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Seafood biopreservation by lactic acid bacteria – A review

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ABSTRACT

Biopreservation is a powerful and natural tool to extend shelf life and to enhance the safety of foods by applying naturally occurring microorganisms and/or their inherent antibacterial compounds of defined quality and at certain quantities. In this context, lactic acid bacteria (LAB) possess a major potential for use in biopreservation because most LAB are generally recognized as safe, and they naturally dominate the microflora of many foods. The antagonistic and inhibitory properties of LAB are due to different factors such as the competition for nutrients and the production of one or more antimicrobially active metabolites such as organic acids (prevailingly lactic and acetic acid), hydrogen peroxide, and antimicrobial peptides (bacteriocins). This review addresses various aspects related to the biological preservation of seafood and seafood products by LAB and their metabolites.

1. Introduction

1.1. Trends and developments

The growing interest of consumers in nutritional aspects and the parallel attention paid on food quality issues have contributed to the increasing consumption of fish and fish products. Usually, this product category is considered as of high nutritional value and highly recommended by nutritionists. However, fish and seafood products are also known to be susceptible to spoilage due to microbiological and biochemical degradation (Dalgaard, Madsen, Samieian, & Emborg, 2006; Mejlholm et al., 2008). Accordingly, the development of effective processing treatments to extend the shelf life of fresh fish products has become a must. In addition, the consumers increasingly demand for high-quality but minimally processed seafood (Campos, Castro, Aubourg, & Velázquez, 2012). In this context, lower levels of salt, fat, acid and sugar and/or the complete or partial removal of chemically synthesized additives have become essential.

In the last years, traditional processes like salting, smoking and canning applied to fish and seafood have decreased in favour of so-called mild technologies involving the application of lower salt concentrations, lower heating temperature and packaging under vacuum (VP)* or under modified atmosphere (MAP; Dalgaard et al., 2006; Emborg, Laursen, Rathjen, & Dalgaard, 2002). However, the drawback of these trends is that safety hurdles are weakened and foodborne illness outbreaks may increase (Cortesi, Panebianco, Giuffrida, & Anastasio, 2009; Mejlholm et al., 2008). Therefore new methodologies are sought to ensure food safety and to extend the shelf-life of foods.

Hitherto, approaches to reduce the risk of food poisoning outbreaks have relied on the search for the addition of efficient chemical preservatives or on the application of more drastic physical treatments such as heating, refrigeration, application of high hydrostatic pressure (HHP), ionizing radiation, pulsed-light, ozone, ultrasound technologies etc. In spite of some possible advantages, such treatments possess several drawbacks and limitations when applied to seafood products. Among these, the toxicity of some commonly used chemical preservatives (e.g., nitrite) (Cleveland, Montville, Nes, & Chikindas, 2001) and the alteration of sensory and nutritional properties of seafood may be exemplarily mentioned. Due to the delicate nature of seafood, physical treatments may induce considerable quality losses (e.g., freezing

Abbreviations: VP, vacuum packed; MAP, modified atmosphere packed; HHP, high hydrostatic pressure; LAB, lactic acid bacteria; LPFP, lightly preserved fish product; SPFP, semi-preserved fish product; GRAS, generally recognized as safe; QPS, qualified presumption of safety; LMM, low-molecular-mass; HMM, high-molecular-mass; HSP, heat shock protein; CSS, cold smoked salmon.

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damage, discolouration in case of HHP and ionizing radiation) (Devlieghere, Vermeiren, & Debevere, 2004; Zhou, Xu, & Liu, 2010).

Among alternative food preservation strategies, particular attention has been paid to biopreservation techniques, which extend the shelf-life and enhance the hygienic quality, thereby minimizing the negative impact on the nutritional and sensory properties. Biological preservation usually refers to the use of a natural or controlled microflora and/or its antimicrobial metabolites (Garcia, Rodriguez, Rodriguez, & Martinez, 2010; Nilsson et al., 2005). Lactic acid bacteria (LAB) are interesting candidates, which can be used for this approach. In fact, they often are naturally present in food products and may act as powerful competitors to contaminating spoilage microorganisms, by producing a wide range of antimicrobial metabolites such as organic acids, diacetyl, acetoin, hydrogen peroxide, reuterin, reutericyclin, antifungal peptides, and bacteriocins. Hence, the last two decades have seen pronounced advancements in using LAB and their metabolites for natural food preservation (Cleveland et al., 2001; Gálvez, Abriouel, López, & Omar, 2007; Nes, 2011; Nilsson et al., 2005).

1.2. Bacterial hazards associated with fish and seafood products

In general, fish and seafood including related products are a risky group of foodstuffs. The diverse nutrient composition of seafood provides an ideal environment for growth and propagation of spoilage microorganisms and common food-borne pathogens (Dalgaard et al., 2006; Emborg et al., 2002). Table 1 presents an overview on the major bacterial hazards associated with aquatic food products.

Pathogenic bacteria found in seafood can be categorized into three general groups (Calo-Mata et al., 2008; Mejlholm et al., 2008): (1) Bacteria (indigenous bacteria) that belong to the natural microflora of fish, such as *Clostridium botulinum*, pathogenic *Vibrio* spp., *Aeromonas hydrophila*; (2) Enteric bacteria (non-indigenous bacteria) that are present due to faecal and/or environmental contamination, such as *Salmonella* spp., *Shigella* spp., pathogenic *Escherichia coli*, *Staphylococcus aureus*; and (3) bacterial contaminants during processing, storage, or preparation for consumption, (such as *Bacillus cereus*, *Listeria monocytogenes*, *Staph. aureus*, *Clostridium perfringens, Cl. botulinum, Salmonella* spp.).

