobic mesophilic bacteria (7.3–8.9). Lactic acid bacteria (4.8–5.8). Bacterial endospores (3.4–5.0). Eumycetes (5.2–5.7).	Enterococcus spp., Streptococcus spp., Lactobacillus spp., Bacillus cereus, Micrococcus spp., Staphylococcus aureus, Clostridium spp.	Candida spp., Saccharomycopsis spp.	Rapsang, & Joshi (2012)
India	Setipinna phasa	Telesech	Collected from market (end products)	Viable counts. Phenotypical and physiological characterization of isolates		Total aerobic mesophilic bacteria (6.4). Lactic acid bacteria (4.2). <i>Bacillus</i> spp. (2.2). <i>Staphylococcus</i> spp. (3.4). <i>Salmonella</i> spp. (<2). <i>Vibrio</i> spp. (<1). Eumycetes (4.1).	Staphylococcus spp., Bacillus spp.		Roy et al. (2014)
India	Setipinna spp.		Collected from market (end products)	Viable counts. Phenotypical and physiological characterization of isolates		Total aerobic mesophilic bacteria (3.8–5.6). Eumycetes (2.4–2.5). Streptococcus spp. (3.0–3.5). Staphylococcus aureus (3.5–4.7). Bacillus cereus (<1). Escherichia coli (<1). Salmonella spp. (abs.).	Bacillus spp., Micrococcus spp.	Fusarium dimerium, Penicillium citrinum, Aspergillus fumigatus, Aspergillus versicolar, Cladosporium spp.	Sarojnalini, & Suchitra (2009)
India	Esomus danricus Puntius sophore Amblypharyngodon mola Channa punctate Mystus vittatus	Utonga- Kupsu Hentak Ngari	Collected from market (end products)	Viable counts Phenotypical and physiological characterization of isolates. Sequencing of 16S rRNA regions of isolates		(aos.). Non-fastidious bacteria (14.0–30.0). Saccharolytic marine bacteria (10.0–18.0).	Bacillus licheniformis, Bacillus aerius, Bacillus altitudinis, Bacillus cereus, Bacillus methylotrophicus, Bacillus pumilus, Bacillus safensis, Bacillus siamensis, Bacillus sonorensis, Bacillus		Singh, Mandal, Lalnunmawii, & Kumar (2018b)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
							subtilis, Bacillus tequilensis, Bacillus vallismortis, Bacillus valezensis, Staphylococcus nepalensis, Staphylococcus cohnii		
India	Esomus danricus Puntius sophore Amblypharyngodon mola Channa punctata Mystus vittatus	Utonga- Kupsu	Collected from market (end products)	Physiological characterization of isolates Sequencing of 16S rRNA regions of isolates			Staphylococcus spp., Staphylococcus piscifermentans, Staphylococcus condimenti, Staphylococcus carnosus		Singh, De Mandal, Mathipi, et al. (2018)
India	Puntius sophore	Ngari	Processed by scientific laboratory	Viable counts. Phenotypical and physiological characterization of isolates		Total aerobic mesophilic bacteria (3.8–6.0). Eumycetes (2.7–3.6). Staphylococcus aureus (3.0–5.4). Streptococcus spp. (3.0–5.5). Escherichia coli (abs.). Salmonella spp. (abs.). Vibrio parahaemolyticus (abs.).	Bacillus cereus, Bacillus subtilis, Bacillus pumilus, Bacillus panthothenticus, Bacillus coagulans, Staphylococcus spp., Micrococcus spp.	Aspergillus fumigatus, Aspergillus sydowi, Cladosporium spp., Penicillium citrinum, Penicillium fellutanum, Penicillium regolosum, Gliocladium penicilloides, Rhizopus spp., Humicola spp.	Taorem, & Sarojnalini (2012)
India	Puntius sophore Esomus danricus Danio spp.	Ngari Hentak Tungtap	Collected from shops (end products)	Viable counts. Phenotypical and physiological characterization of isolates		(abs). Total aerobic mesophilic bacteria (4.7–7.0)y. Lactic acid bacteria (4.6–6.8). Bacterial endospores (3.2–4.2). Bacillus cereus (2.2–2.3). Staphylococcus aureus (<1–3.0). Enterobacteriaceae (3.0–3.5). Yeasts (<1–3.1). Molds (<1).	Lactobacillus fructosus, Lactobacillus amylophilus, Lactobacillus coryniformis, Lactobacillus plantarum, Lactococcus plantarum, Lactococcus lactis, Enterococcus faecium, Bacillus subtilis, Bacillus pumilus, Micrococcus spp.	Candida spp., Saccharomycopsis spp.	Thapa, Pal, & Tamang (2004)
Indonesia	Anabas testudineus	Wadi Betok	Collected from industries (end products)	Viable counts		Total aerobic mesophilic bacteria (4.7–6.4). Lactic acid bacteria (4.3–6.3).			Petrus, Purnomo, Suprayitno, and Hardoko (2013)
Indonesia	Rastrelliger spp.	Peda		Physiological characterization of lactic acid bacteria isolates			Aerococcus spp.		Putra, Suprapto, & Pramono (2018)
Indonesia		Peda Wadi Terasi Pakasam		Phenotypical and physiological characterization of			Lactobacillus spp., Lactobacillus plantarum- pentosus, Lactobacillus acidophilus, Lactobacillus		Rahayu (2003)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
				lactic acid bacteria isolates			fermentum, Lactobacillus curvatus, Lactobacillus murinus, Lactobacillus sakei, Pediococcus acidilactici, Pediococcus pentosaceus, Streptococcus thermophilus, Weissella spp., Weissella confusa, Enterococcus faecium		
Indonesia	Anabas testudineus	Wadi Papuyu	Collected from shop (end products)	Phenotypical and physiological characterization of isolates Identification of isolates with VITEK 2 systemSequencing of 16S and 18S rRNA regions of isolates			Lactobacillus garviae, Staphylococcus warneri- equorum, Bacillus pumilus- altitudinis	Candida lusitaniae- orthopsilosis	Soemarie et al. (2022
Iran	Sardinella spp. Stelophorus spp.	Mahyaveh		Viable counts		Total aerobic mesophilic bacteria (4.7). Total halophilic bacteria (3.7). Lactic acid bacteria (4.1). Enterobacteriaceae (3.4).			Zarei et al. (2012)
Japan	Trachurus japonicas Sardinops melanostica	Aji-Narezushi Iwashi- Nukazuke	Collected from shops (end products)	Viable counts PCR-SSCP	PCR-DGGE	Total aerobic mesophilic bacteria (3.3–7.3). Total halophilic bacteria (5.0–6.1). Total anaerobic mesophilic bacteria (3.8–6.8). Total halophilic anaerobic bacteria (5.2–5.6). Lactic acid bacteria (5.7–6.6). Halophilic lactic acid bacteria (3.5–6.9). Yeasts (3.2–5.6). Halophilic yeasts	Lactobacillus versmoldensis, Lactobacillus acidipiscis, Lactobacillus plantarum, Lactobacillus paralimentarius, Lactobacillus casei, Tetragenococcus halophilus, Tetragenococcus muriaticus		An, Takahashi, Kimura, & Kuda (2010)
Japan		Saba- Narezushi	Collected from producer (end products)	Viable counts. Sequencing of 16S rRNA regions of isolates	High-throughput sequencing of 16S rRNA regions of samples	(3.1–6.7). Total aerobic mesophilic bacteria (8.0)	Lactococcus spp., Lactococcus lactis, Lactobacillaceae spp., Weissella spp.		Doi et al. (2021)
Japan	Carassius carpio	Funazushi		Viable counts	PCR-DGGE	Total aerobic mesophilic bacteria (~4). Lactic acid bacteria	Veisselia spp. Staphylococcus epidermidis, Staphylococcus warneri, Lactobacillus curvatus, Lactobacillus plantarum,		Fujii, Watanabe, Horikoshi, & Takahashi (2011)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Japan	Decapterus spp.	Kusaya	Collected from manufacturers (end products)		High-throughput sequencing of 16S rRNA regions of samples	(~3). Eumycetes (~3).	Lactobacillus acetotolerans, Haloanaerobium spp. Halanaerobium spp., Tissierella spp., Anaerococcus spp., Vagococcus spp., Coriobacteriaceae spp., Dysgonomonas spp.,		Fujii et al. (2016)
Japan			Collected from factory (end products)	Phenotypical and physiological characterization of halophilic proteinase- producing isolates. Sequencing of 16S rDNA regions of halophilic proteinase- producing isolates			Peptostreptococcus spp. Filobacillus spp.		Hiraga et al. (200
Japan	Plecoglossus altivelis	Ayu- Narezushi	Collected from manufacturer (end products) Collected from nature. Processed by scientific laboratory	Viable counts Sequencing of 16S rRNA regions of lactic acid bacteria isolates	High-throughput sequencing of 16S rRNA regions of samples	Total aerobic mesophilic bacteria (4.1–6.0).	Latilactobacillus sakei, Leuconostoc mesenteroides, Lactobacillaceae spp., Enterobacteriaceae spp., Pseudomonadaceae spp.		Hori et al. (2022)
'apan	Scomber japonicus	Saba- Narezushi	Collected from market and retail shop (end products)	Viable counts Phenotypical and physiological characterization of lactic acid bacteria isolates Sequencing of 16S rRNA regions of isolates		Lactic acid bacteria (7.9–9.4). Lactococci (<1–9.8). Yeasts (<1–8.7)	Lactobacillus plantarum, Leuconostoc mesenteroides		Kanno, Kuda, An, Takahashi, & Kim (2012)
Japan	Trachurus japonicus	Narezushi	Collected from manufacturer (end products)	Sequencing of 16S rDNA regions of isolates			Lactobacillus plantarum, Lactobacillus brevis, Lactobacillus parabuchneri, Lactobacillus casei, Pediococcus ethanolidurans, Lactococcus spp., Leuconostoc spp., Citrobacter spp., Clostridium spp., Pseudomonas spp.		Kiyohara et al. (20
Japan	Trachurus japonicus Tribolodon hakonensis	Narezushi	Collected from shops (end products)		Sequencing of 16S rRNA regions of samples		Lactobacillus plantarum, Lactobacillus sakei, Lactobacillus sakei, Lactobacillus acidipiscis, Lactobacillus pobuzihii, Lactobacillus coryniformis, Pediococcus		Koyanagi et al. (20

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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Japan	Seriola quinqueradiata	Kaburazushi	Collected from shop (end products)	Sequencing of 16S rDNA regions of isolates			Tetragenococcus halophilus, Staphylococcus spp., Leuconostoc spp., Lactococcus spp., Clostridium spp., Pseudomonas spp., Escherichia-Shigella spp., Escherichia-Shigella spp., Corynebacterium spp., Oceanobacillus spp., Psychrobacter spp. Bacillus spp., Enterococcus faecium, Lactobacillus sakei, Leuconostoc citreum, Staphylococcus spp.		Koyanagi et al. (2013
Japan	Siganu fuscenses	Suku-Garasu Wata-Garasu	Collected from factories and shops (end products)	Viable counts. Phenotypical and physiological characterization of isolates		Total aerobic mesophilic bacteria (<2–7.7). Total halophilic bacteria (<2–7.5). Total anaerobic mesophilic bacteria (<2–7.6). Total halophilic anaerobic bacteria (<2–7.5).	Tetragenococcus spp.		Kuda, Okamoto, & Yano (2002)
Japan	Trachurus japonicus	Aji-No-Susu	Collected from fisheries and families (end products)	Viable counts Phenotypical and physiological characterization of isolates. Sequencing of 16S rRNA and ITS regions of isolates		Total aerobic mesophilic bacteria (7.5). Total halophilic bacteria (5.0). Lactobacilli (7.2). Halophilic lactobacilli (5.7). Lactococci (7.2). Halophilic lactococci (5.2). Yeasts (4.2). Halophilic yeasts (3.5). <i>Bacillus</i> spp. (3.6). Halophilic <i>Bacillus</i> spp. (3.6). Gram- positive aerobic rods (3.9). Halophilic Gram-positive aerobic rods (3.6). Gram-negative aerobic rods (3.9). Halophilic Gram- negative aerobic rods	Tetragenococcus spp., Lactobacillus rennini, Lactobacillus plantarum	Debaryomyces hansenii, Pichia anomala	Kuda et al. (2009)

