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Diversity of non-starter lactic acid bacteria in autochthonous dairy products from Western Balkan Countries - technological and probiotic properties

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Review paper

Title:

Diversity of non-starter lactic acid bacteria in autochthonous dairy products from Western Balkan Countries - technological and probiotic properties

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Abstract

The aim of this review was to summarize the data regarding diversity of non-starter lactic acid bacteria (NSLAB) isolated from various artisanal dairy products manufactured in Western Balkan Countries. The dairy products examined were manufactured from raw cow's, sheep's or goat's milk or mixed milk, in the traditional way without the addition of commercial starter cultures. Dairy products such as white brined cheese, fresh cheese, hard cheese, yogurt, sour cream and kajmak were sampled in the households of Serbia, Croatia, Slovenia, Bosnia and Herzegovina, Montenegro, and North Macedonia. It has been established that the diversity of lactic acid bacteria (LAB) from raw milk artisanal dairy products is extensive. In the reviewed literature, 28 LAB species and a large number of strains belonging to the Lactobacillus, Lactococcus, Enterococcus, Streptococcus, Pediococcus, Leuconostoc and Weissella genera were isolated from various dairy products. Over 3000 LAB strains were obtained and characterized for their technological and probiotic properties including: acidification and coagulation of milk, production of aromatic compounds, proteolytic activity, bacteriocins production and competitive exclusion of pathogens, production of exopolysaccharides, aggregation ability and immunomodulatory effect. Results show that many of the isolated NSLAB strains had one, two or more of the properties mentioned. The data presented emphasize the importance of artisanal products as a valuable source of NSLAB with unique technological and probiotic features important both as a base for scientific research as well as for designing novel starter cultures for functional dairy food.

Keywords: Western Balkan Countries; Cheeses; Yogurt; Cream; Kajmak; Non-starter lactic acid bacteria; Health benefits

1. Introduction

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Manufacturing of autochthonous dairy products is a tradition that has been preserved for centuries. They have been characterized by great variety, and some of them have been known since ancient times. All cheeses from a certain geographic area represent a potential national treasure and cultural heritage.

Due to its specific geographical location, climate and richness of meadows and pastures the Balkan Peninsula has always been a region suitable for the development of livestock, including the breeding of cattle, sheep and goats. Therefore, milk production and manufacture of various fermented dairy products are a very important agricultural branch. A large part of the Balkan Peninsula is made up of high mountains with small villages, where various dairy products, especially cheeses from raw milk, are manufactured in rural households by traditional technology and without the addition of starter cultures.

Raw milk cheeses are rich in a variety of microbiota. Therefore, they ripen faster and develop more intense flavor than pasteurized or microfiltered milk cheeses (Bachmann et al., 2011; Mrkonjić Fuka et al., 2013; Van Hekken, 2012). Furthermore, during manufacturing and ripening of raw milk cheeses larger amounts of aromatic compounds such as acids, aldehydes, alcohols, esters and sulphur compounds are produced compared to those of cheeses made with pasteurized milk (Kilcawley, 2017). On the other hand, thermal treatment of milk reduces the number of viable microorganisms and associated enzymes as well as some milk proteases and lipases. preventing the formation of the appropriate flavor in pasteurized milk cheeses (Jo, Benoist, Barbano, & Drake, 2018; Pappa, Bontinis, Tasioula-Margari, & Samelis, 2017; Tomasino, Turbes, Lim, WaiteCusic, & Meunier Goddik, 2018). Thus, many cheese consumers choose raw rather than pasteurized milk cheeses (Chambers, Esteve, & Retiveau, 2010; Colonna, Durham, & Meunier-Goddik, 2011). Many authors have studied the sensory characteristics of cheeses produced from different kinds of milk (cow, goat, sheep) and from uncooked and cooked milk (Alonso, Picon, Gaya, & Nunez, 2013; Sant'Ana et al., 2013; Velez, Perotti, Wolf, Hynes, & Zalazar, 2010; Zabaleta et al., 2016). The results shown that the diet of dairy animals has an influence on the flavor of raw milk cheeses (Aprea et al., 2016; Cornu et al., 2009; Kilcawley, Faulkner, Clarke, O'Sullivan, & Kerry, 2018; Martin et al., 2009), together with seasonal effects (Boltar, Čanžek Majhenič, Jarni, Jug. & Baycon Kralj, 2015; Chion et al., 2010). In addition, the characteristics of traditional cheeses are significantly influenced by animal breed, the technology used in cheese manufacturing and the physico-chemical and microbiological qualities of the raw milk (Coulon, Delacroix-Buchet, Martin, & Pirisi, 2004; De Marchi, Bittante, Dal Zotto, Dalvit, & Cassandro, 2007; Johnson, 2017).

In rural households of the Western Balkans, the most common dairy products are fresh young cheese and white brined cheese (known as white-pickled cheese) made from raw milk. Both types of cheeses are manufactured by the addition of rennet to preheated milk at 30°C. The shelf life of fresh young cheeses is short, so they are intended for immediate consumption (Golić et al., 2013; Pešić-Mikulec & Jovanović, 2005; Pogačić et al., 2011; Terzić-Vidojević et al., 2014b), while white brined cheese can be used in the diet after one to six months of ripening (Begovic et al., 2011; Golić et al., 2013; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Nikolic et al., 2008; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic & Topisirovic, 2007; Terzic-Vidojevic et al., 2009a; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a).

Another frequently used dairy product, very popular in the diet among the regional population, is kajmak made from cooked milk. Kajmak is a traditional dairy product with a soft and creamy texture produced by the fermentation of milk fat (Jokovic et al., 2008) that was previously collected from the surface of boiled and then slowly cooled milk. This dairy product is rich in milk fat (about 60%, w/w) and salty. A longer period of fermentation is needed to obtain the final product, which has a thick, creamy consistency (not entirely compact due to milk protein strands) and a rich taste. On the other hand, sweet kajmak is also produced by collecting milk fat from the surface of boiled milk, but without salting and it can be consumed after a short period (Terzić-Vidojević et al., 2014b). Similar to kajmak, mileram is a full-fat dairy product. Mileram is a local homemade product obtained by collecting milk fat from the surface of uncooked milk. It is also called sweet cream because no salt is added during the production process and it is not subject to fermentation (Terzić-Vidojević et al., 2014b).