The presence of indigenous microorganisms in fresh cultured products is usually not a safety concern since they are mainly present at low levels that do not cause a disease, and in case of adequate cooking, food safety hazards are insignificant in those products. Therefore, the real hazard concerns are more related to products where growth of those bacteria is feasible during storage and which are eaten raw or insufficiently cooked (Mejlholm et al., 2008). In this context it has to be mentioned that the development of official guidelines to minimize faecal contamination of shellfish and harvesting waters has strongly reduced the incidence of enteric bacteria in seafood, though these bacteria can still be isolated from various seafood in many countries, indicating the steady potential for transmission to humans (Table 1).

2. Lactic acid bacteria in fish and seafood products

2.1. Lactic acid bacteria as natural contaminants

Usually, LAB are not considered as genuine micro-flora of the aquatic environment, but certain genera, including *Carnobacterium, Enterococcus, Lactobacillus* and *Lactococcus,* have been found associated in fresh and sea water fresh fish (Table 2).

LAB have also been isolated from processed aquatic food products such as lightly preserved fish products (LPFP) and semi-preserved fish products (SPFP). The LPFP category includes fish products preserved by low levels of salt (<6% [w/w] NaCl in the aqueous phase) and, for some products, the addition of preservatives (sorbate, benzoate, NO_2, or smoke) plays some role. The pH of these products is relatively high (>5.0), and they often are packaged under vacuum and need to be stored and distributed at low cooling temperatures (<5 °C). This is a group of high-value delicacy products (cold-smoked, pickled ["gravad"], or marinated fish, brined shellfish) that are typically consumed as ready-to-eat products, without any heat treatment (Mejlholm & Dalgaard, 2007; Mejlholm et al., 2008). LAB dominating vacuum-packaged cold-smoked fish products include the genera of *Lactobacillus*, *Lactococcus, Leuconostoc* and *Carnobacterium* (Gancel, Dzierszinski, & Tailliez, 1997). Many studies have shown that carnobacteria are quite common in chilled fresh and lightly preserved seafood, but at higher storage temperatures (15–25 °C),

Table 1
Bacterial hazards in fish and seafood products – a survey.

Bacteria	Product identified	References
Aeromonas spp.	Fish, shellfish	Fernandes, Flick, & Thomas, 1998; Isonhood & Drake, 2002
Clostridium botulinum Type E	Spores on surface, in intestine, on gills (trout, herring, salmon); vacuum packaged smoked fish products, cans, fermented fish, salted fish	Haagsma, 1991; Hatheway, 1995; Sramova & Benes, 1998; Johnson, 2000
Cl. perfringens	Cod, tuna salad, boiled salmon	Hewitt et al., 1986; Khatib et al., 1994; Aschfalk & Muller, 2002
Escherichia coli	Fresh fish, tuna paste, salted salmon roe, processed seafood	Ayulo, Machado, & Scussel, 1994; Calo-Mata et al., 2008; Asai et al., 1999; Mitsuda et al., 1998; Semanchek & Golden, 1998; Pierard et al., 1999;
Listeria monocytogenes	Ubiquitous, 3–10% human carriers; rarely in seawater or seawater fish, more frequently in freshwater and aquaculture fish, cold smoked products, salted fish products, hot smoked products, raw fish, prawns, mussels, oysters	Hoffman, Gall, Norton, & Wiedmann, 2003; Thimothe, Nightingale, Gall, Scott, & Wiedmann, 2004; Alves, De Martinis, Destro, Vogel, & Gram, 2005; Gudmundsdöttir et al., 2005; Miettinen & Wirtanen, 2005; Beaufort et al., 2007; Calo-Mata et al., 2008; Zunabovic, Domig, & Kneifel, 2011
Salmonella spp.	In intestine (tilapia and carp); prawns, mollusks, alaska pollack; eel and catfish, smoked eel, smoked halibut, dried anchovy	Heinitz, Ruble, Wagner & Tatini, 2000; Ling, Goh, Wang, Neo & Chua, 2002; Olgunoğlu, 2012
Staphylococcus aureus	Contamination from infected persons, fresh fish and fish fillets (*Cynoscion leiarchus*), smoked fish	Ayulo et al., 1994; Eklund, Peterson, Poysky, Paranjpye, & Pelroy, 2004
Vibrio parahaemolyticus	Shellfish, crustaceans on the skin, gills, intestine, fish-balls, fried mackerel (*Scomber scombrus*), tuna (*Thunnus thynnus*), and sardines (*Sardina pilchardus*),	Baffone, Pianei, Bruscolini, Barbieri, & Cierio, 2000; Calo-Mata et al., 2008; Daniels et al., 2000; IDSC, 1997
V. cholera Serovar O1 and O139	Prawns, shellfish, squid, seafood, uncooked fish marinade seviche (*Cilus gilberti*)	Kam, Leung, Ho, Ho, & Saw, 1995; Calo-Mata et al., 2008

Table 2
Reports on lactic acid bacteria isolated from fish.