Table	2	(continued)
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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Japan	Trachurus japonicas Seriola quinqueradiata	Aji-Narezushi Kaburazushi	Collected from manufacturers (end products)	Viable counts Physiological characterization of lactic acid bacteria isolates Sequencing of 16S rRNA regions of isolates		Total aerobic mesophilic bacteria (7.6–8.8). Lactobacilli (7.4–8.5). Lactococci (7.3–8.5). Gram- positive aerobic rods (3.2–3.6). Yeasts (2.8–3.7).	Lactobacillus plantarum		Kuda et al. (2010)
Japan	Sardinops melanosticus Scomber japonicas	Iwahi- Nukazuke Saba- Nukazuke	Collected from shops (end products)	Viable counts Physiological characterization of isolates. Sequencing of 16S rRNA regions of isolates		Lactococci (2.1–7.7). Halophilic lactococci (3.2–7.6). <i>Staphylococcus</i> spp. (<1–3.9). Halophilic <i>Staphylococcus</i> spp. (<1–3.8). Halophilic Gram-positive aerobic rods (<1–3.1). Yeasts (<1–3.9). Halophilic yeasts (<1–6.6).	Tetragenococcus halophilus		Kuda et al. (2012)
Japan	Cobolabis saira	Samma- Narezushi	Collected from manufacturer (end products)		Sequencing of 16S rRNA regions of samples		Lactobacillus sakei, Leuconostoc gelidum, Lactococcus lactis, Lactococcus piscium, Acinetobacter junii, Acinetobacter junisnii, Pseudomonas putida, Rahnella aquatilis		Matsui et al. (2008)
Japan	Plecoglossus altivelis altivelis	Ауи- Narezushi	Collected from manufacturer (end products)		Sequencing of 16S rRNA regions of samples		Lactobacillus fucluensis, Lactobacillus fucluensis, Lactobacillus curvatus, Lactococcus piscium, Lactococcus piscium, Lactococcus lactis, Leuconostoc gasicomitatum, Leuconostoc gasicomitatum, Leuconostoc pseudomesenteroides, Enterococcus faecium, Vagococcus carniphilus, Carnobacterium spp., Brochothrix thermosphacta, Psychrobacter alimentarius, Hafnia alvei, Enterobacter annigenus, Pectobacterium carotovorum, Comamonas spp., Myroides odoratus		Matsui, Saka, Isobe, (Narita (2010)
Japan	Scomber japonicus	Saba- Narezushi	Collected from manufacturer (end products)		Sequencing of 16S rRNA regions of samples		Spp., Myrotaes outoratus Lactobacillus curvatus, Lactobacillus fuchuensis, Lactobacillus sakei, Lactococcus piscium, Lactococcus lactis,		Matsui, Tsuchiya, Isobe, Maeda, & Narita (2013) (continued on next page

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
							Leuconostoc gasicomitatum, Vagococcus carniphilus, Carnobacterium divergens, Brochothrix thermosphacta, Hafnia alvei, Buttiauxella gaviniae, Pseudomonas psychrophile, Shewanella baltica		
Japan		Saba- Narezushi	Collected from manufacturer (end products)	Viable counts Sequencing of 16S rRNA regions of isolates	High-throughput sequencing of 16S rRNA regions of samples	Lactic acid bacteria (9.0).	Lactobacillaceae spp., Pediococcus spp., Lactobacillus spp., Lactobacillus plantarum, Weissella spp., Leuconostocaceae spp., Leuconostoc spp., Lactococcus spp., Enterococcus spp., Staphylococcus spp.		Nakagawa, Kawase, & Hayakawa (2016)
Japan	Carassius auratus grandoculis	Funazushi	Collected from manufacturer (end products)	Physiological characterization of lactic acid bacteria isolates. Sequencing of 16S rRNA regions of isolates			Lactobacillus buchneri		Okada et al. (2018)
Japan	Scombridae spp.		Collected from stores (end products)	Sequencing of 16S rRNA regions of histamine-producing isolates			Tetragenococcus muriaticus		Satomi et al. (2012)
Japan	Cypselurus agoo agoo Coryphaena hippurus Glossanodon semifasciatus		Collected from market (raw materials). Processed by scientific laboratory	Viable counts. Sequencing of 16S rDNA regions of isolates		Total aerobic mesophilic bacteria (4.8–5.1). Total halophilic bacteria (6.2–7.5).	Staphylococcus spp., Tetragenococcus spp.		Taira, Funatsu, Satomi, Takano, & Abe (2007)
Japan		Kusaya	Collected from manufacturers (end products)	Viable counts RFLP analysis	PCR-DGGE	Non-fastidious bacteria (8.6). Total aerobic mesophilic bacteria (8.7). Total anaerobic mesophilic bacteria (9.0).	Pseudomonas halodenitrificans, Marinella spp., Peptostreptococcus spp., Enterococcus spp., Moraxella spp., Thermohalobacter spp., Psychrobacter spp., Halomonas desiderata, Bacteroides caccae, Flavobacterium spp., Fusobacterium spp., Clostridium spp., Eggerthella lenta		Takahashi, Kimura, Mori, & Fujii (2002)
Japan		Funazushi	Collected from grocery store (end products)	Sequencing of 16S rRNA regions of isolates			Lentilactobacillus buchneri		Tanabe et al. (2022
Japan	Carassius buergeri grandoculis	Funazushi	Collected from shops and	Viable counts Physiological characterization of		Lactic acid bacteria (4.4–5.1).	Streptococcus salivarius, Lactobacillus buchneri, Lactobacillus		Tsuda, Kubota, Matsumoto, & Ishin (2012)

Table 2	(continued)
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	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
			manufacturers (end products)	isolates. Sequencing of 16S rRNA regions of isolates			parabucheneri, Lactobacillus plantarum, Lactobacillus alimentarius, Lactobacillus farciminis, Lactobacillus acidipiscis, Lactobacillus casei		
Korea	Raja kenojei		Collected from processing plant (end products)	Viable counts. Physiological characterization of isolates		Total aerobic mesophilic bacteria (7.9).	Photobacturis cuset Photobacterium logei, Vibrio harveyi, Vibrio fluvialis, Vibrio furnissii, Bacillus subtilis, Staphylococcus lentus, Brevibacterium mcbrellneri, Pseudomonas boreopolis, Enterobacter aminigenus		Cho, Jahncke, & Eur (2004)
Korea		Jeotgal	Collected from store (end products)	Viable counts Phenotypical characterization of isolates Sequencing of 16S rDNA regions of isolates		Total aerobic mesophilic bacteria (7.6). Lactic acid bacteria (7.18). Enterobacteriaceae	Lactobacillus spp., Enterococcus- Streptococcus-Pediococcus spp., Leuconostoc-Weissella spp., Leuconostoc mesenteroides,		Cho, & Do (2006)
Korea	Engraulis japonicus	Myeolchi- Jeot	Collected from markets (end products)	isolates Sequencing of 16S rDNA regions of isolates		(<1).	Streptococcus salivarius Sporosarcina spp., Virgibacillus spp., Bacillus spp., Staphylococcus spp., Halomonas spp., Kokuria spp., Psychrobacter spp., Rummeliibacillus spp., Oceanobacillus spp., Amaricoccus spp., Enhydrobacter spp., Lentibacillus spp., Barghavaea spp., Lysinibacillus spp., Tetragenococcus spp., Weissella spp., Lactobacillus spp., Brachybacterium spp., Vibrio spp., Paenibacillus spp., Deinococcus spp., Rhodococcus spp., Rhodococcus spp., Bracilibacillus spp., Gracilibacillus spp., Gracilibacillus spp., Ornithinibacillus spp.,		Guan, Cho, & Lee (2011)
Korea	Raja pulchra		Collected from restaurant and market (end products)	Viable counts Sequencing of 16S rDNA regions of samples and isolates	Epifluorescence microscopyReal- time PCR	Bacteria (7.6–7.9).	Enterococcus spp. Gammaproteobacteria spp., Pseudomonadaceae spp., Pseudomonas spp., Pseudomonas caeni, Psychrobacter spp., Psychrobacter maritimus,		Jang, Kim, Hwang, a Cho (2017)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
							Aeromonadales spp.,		
							Bacilli spp.,		
							Carnobacteriaceae spp., Carnobacterium spp.,		
							Carnobacterium mobile,		
							Carnobacterium funditum,		
							Carnobacterium iners,		
							Carnobacterium inhibens,		
							Carnobacterium jeotgali, Carnobacterium		
							maltaromaticum,		
							Atopostipes spp., Bacillales		
							spp., Planococcaceae spp.,		
							Sporosarcina spp.,		
							Filibacter spp., Clostridia spp., Tissierella spp.,		
							Halomina spp., Haloarcula		
							spp., Nitrosopumilus spp.,		
							Facklamia tabacinalis,		
							Vagococcus salmoninarum,		
							Trichococcus pasteurii, Trichococcus palustris,		
							Kytococcus sedentarius,		
							Micrococcus yunnanensis		
Korea	Glyptocephalus	Jeotgal			Real-time		Lactobacillus spp.,		Jung, Lee, Jin, Jeon
	stelleri				PCRSequencing		Lactobacillus sakei,		& Park (2014)
					of 16S rRNA regions of		Weissella spp., Pseudomonas spp., Serratia		
					samples		spp.		
Korea	Engraulis japonicus	Myeolchi-	Collected from		Real-time PCR		Tetragenococcus spp.,		Jung, Lee, Chun, &
		Aekjeot	nature. Processed		Sequencing of		Alkalibacillus spp.,		Jeon (2016)
			by scientific		16S rRNA regions		Lentibacillus spp.,		
Korea	Verasper variegates	Gajami-	laboratory Collected from	Phenotypical	of samples Sequencing of		Chromohalobacter spp. Lactobacillus sakei,		Kim, Kim, Turner, &
Korea	verusper vurieguies	Sikhae	manufacturer (end	characterization of	16S rDNA regions		Lactobacillus graminis,		Lee, 2014
			products)	isolates. Sequencing	of samples		Lactobacillus alimentarius,		, ,
				of 16S rDNA regions			Lactobacillus fructivorans,		
				of isolates			Leuconostoc mesenteroides,		
							Weissella thailandensis, Weissella hellenica,		
							Weissella halotolerans,		
							Bacillus subtilis, Bacillus		
							amyloliquefaciens		
Korea	Gadus	Sikhae	Processed by		High-throughput		Lactobacillus sakei,		Kim, Kim, Turner,
	chalcogrammus		scientific laboratory		sequencing of 16S rRNA regions of		Weissella hellenica, Weissella cibaria,		and Lee (2014)
			laboratory		samples		Psychrobacter arcticus,		
							Pantoea spp., Enterobacter		
							cowanii, Leuconostoc spp.		
Korea		Jeotgal	Collected from	Sequencing of 16S			Weissella thailandensis-		Kim et al. (2017)
			market (end products)	rRNA regions of isolatesMALDI-TOF			paramesenteroides, Weissella halotolerans		
			products)	MS			measella natototerans		