Hard cheeses are another group of dairy products made in the countries of the Western Balkans (Bojanic Rasovic, Mayrhofer, Martinovic, Dürr, & Doming, 2017; Čanžek Majhenič, Rogelj, & Perko, 2005; Čanžek Majhenič, Mohar Lorberg, & Rogelj, 2007; Levkov & Kakurinov, 2012; Levkov, Srbinovska, & Gjorgovska, 2014; Levkov, Mojsova, Nastova, Srbinovska, & Gjorgovska, 2017; Mrkonjić Fuka, Engel, Skelin, Redžepović, & Schloter, 2010; Mrkonjić Fuka et al., 2013; Paveljšek, Trmčić, Hacin, & Rogelj, 2014; Skelin et al., 2012). The main characteristics of hard cheeses are their very low moisture content and longer shelf life. They represent the most common cheeses in the warmer regions of the Western Balkan Countries (WBC) such as the Adriatic Sea

coast, North Macedonia and Montenegro. Aside from the hard consistency these cheeses have a strong flavor, so they are consumed throughout the year in smaller quantities.

A specific type of semi-hard cheese matured in lambskin or sheepskin sacks, so called "Sir iz mišine", is characteristic of the regions of Croatia, Bosnia and Herzegovina and Montenegro (Frece et al., 2016). When removed from the sack, the cheese is dried in the form of lumps of different sizes. The taste is moderately salty and spicy, typical of the type of milk. Due to its unique organoleptic properties, this type of cheese is a favorite in the diet of the local consumers.

Dairy products, especially those manufactured from raw milk are rich in numerous useful and harmful microbiota. Among the useful microorganisms are non-starter lactic acid bacteria (NSLAB) (Bluma, Ciprovica, & Sabovics, 2017; Domingos-Lopes, Stanton, Ross, Dapkevicius, & Silva, 2017; Settani & Moschetti, 2010). Lactic acid bacteria (LAB) are naturally present in milk, but the origin and quality of milk, environmental conditions like livestock diet (grass, hay etc.), seasons, altitude of pasture, and manufacturing process of dairy products, and hygienic conditions during manipulation of the milk all have a significant impact on what microbial populations are present (Gobbetti, De Angelis, Di Cagno, Mancini, & Fox, 2015; Siezen et al., 2010; Tilocca et. al., 2020).

The genera Lactococcus, Lactobacillus, Enterococcus, Streptococcus, Pediococcus, Leuconostoc and Weissella are each part of the heterogeneous NSLAB community (Bluma, Ciprovica, & Sabovics, 2017; González, Fernández Cuadrillero, Castro, Bernardo, & Tornadijo, 2015; Montel et al., 2014), and they share many common physiological features. The main recognizable characteristic of LAB is their ability to convert fermentable carbohydrates into organic acids, alcohols, and carbon dioxide via homo- or heterofermentative metabolism (Bintsis, 2018a; Widyastuti, Rohmatussolihat, & Febrisiantosa, 2014). These compounds, the end products of metabolism, exhibit an inhibitory effect on the growth of pathogenic and spoilage microorganisms and thereby prolong the shelf life of fermented foods. In addition to organic acids (mainly lactic and acetic acid) many LAB strains have the ability to produce other antimicrobial compounds such as hydrogen peroxide and antifungal peptides, but bacteriocins have the greatest significance (Des, Ross, & Hill, 2018; Reis, Paula, Casarotti, & Penna, 2012; Settanni & Corsetti, 2008). Thanks to their ability to produce these compounds LAB enable biopreservation and improve food safety. Besides preserving foods, through some of their metabolic properties LAB significantly affect changes in the organoleptic characteristics of fermented food, such as the development of the distinctive flavor and texture of the final product. Moreover, fermented food is enriched with vitamins, proteins, essential amino acids and essential fatty acids, which contribute to the increase of nutritional value (Câmara et al., 2019; Widyastuti, Rohmatussolihat, & Febrisiantosa, 2014).

In addition, LAB are recognized as bacteria with probiotic features as they contribute to the improvement of consumers' health. According to a WHO expert panel, probiotics are defined as 'live microorganisms which when administered in adequate amounts confer a health benefit on the host' (Pineiro et al., 2008). The consumption of fermented foods enriched in probiotic bacteria exerts beneficial effects on the consumer's health through direct actions of the live microbial cells ("probiotic effects") or through indirect effects by secondary metabolites with health-promoting properties produced by probiotic bacteria during fermentation (postbiotics) (Divya, Varsha, Nampoothiri, Ismail, & Pandey, 2012; Hayes, Ross, Fitzgerald, & Stanton, 2007; Muhammad, Ahmad, & Shah, 2018). Taking into consideration the fact that LAB are food-grade bacteria, as well as their significance in food fermentation, LAB are denoted as "generally recognized as safe" (GRAS) (Bourdichon et al., 2012; Hempel et al., 2011).

Many reports on LAB from different niches, describing their technological and potential for probiotic properties and application in the food industry, are available in literature (Bintsis, 2018b; Montel et al., 2014; Ravyts, De Vuyst, & Leroy, 2012; Zielińska & Koloźyn-Krajewska, 2018). A major part of a review article by Taneva-Angelova, Balabanova, Boyanova, and Beshkova (2018) is devoted to describing the technological process of producing various traditional fermented milk products from all Balkan Peninsula countries, while data on LAB have been given generally per groups of milk products. In contrast, the main focus of this review is for the first time to relate the technological and probiotic properties of NSLAB isolated from numerous artisanal and autochthonous dairy products produced in rural households of the WBC.

2. Prevalence of LAB in different types of WBC dairy products

In rural parts of the Western Balkans, a number of various artisanal dairy products are manufactured in households in the traditional way, mainly from raw cow's, ewe's and goat's milk and without the addition of a commercial starter culture. This region has a long tradition of producing fermented products that has been passed down from generation to generation. The dairy products involved in this review were collected from specific localities across Serbia, Croatia, Slovenia, Bosnia and Herzegovina, North Macedonia and Montenegro.

2.1. White brined (white-pickled) cheeses

White brined cheeses are the most commonly found types in Serbia, Montenegro, Bosnia and Herzegovina, and North Macedonia regions (Table 1). These cheeses are traditionally produced from raw milk, mainly in areas with higher altitude mountains like Zlatar, Stara Planina, Radan, Golija, Javor, Vlašić, Galičica and many other similar localities. White brined cheeses are full-fat cheeses of intense flavor, dry-salted, ripened and stored in brine. They are usually consumed after several months of ripening and have a particular flavor depending on the milk used (cow's, ewe's and goat's milk or a mixture of two types of milk) and their microbiota varies depending on the ripening period (Begovic et al., 2011; Levkov, Srbinovska, & Gjorgovska, 2014; Levkov, Mojsova, Nastova, Srbinovska, & Gjorgovska, 2017; Mojsova et al., 2013; Nikolic et al., 2008; Paveljšek, Trmčić, Hacin, & Rogelj, 2014; Pešić-Mikulec & Jovanović, 2005; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic et al., 2009a; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, 2015b). The ripening period also affects the specific texture and flavor of the final product (Asteri et al., 2009; Callon, Berdagué, Dufour, & Montel, 2005; Farahani, Rasooli, & Owlia, 2017; Pino et al., 2019; Saiki et al., 2018).