Lactic acid bacteria	Product identified	References
Lactobacillus spp.	Arctic charr Atlantic cod Atlantic salmon Brown trout Herring Sturgeon fish Various fish	Kvasnikov, Kovalenko, & Materinskaya, 1977; Schrøder, Clausen, Sandberg, & Raa, 1980; Strøm & Olafsen, 1990; Olsen, Aagnes, & Mathiesen, 1994; Ringø, Bendiksen, Gausen, Sundsfjord, & Olsen, 1998; Ringø & Gatesoupe, 1998; Westerdahl, Joborn, Olsson, Kjelleberg, & Conway, 1998; Gonzalez, Enicinas, Garcıa Lopez, & Otero, 2000; Ringo, 2004; Bucio, Hartemink, Schrama, Verreth, & Rombouts, 2006; Ghanbari, Rezaei, Jami, & Nazari, 2009.
Carnobacterium spp.	Arctic charr Rainbow trout Brown trout Various fish	Ringø & Gatesoupe, 1998; González et al., 2000; Jöborn, Dorsch, Olsson, Westerdahl, & Kjelleberg, 1999; Gonzalez et al., 2000; Ringo, 2004
Aerococcus spp.	Atlantic salmon	Westerdahl et al., 1998; Ringo, 2004
Enterococcus spp.	Common carp Brown trout	Kvasnikov et al., 1977; Cai, Suyanandana, Saman, & Benno, 1999; Gonzalez et al., 2000; Ringo, 2004; Campos, Rodríguez, Calo-Mata, Prado & Barros-Velazquez, 2006
Lactococcus spp.	Common carp Brown trout	Cai et al., 1999; Gonzalez et al., 2000; Campos et al., 2006
Leuconostoc spp.	Arctic charr	Ringo, 2004
Pediococcus ssp.	Common carp, Rohu	Cai et al., 1999; Halami, Chandrashekar, & Joseph, 1999
Streptococcus spp.	Arctic charr Atlantic salmon Carp, Eel, European Eel, Japanese Goldfish Rainbow trout Various salmonids Turbot Yellowtail	Ringø & Olsen, 1999; Ringø et al., 2000; Ringo, 2004
Vagococcus spp.	Brown trout	Gonzalez et al., 2000
Weissella hellencia	Flounder	Byun, Park, Benno, & Oh, 1997

other species including *Enterococcus* spp. could dominate the microbial spoilage community of seafood (Dalgaard et al., 2003; Emborg et al., 2002).

Fish products with a high salt content (>6% NaCl in aqueous phase) or with a pH below 5.0 and to which preservatives (benzoate, sorbate, nitrate) are added are defined as "semi-preserved" (Mejlholm et al., 2008). Typically, the European products (e.g., salted and/or marinated herring, anchovies, caviar) are distributed at cooled temperatures (<10 °C). In marinated or dried fish, salted and fermented fish, the lactic acid microflora can be quite diverse, since the presence of lactobacilli and pediococci has been reported. Table 3 summarizes the most relevant species isolated from different ready-to-eat seafood products.

2.2. Biopreservation using lactic acid bacteria

Biopreservation of fish and seafood products is an alternative to meet safety standards and to control microbial deterioration without negative impact on the sensory quality of the product. The selection of LAB possessing the GRAS (generally recognized as safe) status (US Food and Drug Administration) as protective cultures is generally agreed as beneficial for extending the shelf-life of seafood products (Calo-Mata et al., 2008; Leroi, 2010). Likewise, they also fulfil the QPS (qualified presumption of safety) requirements (EFSA, 2007). Seafood-borne LAB are often able to grow even at refrigerated temperatures and are compatible to the seafood environment (modified-atmosphere packaging, low pH, high salt concentrations, presence of additives like, e.g., lactic acid or acetic acid). Importantly, their growth can also suppress more potent spoilage germs by means of antagonistic and inhibitory activities (either through the competition for nutrients or the production of one or more antimicrobially active metabolites; Nilsson, 1997; Nilsson, Gram, & Huss, 1999; Nilsson et al., 2005; Nes, 2011). Hence LAB usually meet the necessary requirements for biopreservation of seafood products, which are dealt with below.

2.2.1. Requirements of biopreservation cultures

When using live microbial antagonists in seafood biopreservation, there are a number of criteria and requirements, which must be taken into account (Calo-Mata et al., 2008; Leroi, 2010). Primarily, consumer protection is the most important aspect, in particular in terms of ready-to-eat seafood, but also for other types of this food category since cross-contamination, both at the retail and consumer level, is possible. Furthermore, the extent to which such protective cultures or their metabolites may affect the sensory attributes of the seafood product should be taken into consideration. Hence, protective cultures should not cause any detrimental effects on the target food. Since certain LAB may also contribute to spoilage or at least to some degradation of food ingredients in a number of foods, it is essential to consider their effect on chemical, physical and sensory quality parameters (Castellano, Gonzalez, Carduza, & Vignolo, 2010). Another important requirement for a successful application of protective cultures is their ability to produce sufficiently active antagonistic metabolites against a broad spectrum of relevant food-borne pathogen and/or spoilage bacteria and fungi. In addition, the capability of surviving adverse conditions encountered during technological treatments and maintaining inhibitory activities during storage are of great significance. In general, the most relevant requirements of biopreservative agents can be summarized according to Fig. 1.