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Table 2	(continued)
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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Korea	Glyptocephalus stelleri	Gajami- Sikhae	Collected from manufacturer (end products)	Viable countsMALDI- TOF MS		Lactic acid bacteria (~7).	Latilactobacillus sakei, Latilactobacillus curvatus, Leuconostoc mesenteroides, Leuconostoc gelidum, Levilactobacillus brevis, Lactiplantibacillus plantarum		Kim et al. (2022)
Korea	Chromis notata Spratelloides gracilis	Jeotgal	Collected from market (end products)	Phenotypical and physiological characterization of isolates	Sequencing of 16S rRNA regions of samples		Tetragenococcus halophilus, Tetragenococcus muriaticus, Halanaerobium saccharolyticum, Chromohalobacter spp., Halomonas spp., Psychrobacter spp., Staphylococcus nepalensis,		Kim, & Park (2014c)
Korea	Engraulis japonicus	Myeolchi- Aekjeot	Processed by scientific laboratory		Sequencing of 16S rRNA regions of samples		Staphylococcus equorum Tetragenococcus spp., Psychrobacter spp., Salinivibrio spp., Halanaerobium spp., Staphylococcus spp., Pseudomonas spp., Photobacterium spp.		Lee et al. (2015)
Korea	Engraulis japonicus	Myeolchi- Aekjeot	Collected from markets (end products)		High-throughput sequencing of 16S rRNA regions of samples		Tetragenococcus spp., Halanaerobium spp., Lactobacillus spp., Lactococcus spp., Leuconostoc spp.		Lee, Choi, Hwang, Hong, & Lee, 2016
Korea	Trichiuridae spp. Engraulidae spp.	Galchi- Jeotgal Myeolchi- Jeotgal	Collected from market (end products)	Sequencing of 16S rRNA regions of isolatesMALDI-TOF MS	PCR-DGGE		Pediococcus spp., Pediococcus acidilactici, Pediococcus pentosaceus, Tetragenococcus halophilus, Tetragenococcus halophilus, Tetragenococcus muriaticus, Leuconostoc mesenteroides, Leuconostoc citreum, Leuconostoc gelidum, Enterococcus spp., Enterococcus devriesei, Enterococcus faecium, Weissella viridescens, Weissella halotolerans, Weissella paramesenteroides, Staphylococcus epidermidis, Lactobacillus sakei, Lactobacillus sakei, Stephylococcus spi. Synechococcus spp., Synechococcus spp.		Lee, Cho, Kim, & Ki (2018)
Korea		Myeolchi- Jeot	Collected from store (end products)	Viable counts. Phenotypical and physiological		Total aerobic mesophilic bacteria (4.1–4.6).	Stabhylococcus sylosus, Bacillus licheniformis, Bacillus coagulans, Micrococcus luteus		Mah, Ahn, Park, Sung, & Hwang (2003)

Table 2 (continued)
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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Korea	Beringraja pulchra		Collected from nature. Processed by scientific laboratory	characterization of isolates Viable counts	High-throughput sequencing of 16S rRNA regions of samples	Total aerobic mesophilic bacteria (4.0). Marine bacteria (7.6). Lactic acid bacteria (1.2). Coliforms (0.6). Salmonella spp. (<1).	Pseudoalteromonas spp., Aerococcaceae spp., Pseudomonadaceae spp., Moraxellaceae spp.		Park, Kim, & Kim (2020)
Korea	Engraulis japonica	Myeolchi- Jeot		Viable counts	High-throughput sequencing of 16S rRNA regions of samples	Shigella spp. (<1). Total aerobic mesophilic bacteria (6.6–8.4). Lactic acid bacteria (6.1–8.3).	Tetragenococcus muriaticus, Tetragenococcus halophilus, Tetragenococcus doogicus, Synechococcus spp., Lactobacillus sakei, Erysipelothrix rhusiopathiae, Anabaena lemmermannii, Stanbuleoccus aguarum		Song et al. (2018)
Korea		Hongeo	Collected from processing plant (end products)		Shotgun sequencing of whole genomes of samples		Staphylococcus equorum Psychrobacter spp., Pseudomonas spp., Clostridium spp., Oblitimonas spp., Staphylococcus spp., Enterococcus spp., Carnobacterium spp., Jeotgalibaca spp., Marinilactibacillus spp., Lactobacillus spp., Aerococcus spp., Virgibacillus spp., Streptococcus spp., Lysinibacillus spp., Listeria spp., Acinetobacter spp., Vagococcus spp., Fusobacterium spp.		Zhao, & Eun (2020
Laos	Cyclocheilichthys repasson Henicorhynchus siamensis	Pa-Som	Processed by scientific laboratory		PCR-DGGE		Ausobacterium spp. Lactococcus spp., Lactococcus lactis, Weissella spp., Weissella paramesenteroides, Macrococcus spp., Plesiomonas shigelloides, Clostridium spp., Pediococcus spp., Staphylococcus spp., Staphylococcus sciuri, Staphylococcus sciuri, Enterococcus spp.		Marui et al. (2014

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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Malaysia	Stolephorus spp.	Budu	Collected from factory (end products)	Phenotypical and physiological characterization of lactic acid bacteria isolates			Lactobacillus casei, Lactobacillus plantarum, Lactobacillus paracasei		Liasi et al. (2009)
Malaysia		Budu	Collected from producers (end products)	Viable counts		Escherichia coli (abs.). Coliforms (abs.). Vibrio parahaemolyticus (abs.). Vibrio cholerae (abs.).			Rosma, Afiza, Wan Nadiah, Liong, & Gulam (2009)
Malaysia	Stolephorus spp.	Budu	Collected from factory (end products)	Viable counts. Physiological characterization of isolates		Total aerobic mesophilic bacteria (3.2). Total halophilic bacteria (3.1). Total proteolytic bacteria (~3.5). Lactic acid bacteria (<1). Yeats (<1). Yeats (<1). Molds (<1).	Micrococcus luteus, Staphylococcus arlettae, Staphylococcus cohnii, Staphylococcus consus, Staphylococcus xylosus, Lactobacillus plantarum, Lactobacillus plantarum, Lactobacillus delbrueckii, Pediococcus pentosaceus, Pediococcus acidilactici, Lactococcus lactis, Corynebacterium spp., Rahnella aqualitis, Enterobacter spp.	Saccharomyces cerevisiae, Candida famata, Candida parasilopsis, Candida glabrata	Yuen, Yee, & Anton (2009)
Malaysia			Collected from factories (end products)	Viable counts. Physiological characterization of isolates		Total aerobic mesophilic bacteria (4.9–5.5). Total proteolytic bacteria (3.6–4.0).	Bacillus anyloliquefaciens, Bacillus subtilis, Bacillus humi, Staphylococcus carnosus, Staphylococcus intermedius, Staphylococcus condiment		Zaman, Bakar, Selamat, & Bakar (2010)
Malaysia		Budu	Collected from shop (end products)		High-throughput sequencing of 16S rRNA regions of samples		Tetragenococcus spp., Halanaerobium spp., Staphylococcus spp., Acinetobacter spp., Weissella spp., Pseudomonas spp., Bacillus spp., Psychrobacter spp., Corynebacterium spp., Lentibacillus spp., Kocuria spp., Paracoccus spp., Brevibacterium spp., Comamonas spp.		Zoqratt, & Gan (2021)
Myanmar		Yegyo Ngapi	Collected from market (end products)	Viable counts Phenotypical characterization of isolates RFLP analysisSequencing of 16S rRNA regions of isolates	Sequencing of 16S rRNA regions of samples	Halophilic lactic acid bacteria (5.3–6.3).	Containonta's spp. Tetragenococcus spp., Tetragenococcus muriaticus, Tetragenococcus halophilus, Staphylococcus epidermidis, Clostridium spp., Clostridium botulinum, Clostridium haemolyticum, Eubacterium tarantellae, Halanaerobium fermentans,		Kobayashi et al. (2016)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
							Alkalibacillus spp., Alloiococcus spp., Bacillus spp., Candidatus Arthromitus, Lactobacillus spp., Sporosarcina spp.		
Myanmar		Ngachin	Collected from market (end products)	Viable counts Phenotypical and physiological characterization of lactic acid bacteria isolates RFLP analysis Sequencing of 16S rRNA regions of isolates		Lactic acid bacteria (8.0–9.5).	Lactobacillus plantarum, Lactobacillus farciminis, Lactobacillus reuteri, Lactobacillus futsaii, Weissella paramesenteroides, Pediococcus pentosaceus		Moe, Thwe, et al. (2015)
Myanmar	Puntius schwanenfeldii	Ngachin	Collected from market (end products)	Sequencing of 26S rRNA regions of malachite green- degrading isolates				Debaryomyces nepalensis	Moe, Wilaipun, et al (2015)
Myanmar	Barbonymus schwanenfeldii Labeo rohita Chitala ornata	Nga-Chin Ngagyin-Chin Ngaphae- Chin	Collected from market (end products)	Phenotypical characterization of lactic acid bacteria isolates Sequencing of 16S rRNA regions of isolates			Lactobacillus plantarum, Lactobacillus pentosus, Lactobacillus farciminis		Thwe et al. (2011)
Philippines	Chanos chanos	Burong Bangus	Collected from marketProcessed by scientific laboratory	Viable counts Physiological characterization of isolates		Non-fastidious bacteria (3.5). Lactic acid bacteria (5.4).	Enteroccus faecalis, Tetragenococcus muriaticus, Lactobacillus delbrueckii, Carnobacterium divergens		Arcales, & Alolod (2018)
Philippines		Burong Isda	Collected from markets (end products)		PCR-DGGE		Bacillus spp., Lactobacillus pontis, Lactobacillus plantarum		Dalmacio, Angeles, Larcia, Balolong, & Estacio (2011)
Philippines VietnamThailand			Collected from supermarket (end products)	Viable counts Physiological characterization of histamine-forming bacteria isolates		Total aerobic mesophilic bacteria (2.1).	Bacillus coagulans, Bacillus megaterium		Tsai et al. (2006)
Saudi Arabia		Hout-Kasef	Collected from market (end products)	Viable counts. Phenotypical and physiological characterization of isolates		Total aerobic mesophilic bacteria (3.8). Total halophilic bacteria (4.3). Coliforms (<1). <i>Staphylococcus</i> spp. (3.2). <i>Vibrio</i> spp. (<1). <i>Yersinia</i> spp. (<1). <i>Campylobacter</i> spp. (<1). <i>Listeria</i> monocytogenes	Bacillus spp., Bacillus subtilis, Bacillus mycoides, Bacillus licheniformis, Bacillus pumilus, Staphylococcus spp., Staphylococcus aureus, Staphylococcus hominis, Staphylococcus xylosus, Staphylococcus saprophyticus, Staphylococcus cahnii		Gassem (2019)

Listeria monocytogenes

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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
						(abs.). Eumycetes			
South Korea	Raja kenojel	Hongeo	Collected from market. Processed by scientific laboratory	Viable counts	Sequencing of 16S rRNA regions of samples	(1.3). Total aerobic mesophilic bacteria (6.1).	Pseudomonas caeni, Thiopseudomonas spp., Tissierella spp., Sporosarcina spp.,		Zhao et al. (2019)
Fhailand		Pla Som Fug	Collected from market (end products)	Phenotypical and physiological characterization of lactic acid bacteria isolates. Sequencing of 16S rDNA regions of lactic acid bacteria isolates			Atopostipes spp. Weissella cibaria, Weissella confusa		Deatraksa et al. (2018)
Thailand	Oreochromis niloticus	Plasom		Phenotypical characterization of isolates. Sequencing of 16S rDNA regions of lactic acid bacteria isolates			Streptococcus salivarius, Enterococcus faecalis		Hwanhlem et al. (2011)
Thailand	Barbodes gonionotus	Plaa-Som	Collected from factory (end products)	ARDRASequencing of 16S rDNA regions of lactic acid bacteria isolates			Lactobacillus plantarum, Lactobacillus fermentum, Pediococcus pentosaceus, Weissella cibaria, Streptococcus bovis, Lactococcus garvieae		Kopermsub, & Yunchalard (2010
ThailandLaos	Channa striata Trichopodus trichopterus Cirrhinus molitorella	Plaa-Ra Pa-Daek	Collected from markets (end products)		PCR-DGGE		Tetragenococcus muriaticus, Tetragenococcus halophilus, Halanaerobium fermentans, Lactobacillus spp., Weissella spp., Pediococcus spp., Clostridium spp., Sphingobium spp.		Marui et al. (2015
Thailand		Pla Jaw Pla-Jom Pla-Som Pla-Ra Pla-Ra-Taung Pla-Ra Sub Nham-Pla	Collected from markets (end products)	Sequencing of 16S rRNA regions of isolates			Enterococcus faecalis, Enterococcus faecium, Enterococcus faecium, Enterococcus thailandicus, Lactobacillus acidipiscis, Lactobacillus farciminis, Lactobacillus futsaii, Lactobacillus plantarum, Lactobacillus plantarum, Lactobacillus plantarum, Lactobacillus paracasei, Lactobacillus paracasei, Lactobacillus pobuzihii, Pediococcus pentosaceus, Pediococcus halophilus,		Miyashita et al. (2012)