Table 1

Results have shown that in the white brined cheeses, regardless of the ripening period, the most common LAB genera are: Lactobacillus (Lb.), Lactococcus (Lc.), Enterococcus (E.) and Leuconostoc (Ln.) (Figure 1). Similar results were obtained by other authors who have examined the NSLAB populations of artisanal white brined cheeses during ripening (Bintsis & Papademas, 2002; Hayaloglu, 2016; Madrau et al., 2006; Manolopoulou et al., 2003; Slyvka, Tsisaryk, Dronyk, & Musiy, 2018; Stojiljkovic, 2018). Lactococci are not usually isolated from cheeses older than 30 days except in Macedonian cheeses (Mojsova et al., 2013) (Figure 1). The inhibitory effect of low pH and high salt concentration throughout cheese ripening has been considered the main reason for their rapid decline in older cheeses (Fusco, Quero, Poltronieri, Morea, & Baruzzi, 2019; Susilowati, Laia, & Purnomo, 2018). Many authors investigating LAB populations from white brined cheeses manufactured in different geographical regions, such as Lighvan, Tulum, Feta and Teleme cheeses, also noticed that lactococci decreased significantly after 30 days of ripening (Edalatian, Najafi, Mortazavi, & Mayo, 2012; Gurses & Erdogan, 2006; Tzanetakis & Litopoulou-Tzanetaki, 1992). Similar to lactococci, leuconostocs were present in younger cheeses, while lactobacilli and enterococci, which are less sensitive to low pH and high salt concentration (Dabevska-Kostoska, Velickova, Kuzmanova, & Winkelhausen, 2015), were found in all ripening stages of WBC white brined cheeses (Begovic et al., 2011; Golić et al., 2013; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Levkov, Mojsova, Nastova, Srbinovska, & Gjorgovska, 2017; Mojsova et al., 2013; Nikolic et al., 2008; Terzic-Vidojevic, Vukašinovic, Veljovic, Ostojic & Topisirovic, 2007; Terzic-Vidojevic et al., 2009a; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a). Streptococci and pediococci were isolated sporadically from a few kinds of 1 to 20-day-old cheeses (Begovic et al., 2011; Golić et al., 2013; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a). Similar data were described by Barouei et al. (2011); Edalatian, Najafi, Mortazavi, and Mayo (2012) and Hayaloglu (2016) who studied the diversity and evolution of LAB microbiota during ripening of white brined cheeses.

There are significant differences in the occurrence of certain LAB genera in cheeses produced from different types of milk and in different households, as well as in cheeses of varying ripening periods (Figure 1). Lactobacilli were predominant (about 70%) in 30-day-old BGZLS (letters represent different geographic locations) (Veljovic et al., 2007) and BGGJ cheeses (Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011) but also in 10-day-old BGGO cheese (Terzić-Vidojević et al., 2014a). In addition, enterococci represented 50% of microbiota in 60-day-old BGZLS cheese (Veljovic et al., 2007) and 57% in 5-day-old BGGJ cheese (Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011). On the other hand, enterococci were present at a rate of 38% in BGGO 1 day and 60-day-old cheeses (Terzić-Vidojević et al., 2014a). Four Macedonian cheeses, marked A, B, C and D, 7 and 90 to 100-day-old, contained lactobacilli, but enterococci were not detected in two nor leuconostocs in three 90 to 100-day-old cheeses (Levkov, Mojsova, Nastova, Srbinovska, & Gjorgovska, 2017). Additionally, lactococci, streptococci and pediococci were not isolated from any of the Macedonian cheeses analyzed (Levkov, Mojsova, Nastova, Srbinovska, & Gjorgovska, 2017) (data not shown). It should be emphasized that sampling of these cheeses was performed in diverse households among which there is a variation in the manufacturing technology and environmental conditions. These differences might explain the variation in the percentage of lactobacilli, enterococci and other LAB genera isolated from various cheeses.

Fig. 1.

More specifically, data on LAB species in certain cheeses are presented in Figure 2. *Lactobacillus plantarum* was the predominant *Lactobacillus* species in Pirot, Golija, Radan and Vlasina cheeses as well as in white brined cheeses from South Morava, Eastern Serbia and North Macedonia followed by *Lb. paracasei* subsp. *paracasei* found in Bukuljac and Zlatar BGZLS cheeses, *Lb. casei/paracasei* in Zlatar BGNV cheese, *Lb. paraplantarum* in Pirot and Radan cheeses, *Lb. brevis* in Pirot and Zlatar BGZLS cheeses and *Lb. paraplantarum* and *Lb. delbrueckii* in Radan and Pirot cheeses (Begovic et al., 2011; Golić et al., 2013; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Levkov, Mojsova, Nastova, Srbinovska, & Gjorgovska, 2017; Nikolic et al., 2008; Terzic-Vidojevic, Vukašinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2009a, 2013, 2014a).

The largest number of different LAB species including Lb. fermentum, Lb. sucicola, Lb. rhamnosus, Lb. reuteri, Lb. helveticus, Lb. curvatus, Lb. lindneri, Lb. salivarius and Lb. delbrueckii, was found in Golija and North Macedonia (Golić et al., 2013; Levkov, Mojsova, Nastova, Srbinovska, & Gjorgovska, 2017; Terzić-Vidojević et al., 2014a) while in 90-day-old Zlatar BGNV cheese (Terzic-Vidojević et al., 2009a) heterofermentative species Lb. parabuchneri was identified (Figure 2). Results obtained by Edalatian, Najafi, Mortazavi, and Mayo (2012), Ehsani, Hashemi, Afshari, and Aminzare (2018), Hassanzadazar and Ehsani (2013), Slyvka, Tsisaryk, Dronyk, and Musiy (2018), Sofu and Ekinci (2016) and Tzanetakis and Litopoulou-Tzanetaki (1992) described the diversity of LAB in Lighvan, Koopeh, Ezine, Carpathian, Feta and Teleme white brined cheeses during ripening. They also found Lb. plantarum to be the dominant Lactobacillus species followed by Lb. casei, Lb. paracasei and Lb. brevis, while the species Lb. fermentum, Lb. rhamnosus, Lb. curvatus, Lb. delbrueckii and Lb. helveticus were less widely distributed (Edalatian, Najafi, Mortazavi, & Mayo, 2012; Gurses & Erdogan, 2006; Sofu & Ekinci, 2016). On the other hand, Hosono, Iseki, Otani, and Takahashi (1992) reported that in Beyaz Peynir cheese Lb. casei subsp. casei was the most dominant species among lactobacilli, and Sengul (2006) isolated 18 Lb. fermentum and 17 Lb. parabuchneri strains from Civil cheese. Based on the above results we concluded that Lb. plantarum, Lb. casei and Lb. paracasei are the most common Lactobacillus species in white brined cheeses.