2.2.2. Antimicrobial components from lactic acid bacteria

Table 4 presents a survey of the diversity of antimicrobials produced by LAB. The most relevant antimicrobial substance produced by LAB is lactic acid and the concomitant reduction of pH (Stiles, 1996). Lactic acid is also produced by other genera (e.g. *Brochothrix*). The antimicrobial effect of organic acids in food ecosystem lies in the reduction of pH, as well as the nature of the un-dissociated form of the organic acid, which inhibits the growth of unwanted microorganisms (Gould, 1991). In addition, LAB produce various other antimicrobial compounds, which can be classified as low-molecular-mass (LMM) compounds such as hydrogen peroxide (H_2O_2), carbon dioxide (CO_2), diacetyl (2,3-butanedione), and high-molecular-mass (HMM) compounds like bacteriocins

Table 3
Reports on lactic acid bacteria isolated from ready-to-eat seafood products.

Product type	Lactic acid bacteria	References
Brine shrimp	*Aerococcus viridans*	Dalgaard & Jørgensen, 2000; Dalgaard et al., 2003
	Carnobacterium divergens	
	C. maltaromaticum,	Mejlholm, Bøknæs, & Dalgaard, 2005
	C. spp.	Dalgaard & Jørgensen, 2000; Dalgaard et al., 2003
	Enterococcus faecalis	Dalgaard & Jørgensen, 2000; Dalgaard et al., 2003; Mejlholm & Dalgaard, 2007
	Ent. gallinarum	Dalgaard & Jørgensen, 2000; Dalgaard et al., 2003
	Ent. malodoratus	Mejlholm & Dalgaard, 2007
	Lactobacillus curvatus	Dalgaard & Jørgensen, 2000; Dalgaard et al., 2003
	Lb. spp.	From & Huss, 1990
	Lb. sakei	Mejlholm & Dalgaard, 2007
	Lactococcus garvieae	Dalgaard & Jørgensen, 2000; Dalgaard et al., 2003
	Streptococcus sp.	From & Huss, 1990
Cold smoked fish	*C. divergens*	Leroi, Joffraud, Chevalier, & Cardinal, 1998
	C. piscicola/maltaromaticum	Paludan-Müller, Dalgaard, Huss, & Gram 1998; Leroi et al., 1998; Gonzalez-Rodriguez, Sanz, Santos, Otero, & Garcia-Lopez, 2002; Olofsson, Ahrné, & Molin, 2007
	Ent. faecalis	Gonzalez-Rodriguez et al., 2002
	Ent. spp.	Lyhs, Björkroth, Hyytiä, & Korkeala, 1998
	Lb. alimentarius	Leroi et al., 1998
	Lb. casei ssp. *tolerans*	Gonzalez-Rodriguez et al., 2002
	Lb. coryneformis	
	Lb. curvatus	Truelstrup, Hansen, & Huss, 1998; Lyhs, Björkroth, & Korkeala, 1999; Jorgensen, Dalgaard, & Huss, 2000; Gonzalez-Rodriguez et al., 2002
	Lb. delbrueckii ssp. *delbrueckii*	Gonzalez-Rodriguez et al., 2002
	Lb. farciminis	Leroi et al., 1998
	Lb. homohiochii	Gonzalez-Rodriguez et al., 2002
	Lb. plantarum	Gancel et al., 1997; Hansen & Huss, 1998; Lyhs et al., 1999; Gonzalez-Rodriguez et al., 2002
	Lb. pentosus	Gancel et al., 1997
	Lb. sakei	Leroi et al., 1998; Truelstrup Hansen & Huss, 1998; Lyhs et al., 1999; Jorgensen et al., 2000; Gonzalez-Rodriguez et al., 2002
	Lc. spp.	Paludan-Müller et al., 1998
	Leuconostoc carnosum	Hansen & Huss, 1998
	Leuc. citreum	Lyhs et al., 1999
	Leuc. gelidum	Hansen & Huss, 1998
	Leuc. mesenteroides	Hansen & Huss, 1998; Lyhs et al., 1999
	Weissella kandleri	Gonzalez-Rodriguez et al., 2002
Fermented fish	*Lb. acidophilus*	Tanasupawat, Shida, Okada & Komagata, 2000
	Lb. brevis	Lee, Jun, Ha, & Paik, 2000
	Lb. pentosus	Paludan-Müller et al., 1998; Tanasupawat, Okada & Komagata, 1998
	Lb. plantarum	Tanasupawat et al., 1998
	Lc. lactis	Lee et al., 2000
	Lc. lactis ssp. *lactis*	Paludan-Müller et al., 1998
	Leuc. citreum	
	Pediococcus pentosaceus	
Salted, marinated or dried fish	*C.* spp.	Basby, Jeppesen, & Huss, 1998
	Ent. faecalis, Ent. faecium	Thapa, Pal, & Tamang, 2006
	Lb. alimentarius, Lb. buchneri	Lyhs, Korkeala, & Björkroth, 2002
	Lb. delbrueckii ssp. *lactis*	
	Lb. plantarum	
	Lc. lactis	Thapa et al., 2006
	Leuc. mesenteroides	
	Ped. pentosaceus, W. confusa	
Seafood salad	*C. piscicola*	Andrighetto et al., 2009
	Ent. spp., *Ent. faecalis,*	
	Lb. curvatus	
	Lb. malfermentans	
	Lb. paraplantarum	
	Lb. sanfranciscensis	
	Lc. lactis	
	Leuc. mesenteroides	
	Leuc. pseudomesenteroides	
	Ped. spp.	
	Str. parauberis	
	Vagococcus spp.	
	W. spp.	
Sugar-salted (Gravad) fish	*C. divergens, C. piscicola*	Lyhs et al., 2002
	Lb. curvatus ssp. *melibiosus*	
	Lb. curvatus ssp. *curvatus*	
	Lb. curvatus, Lb sakei	Leisner, Millan, Huss, & Larsen, 1994
	Lb. sakei	Jeppesen and Huss, 1993; Lyhs et al., 2002
	Leuc. spp.	Leisner et al., 1994
	W. viridescens	