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Eumycetes

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Table 2 (continued) Country of origin

Fish species

Local name

Collection and

Analytical methods

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Thailand				Phenotypical characterization of halophilic proteinase- producing isolates. Sequencing of 16S rRNA regions of halophilic proteinase- producing isolates			paramesenteroides, Weissella thailandensis, Weissella viridescens, Aerococcus viridans Halobacillus spp.		Namwong et al. (2006)
Thailand	Stolephorus spp.		Collected from factories (end products)		High-throughput sequencing of 16S rRNA regions of samples		Halanaerobium spp., Lentibacillus spp., Halomonas spp., Tetragenococcus spp., Peptostreptococcus spp., Peptoniphilus spp., Gallicola spp., Fusobacterium spp., Vagococcus spp.		Ohshima et al. (2019)
Thailand	Channa striatus	Plaa-Som	Collected from producer (end products)	Viable counts Phenotypical characterization of isolates. Sequencing of 16S rRNA and ITS regions of isolates		Lactic acid bacteria (7.0–9.0). Yeasts (5.0–6.0).	Lactobacillus plantarum, Lactobacillus acidophilus, Lactobacillus alimentarius, Lactobacillus farciminis, Lactobacillus kimchii, Lactobacillus plantarum, Pediococcus plantarum, Staphylococcus spp., Weissella confusa, Lactococcus garviae	Zygosaccharomyces rouxii	Paludan-Müller et al. (2002a)
Thailand	Cirrhina microlepis	Som-Fak	Collected from manufacturer (end products)	Viable counts Phenotypical characterization of lactic acid bacteria and Gram-negative bacteria isolatesRAPD analysis		Total aerobic mesophilic bacteria (9.3). Lactic acid bacteria (9.0–9.5).	Lactobacillus pentosus, Lactobacillus plantarum, Lactobacillus paracasei, Weissella confusa, Pediococcus pentosaceus, Aeromonas spp.		Paludan-Müller, Valyasevi, et al., 2002
Thailand	Henicorhynchus siamensis Trichogaster tricopterus Channa striatus	Pla-Ra	Collected from factories (end products)		High-throughput sequencing of 16S rRNA regions of samples		Tetragenococcus spp., Staphylococcus spp., Lactobacillus spp., Virgibacillus spp., Lentibacillus spp., Anaerococcus spp., Bacillus spp., Brevibacterium spp., Clostridium spp., Corynebacterium spp., Halanaerobium spp., Paraclostridium spp.		Phewpan et al. (2020)
Thailand	Clarias macrocephalus Clarias gariepinus	Pla-Duk-Ra	Collected from farm (raw materials). Processed by	Viable counts		Total aerobic mesophilic bacteria (6.4). Lactic acid bacteria	r a accountaint opp		Pongsetkul, & Benjakul (2021)
									(continued on next page)

Microbial counts

Bacteria

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
			scientific laboratory			(3.3). Salmonella spp. (abs.). Staphylococcus aureus (1.6). Bacillus cereus (<1). Clostridium perfringens (<1). Escherichia coli (1.4). Eumycetes (2.0).			
Thailand	Priacanthus tayenus Nemipterus japonica Sphyraena langsar Sphyraena obtusata Saurida tumbil Trichiurus leptorus	Som-Fug	Processed by scientific laboratory	Viable counts		Lactic acid bacteria (~8).			Riebroy, Benjakul, Visessanguan, & Tanaka (2007)
Thailand		Pla-Ra	Collected from market (end products)		High-throughput sequencing of 16S rRNA regions of samples		Tetragenococcus muriaticus, Halanaerobium fermentans, Lactobacillus rennini		Rodpai et al. (2021)
Thailand	Rastrelliger neglectus Rachycentron canadus Otolithes ruber Nemipterus hexodon	Pla-Ra		Viable counts		Total aerobic mesophilic bacteria (4.9–6.8). Lactic acid bacteria (<1–4). Staphylococcus aureus (abs.). Vibrio parahaemolyticus (abs.). Clostridium perfringens (abs.).			Sangjindavong, Chuapoehuk, Runglerdkriangkrai, Klaypradit, & Vareevanich (2008)
Thailand		Nam-Pla	Collected from markets (end products)	Phenotypical and physiological characterization of isolates Sequencing of 16S rRNA regions of isolates			Tetragenococcus halophilus, Tetragenococcus muriaticus		Sitdhipol et al. (2013)
Thailand		Plaa-Ra	Collected from factory and market	Sequencing of 16S rRNA regions of isolates			Halobacterium piscisalsi, Natrinema gari		Tapingkae, Tanasupawat, Parkin, Benjakul, & Visessanguan (2010)
Thailand		Nam-Pla	Collected from factory (end products)	Phenotypical and physiological characterization of isolates DNA-DNA hybridization			Tetragenococcus halophilus, Tetragenococcus muriaticus		Thongsanit, Tanasupawat, Keeratipibul, & Jatikavanich (2002)
Thailand			Collected from factories (end products)	Phenotypical and physiological characterization of halophilic lactic acid			Tetragenococcus halophilus		Udomsil, Rodtong, Tanasupawat, & Yongsawatdigul (2010)

Table 2 (continued)

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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Thailand		Plar-Ra		bacteria isolates RFLP analysis. Sequencing of 16S rRNA regions of halophilic lactic acid bacteria isolates Sequencing of 16S rRNA regions of			Staphylococcus hominis		Wilaipun, Zendo, Okuda, Nakayama,
Turkey	Sardina pilchardus		Collected from nature. Processed by scientific laboratory	isolates Viable counts		Total aerobic mesophilic bacteria (3.9–5.6). <i>Staphylococcus aureus</i> (<1). Eumycetes (<1). Lactic acid bacteria (3.9–5.5).			Sonomoto (2008) Kilinc, Cakli, Tolasa & Dincer (2006)
Vietnam				Physiological characterization of collagenase- producing isolates			Bacillus subtilis		Tran, & Nagano (2002)
AUSTRALIA New Zealand	Pseudocaranx dentex Arripis trutta Macruronus novaezelandiae		Collected from retail shop (raw materials). Processed by scientific laboratory	Viable counts		Lactic acid bacteria (~8.7).			Khem, Young, Robertson, & Brook (2013)
EUROPE Faroe Islands	Melanogrammus aeglefinus Gadus morhua Pollachius virens		Collected from industry (end products)		High-throughput sequencing of 16S rRNA regions of samples		Photobacterium spp., Psychrobacter spp., Pseudoalteromonas spp., Shewanella spp., Moritella spp., Pseudomonas spp., Cetobacterium spp., Acinetobacter spp., Proteus spp., Vibrio spp., Bacteroides spp., Lysinibacillus spp., Myroides spp.,		Bahrndorff et al. (2022)
Iceland	Dipturus batis		Collected from establishment	Viable counts. Sequencing of 16S rRNA regions of isolates	Sequencing of 16S rRNA regions of samples	Total aerobic mesophilic bacteria (6.0–9.0). Total anaerobic mesophilic bacteria (5.0–8.0).	Carnobacterium spp. Pseudomonas spp., Oceanisphaera donghaensis, Psychrobacter spp., Carnobacterium divergens, Pseudoalteromonas spp., Providencia rettgeri, Rheinheimera spp., Vagococcus salmoninarum, Arthrobacter oxidans, Corynebacterium spp.,		Reynisson, Marteinsson, Jónsdóttir, Magnússon, & Hreggvidsson (2012

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Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Iceland	Somniosus microcephalus	Hákarl	Collected from ecommerce (end products)	Viable counts	ELFA PCR-DGGE Sequencing of 16S rRNA regions of samples. Real- time PCR	Total aerobic mesophilic bacteria (1.0-5.7). Lactobacilli (<1-1.6). Lactococci (2.0-4.5). Pseudomonadaceae (<1). Enterobacteriaceae (<1). Pseudomonas aeruginosa (abs.). Eumycetes (<1).	Paenibacillus amylolyticus, Photobacterium phosphoreum, Aliivibrio fischeri, Aliivibrio wodanus, Aliivibrio logei, Micrococcus luteus, Atopostipes suicloacalis, Idiomarina spp., Aerosphaera taetra Tissierella creatinophila, Anaerosalibacter massiliensis, Murdochiella massiliensis, Sporanaerobacter acetigenes, Pontibacillus marinus, Pseudomonas spp., Abyssivirga spp., Oceanobacillus spp., Lactococcus spp., Alkalibacterium spp., Photobacterium spp., Anaerobacillus spp., Staphylococcus spp., Listeria spp.,	Candida tropicalis, Candida glabrata, Candida garapsilosis, Candida zeylanoides, Saccharomyces cerevisiae, Debaryomyces spp., Torulaspora spp., Yamadazyma spp., Sporobolomyces spp., Cladosporium tenuissimum, Moristroma quercinum, Alternaria spp., Phoma spp., Epicoccum spp.	Osimani et al. (2019
Italy	Engraulis encrasicolus		Collected from market. Processed by scientific laboratory	Viable counts		Total aerobic mesophilic bacteria (2.0–3.3). Total halophilic bacteria (1.2–1.6). Lactococci (1.1–1.7). Lactobacilli (1.0–2.0). Enterobacteriaceae (1.0–1.8). <i>Staphylococcus</i> spp. (1.3–2.7)	лыста эрр.,		Alfonzo et al. (2018)
Italy	Engraulidae spp.			RFLP analysis Sequencing of 16S rRNA regions of halophilic archaea isolatesRAPD analysis		(1.3-2.7)	Haloarcula marismortui		Moschetti et al. (2006)
Italy	Thunnus albacares Xiphias gladius Seriola lalandi		Collected from producer (end products)	Viable counts Sequencing of 16S rRNA regions of lactic acid bacteria isolatesREP-PCR	High-throughput sequencing of 16S and 26S rRNA regions of samples	Lactic acid bacteria (7.6–9.1). Staphylococcus spp. (2.6–5.9). Enterobacteriaceae (<1 –4.5). Pseudomonadaceae (<1 –5.1). Enterococcus spp. (<1 –5.0). Eumycetes (4.2–5.6).	Latilactobacillus sakei, Latilactobacillus curvatus, Clostrium spp., Peptostreptococcus spp., Staphylococcus succinus	Kurtmaniella zeylanoides, Rhodotorula mucilaginosa, Debaryomyces hansenii, Galactomyces spp., Galactomyces geotrichum, Pichia fermentans	Belleggia et al. (2022