As can be seen in Figure 2 Lc. lactis was the species found in most WBC white brined cheeses during earlier ripening periods (Begovic et al., 2011; Golić et al., 2013; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Nikolic et al., 2008; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a). Lactococcus lactis was isolated from fresh Lighvan and Tulum cheeses (Edalatian, Najafi, Mortazavi, & Mayo, 2012; Gurses & Erdogan, 2006), from Anevato cheese up to 15-day-old (Hatzikamari, Litopoulou-Tzanetaki, & Tzanetakis, 1999) and from Greek white brined cheese up to 15-day-old (Litopoulou-Tzanetaki & Tzanetakis, 1992). In contrast, Mojsova et al. (2013) and Prodromou, Thasitou, Haritonidou, Tzanetakis, and Litopoulou-Tzanetaki (2001) isolated Lc. lactis species from Macedonian and Orinotyri 90-day-old cheeses. On the other hand, Lc. garvieae was detected in limited numbers in cheeses from Golija and Eastern Serbia (Golić et al., 2013; Terzić-Vidojević et al., 2014a), and in white brined Orinotyri and Bryndza cheeses from the Greek and Carpathian mountains, respectively (Prodromou, Thasitou, Haritonidou, Tzanetakis, & Litopoulou-Tzanetaki, 2001; Slyvka, Tsisaryk, Dronyk, & Musiy, 2018). Ruggilero et al. (2018) examined the viability of Lc. lactis subsp. lactis in model cheeses during 6 months of ripening by both culture dependent and culture independet methods. They found 3-4 log CFU/g of Lc. lactis at the end of ripening period using reverse transcription quantitative polymerase chain reaction (RT-qPCR) analysis, but they did not detect viable Lc. lactis by traditional plating on M17 medium, concluding its viable but not cultivable state.

Fig. 2.

Enterococci are widespread in white brined cheeses because they are a salt-resistant group of LAB (Elkenany, Elsayed, Eltaysh, Zakaria, & El-Baz, 2018) and they are also well adapted to the entire cheese manufacturing process (Edalatian, Najafi, Mortazavi, & Mayo, 2012). *Enterococcus faecalis* and *E. faecium* are approximately equally represented in WBC white brined cheeses followed by *E. durans* (Figure 2) (Begovic et al., 2011; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Golić et al., 2013; Nikolic et al., 2008; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic et al., 2009a; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a). Edalatian, Najafi, Mortazavi, and Mayo (2012) reported similar results. On the other hand, *E. faecium* was detected in Greek and Carpathian Bryndza white brined cheeses as the dominant *Enterococcus* species (Litopoulou-Tzanetaki & Tzanetakis, 1992; Slyvka, Tsisaryk, Dronyk, & Musiy, 2018). Prodromou, Thasitou, Haritonidou, Tzanetakis, and Litopoulou-Tzanetaki (2001) described the dominant prevalence of *E. faecalis* over *E. faecium* strains in Orinotyri cheese, while *E. durans* was the dominant *Enterococcus* species in Macedonian cheeses (Levkov, Mojsova, Nastova,

Srbinovska, & Gjorgovska, 2017) and in each stage of Ezin cheese making (Sofu & Ekinci, 2016). The results confirmed that *E. faecium*, *E. faecalis* and *E. durans* are the most frequently isolated enterococci from white brined cheeses.

As presented in Figure 1 the oldest white brined cheese from WBC from which leuconostocs were isolated was 20-day-old, with the exception of one 90 to 100-day-old Macedonian cheese from Štip in which leuconostocs were also detected. Similar findings were referred by Sofu and Ekinci (2016) and Litopoulou-Tzanetaki and Tzanetakis (1992) who identified leuconostocs in 1 to 30-day-old white brined cheeses. The authors who have studied the LAB of white brined cheeses found *Ln. mesenteroides* and *Ln. pseudomesenteroides* as the main representatives of heterofermentative LAB in Radan, Golija, Vlasina, Pirot and Macedonian cheeses, and in cheeses of the South Morava and Eastern Serbia regions (Figure 2), as well as in Carpatian and Turkish white brined cheeses (Begovic et al., 2011; Golić et al., 2013; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Levkov, Mojsova, Nastova, Srbinovska, & Gjorgovska, 2017; Slyvka, Tsisaryk, Dronyk, & Musiy, 2018; Sofu & Ekinci, 2016; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzić-Vidojević et al., 2014a). *Leuconostoc garlicum* was present in Pirot cheeses (Begovic et al., 2011; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b) and *Ln. citreum* was identified in Vlasina cheeses (Terzic-Vidojevic et al., 2013) (Figure 2).

Streptococcus (S.) strains such as Streptococcus thermophilus (Figure 2) were found in very low proportions in Radan, Golija and Pirot cheeses (Begovic et al., 2011; Golić et al., 2013; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzić-Vidojević et al., 2014a), while S. equinus/bovis was detected in cheeses of the South Morava and Eastern Serbia regions (Golić et al., 2013). Interestingly, S. bovis was isolated from cow feces, since this species dominates the intestinal tract of cows (Gelsomino, Vancanneyt, Cogan, Condon, & Swings, 2002). All these cheeses, from which LAB streptococci were isolated, were 1 to 3-day-old (Figure 1). Additionally, streptococci were found in white brined Feta and Ezine cheeses during ripening (Rantsiou, Urso, Dolci, Comi, & Cocolin, 2008; Sofu & Ekinci, 2016).

Pediococcus pentosaceus was isolated from 15-day-old Vlasina cheese (Figure 1 and Figure 2) (Terzic-Vidojevic et al., 2013). These data are in accordance with data referred to previously, where *P. pentosaceus* was detected in the analysis of raw milk and fresh stages of Lighvan cheese and 1, 15 and 30-day-old Feta cheese (Edalatian, Najafi, Mortazavi, & Mayo, 2012; Tzanetakis & Litopoulou-Tzanetaki, 1992). The exception was the isolation of pediococci from 120-day-old Radan cheese (Figure 1) (Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011).

2.2. Fresh (young) cheeses

Fresh cheeses are the second group of artisanal cheeses manufactured mainly in country households of Bosnia and Herzegovina, Croatia and Serbia (Table 1). The consistency of fresh cheeses is soft or creamy. They are manufactured from different types of raw milk (cow, sheep and goat milk) by traditional methods without adding commercial starter cultures and without ripening (Golić et al., 2013; Pešić-Mikulec & Jovanović, 2005; Pogačić et al., 2010; Terzić-Vidojević et al., 2014b). Therefore, they are often consumed immediately after manufacturing. These cheeses are used daily in the diet as an addition to a meal or for the preparation of salty and sweet dishes, since the majority of fresh cheeses are made without salt. Apart from the fact that these cheeses are unsalted, they belong to the group of low-fat cheeses, so they are suitable for the diet of people who suffer from increased cholesterol and triglycerides as well as high blood pressure. Since fresh cheeses are produced from raw milk they abound in a large number of different species and strains of LAB that possess valuable technological and probiotic properties (Yu et al., 2012; Zhong et al., 2016). Indigenous raw milk microbiota have an impact on the organoleptic characteristics of the final dairy product especially on their flavor (Tilocca et al., 2020). The diversity of the natural population of LAB is of great importance for eventual application in the food and pharmaceutical industry, as well as for fundamental research (Bintsis, 2018b).