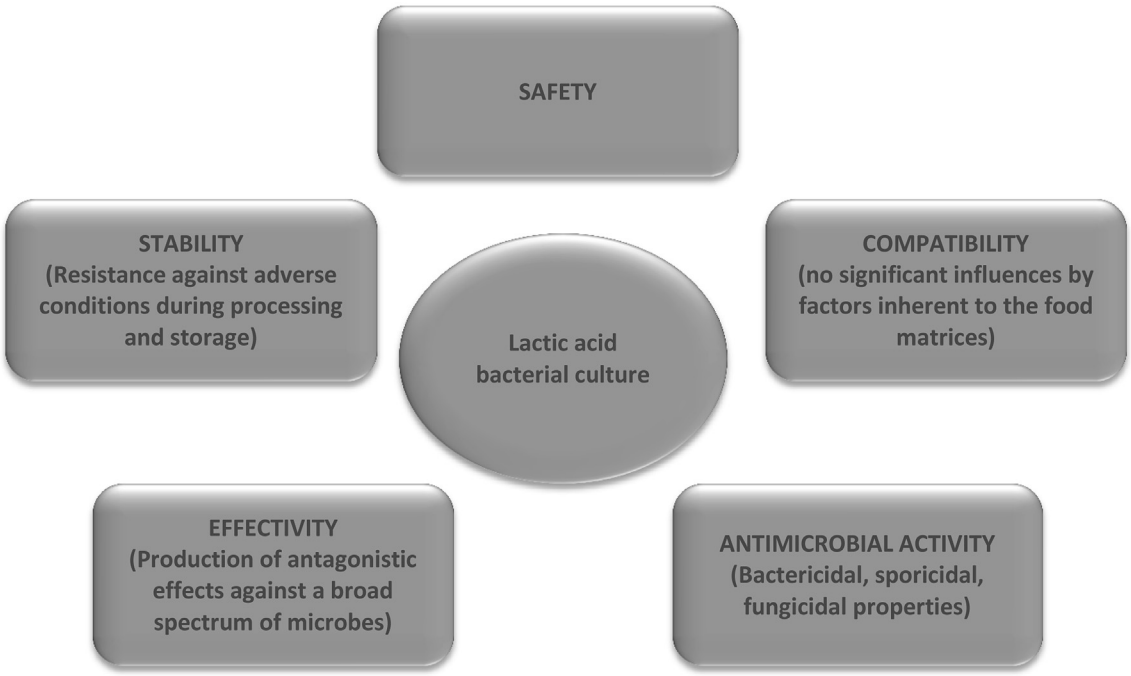

Fig. 1. Principles of potential LAB protective cultures and/or their inhibitory metabolites.

(Nes, 2011). The production of bacteriocins by LAB is very significant for applications in food systems and thus, unsurprisingly, these have been most extensively investigated. Among numerous bacteriocins so far characterized, nisin is best defined, and the only purified bacteriocin preparation approved for use in food products (Cleveland et al., 2001; Gálvez et al., 2007; Garcia et al., 2010; Nes, 2011; Nilsson, 1997; Nilsson et al., 1999).

2.2.3. Understanding LAB adaptation to stressful environments

Seafood biopreservation strategies reinforce the need for having robust LAB since they have to survive steps of food processing, to resist the food environment and to express specific functions under unfavourable conditions. The ability to quickly respond to stress is essential for survival, and it is now well established that LAB, like other bacteria, have evolved defence mechanisms against stress

Table 4
Antimicrobials produced by lactic acid bacteria- a concise survey.