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Clupea harengus Scomber scombrus	Maatjes	Collected from producer (end products)	Viable counts		Total aerobic mesophilic bacteria (3.6–5.6). Hydrogen sulphide producing bacteria (<2). Total psychrotrophic bacteria (3.6–5.0). Lactic acid bacteria			Lyhs et al. (2007)
Scomber scombrus					(<2–3.7). Enterobacteriaceae (<2–3.0).			
			Phenotypical characterization of lactic acid bacteria isolates			Lactobacillus sakei, Lactobacillus curvatus, Leuconostoc mesenteroides, Weissella hellenica, Enterococcus faecium		Dapkevicius, Nout, Rombouts, Houben & Wymenga (2000
	Rakfisk	Collected from producers (end products)	Viable counts. Sequencing of 16S rRNA regions of isolates	Sequencing of 16S rRNA regions of samples. High- throughput sequencing of 16S rRNA regions of samples	Total aerobic mesophilic bacteria (~7). Fastidious bacteria (~7). Lactic acid bacteria (~7). Enterobacteriaceae (<1-~ 3). Yeast (<1-~ 1).	Psychrobacter spp., Lactobacillus spp., Lactobacillus sakei, Lactobacillus curvatus, Psychrobacter spp., Leuconostoc spp., Carnobacterium spp., Carnobacterium maltaromaticum, Carnobacterium divergens, Pediococcus spp., Yersinia- Serratia-Rahnella spp., Halomonas spp., Pseudoalteromonas spp., Brochothrix spp., Enterobacteriaceae spp.,		Bjerke et al. (2019)
Engraulis encrasicholus		Collected from landing centre (raw materials). Processed by scientific laboratory	Viable counts		Total psychrotrophic bacteria (1.8–1.9). Total halophilic bacteria (1.5–5.3). Enterobacteriaceae (<1). <i>Enterococcus</i> spp. (<1).			Hernandez-Herrero et al. (2002)
Engraulis encrasicholus		Collected from factory (end products)	Viable counts		Total aerobic mesophilic bacteria (~2.5). Total psychrotrophic bacteria (~2.5). Enterobacteriaceae (<1).			Pons-Sánchez- Cascado, Veciana- Nogués, & Vidal- Carou (2003)
	encrasicholus Engraulis	Engraulis encrasicholus	EngraulisCollected from landing centre (raw materials). Processed by scientific laboratoryEngraulisCollected from factory (end	Engraulis encrasicholusCollected from producers (end products)Viable counts. Sequencing of 16S rRNA regions of isolatesEngraulis encrasicholusCollected from landing centre (raw materials). Processed by scientific laboratoryViable counts	isolates Rakfisk Collected from producers (end producers) (end producers) (end producers) (end revening of 16S rRNA regions of samples. High-throughput sequencing of 16S rRNA regions of samples. High-throughput sequencing of 16S rRNA regions of samples free constraints and the set of t	isolates Rakfisk Collected from producers (end products) Sequencing of 165 rRNA regions of iso rRNA regions of iso rRNA regions of iso rRNA regions of isolates rRNA regions of isolates Regraulis Engraulis Collected from Ianding centre (raw materials). Processed by scientific Iaboratory Collected from factory (end products) Viable counts Collected from factory (end products) Collected from factory	Rakfisk Collected from produces (end products) Viable counts. Sequencing of 165 rRNA regions of isolates Sequencing of 165 from regions of samples. High throughput sequencing of 165 rRNA regions of regions of reg	Forgrauiis Collected from producers (end producers) Viable counts. Sequencing of 165 Sequencing of 165 isolates Sequencing of 165 rRNA regions isolates Total aerobic mesophile bacteria (1-7). Setaidou producers pp., 2-7). Catical call producers pp., 2-7). Catical call producer

Table 2 (continued)	
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Spain	Engraulis encrasicholus		Collected from		independent			
			producer (end products)	Viable counts Physiological characterization of isolates		Total aerobic mesophilic bacteria (3–9–4.1). Total halophilic bacteria (2.0–3.6). Enterobacteriaceae ($<$ 1). <i>Staphylococcus</i> spp. (2.0–4.1). Lactic acid bacteria (2.3–2.7). <i>Enterococcus</i> spp. ($<$ 1).	Kocuria varians, Staphylococcus chromogenes, Aerococcus viridans, Enterobacter cloacae	Pons-Sánchez- Cascado, Veciana- Nogués, Bover-Cid, Mariné-Font, & Vida Carou (2005)
Sweden	Clupea harengus var. membras	Surströmming	Collected from retail shop (end products)	Viable counts Phenotypical and physiological characterization of anaerobic isolates DNA-DNA hybridization. Sequencing of 16S rRNA regions of isolates		Total halophilic anaerobic bacteria (5.7–6.7).	Haloanaerobium praevalens, Tetragenococcus halophila	Kobayashi, Kimura, (Fujii (2000)
Sweden	Clupea harengus var. membras	Surströmming	Collected from ecommerce (end products)	Viable counts	ELFA. High- throughput sequencing of 16S rRNA regions of samples	Total aerobic mesophilic bacteria ($4.1-5.7$). Total halophilic bacteria ($5.0-6.7$). Total halophilic anaerobic bacteria ($5.6-7.0$). Lactobacilli ($<1-4.6$). Halophilic lactobacilli ($5.6-7.1$). Lactococci ($<1-4.8$). Halophilic lactococci ($<1-5.6$). Enterobacteriaceae ($<1-1.3$). Pseudomonadaceae ($<1-2.1$). <i>Staphylococcus</i> spp. ($2.6-5.8$). Hydrogen sulphide producing bacteria (<2). <i>Salmonella</i> spp. (abs.). <i>Eunycetes</i> ($<1-9.0$). Halophilic	Alkalibacterium gilvum, Carnobacterium spp., Tetragenococcus halophilus, Halanaerobium praevalens, Clostridüsalibacter spp., Porphyromonadaceae spp., Psychrobacter celer, Ruminococcaceae spp., Marinilactibacillus psychrotolerans, Streptococcus infantis, Salinivibrio costicola	Belleggia et al. (2024

Table 2 (continued)

Country of origin	Fish species	Local name	Collection and production point	Analytical methods Culture-dependent	Culture- independent	Microbial counts (Log cfu g ⁻¹)	Bacteria	Eumycetes	Reference
Greenland	Mallotus villotus		Collected from nature		High-throughput sequencing of 16S rRNA regions of samples	eumycetes (<1).	Lactococcus spp., Streptococcus spp., Propionibacterium spp., Escherichia-Shigella spp., Enterobacteriaceae spp.		Hauptmann et al. (2020)

Japanese Narezushi and its variants.

The lactobacilli community comprises more than 260 different species, often associated with nutritional quality improvement of foods and health-promoting properties for humans (Zheng et al., 2020). Among lactobacilli, *Lactiplantibacillus plantarum* (basonym *Lactobacillus plantarum*), *Latilactobacillus sakei* (basonym *Lactobacillus sakei*), *Latilactobacillus curvatus* (basonym *Lactobacillus sakei*), *Latilactobacillus curvatus* (basonym *Lactobacillus sakei*), *vert* frequently detected species in fermented fish and fish-based products.

L. plantarum colonizes many ecological niches due to its numerous and efficient regulatory and transport activities (Sabo, Vitolo, González, & Oliveira, 2014). *L. plantarum* was described as a key microorganism in the food industry, as it took part in the fermentation of many products, including dairy products, sourdough, and fermented sausages (Sabo et al., 2014). Furthermore, rapid lactic acid synthesis, acid tolerance, and bacteriocin production by *L. plantarum* were reported (Dalmacio et al., 2011; An et al., 2010; Fujii et al., 2011). Noteworthy, Zeng et al. (2014) evidenced the aminopeptidase activity by *L. plantarum* strains isolated from *Suan Yu*, thus demonstrating their contribution to the flavour, texture, and taste of the end product.

L. sakei was first isolated from fermented sausage and showed specialized physiological and biochemical properties that, compared to other lactobacilli, allow a high adaption to meat and fish environment (Dai et al., 2013). Among the pro-technological capacities of L. sakei, the production of bacteriocins and self-protection from bacteriocins synthetized from other competitors represent advantageous characteristics to compete and colonize various ecosystems (Kim, Kim, Turner, & Lee, 2014). Moreover, the metabolic activity of L. sakei contributed to flavour and texture definition of fermented fish and fish-based products (Matsui et al., 2008; Nordvi et al., 2007). In fact, an increase in glutamic acid, the main compound responsible of the umami taste, after the inoculation of meat constituents with crude cell extract of L. sakei, was registered in Samma-Narezushi (Matsui et al., 2008). Also, Nordvi et al. (2007) analysed the volatile substances profile of fermented fish product prepared with the addition of L. sakei as starter culture; in the inoculated product, volatile compounds such as alcohols, alkanes, aldehydes, and ketones were released, likely due to the metabolic activity of the L. sakei culture.

As *L. sakei*, another lactic acid bacteria species normally involved in fermentation of animal tissues is represented by *L. curvatus*. This latter species has frequently been used as starter culture in fermented sausages due to rapid acidification, hydrolysis of muscle protein, and inhibition of pathogenic microorganisms (Janßen, Eisenbach, Ehrmann, & Vogel, 2018). Several studies focused on characterization of bacteriocinogenic *L. curvatus* strains for their application in food matrices. For example, Gómez-Sala et al. (2019) revealed the biotechnological potential of a multi-bacteriocinogenic strain of *L. curvatus* derived from dry-salted cod (*Gadus morhua*). Moreover, the suppressing activity against *Listeria monocytogenes* from *L. curvatus* has extensively been demonstrated (Barbosa, Todorov, Jurkiewicz, & Franco, 2015; Barbosa, Todorov, Jurkiewicz, et al., 2015; de Castilho, Todorov, Oliveira, Bersot, & Nero, 2020).

In high-salt fermented fish and fish-based products, species of Tetragenoccus, especially Tetragenococcus halophilus and Tetragenococcus muriaticus, were the most represented taxa of lactococci. Both species were described as taste and flavour enhancers in fermented foods characterized by high salinity levels (Lee et al., 2015; Chuon et al., 2013; Marui et al., 2015). T. halophilus and T. muriaticus were reported to survive and grow in foods accounting for salt concentrations up to 30% (Li et al., 2022; Udomsil et al., 2010). The capability to maintain a great osmotic balance between the cytoplasm and the external environment by the accumulation of solutes was indeed evidenced in such species of lactic acid bacteria (Marui et al., 2015; Udomsil et al., 2010). However, the knowledge and the applications of T. halophilus appeared more frequently documented in respect to T. muriaticus. In fact, T. halophilus was reported to greatly improve the volatile component profile of foods through the reduction of dimethyl disulfide, an organic chemical compound causing a faecal note, and the production of desirable

compounds, such as 1-propanol, 2-methylpropanol, and benzaldehyde (Ohshima et al., 2019; Fukui et al., 2012). Also, a major exopolysaccharide production from T. halophilus was documented; recently, Zhang et al. (2022) and Yang et al. (2022) demonstrated the antioxidant activity, the cryoprotective capability, and the moderate emulsifying capacity of exopolysaccharide fractions synthetized by T. halophilus strains to be applied in the food industry. It is noteworthy that the role of Tetragenococcus on BAs formation is still controversial, as the implication of this genus in either generating or reducing such compounds in fermented fish was described (Lee, Choi, et al., 2016; Kim, Lee, Chun, Jeong, & Jeon, 2019; Chun et al., 2019; Jeong, Heo, & Lee, 2017; Ohshima et al., 2019; Kuda et al., 2012; Udomsil et al., 2010). Interestingly, the genetic determinants of amino acids decarboxylation to produce the corresponding BAs were generally considered strain specific (Ladero et al., 2012). With the aim of obtaining safe starter cultures capable of driving the whole fermentation process of fermented fishbased products, strains belonging to Tetragenococcus spp. should be evaluated and selected for the absence of such genetic determinants (Jeong et al., 2017).

Based on the available literature, the genus Lactococcus undoubtedly belongs to the microbial groups that were most well-adapted to the environment of fermented fish. This microbial group is widely distributed in fish, as confirmed by its frequent isolation from fish intestine (Kim, 2014d; Małaczewska & Kaczorek-Łukowska, 2021). The recurrent identification of Lactococcus spp. in Chouguiyu (Dai et al., 2013; Yang et al., 2021; Wang et al., 2021) and Narezushi (Kiyohara et al., 2012; Doi et al., 2021; Matsui et al., 2010; Matsui et al., 2013; Matsui et al., 2008; Koyanagi et al., 2011; Nakagawa et al., 2016) suggested their occurrence in the raw materials generally used for the preparation of these fermented fish-products. Lactococcus was positively correlated with the following features: i) production of volatile components and free fatty acids mainly associated with sweet and umami flavour, ii) improvement of physical properties of the end products, and iii) inhibition of BA synthesis (Zang et al., 2022; Zhao et al., 2021). Among Lactococcus species, Lactococcus lactis was the most frequently identified in fermented fish-based products. It is worth noticing that L. lactis was implied in the production of aromatic compounds, surfactants, and nisin, a bacteriocin characterized by a wide spectrum of antibacterial activity against Gram-positive bacteria (Małaczewska & Kaczorek-Łukowska, 2021). Among other functions, such species was reported to decrease the accumulation of substances that are negatively correlated with the fish freshness in Chouguiyu, as the total volatile basic nitrogen (TVB-N) and thiobarbituric acid reactive substances (TBARS) (Bao et al., 2018).