Based on available data given in Figure 3A lactococci were the predominant LAB in Serbian fresh cheeses (87.5 %) (Pešić-Mikulec & Jovanović, 2005) and Croatian fresh cheeses known as Karakačanski Skakutanac (10⁷-10⁸ CFU/g) (Pogačić et al., 2011). On the other hand, the number of lactobacilli, enterococci and leuconostocs in Karakačanski Skakutanac cheeses ranged between 10² and 10³CFU/g, while no data for streptococci and pediococci were reported. *Lactobacillus versmoldensis*, *Lc. lactis* subsp. *lactis*, *E. faecalis* and *Ln. pseudomesenteroides* were the species isolated from this cheese (Pogačić et al., 2011) (Figure 3B).

Lactococcus spp. are the most commonly isolated LAB from artisanal dairy products (Hayaloglu, 2016; Tilocca et al., 2020) and *Lc. lactis* is main representative of LAB species in fresh cheeses of WBC (Golić et al., 2013; Mrkonjić Fuka, Engel, Skelin, Redžepović, & Schloter, 2010; Pogačić et al., 2011; Terzić-Vidojević et al., 2014b) and in many other fresh raw milk cheeses (Castro et al., 2016a; Fernández, Alegría, Delgado, Martín, & Mayo, 2011; Feutry et al., 2012) (Figure 3). Many authors consider lactococci to be the group of LAB that play a

leading role in the acidification of milk at the beginning of cheese mantufacturing (Delcenserie et al., 2014; Luiz et al., 2017; Veljovic et al., 2007). Besides lactose fermentation, the decrease of milk pH, curd formation and prevention of the growth of pathogenic and spoilage bacteria, *Lc. lactis* strains isolated from Leben (Tunisian fermented milk) produced 35 volatile compounds which were mainly ketones, amino acids and sulphur compounds (Ziadi, Wathelet, Marlier, Hamdi, & Thonard, 2008). Aldehydes were considered as particularly for the flavor formation in naturally fermented milk (Gadaga, Viljoen, & Narvhus, 2007; Morales, Fernández-García, Gaya, & Nuñez, 2003; Nájera-Domínguez, Gutiérrez-Méndez, Nevárez-Moorillon, & Caro-Canales, 2014). It has also been shown that the flavor derived from amino acid catabolism by *Lc. lactis* during milk fermentation is much more intense than that obtained during ripening (Ziadi et al., 2010). According to these results, it can be concluded that the pronounced flavor of fresh cheeses is primarily due to the activity of *Lc. lactis* strains in the first hours of milk fermentation.

Fig. 3

Enterococci are part of the dominant microbiota in raw milk cheeses (Jamaly, Benjouad, Comunian, Daga, & Bouksaim, 2010; Morandi, Brasca, Andrighetto, Lombardi, & Lodi, 2006; Terzić-Vidojević et al., 2015b). Enterococci and leuconostocs were the most numerous LAB in Croatian fresh cheeses from the Prigorje, Zagorje and Bilogorsko-Podravska regions (Golić et al., 2013), while in Travnik young cheeses (from Bosnia and Herzegovina) lactococci, enterococci and leuconostocs were almost equally represented (25.7%, 26.2% and 27.9%, respectively) (Terzić-Vidojević et al., 2014b) (Figure 3A). Results presented in Figure 3A show that Enterococcus spp. have been significantly presented in some unripened cheeses (Golić et al., 2013; Terzić-Vidojević et al., 2014b), and in lower numbers in others (Pogačić et al., 2011), while in some fresh cheeses enterococci were not detected (Pešić-Mikulec & Jovanović, 2005). As could be seen in Figure 3B E. faecalis, followed by E. faecium and E. durans, are common in fresh cheeses of the WBC (Golić et al., 2013; Pogačić et al., 2011; Terzić-Vidojević et al., 2014b). These three *Enterococcus* species are the most common microbiota in raw milk cheeses (Martin-Platero, Valdivia, Maqueda, & Martínez-Bueno, 2009; Nieto-Arribas et al., 2011; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, b; 2015b; Veljovic et al., 2007), contributing to cheese flavor and texture (Martino, Quintana, Espariz, Blancato, & Magni, 2016; Sarantinopoulos et al., 2001). Furthermore, many strains of enterococci produce bacteriocins, the so-called enterocins, that are active against pathogens and spoilage bacteria, so they have a significant role in food biopreservation (Elkenany, Elsayed, Eltaysh, Zakaria, & El-Baz, 2018; Giraffa, 2003; Sarantinopoulos et al., 2002; Veljovic et al., 2009).

Leuconostocs were found in Croatian fresh cheeses and young cheeses from Bosnia and Herzegovina (Golić et al., 2013; Pogačić et al., 2011; Terzić-Vidojević et al., 2014b), while in Serbian fresh cheeses leuconostocs were not found (Figure 3A) (Pešić-Mikulec & Jovanović, 2005). Since leuconostocs are normally found on the surface of plants, many traditional cheeses produced from raw milk contain Leuconostoc species as part of NSLAB (Alegria, Delgado, Flórez, & Mayo, 2013; Begovic et al., 2011; Franciosi, Settanni, Cologna, Cavazza, & Poznanski, 2011; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Mojsova et al., 2013; Nieto-Arribas, Seseña, Poveda, Palop, & Cabezas, 2010; Terzic-Vidojevic et al., 2013, 2014a). As heterofermentative LAB, *Leuconostoc* spp. produces carbon dioxide from carbohydrates and dextran from sucrose, influencing the texture of the final product (Dror et al., 2018; Hemme & Foucaud-Sheunemann, 2004). Since leuconostcs have a weak ability to ferment lactose, they have no significant effect on the acidification process. However, leuconostocs grow in association with acid-producing lactococci. Lowering pH by lactococcal activity accelerates the metabolism of citrate positive (cit+) leuconostoc strains which produce aromatic compounds important for cheese flavor (McSweeney & Sousa, 2000; van Mastrigt, Egas, Abee, & Smid, 2019). The sensory properties of starter-free cheeses are influenced by proteolytic, lipolytic and aminopeptidase activities of leuconostocs (Cardamone et al., 2011; Yeluri Jonnala, McSweeney, Sheehan, & Cotter, 2018). Leuconostoc mesenteroides and Ln. pseudomesenteroides are two species-previously described as the most common Leuconostoc species in dairy products (Båth, Persson, Schnürer, & Leong, 2012; Montel et al., 2014), as well as in Croatian fresh cheeses and cheeses from Bosnia and Herzegovina (Golić et al., 2013; Pogačić et al., 2011; Terzić-Vidojević et al., 2014b) (Figure 3B).