Antimicrobial	Category	Subcategory	Remarks	Examples	References
Bacteriocin	Class I Lantibiotics, lanthionine containing, Class II Non-modified heat stable bacteriocins	Type A	Elongated molecules, molecular mass 2–5 kDa,	Nisin A	Gross & Morell, 1971
		Type B	Globular molecules; molecular mass 1.8–2.1 kDa	Mersacidin	Niu & Neu, 1991
		Subclass IIa	Pediocin like bacteriocins, listericidal, small (<10 kDa), narrow spectrum bacteriocins	Pediocin PA-1/AcH Leucocin A	Henderson, Chopko, & Van Wasserman, 1992; Motlagh et al., 1992; Hasting et al., 1991
		Subclass IIb	Two peptide bacteriocins, small (<10 kDa)	Lactococcin G Lactacin F	Nissen-Meyer, Holo, Håvarstein, Sletten, & Nes, 1992; Alison, Frémaux, & Klaenhammer, 1994
		Subclass IIc	Cyclic bacteriocins, small (<10 kDa)	Entrocin AS-48 Gassericin A Lactocyclicin Q	Samyn et al., 1994 Kawai, Saito, Kitazawa, & Itoh, 1998 Sawa et al., 2009
		Subclass IId	Non-pediocin single linear bacteriocin, small (<10 kDa)	Lactococcin A Lacticin Q	Holo, Nilssen, & Nes, 1991; Fujita, Ichimasa, Zendo, Koga, & Yoneyama, 2007
	Bacteriolysins		Non-bacteriocin lytic proteins, large, heat labile proteins, often murein hydrolases	Entrolysin A	Nilsen, Nes, & Holo, 2003
Organic acid	Lactic acid	Major metabolite of LAB fermentation. Active against putrefactive and Gram-negative bacteria, some fungi			Woolford 1975; Lindgren & Dobrogosz, 1990
	Acetic and propionic acids	More antimicrobially effective than lactic acid. Active against Putrefactive bacteria, clostridia. some yeasts and fungi			Ahamad & Marth 1989; Wong & Chen 1988; Richards, Xing, & King, 1995
Other	Hydrogen peroxide	Active against pathogens and psychotropic spoilage organisms e.g. *Staphylococcus aureus*, *Pseudomonas* sp.			Davidson, Post, Braner, & McCurdy, 1983; Cords & Dychdala, 1993
	Carbon dioxide	Active against Gram positive and specially Gram-negative psychrotrophic bacteria e.g. *Enterobacteriaceae* and *Listeria*			Devlieghere & Debevre, 2000; Ouwehand & Vesterlund, 2004
	Diacetyl	Active against Gram positive and Gram-negative bacteria e.g. *Listeria, Salmonella, Yersinia, E. coli*, and *Aeromonas*			Jay, 1982; Ouwehand & Vesterlund, 2004
	Fatty acids	Active against Gram-positive bacteria and some fungi			Gould, 1991
	Reuterin	Active against broad spectrum of Gram-positive and Gram-negative bacteria, yeast, fungi and protozoa e.g. species of *Salmonella, Shigella, Clostridium, Staphylococcus, Listeria, Candida*, and *Trypanosoma*			Axelsson, Chung, Dobrogosz, & Lindgren, 1989

that allow them to withstand harsh conditions and sudden environmental changes. While genes implicated in stress responses are numerous, in LAB the characterization of their actual role and regulation differs widely between species (Champomier -Vergès, Zagorec, & Fadda, 2010). Indeed, The functional conservation of several stress proteins (for example, HS proteins, Csp etc.) and some of their regulators (e.g. HrcA, CtsR) render even more striking the potentials of LAB for use in biopreservation (van de Guchte et al., 2002).

Cold acclimation of selected LAB constitutes a real advantage in bacterial competition against spoilage and pathogenic psychrotrophic bacteria. These LAB can rapidly adapt to a temperature downshift and can continue to grow at a reduced rate after a temperature downshift to about 20 °C below the optimal growth temperature. Although more important temperature downshifts lead to growth arrest, there are some LAB isolates, which are compatible with this situation (Garnier et al., 2010). To withstand cooling temperature, LAB have developed a cold-shock response, which is based on the synthesis of a number of cold-induced proteins (CIPs). Most proteins include a family of closely related low-molecular weight (~7.5 kDa) proteins termed cold-shock proteins (CSP) (Phadtare, 2004). CSP proteins or corresponding genes, as part of the cold-adaptive response, were detected and/or identified in several strains of LAB such as *Lactobacillus lactis* ssp. *cremoris*, *Streptococcus thermophilus*, *Pediococcus pentosaceus*, *Enterococcus faecalis*, *Lactobacillus acidophilus*, *Lactobacillus casei*, *Lactobacillus plantarum* and *Streptococcus pyogenes* (van de Guchte et al., 2002). Similar to other Gram positive bacteria, heat shock response in LAB is characterized by the induction of a set of heat shock proteins (HSP) (Champomier-Vergès et al., 2010). By a proteomic approach using 2D PAGE gels, heat shock treatment of *Lactococcus lactis* strongly induced DnaK, GroEL, and GroES (Auffray, Gansel, Thammavongs, & Boutibonnes, 1992; Whitaker & Batt, 1991). These proteins are well-known chaperones, which hold up folding and maturation of emerging or denatured proteins (Kaufman, 1999).

In LAB three types of starvation conditions (i.e. carbohydrate starvation, phosphate starvation, and nitrogen [amino acids] starvation) have been largely studied, but the majority of the reports relates to carbohydrate starvation. Using 2D-electrophoresis it has been established that starvation induced the synthesis of specific proteins in LAB. In *Lb. acidophilus*, 16 proteins are induced in stationary phase (Hartke, Bouche, Gansel, Boutibonnes, & Auffray, 1994).