The reviewed research papers dealing with the microbiota of Thai and Korean fermented fish-based products often reported the identification of Weissella spp. The latter genus comprises microorganisms inhabiting various ecological niches, such as soil, sludge of milking machines, marshy sediments, lake water, plants, digestive tracts of humans and animals, and numerous fermented foods (Fusco et al., 2015). Interestingly, Weissella spp. played a crucial role during the fermentation processes of Suan Yu (Liu et al., 2021; Yang, Jiang, et al., 2020; Wang, Xu, et al., 2020) and Plaa-Som (Marui et al., 2014; Kopermsub, & Yunchalard, 2010; Paludan-Müller, Madsen, et al., 2002; Miyashita et al., 2012; Deatraksa et al., 2018). In such foods, the addition of sugar and other carbohydrate sources may have advantaged Weissella spp. during the initial phases of fermentation. Weissella spp. were reported to inhibit a broad-spectrum of common foodborne pathogens and to synthetize bacteriocins (Deatraksa et al., 2018; Kim et al., 2017). To date, six bacteriocins produced by Weissella were detected, including weissellicin 110, obtained for the first time by a Weissella strain isolated from a Thai fermented fish product (Srionnual, Yanagida, Lin, Hsiao, & Chen 2007; Fusco et al., 2015). Another common peculiarity of Weissella spp. was the production of considerable amounts of exopolysaccharides, whose application in the food sector as texture improvers is constantly increasing (Kavitake, Devi, & Shetty, 2020; Deatraksa et al., 2018).

As evidenced in the selected research papers, *Pediococcus* spp. (e.g., Pediococcus pentosaceus) were generally isolated from Thai fermented fish-based products (Kopermsub & Yunchalard, 2010; Paludan-Müller, Madsen, et al., 2002; Paludan-Müller, Valyasevi, et al., 2002; Miyashita et al., 2012; Marui et al., 2015). Holzapfel, Franz, Ludwig, and Dicks (2015) reported that this genus may naturally be associated with plants and fruits and suggested its adaptation and contribution to the fermentation of plant materials and processed meat. Numerous studies investigating the potential pro-technological roles exerted by P. pentosaceus isolates during the fermentative process of foods were retrieved from the scientific literature (Gupta et al., 2021; Li et al., 2021; Li et al., 2022; Nie, Lin, & Zhang, 2014; Lee et al., 2014; Skariyachan, & Govindarajan, 2019). As an example, Li et al. (2021) tested a Pediococcus pentosaceus strain for the production of fermented tilapia sausage, and the results suggested a broad spectrum of advantages, including: i) a rapid flesh gelation through the synthesis of organic acids, thus playing a crucial part in the formation and improvement of physico-chemical properties; ii) a fast fermentation process that reduced the colonization of amine-producing Enterobacter spp., Citrobacter spp., and Streptococcus spp.; iii) a good removal rate of BAs, likely due to their accumulation into P. pentosaceus cells through the corresponding transporters. Moreover, a strong proteolytic activity able to modify the final texture and flavor of the end products was observed for P. pentosaceus strains both in grass carp sausage (Nie et al., 2014) and tilapia sausage (Li et al., 2022).

Although generally encountered as a minority group, Leuconostoc spp. were detected in a great number of the fermented fish-based products considered in the present review. This genus was mainly associated with plant materials and various fermented vegetable products (Björkroth, Dicks, Endo, & Holzapfel, 2015). Interestingly, Leuconostoc spp. were recurrently identified in Narezushi (Koyanagi et al., 2013; Kanno et al., 2012; Koyanagi et al., 2011; Matsui et al., 2008; Hori et al., 2022; Matsui et al., 2010; Matsui et al., 2013; Kiyohara et al., 2012; Nakagawa et al., 2016) and Gajami-Sikhae (Kim, Kim, Turner, & Lee, 2014; Kim, Kim, Turner, Kim, et al., 2014; Kim et al., 2022) that were produced using rice, grains, and other vegetable ingredients. The central role of Leuconostoc spp. in the aroma formation of many fermented foods by the production of diacetyl, acetate, and ethanol, and in the texture development by the production of exopolysaccharides has already reported (Hemme, & Foucaud-Scheunemann, 2004), thus suggesting the same role in fermented fish-based products. Moreover, Leuconostoc spp. showed antimicrobial activities against Salmonella spp., L. monocytogenes, Pseudomonas aeruginosa, Vibrio parahaemolyticus, E. coli, S. aureus, and Bacillus subtilis (Toushik et al., 2022; Nakamura et al., 2012; Paray, Rather, Al-Sadoon, & Hamad, 2018).

Based on the reviewed scientific literature, Enterococcus spp. were identified in several fermented fish-based products worldwide. Enterococci are ubiquitous bacteria that can be found in soil, surface waters, and on plants and vegetables, even if they predominate in the digestive tract of humans and animals. Also, fermented foods, including cheeses and fermented sausages, usually contain enterococci, that shape taste and flavor profiles of the products (Yang, Wu, et al., 2022; Zhao et al., 2021; Hwanhlem et al., 2011). Some Enterococcus strains acted as bacteriocin producers, showing an antagonistic activity against Salmonella spp., L. monocytogenes, S. aureus and B. cereus (Molinos et al., 2009; Izquierdo, Wagner, Marchioni, Aoude-Werner, & Ennahar, 2009). Nevertheless, enterococci potentially harbour genes correlated with decarboxylase activity, and were indeed associated with the production of BAs in fermented tilapia sausages (Zhao et al., 2021; Pleva et al., 2012). Moreover, immunocompromised patients and those admitted to intensive care were subjected to nosocomial infections caused by Enterococcus spp., that may possess virulence factors promoting pathogenicity (Biswas, Sharma, & Joshi, 2019). It is noteworthy that Enterococcus faecalis and Enterococcus faecium were reported as the major responsible for enterococcal-related infections (Lerma et al., 2014). The same species were detected in numerous fermented fish-based products

considered, thus supporting the application of prevention strategies to control their spread throughout food chain.

As shown by literature search, Streptococcus spp. were frequently identified in different fermented fish-based products worldwide, albeit with a supposed limited role. Streptococcus spp. were described as commensal microorganisms generally found on the mucous membranes of the respiratory, digestive, and genitourinary tracts of humans and other warm-blooded animals, as well as on their skin (Toit, Huch, Cho, & Franz, 2014). For these reasons, the occurrence of streptococci in fermented fish-based preparations may be attributed to the use of inadequate hygiene practices during their production process. Members of Streptococcus are considered spoilage microorganisms able to grow on modified atmosphere-packaged meat products (Koort, Coenye, Vandamme, & Björkroth, 2006; Fernández-No et al., 2012) and can sporadically be causative agents of human diseases (Kopermsub & Yunchalard, 2010). Noteworthy, Streptococcus salivarius, isolated from Plaa-som (Hwanhlem, et al., 2011), Jeotgal (Cho, & Do, 2006), Funazushi (Tsuda et al., 2012), and Rakfisk (Bjerke et al., 2019) was reported to positively influencing the texture and flavor of these fermented fishbased foods. Moreover, the same Streptococcus species proved to be able to synthetize γ -aminobutyrric acid in dairy products and other functional fermented foods (Hwanhlem, et al., 2011), thus suggesting a similar role in fermented fish-based products.

Created in 1989 from a group of Lactococcus-motile strains, the genus Vagococcus is widely distributed in the aquatic environment, as confirmed by its frequent isolation from various fish and shellfish species (Wullschleger et al., 2018). Hence, the recurrent identification of Vagococcus species in fermented fish-based products included in the present study, especially in the early steps of the production process, may be attributed to their occurrence in the raw material (Fujii et al., 2016). A few data on the metabolic activities of Vagococcus spp. were obtained from the scientific literature (Yang, Wu, et al., 2022; Yang et al., 2021; Wang et al., 2021). On the one hand, Yang, Wu, et al. (2022) attributed the improved protease activity and the formation of umami taste in Chouguiyu to various microbial taxa, including Vagococcus. Also, this genus was closely associated to the free amino acid profile of different brands of fermented Cyprinus carpio (Yang et al., 2021). On the other hand, Wang et al. (2021) reported the correlation between Vagococcus spp. and 1-octen-3-ol, trimethylamine, and phenol characterizing the "stinky" off-flavor in fermented Siniperca chuatsi. It is noteworthy that several Vagococcus species were considered among the most significant cold-water pathogens, being associated with fish diseases in salmonid species (Saticioglu, Yardimci, Altun, & Duman, 2021; Dallagnol, Pescuma, Espínola, Vera, & Vignolo, 2021). Regarding pathogenicity of Vagococcus to humans, limited research on severe clinical manifestations was conducted. In fact, a case of Vagococcus bacteremia was reported for the first time by Matsuo et al. (2021) only in 2021.

4.2. Staphylococcus spp.

To date, 64 validly published species are comprised under the genus Staphylococcus (Parte, Carbasse, Meier-Kolthoff, Reimer, & Göker, 2020). Members of such taxonomical group inhabit skin, skin glands, and mucous membranes of warm-blooded animals, and can also be detected in soil, dust, air, and foodstuff. Staphylococci are aerobic or facultatively anaerobic, non-motile, non-spore forming microorganisms and utilize glucose as the major energy source by respiratory and fermentative pathways. Staphylococci species can exhibit a great resistance under stressful environmental conditions, tolerating water activities lower than 0.90 and extremely high levels of salt. Although most species result nutritionally fastidious and require several micronutrients to proliferate, the proteolytic and lipolytic activities of Staphylococcus spp. allow their adaptation to diversified fermented products. Moreover, the occurrence of some staphylococci species in fermented foods was usually correlated with enhanced sensorial properties. It is noteworthy that staphylococci are generally categorized as coagulase-positive

species and coagulase-negative species, depending on the capability to secrete coagulase, a protein enzyme implicated in blood coagulation. Coagulase-negative staphylococci, rarely implied in opportunistic infections in humans, were suggested as starter or adjunctive cultures because of their wide range pro-technological activities, as nitrate reductase activity, antioxidant activity, and exopolysaccharide production (Gillaspy, & Iandolo, 2009; Khusro, & Aarti, 2022).

The adaptation of Staphylococcus spp. to fermented fish-based products, these latter characterized by a significant presence of nutritional compounds and high amount of salt, appears glaring. Staphylococcus carnosus, Staphylococcus cohnii, Staphylococcus epidermidis, Staphylococcus equorum, Staphylococcus lentus, and Staphylococcus xylosus were among the most represented species detected in the fermented fish-based products herein considered. Zeng et al. (2017) isolated 27 S. xylosus strains from Suan Yu, and highlighted their lipolytic, proteolytic, and enzymatic activities. The protein hydrolysis and volatile formation by staphylococci strains was confirmed by Udomsil, Rodtong, Tanasupawat, & Yongsawatdigul (2015), reporting an umami taste improvement through the production of glutamic acid in fish sauce. Antibacterial effects against E. coli, P. aeruginosa, and S. aureus by staphylococci strains isolated from Indian traditional fermented meat and fish products were also reported by different authors (Borah, Gogoi, Adhikari, & Kakoti, 2016; Singh, De Mandal, Mathipi, et al., 2018). Regarding the role of Staphylococcus spp. on BAs production (Hernández-Herrero, Roig-Sagués, Rodríguez-Jerez, & Mora-Ventura, 1999; Rapsang, & Joshi, 2012) or degradation (Devi et al., 2015; Zaman et al., 2010) in seafood products, conflicting results were described in the scientific literature. A further evaluation of metabolic pathways implied in BAs accumulation or reduction by staphylococci was indeed suggested (Jeong et al., 2017). Worthy to mention is that enterotoxin release from coagulase-negative staphylococci represents a topic of debate. Commonly, this bacterial group demonstrated scarce enterotoxigenic production attributes (Khusro, & Aarti, 2022). However, numerous studies suggested that coagulase-negative staphylococci strains used in food production cannot necessarily be regarded as safe (Khusro, & Aarti, 2022). In fact, Zell et al. (2008) conducted a comprehensive analysis of toxin release associated with coagulasenegative staphylococci in food matrices, including fermented fishbased products, and the results showed that 18 out of the 35 tested strains were able to produce toxins, especially SED and SEH enterotoxins.