Lactobacilli were found in low proportions in Serbian fresh cheeses (Pešić-Mikulec & Jovanović, 2005), Croatian Karakačanski Skakutanac (Pogačić et al., 2011) and Croatian fresh cheeses from Prigorje, Zagorje and Bilogorsko-Podravska regions (Golić et al., 2013). On the other hand, in Travnik young cheeses one-fifth of total determined LAB were lactobacilli (Terzić-Vidojević et al., 2014b) (Figure 3A). Results reported previously showed that one-day-old Zlatar cheese (Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007), 5 and 10-day-old Radan cheeses (Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011) as well as 5-day-

old Vlasina cheese (Terzic-Vidojevic et al., 2013) contained only a few or no lactobacilli (Figure 1). In addition, three samples of one-day-old Golija cheese contained between 16.7 to 18.9 % *Lactobacillus* isolates (Golić et al., 2013; Terzić-Vidojević et al., 2014a). The main reason for the fact that lactobacilli are present both in young and ripened cheeses is that in addition to lactose they can use other carbon sources, such as citrate and many other carbohydrates (Díaz-Muñiz & Steele, 2006; Frau, Nuñez, Gerez, Pece, & Font, 2016). Non-starter lactobacilli showed significant proteolytic and lipolytic potential and contribute to flavor development and improve the sensory characteristics of cheese (Duan et al., 2019; Morea, Matarante, Di Cagno, Baruzzi, & Minervini, 2007). The most common *Lactobacillus* species in fresh cheeses of the WBC are *Lb. casei* and *Lb. plantarum* (Figure 3B). These two lactobacilli species were dominant in raw milk cheeses such as Zlatar cheese (Veljovic et al., 2007), Radan cheeses (Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011), Golija cheeses (Golić et al., 2013; Terzić-Vidojević et al., 2014a) and Vlasina cheeses (Terzic-Vidojevic et al., 2013).

2.3. Hard cheeses

Hard cheeses form a very heterogeneous group of cheeses, different in shape, properties and technology of production. They have a moisture content below 40%, since they are exposed to pressure that forces the drainage of the whey during the manufacturing process, and therefore have a longer shelf life than soft cheeses. Furthermore, hard cheeses have higher fat content in dry matter compared to some other types of cheese. One of the main characteristics of hard cheeses is their long ripening period. They are manufactured from cow's, sheep's and goat's milk or from a mixture of types of milk. Traditional hard cheeses produced in the Western Balkans, such as Kashkaval, Pirot cheese, Trappist cheese, Njeguši cheese, Istrian cheese, Tolminc cheese, Krcki cheese, Paski cheese, Karst cheese and Macedonian Beaten cheese, are known worldwide. The unique organoleptic properties of autochthonous cheeses are influenced by specific geographical and pedoclimatic characteristics, milk quality and technology of cheese manufacturing (Micari, Sarullo, Sidari, & Caridi, 2007). In addition, NSLAB found in cheese originating from raw milk, dairy equipment and the environment during cheese manufacturing and ripening have a great impact on the final flavor and texture (Kilcawley, 2017; Steele, Broadbent, & Kok, 2013). Hard cheeses are used daily in the diet as part of a cold meal with bread, as an appetizer or as an addition to various types of salads, sandwiches, pizza and many other dishes.

There are not many published data pertaining to the LAB population in hard cheeses from WBC. Results reported by Mrkonjić Fuka, Engel, Skelin, Redžepović, and Schloter (2010), Mrkonjić Fuka et al. (2013) and Levkov and Kakurinov (2012), which describe LAB isolated from four types of hard cheeses produced in Croatia (Istrian, Krcki and Paski cheese) and in North Macedonia (Beaten cheese), are listed in Table 2. Although we found little data referring to LAB microbiota of WBC hard cheeses, 13 LAB species were isolated from the hard cheeses mentioned (Table 2). Each of them contributed to the specificity of the final flavor and/or texture of the cheese.

Table 2

The most common species isolated from Istrian, Krcki and Paski cheeses were *Lc. lactis* and *Lc. raffinolactis* (Paski cheeses) in both young and old cheeses (Mrkonjić Fuka, Engel, Skelin, Redžepović, & Schloter, 2010; Mrkonjić Fuka et al., 2013). *Lactococcus lactis* subsp. *lactis* (28.3%) and *Lc. raffinolactis* (4.4%) were also the main lactococci isolated from Spanish semi-hard San Simón da Costa Cheese (González, Fernández Cuadrillero, Castro, Bernardo, & Tornadijo, 2015). Beaten cheeses had a similar number of lactobacilli and lactococci in both one-day-old and 45-day-old cheeses (Table 2), but no enterococci, leuconostocs or streptococci were described in these cheeses (Levkov & Kakurinov, 2012). In addition, *Leuconostoc* spp. and *Streptococcus* spp. were not found in Istrian cheeses (Mrkonjić Fuka, Engel, Skelin, Redžepović, & Schloter, 2010) while dairy streptococci such as *S. thermophilus* and *S. macedonicus* were not found in Istrian, Krcki and Paski cheeses (Mrkonjić Fuka et al., 2013) (Table 2).

Lactobacillus curvatus was isolated from 0 and 120-day-old Istrian cheeses (Mrkonjić Fuka, Engel, Skelin, Redžepović, & Schloter, 2010) while 45 and 90-day-old Istrian cheeses contained other lactobacilli such as Lb. casei/paracasei, Lb. plantarum, Lb. acidipiscis and Lb. amylovorum (Mrkonjić Fuka et al., 2013) (Table 2). The species Lb. acidipiscis was also isolated from Krcki cheeses (Table 2). This information is not surprising since Lb. acidipiscis was isolated from traditional Japanese fermented fish products (An, Takahashi, Kimura, & Kuda, 2010) and the Istrian Peninsula and the island of Krk are located along the Adriatic Sea.