2.3. Application in seafood and seafood products

Since some psychrotrophic pathogenic and spoilage bacteria can survive and grow in lightly preserved fish products, research has been conducted on this subject. Next to the raw bivalve molluscs, LPFP and SPFP constitute the most dangerous group of fish products. Almost any of the pathogenic organisms listed in Table 1 may be transferred via these products. Particularly, the presence and growth of *L. monocytogenes* is of major concern. *L. monocytogenes* has frequently been isolated from LPFP like cold smoked salmon (CSS). This organism is a frequent contaminant in the raw material: it survives the salting and cold-smoking (<30 °C) process and it is able to grow in the final product at chilling temperature (Table 1). In this regard, the use of lactic acid bacteria isolated from seafood and/or their bacteriocins have proved successful in preventing or delaying the growth of this pathogen under conditions mimicking those existing in lightly preserved fish products (Table 5).

Based on the reports on the application of LAB protective culture and/or their bacteriocins in seafood products, the recognized strengths of biopreservative agents can be summarized as follows: (1) promoting extended shelf life of seafood during storage time, (2) contributing to decreased risk for transmission of foodborne pathogens in LPFP and SPFP, (3) amelioration of economic losses due to seafood spoilage, (4) allowing reduced application of chemical preservatives and drastic physical treatments such as heating, refrigeration, etc. also causing better preservation nutritional quality of food, (5) good option for the industry due to cost effective technology, and (6) a proper response to consumer demands for minimally processed, safe, preservative-free foods (Gálvez et al., 2007).

However, there are also some drawbacks that must be considered. The effectiveness of protective cultures and/or their inhibitory compounds in food can be limited by a range of factors such as the narrow activity spectrum of some agents, the spontaneous loss of bacteriocinogenicity (genetic instability), limited diffusion behaviour in solid matrices, inactivation through proteolytic enzymes or binding to food ingredients such as lipids, poor adaptation of the culture to (refrigerated) food environments, low production levels and the emergence of bacteriocin-resistant bacteria. In addition, most LAB protective cultures are not capable of surviving commercial heat treatment processes and therefore usually are added by dipping or spraying only after heat treatment. This increases the costs and bears the problem of product supplementation with viable microbial cells (Devlieghere et al., 2004).

3. Regulatory issues in biopreservation of seafood and seafood products

At present, three major challenges severely restrict the application of seafood biopreservatives: (1) issues relating to microbial safety, (2) regulatory aspects, and (3) the formulation of microorganism.

In general, there are stringent regulatory requirements for the use of naturally-occurring antimicrobial cultures and substances, such as bacteriocins, in food preservation. As one of the key regulatory aspects, protective cultures selected for biopreservation need to take into account their impact on the nutritional and sensory features of perishable products. Presumably, this is one of the main reasons for which in spite of more studies in other food sectors, the information on the application of LAB or bacteriocins to seafood is limited. In case of protective cultures, safety aspects (e.g., production of histamine) of the bioprotective bacteria should be considered. However, it is important to note that in seafood the production of histamine connected to bioprotective LAB has not been reported so far. Furthermore, promising strains of LAB selected for seafood preservation did not exhibit any problematic resistance to antibiotics nor possess potential cytotoxicity (Pilet & Leroi, 2011).

Using the direct application of bacteriocins to seafood, likewise, regulatory aspects of these substances must be met. In analogy, bacteriocins should not exert deleterious effects on sensory properties of the foods. The bacteriocin has to be stable during storage and, if the activity depends upon residual concentrations, it has to be consistent throughout the shelf-life of the food. Approved by the U.S. Food and Drug Administration (FDA) in 1988 for use in pasteurized processed cheese spreads, nisin is currently the only purified bacteriocin approved for food use in the U.S, which is used for fish and seafood product packaging in the form of coated or impregnated film (Jones, Salin, & Williams, 2005).

Although encouraging results had been achieved in controlling the growth of *L. monocytogenes* by using LAB protective cultures or/and their bacteriocins in seafood, so far potential bioprotective bacterial formulations for seafood products are not included in the list of micro-organisms judged suitable for QPS status (Leroi, 2010).

Table 5
Survey of literature dealing with biopreservation of fish and seafood products.