4.3. Bacillus spp.

With 104 validly published species, the genus Bacillus comprises highly heterogeneous microorganisms (Parte et al., 2020; Logan, & Vos, 2015). Bacillus spp. appear as rod-shaped, straight, or slightly curved cells, arranged in pairs, in chains, or as single cells, with variable morphology and size depending on the species. Such ubiquitous bacterial genus includes either motile or non-motile microorganisms, Grampositive or Gram-negative, aerobes, facultative anaerobes, or strictly anaerobes. Usually, Bacillus spp. were isolated from soil or matrices directly or indirectly in contact with soil, however, its presence was ascertained also in other environments, as clinical specimens, pharmaceutical products, foodstuff, and water. The occurrence of Bacillus spp. in such a wide range of habitats was attributed to the great adaptive capacity of its species, ranging from psychrophilic to thermophilic strains, acidophilic to alkaliphilic, and salt tolerant to halophilic. Significantly, Bacillus spp. can develop endospores, that are structures resistant to several hostile conditions, including heat, radiations, disinfectants, and shortage of nutrients (Logan & Vos, 2015). Since the aquatic environment does not represent the ideal habitat for the growth of Bacillus spp., their frequent isolation from fermented fish-based products was ascribable to contamination of the raw materials throughout production or to their ability to survive to adverse environments. The establishment of favorable conditions during the early stages of the fermentative process

allowed the proliferation of several *Bacillus* species able to use amino acids and organic acids as carbon or energy sources.

Of note, Bacillus subtilis, Bacillus licheniformis, and Bacillus pumilus were recurrently isolated from fermented fish-based products considered in the present literature search. During fermentation of fish-based products, the contribution of Bacillus spp. on the generation of aroma compounds was reported. In fact, the metaproteomic analysis conducted by Ji et al. (2017) on the traditional Chinese fermented fish Siniperca chuatsi allowed the identification of 31 different proteases belonging to proteolytic bacterial genera, including Bacillus. With the aim of producing a modern and standardized version of Lanhouin, Anihouvi, Kpoclou, and Hounhouigan (2012) tested the application of B. subtilis and B. licheniformis as starter cultures in pasteurized fish flesh and obtained a promising final product with desirable taste and aroma. In addition, the synthesis of bioactive proteins by the *B. subtilis* strain A26, starting from fermented protein hydrolysates containing powdered fish flesh, was investigated by Jemil et al. (2014). The same authors reported that the fish-based product fermented by B. subtilis A26 was characterized by improved solubility, foaming and emulsifying properties, antioxidant action, and different antimicrobial activities (Jemil et al., 2014), thus suggesting its potential application as starter culture. Regarding the production of BAs, their increase during the fermentation of fish-based products, due to Bacillus species, was described by several studies (Tsai et al., 2006; Lin, Liu, Lee, Hwang, & Tsai 2012; Mah et al., 2003). Contrarily, numerous studies demonstrated that Bacillus species were not involved in BAs production or could have even been able to degrade them (Zaman et al., 2010; Thapa et al., 2004; Lee, Kung, Huang, Huang, & Tsai, 2016).

4.4. Other noteworthy bacterial groups

As emerged from the analysis of the reviewed literature, Micrococcus spp. frequently characterized the microbiota of fermented fish preparations manufactured in Northeast India, such as Shidal, Lonailish, Tungtap, Ngari, and Hentak (Majumdar, & Basu, 2010; Majumdar et al., 2016b; Taorem, & Sarojnalini, 2012; Majumdar et al., 2015; Rapsang, & Joshi, 2012; Thapa et al., 2004; Majumdar et al., 2005; Sarojnalini, & Suchitra, 2009). Members of Micrococcus are Gram-positive, halotolerant, and strictly aerobic bacteria, usually isolated from a wide variety of terrestrial and aquatic ecosystems, and, mostly, from the skin of warmblooded animals, including humans (Busse, 2015). The frequent isolation of Micrococcus spp. during the initial stages of production of fermented fish-based foods suggested the application of scarce hygiene practices during raw material handling. Of note, the proteolytic and lipolytic activities of Micrococcus spp. during the fermentation process of fish-based products, as well as the weak production of BAs, were reported by different studies (Yuen et al., 2009; Lopetcharat, & Park, 2002; Mah et al., 2003).

Based on the considered scientific studies, Pseudomonas spp. deeply influenced the alkaline fermentation process of skates (Zhao et al., 2019; Zhao, & Eun, 2020; Reynisson et al., 2012; Cho et al., 2004; Jang et al., 2017; Park et al., 2020) and Hákarl (Osimani et al., 2019), thus resulting as one of the key microbial taxa involved in the production of these fermented foods. The genus Pseudomonas comprises ubiquitous Gramnegative microorganisms that are generally unable to grow under pH values of 4.5 or lower (Palleroni, 2015). In the absence of a carbohydrate source, the fermentation of fish is generally characterized by the establishment of a slightly acid or alkaline environment that supports the proliferation of Pseudomonas species. Members of Pseudomonas were reported to possess strong proteolytic and urease activities, thus increasing the ammonia nitrogen content in Hongeo (Zhao et al., 2019). In addition, degradation pathways of trimethylamine regulated by Pseudomonas species were documented in skates and Hákarl (Reynisson et al., 2012; Osimani et al., 2019). It is noteworthy that human opportunistic pathogen species as Pseudomonas fluorescens (Scales, Dickson, LiPuma, & Huffnagle, 2014) and Pseudomonas putida (Fernández et al.,

2015) were detected in different fermented fish-based products as *Momoni*, the West African fish-carbohydrate meal *Enam Ne-Setaakye*, *Hákarl*, and *Samma-Narezushi*, thus justifying the application of monitoring strategies to avoid risks for the consumers' health (Sanni et al., 2002; Asiedu, & Sanni, 2002; Osimani et al., 2019; Matsui et al., 2008).

As evidenced by the scientific literature, the microbiota of both Korean (Lee et al., 2015; Guan et al., 2011; Kim, Kim, Turner, Kim, et al., 2014; Jang et al., 2017; Zhao, & Eun, 2020; Lee et al., 2018) and European (Bahrndorff et al., 2022; Reynisson et al., 2012; Bjerke et al., 2019; Belleggia et al., 2020) traditional fermented fish-based products usually comprised Psychrobacter spp. among the most represented bacterial groups. Psychrobacter spp. include Gram-negative, aerobic, halotolerant, and psychrotrophic microorganisms, commonly isolated from the aquatic environment (open sea, deep sea, sea ice, and skin and gills of fish) (Juni, 2015). The fermentation temperature of fish-based products played a crucial role on the growth of Psychrobacter, whose species have characterized the early stages of the process or even the entire fermentation. As described by Skåra et al. (2015), the use of low temperatures in preparing fermented fish slowed the microbial metabolic activities interfering with lactic acid bacteria proliferation, thus allowing the dominance of psychrotrophic microorganisms, as Psychrobacter spp. A consistent amino acid metabolism was also associated with Psychrobacter spp., with nitrogen compound accumulation, formation of umami-related peptides, and flavor development in different fermented fish (Bhutia, Thapa, Shangpliang, & Tamang, 2021; Yang, Wu, et al., 2022; Zhao, & Eun, 2020).

Based on the research papers herein reviewed, the occurrence of *Halanaerobium* spp. in fish sauces was largely demonstrated (Lee et al., 2015; Lee, Choi, et al., 2016; Ohshima et al., 2019; Wang et al., 2018; Wang, Li, et al. (2020); Wang et al., 2022; Zoqratt, & Gan, 2021). *Halanaerobium* spp. comprise Gram-negative, strictly anaerobic, moderately or extremely halophilic microorganisms that prefer neutral or slightly alkaline pH levels (Oren, 2015). Moreover, members of *Halanaerobium* were usually isolated from hypersaline anaerobic environment (Oren, 2015). Jung, Lee, Lee, & Jeon (2013) described *Halanaerobium* spp. as potential indicators of over-fermentation process and putrefaction in seafood due to the production of acetate, butyrate, and methylamines, causing off-flavors and taste changes. Moreover, the synthesis of BAs, in particular putrescine, was attributed to *Halanaerobium* spp. during the fermentation of *Myeolchi-aekjeot* and *Yu-Lu* (Lee et al., 2015; Wang et al., 2018).

The genus Halomonas was usually identified in heavily salted fermented fish-based products included in the present review (Kim, & Park, 2014; Guan et al., 2011; Ohshima et al., 2019; Wang et al., 2018; Wang, Li, et al., 2020; Du et al., 2019; Ma et al., 2021). Halomonas species are Gram-negative, mainly aerobic, halotolerant or moderately halophilic, and nutritionally versatile bacteria (Ventosa, de la Haba, Arahal, & Sánchez-Porro, 2015). Interestingly, Halomonas spp. were commonly isolated from saline environments, including solar salt facilities, intertidal estuaries, the open ocean, and hypersaline lakes (Ventosa et al., 2015). The influence of Halomonas spp. in flavor formation of fermented fish-based, through the release of volatile compounds and lipolytic enzymes, was documented by Wang, Li, et al. (2020) and Ohshima et al. (2019) in fish sauce. Of great interest is the ability of degrading BAs exerted by several Halomonas strains. In fact, the decrease in cadaverine, phenethylamine, putrescine, tryptamine, tyramine, and histamine in fermented fish sauce, and the chemotactic movement toward histamine in vitro were reported (Xu, Liu, Xu, Wang, & Jiang, 2016; Perez et al., 2020; Wang, Li, et al., 2020; Perez et al., 2021; Wang et al., 2018), thus indicating its potential use as starter culture to limit risks related to BAs.

4.5. Pathogenic microorganisms

The manufacturing of fermented fish-based products relies on the application of traditional practices handed down over time. Although these ancient practices allow the conservation of such a perishable food to be obtained, the use of improper hygiene conditions during preparation, transport and sale of the end product might reduce their safety (Novoslavskij et al., 2016). Consequently, the occurrence of foodborne pathogens in fermented fish-based products may represent a considerable risk for the consumers' health.

Among pathogenic microorganisms, Clostridium spp. encompass ubiquitous Gram-positive endospore-forming bacteria, whose occurrence in fermented fish-based products included in the present literature review was commonly reported (Chuon et al., 2013; Qiu et al., 2022; Nie et al., 2022; Zhang et al., 2016; Devi et al., 2015; Kiyohara et al., 2012; Rapsang, & Joshi, 2012; Koyanagi et al., 2011; Takahashi et al., 2002; Zhao, & Eun, 2020; Marui et al., 2014; Phewpan et al., 2020; Marui et al., 2015; Kobayashi et al., 2016). The genus Clostridium is constituted by numerous pathogenic bacteria that cause severe or even fatal diseases in humans (e.g., Clostridium botulinum). Of note, Keisam, Tuikhar, Ahmed, & Jeyaram (2019) analyzed 247 samples of various Indian spontaneously fermented fish-based preparations and attested the occurrence of C. botulinum in 44% of the samples. In addition, the foodborne pathogens C. perfringens and Clostridium difficile were also detected in the same fermented products (Keisam et al., 2019). Recently, Hamad et al. (2022) isolated C. botulinum from 40% of tested Egyptian Feseekh and suggested the use of novel biocontrol practices by means of probiotic bacteria. The urgency to reduce or eliminate the risks represented by pathogenic Clostridium species was also confirmed by outbreak of foodborne botulism associated with consumption of Feseekh in Canada (Walton et al., 2014).

As evidenced in the considered research articles, Vibrio spp. were frequently associated with Chinese fermented fish-based products, as fish sauce (Wang et al., 2018; Du et al., 2019; Wang et al., 2022), Yucha (Hu et al., 2020; Zhang et al., 2016), Chouguiyu (Yang, Liu, et al., 2020; Yang et al., 2021; Xu et al., 2022; Wang et al., 2021), Suanzhayu (Yang, Jiang, et al., 2020) and fermented Ctenopharyngodon idellus (Zhao et al., 2022) and Siniperca chuatsi (Wang et al., 2021). In addition, the pathogenic species Vibrio fluvialis was identified in fermented skate skin (Cho et al., 2004). Vibrio spp. include numerous Gram-positive pathogenic species for humans that can cause infections of the gastrointestinal tract with different symptoms, as mild enteritis, vomiting, and fulminant diarrhea. Vibrio spp. inhabit aquatic environments including rivers, streams, ponds, and coastal areas and their associated animals and plants (Farmer, Janda, Brenner, Cameron, & Birkhead, 2015). Hence, the raw materials and related fermented fish-based products may constitute a reservoir of such microbial genus.