The main lactobacilli isolated from semi-hard raw milk San Simón da Costa cheese and from 2, 6, 9 and 13-months-old hard raw-milk PDO Grana Padano cheeses were *Lb. casei* subsp. *casei* and *Lb. paracasei* subsp. *paracasei* (González, Fernández Cuadrillero, Castro, Bernardo, & Tornadijo, 2015; Pogačić et al., 2013). *Lactobacillus brevis* was isolated from 45-day-old Paski cheese (Mrkonjić Fuka et al., 2013). Similar data were

reported by Veljovic et al. (2007) who detected *Lb. brevis* in 45-day-old Zlatar cheese. The majority of the NSLAB population of Cheddar cheeses was composed of *Lb. casei*, *Lb. paracasei*, *Lb. plantarum*, and *Lb. rhamnosus* (Stefanovic et al., 2018). De Angelis et al. (2001) found 37% *Lb. plantarum/pentosus* isolates, 18% *Lb. casei/paracasei* isolates, 15% *Lb. brevis* isolates, 9% *Lb. curvatus* isolates, 6% *Lb. fermentum* isolates, 3% *Lb. casei* subsp. *pseudoplantarum* isolates, and 1% *Lb. rhamnosus* isolates from 12 samples of Italian Pecorino-like cheeses made from sheep's milk These results support the assumption that the composition of the LAB microbiota in cheeses depends on the environment, LAB present in raw milk-derived mainly from plants and milk equipment and all phases of cheese-making process (Franciosi, Settanni, Cologna, Cavazza, & Poznanski, 2011; Tilloca et al., 2020). In addition, techniques used to monitor bacterial composition are very important to find out more about LAB population of cheeses during and after the production process.

Enterococci were detected in low numbers in Istrian cheeses (Mrkonjić Fuka, Engel, Skelin, Redžepović, & Schloter, 2010), in Krcki and Paski cheeses (Mrkonjić Fuka et al., 2013) (Table 2). The exceptions were 45 and 90-day-old Istrian cheeses (Mrkonjić Fuka et al., 2013) where enterococci were present in higher numbers (42-45% of operational taxonomical units (OTUs) 90–100% sequence similarity). Enterococci were found in many types of hard cheeses and the dominant species was mainly *E. faecalis* isolated from hard Manchego cheese (Nieto-Arribas et al., 2011), Armada cheese (Herreros, Fresno, González Prieto, & Tornadijo, 2003), Roncal and Idiazabal cheeses (Arizcun, Barcina, & Torre, 1997) Ezine cheese (Başar Uymaz, Akçelik, & Yüksel, 2019), as well as San Simón da Costa cheese (González, Fernández Cuadrillero, Castro, Bernardo, & Tornadijo, 2015).

Some aroma compounds present in hard cheeses could originate from the metabolic activity of leuconostocs. The species *Ln. mesenteroides* was found in Istrian, Krcki and Paski cheese (Mrkonjić Fuka et al., 2013) while *Ln. citreum* was isolated only from Paski cheese (Table 2). Leuconostocs were the most frequent in 45 and 90-day-old Paski cheeses (Mrkonjić Fuka et al., 2013). In semi-hard San Simón da Costa cheese 7.9% of all leuconostcos belonged to the species *Ln. mesenteroides* (González, Fernández Cuadrillero, Castro, Bernardo, & Tornadijo, 2015). Leuconostocs as heterofermentative LAB produce lactic acid and CO₂, as well as the flavor components diacetyl and acetoin (Hill & Kethireddipalli, 2013). For the flavor development of dairy products, a combination of citrate positive LAB (e.g. *Lc. lactis* subsp. *lactis* and *Ln. mesenteroides* subsp. *cremoris*) is very important since it is responsible for specific flavor and small eyes significant for the final sensorial properties of semi-hard and hard cheeses (Hache et al., 1999). Such a combination of lactococci and leuconostocs was detected in Istrian, Krcki and Paski cheeses (Mrkonjić Fuka et al., 2013) which are in high demand on the market.

The species of *Weissella* (*W*.) and *Pediococcus* (*P*.) genera are often present in fermented foods along with other LAB (Adesulu-Dahunsi, Sanni, & Jeyaram, 2017; Amari et al., 2013). Except for *W. hellenica*, which was found in 0, 45 and 90-day-old Krcki cheeses, *Weissella paramesenteroides*, (formerly *Ln. paramesenteroides*) was detected in 45 and 90-day-old Istrian cheeses (Mrkonjić Fuka et al., 2013) and *P. pentosaceus* was isolated from 90-day-old Krcki and Paski cheeses (Table 2). *Weissella* spp. produce gas from carbohydrates, bacteriocins, exopolysaccharides (EPS) and hydrolytic enzymes (Lynch et al., 2015) and may influence the organoleptic characteristics of cheeses such as texture and aroma. *Weissella paramesenteroides* and *W. hellenica* have been detected in different types of raw-milk cheeses (Di Cagno et al., 2007; Gerasi, Litopoulou-Tzanetaki, & Tzanetakis, 2003; Morales, Morales, Hernández, & Hernández-Sánchez, 2011). Morea, Baruzzi, Cappa, and Cocconcelli (1998) reported that *W. hellenica* 1M30 is good for production of Mozarella cheese due to its high acidification and proteolytic activity.

On the other hand, Irmler et al. (2013) and Tzanetakis and Litopoulou-Tzanetaki (1989) reported the importance of the complex biochemical activity of non-starter *P. pentosaceus* isolates of dairy origin. By various enzymatic activities (protease, peptidase, and esterase) and by production of acetate from lactate and diacetyl from glucose *P. pentosaceus* might significantly improve cheese flavor. Some authors concluded that pediococci achieve better effect on flavor development during cheese ripening in association with other NSLAB than when applied solely (Afshari et al., 2020). In addition, some strains of *P. pentosaceus* produce a pediocin-like bacteriocin with anti-listerial and anti-fungal activity (Dalie, Deschamps, Atanasova-Penichon, & Richard-Forget, 2010; Jang, Lee, Jang, Choi, & Suh, 2015).

2.4. Other types of dairy products

2.4.1. Kajmak and sweet cream

Kajmak is a specific dairy product manufactured in Serbia, Montenegro, Bosnia and Herzegovina, as well as in Turkey, Afganistan and Iran. Its texture is soft and creamy because kajmak contains over 80% fat in dry matter (Jokovic et al., 2008). There are two types of kajmak (Table 1): salted kajmak made by fermentation of milk fat over a longer period (Jokovic et al., 2008) and unsalted (sweet) kajmak made without fermentation and ready to eat immediately after producing (Terzić-Vidojević et al., 2014b). Kajmak is obtained by light separation

of milk fat on the surface of boiled milk. The layers of milk fat are collected in suitable containers, salted and placed in cold rooms (about 15°C) for ripening during a few days (young kajmak) or few months (old kajmak) depending on the request of the consumers. Old kajmaks are consumed predominantly in Serbia and Montenegro, while in Bosnia and Herzegovina sweet kajmak is very often on the table of consumers. It can be used by spreading on bread, by combining with cheese or in addition to various dishes.

Sweet cream is a product also obtained by light separation of milk fat but on the surface of uncooked milk during 2-3 days at lower temperature. After that period the cream is collected with a spoon and poured usually into a glass vessel. The use of sweet cream in households is widespread. Similar to kajmak, sweet cream can be used as a spread on bread slices, for mixing with low-fat cheeses, or in addition to various dishes especially soups. Most often sweet cream is used for preparing whipped cream for cakes and fruit salads.