Product	Protective culture/bacteriocin employed	Reported effects	References
Fish fillet			
Catfish	*Lc. lactis* ssp. cremoris ATCC 19257	Improved odour and appearance	Kim & Hearnsberger, 1994
Catfish	*Bifidobacterium adolescentis, Bif. infantis*, or *Bif. longum*	Extended shelf-life	Kim, Hearnsberger, Vickery, White, & Marshall, 1995
Horse Mackerel	*Ped.* spp. (Bac+, Bac-)	Improved sensory quality	Cosansu, Mol, Ucok Alakavuk, & Tosun, 2011
Indian mackerel	*Ped. acidilactici, Ped. pentosaceous, Str. thermophilus, Lc. lactis, Lb. plantarum, Lb. acidophilus and Lb. helveticus.*	Controlled spoilage bacteria and amines	Sudalayandi & Manja, 2011
Rainbow trout	nisin-containing aqueous solution of *Lc. lactis* ssp. *lactis* NCFB 497	No effect	Kisla & Ünlütürk, 2004
Salmon	*Lb. sakei* LAD and *Lb. alimentarius* BJ33	Improve sensory attributes	Morzel, Fransen, & Arendt, 1997
Sardine	Nisin	Inhibited fish spoilage flora	Elotmani & Assobhei, 2004
Tilapia	*Lb. casei* DSM 120011 (A) and *Lb. acidophilus* 1M	Improved biochemical quality criteria and microbial aspects	Ibrahim & Salha, 2009
Tilapia	*Lb. casei* DSM 120011 and *Lb. acidophilus*	Extended shelf-life and safety	Daboor & Ibrahim, 2008
Turbot, VP and MAP	EntP-producing enterococci	Anti-listerial, anti-staphylococcal, and anti-bacilli	Campos et al., 2012
VP fresh plaice	*Bif. bifidum*	Inhibited *Pseudomonas* spp. and *Pseudomonas phosphoreum*	Altieri, Speranza, Del Nobile & Sinigaglia, 2005
VP rainbow trout	*Lb. sakei* CECT 4808 and *Lb. curvatus* CECT 904T	Extended shelf-life	Katikou, Ambrosiadis, Koidis & Georgakis, 2007
VP rainbow trout	Sakacin A-producing strain of *Lb. sakei* (Lb706)	Inhibited *L. monocytogenes*	Aras Husar, Kaban, Hisar, Yanik, & Kaya, 2005
Cold smoked fish			
CO_2 packed cold smoked salmon	Nisin	Reduced *L. monocytogenes*	Nilsson, 1997; Nilsson et al., 1999.
Cold smoked salmon	Sakacin P	Inhibited *L. monocytogenes*	Aasen et al., 2003
Cold smoked salmon	*C. maltaromaticum* CS526	Inhibited *L. monocytogenes*	Yamazaki, Suzuki, Kawai, Inoue, & Montville, 2003
Cold smoked salmon	*C. divergens* V41 *C. divergens* V1 *C. divergens* SF668	Inhibited *L. monocytogenes*	Brillet, Pilet, Prévost, Cardinal, & Leroi, 2005
Cold smoked salmon	*Lb. sakei*	Inhibited *L. innocua*	Weiss & Hammes, 2006
Cold smoked salmon	*Lb. casei*, *Lb. plantarum* and *C. maltaromaticum*	Inhibited innocua	Vescovo, Scolari, & Zacconi, 2006
Cold smoked salmon	*Lb. casei* T3 and *Lb. plantarum* PE2	Inhibited *L. innocua*	Vescovo et al., 2006
Cold smoked salmon	*Ent. faecium* ET05	Inhibited *L. innocua*	Tomé, Pereira, Lopes, Gibbs, & Teixeira, 2008
Cold smoked salmon	*C. divergens* M35 (bac+)	Inhibited *L. monocytogenes*	Tahiri, Desbiens, Kheadr, & Lacroix, 2009
VP cold smoked salmon	*C.* spp.	Improve sensory characteristics	Leroi, Arbey, Joffraud, & Chevalier, 1996
VP cold smoked salmon	*C. piscicola* V1, *C. divergens* V41 and Divercin V41,	Inhibited *L. monocytogenes*	Duffes, Corre, Leroi, Dousset, & Boyaval, 1999; Duffes, Leroi, Boyaval, & Dousset, 1999; Nilsson et al., 2004
VP cold-smoked rainbow trout	Nisin	Inhibited *L. monocytogenes*	Nykanen, Weckman, & Lapvetelainen, 2000
VP cold-smoked salmon	Sakacin P-producing *Lb. sakei* and Sakacin P	Inhibited *L. monocytogenes*	Katla et al., 2001
Shrimp			
Brine shrimp	Nisin Z, Carnocin UI49 and crude Bavaricin A	Improved quality and extended shelf life	Einarsson & Lauzon, 1995
Chilled shrimp	Nisin	Inhibited *Pseudomonas* spp. and H_2S producing bacteria	Shirazinejad, Noryati, Rosma, & Darah, 2010
Cooked shrimp	*Lc. piscium* CNCM I-4031	Inhibited *Brochothrix thermosphacta* and improved sensory indices	Fall, Leroi, Cardinal, Chevalier, & Pilet, 2010
Cooked shrimps	*C. maltaromaticum*	No effect	Laursen et al., 2005
VP cooked shrimp	*Lc. piscium* EU2241 and *Leuc. gelidum* EU2247	Inhibited *L. monocytogenes* and *Staph. aureus*	Matamoros et al., 2009

Comprehensive proof of antagonistic effects, precise taxonomic data and strong evidence in terms of safety are still needed for obtaining this status.

4. Conclusion and future perspectives

During the last 20 years, research activities were undertaken to study the application of protective cultures as biopreservatives in seafood matrices. Either deliberately added or produced *in-situ*, this strategy has been discovered to play a potential role in the control of undesirable microorganisms. In addition, the establishment of beneficial bacterial populations is promoted. However, LAB based antagonisms do not necessarily alleviate practical food safety issues in general, as they may be efficient only in a narrow range of food environment (pH, fat content, etc.) and this limits their application in many seafood products. Thus, a case-to-case consideration of applying such a bioprotectant to a certain single food matrix is essential.

It is expected that performing additional studies to select appropriate LAB strains and corresponding combinations to limit the growth of both the pathogenic and spoilage microflora and, furthermore, investigating of the individual nature of the strains and the mechanisms underlying the inhibitory potential will definitively result in the optimization of biopreservation.

Novel techniques such as genomics, proteomics, metabolomics, and system biology, will open up new avenues for the in-depth interpretation of biological data and may enable the development of predictive models estimating safety and shelf life issues of seafood products. By combining classical with molecular tools these new methods possess some big potential in exploring and designing valuable LAB functions allowing to develop not only safer traditional but also innovative seafood products.

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