It is worthy to mention that the species S. aureus and B. cereus were occasionally detected in fermented fish-based products. The first foodborne pathogen is a coagulase-positive staphylococcus implicated in food poisonings, due to enterotoxin production, and nosocomial infections (Schleifer, & Bell, 2015). The second is a human pathogen inducing foodborne intoxications and opportunistic infections (Logan & Vos, 2015). In more detail, S. aureus was identified in Sanbao larger yellow croaker (Zhang et al., 2015), Hout-Kasef (Gassem, 2019) and Tungtap (Rapsang, & Joshi, 2012), whereas B. cereus was detected in Lanhouin (Anihouvi et al., 2007), fish sauce (Xiao et al., 2014), Tungtap (Rapsang, & Joshi, 2012), and different fish products from Northeast India (Singh, De Mandal, Lalnunmawii, et al.. 2018; Taorem, & Sarojnalini, 2012). It is noteworthy that a lack of investigations regarding the presence of toxins synthesized by S. aureus and B. cereus in fermented fish and fish-based products clearly emerged from the scientific literature. Interestingly, Bhutia, Thapa, and Tamang (2021) assessed the microbiological quality of traditionally preserved fish products of India by detecting the enterotoxins of potential pathogenic bacteria. In the same study, the occurrence of Bacillus diarrheal enterotoxins and staphylococcal enterotoxins was evidenced in 53.3 and 36.4% of tested fish products, respectively (Bhutia, Thapa, & Tamang, 2021). For this reason, although no recurrent outbreaks due to consumption of fermented fish and fish-based products were reported, the occasional presence of S. aureus and B. cereus in these food matrices suggests the

need for closer surveillance of a probably underestimated issue (Thapa et al., 2004).

4.6. Eumycetes

Yeasts and molds assumed over time an increasing attention by the food industry due to their metabolic versatility. To date, several popular fermented foods were produced by applying fungi as starter cultures that allowed the development of unique sensory features through the synthesis of enzymes and appreciated volatile compounds (Copetti, 2019). To the authors' knowledge, the role and the application of eumycetes in fermentative processes of fish-based products were poorly investigated by the scientific community. However, the detection and identification of yeasts and molds in such foods were repeatedly reported. As described by Musa, Kasim, Gunny, & Gopinath (2018), eumycetes capable of inhabiting hypersaline environments, as saline water, saline soil, and salted food products, are common. Indeed, eumycetes encompass salt-adapted or salt-tolerant microorganisms that can survive under high salt concentrations for their ability to balance the higher external osmotic pressure (Musa et al., 2018).

As emerged by the reviewed literature, members of Candida were identified in different fermented fish-based products worldwide (Clementine et al., 2012; Chuon et al., 2013; Yang, Jiang, et al., 2020; Rapsang, & Joshi, 2012; Thapa et al., 2004; Soemarie et al., 2022; Yuen et al., 2009; Osimani et al., 2019). As recently reported by Pereira et al. (2022), Candida spp. colonize a wide variety of ecological habitats due to their metabolic versatility and resistance to stress factors. In fact, Candida cells have already been isolated from skin or mucosae of warmblooded animals, cheese, coffee, cocoa, vegetables, meat and fermented beverages (Pereira et al., 2022). Candida spp. are widely used in the food industry for their ability to synthesize numerous metabolites, including exopolysaccharides, ethanol, and citric acid (Kieliszek et al., 2017). During the fermentation of fish-based products herein considered, the production of aromatic compounds (e.g., esters) derived by lipolytic and proteolytic activities of Candida spp. was reported (Zang et al., 2022; Zang et al., 2020; Osimani et al., 2019; Yuen et al., 2009). It is worth noticing that Candida glabrata, Candida parapsilosis, and Candida tropicalis, usually associated with fungal bloodstream infections in immunocompromised patients (Pfaller et al., 2001), were detected in Hákarl (Osimani et al., 2019), Budu (Yuen et al., 2009) and Adjuevan (Clementine et al., 2012), thus highlighting the need of further investigations for a proper risk assessment.

Based on the scientific studies considered, the species Debaryomyces hansenii characterized the microbiota of various fish-based products, as Momoni (Sanni et al., 2002), Aji-no-susu (Kuda et al., 2009), Hákarl (Osimani et al., 2019), fish sausage (Belleggia et al., 2022), and Adjuevan (Clementine et al., 2012). D. hansenii was isolated for the first time from marine environments, moreover, it is well adapted to habitats with low water activity, including fermented foodstuff (Breuer, & Harms, 2006). Of note, the ability of D. hansenii to synthetize, accumulate and store lipids resulted beneficial for its application in biotechnological productions (Breuer, & Harms, 2006). Indeed, sensory quality enhancement of Suan Yu was attributed by Zang et al. (2022) to free fatty acid metabolism of Debaryomyces spp. Of note, numerous D. hansenii strains proved to have great efficiency as biological control agents of pathogenic filamentous fungi in foodstuff, as fruits, dairy products, processed meat, and cereals (Medina-Córdova, Rosales-Mendoza, Hernández-Montiela, & Angulo, 2018).

Finally, *Saccharomyces cerevisiae* was detected in *Adjuevan* (Clementine et al., 2012), *Budu* (Yuen et al., 2009), *Suan Yu* (Zeng et al., 2016), and *Hákarl* (Osimani et al., 2019). Goddard, & Greig (2015) hypothesized the non-adaption of *S. cerevisiae* to a specific ecological niche, but rather emphasized its capability to inhabit and persist in many different environments. *S. cerevisiae* represents a valuable species for a wide variety of industrial applications, and its experimental use also in fish fermentation was extensively documented (Parapouli, Vasileiadis,

Afendra, & Hatziloukas, 2020; Gao, Xia, Li, & Liu, 2019; Zang, Xu, Xia, Jiang, et al., 2018; Zang et al., 2020, 2022; Liao, Xu, Jiang, & Xia, 2019; Sun, Hua, et al., 2022; Li & Xu, 2021; Xu, Xie, Xia, Regenstein, & Gao, 2018; Zang Xu, Xia, Yu, et al., 2018; Xu, Li, Xia, Zang, & Gao, 2019). In more detail, Xu et al. (2019) demonstrated that the strain *S. cerevisiae* 31 influenced flavor formation in fish paste made with carp, through lipolysis and release of polyunsaturated fatty acids. In addition, Zang, Xu, Xia, Jiang, et al. (2018) showed that the same *S. cerevisiae* strain positively affected phospholipid molecular species composition in *Suan Yu*, thus influencing both sensory characteristics and nutritional properties of the end product.

4.7. Archaea

The archaea domain is constituted by microorganisms that are able to survive under severe environmental conditions, such as extreme acidity, alkalinity, temperature, pressure and radiation, and hypersaline waters (Nagrale, & Gawande, 2018). To date, knowledge of archaea biology is limited in respect to the other domains, but recent technological advances in DNA sequencing and bioinformatic allowed an accelerated reconstruction of archaea genomes and thus the definition of new taxonomic groups (Baker et al., 2020). Moreover, the functional roles of archaea members in industrial and biotechnological applications are constantly increasing, thanks to the production of enzymes and biocatalysts accelerating fermentation processes (Nagrale, & Gawande, 2018). As far as the authors are aware, a few scientific papers dealt with the determination of archaea members in fermented fish-based products (Das et al., 2020; Jang et al., 2017; Tapingkae et al., 2010). Das et al. (2020) analyzed 101 Indian fermented fish samples containing over 20% of salt and evidenced a higher relative abundance of archaea (74.5%) over bacteria (25.4%). In the same study, the potential decisive role on flavor and bioactivities of archaea members in highly salted fermented fish products was suggested (Das et al., 2020). Tapingkae et al. (2010) isolated 156 halophilic archaea from different fishery products, including fish sauces and Pla-ra. Among archaea isolates, four strains belonging to the Natrinema and Halobacterium genera exhibited a remarkable histamine degradation activity (Tapingkae et al., 2010). The study of Jang et al. (2017) investigated the prokaryotic community composition of fermented skate. These prokaryotes consisted of a smaller portion of archaea members than bacterial ones, which were described as more competitive under pH values comprised between 8.4 and 8.9 (Jang et al., 2017).

5. Conclusions

Fermentation represents one of the most valuable methods to preserve fish, with the aim of guaranteeing a precious source of livelihood and curbing post-harvest losses. The analysis of the available scientific literature highlighted that most of the unique fish-based delicacies herein considered were merely realized based on traditional empirical methods mainly developed in Southeast Asian countries as well as in Western African and Northern European countries.

As emerged by studies applying culture-dependent methods, the microbial composition of fermented fish and fish-based products was characterized by the occurrence of microbial groups usually associated with food fermentation, namely lactic acid bacteria, staphylococci, *Bacillus* spp., and yeasts. As for potential pathogenic microorganisms, the absence of Enterobacteriaceae, *Campylobacter* spp., *Listeria* spp., and *C. perfringens* was observed, whereas the detection of *S. aureus* and *B. cereus* was occasionally reported.

Based on studies on microbial isolates and on the use of cultureindependent methods, a more accurate overview on the dominant taxa was depicted. In more detail, the fermentative processes of fish-based products were generally guided by lactobacilli or *Tetragenococcus* spp., depending on the salt concentration. The predominance of lactobacilli was observed in fermented fish products with low salt levels, whereas the occurrence of *Tetragenococcus* spp. was favored by high concentrations of salt. The most frequently detected species of lactobacilli were *L. plantarum, L. sakei*, and *L. curvatus*. The species *T. halophilus* and *T. muriaticus* were the most represented within the genus *Tetragenococcus*, and both played significant roles in taste and flavor enhancement. Moreover, among the other genera of lactic acid bacteria, *Lactococcus* spp., *Pediococcus* spp., *Leuconostoc* spp., *Weissella* spp., *Enterococcus* spp., *Streptococcus* spp., and *Vagococcus* spp. were frequently identified, although usually showing a secondary role during the production process.

Non-pathogenic *Staphylococcus* and *Bacillus* species confirmed their great adaptation to this type of fermented products. Of note, selected strains also exhibited: i) valuable enzymatic activities to enhance sensory traits of the end products, ii) antimicrobial activities against foodborne pathogens and iii) human probiotic potential.

Other minor bacterial populations recurrently detected in fermented fish-based preparations included *Micrococcus* spp., *Pseudomonas* spp., *Psychrobacter* spp., *Halanaerobium* spp., and *Halomonas* spp.

As for human pathogenic bacteria, the occurrence of *Clostridium* spp., *Vibrio* spp., *S. aureus*, and *B. cereus* was sporadically documented.

To the authors' knowledge, the role of yeasts in the fermentation process of fish-based products has poorly been investigated, however, the dominance of *Candida* spp., *Debaryomyces* spp., and *Saccharomyces* spp. was evidenced.

Regarding members of the archaea domain, further research is needed to better clarify their contribution in fermentation of fish-based foods. Of note, archaea include microorganisms that are well adapted to extreme salt concentrations and capable of producing novel valuable enzymes, thus suggesting a complex and still unexplored involvement of such microbial group in fish fermentation.

The quality of fermented foods depends on their sensory characteristics (texture, flavor, aroma, and visual aspect) and safety, both strictly connected with metabolic activities of occurring microorganisms. Regarding fermented fish and fish-based products, the contribution of microbial groups on their sensory profile was already investigated by numerous studies available in the scientific literature (Feng et al., 2021; Xu et al., 2021). As for the safety aspect of the same products, the information collected in the present review substantiate their microbiological safety, although the presence of microbial genetic determinants associated with BAs production should be specifically evaluated. Moreover, the absence of foodborne pathogens in fermented fish and fish-based products is very likely related to the proliferation of specific microbial taxa more adapted to this type of environment, based on raw materials, added ingredients, and production conditions. Hence, the present literature review could serve as comprehensive database for the scientific community, and as reference for the food industry in order to select the preeminent microorganisms involved in the natural fermentation of fish and formulate tailored starters or adjunctive cultures for product improvement.

CRediT authorship contribution statement

Luca Belleggia: Conceptualization, Writing – review & editing. Andrea Osimani: Conceptualization, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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