Analyzing the LAB population in kajmaks and creams, it can be concluded that similar diversity was obtained, even though kajmak is made from cooked milk. Thirteen LAB species were detected in salted kajmaks (Jokovic et al., 2008), whereas 11 LAB species were isolated from unsalted kajmaks and 10 LAB species were detected from sweet creams (Terzić-Vidojević et al., 2014b) (Table 2). Rarely present LAB species such as *Lb. kefiri* and *Lb. kefiranofaciens* found in kefir grains and some cheeses (Bosch et al., 2006; Dolci, Alessandria, Zeppa, Rantsiou, & Cocolin, 2008; Jokovic et al., 2008) were isolated. Enterococci and lactobacilli that are less sensitive to the increased salt content and acidity of the environment were also isolated (Terzić-Vidojević et al., 2014b). On the other hand, sweet kajmaks and sweet creams are consumed immediately after manufacturing, so a lower number of LAB species were found. However, phenotypic and genotypic diversity of LAB species and strains present in all three dairy products is impressive and that is the reason why these products are very aromatic and delicious and therefore highly sought on the market.

Lactobacilli (*Lb. plantarum*, *Lb. paracasei* and *Lb. curvatus*) are predominant in older samples of salted kajmaks, contributing to flavor development in the final product, unlike the lactococci which were present in young sweet kajmaks and creams (Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Joković, Rajković, Veljović, Tolinački, & Topisirović, 2014; Rajković & Joković, 2015; Terzić-Vidojević et al., 2014b).

The main role of *Lc. lactis* is acidification of milk and therefore it is probably the most isolated LAB species from dairy products (Dolci, Alessandria, Zeppa, Rantsiou, & Cocolin, 2008; Luiz et al., 2017; Song, In, Lim, & Rahim, 2017). Lactococcus lactis was predominant in up to one-month-old samples of kajmak (Table 2) followed by Lc. raffinolactis isolated from 5-day-old salted kajmak and 2-day-old sweet kajmak and Lc. garvieae found in 30-day-old salted kajmak and 2-day-old sweet cream. Lactococcus raffinolactis (formerly known as Streptococcus raffinolactis) and Lc. garvieae have been isolated from dairy products by other authors (Chebeňová-Turcovská, Ženišova, Kuchta, Pangallo, & Brežná, 2011; Dolci, Alessandria, Zeppa, Rantsiou, & Cocolin, 2008; El-Baradei, Delacroix-Buchet, & Ogier, 2008; Ouadghiri, Amar, Vancanneyt, & Swings, 2005). Although Lc. raffinolactis is naturally present in raw milk and dairy products, this lactococcal species has a weak caseinolytic activity so it is not currently used as a starter culture in the dairy industry (Kimoto-Nira et al., 2012). During the phenotypic characterization of LAB isolated from sweet kajmaks it was determined that the strain Lc. raffinolactis BGTRK10-1 showed aggregation ability which will be discussed below (Miljkovic et al., 2018; Terzić-Vidojević et al., 2014b). Despite the findings that Lc. garvieae was originally isolated from udder mastitis and was also considered a major pathogen for fish (Eyngor et al., 2004), the prevalence of *Lc. garvieae* in some artisanal Italian and Spanish cheeses has been examined (Fernández, Alegriá, Delgado, & Mayo. 2010; Fortina et al., 2007; Fortina, Ricci, & Borgo, 2009). The authors concluded that most Lc. garvieae strains showed positive influence on the typical sensory characteristics of traditional raw milk cheeses.

Enterococci spp. were present both in older and in younger samples of kajmaks and creams (Table 2). Enterococci are generally the most commonly isolated LAB genera from dairy products of Southern Europe (Giraffa, 2003). Enterococcus faecium, E. faecalis, and E. durans are the most common species of enterococci found in raw milk dairy products (Begovic et al., 2011; Golić et al., 2013; Jokovic et al., 2008; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic et al., 2009a; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, b). In addition, E. italicus was identified in a low percentage in sweet kajmaks and was also found in an artisanal Italian the Toma piemontese cheese (Fortina, 2003; Terzić-Vidojević et al., 2014b). Results reported by Fortina et al. (2008) showed that E. italicus strains were associated with low virulence profiles. They concluded that certain E. italicus strains could be applied in the dairy industry. Enterococci produce many volatile compounds and contribute to the formation of the cheese aroma, especially during ripening (Abeijón, Medina, Katz, & González, 2006; Giraffa, 2002; Rasouli Pirouzian, Hesari, Farajnia, Moghaddam, & Ghiassifar, 2012). Furthermore, their proteolytic and lipolytic activity, bacteriocin production and probiotic

characteristics are significant features. Accordingly, there is the possibility of using certain enterococci strains in the dairy industry as part of starter cultures (Centeno, Menéndez, Hermida, & Rodríguez-Otero, 1999; Giraffa, 2003; Mrkonjic Fuka, Zgomba Maksimovic, Tanuwidjaja, Hulak, & Schloter, 2017; Popović et al., 2018).

Leuconostocs were isolated in high percentages from both salted (42.1%) and sweet kajmaks (31.3%) while from sweet cream leuconostocs were 4.2% of the total isolated LAB (Jokovic et al., 2008; Terzić-Vidojević et al., 2014b) (Table 2). Reviewing the previously published data we concluded that leuconostocs could be present both in young and long-ripened dairy products (Başar Uymaz, Akçelik, & Yüksel, 2019; Båth, Persson, Schnürer, & Leong, 2012; Begovic et al., 2011; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Joković, Rajković, Veljović, Tolinački, & Topisirović, 2014; Golić et al., 2013; Mojsova et al., 2013; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, b). The most frequent species in kajmak and sweet cream samples were *Ln.mesenteroides* followed by *Ln. pseudomesenteroides* and *Ln. lactis* (Table 2). Leuconostocs are a very important group of LAB for the development of desirable organoleptic properties in the final dairy products. Although they have poor acidification and proteolytic activities they produce diacetyl, acetate and ethanol contributing to the final flavor (Alegría, Delgado, Flórez, & Mayo, 2013; Nieto-Arribas, Seseña, Poveda, Palop, & Cabezas, 2010; Pederson, Ristagno, McSweeney, Vogensen, & Ardö, 2013). Furthermore, increasing the viscosity and also the specific texture of dairy products is enabled by their ability to produce dextran (Dror et al., 2018; Hemme & Foucaud-Sheunemann, 2004; Park, Ahn, Kim, & Chung, 2013).

Low levels of *S. thermophilus* were found in a 2-day-old sweet cream sample (Terzić-Vidojević et al., 2014b) and in a 5-day-old salted kajmak sample analyzed by the enrichment technique (Jokovic et al., 2008). According to data described previously *S. thermophilus* was isolated in low level from 1 and 5-day-old Golija and Radan cheeses (Golić et al., 2013; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Terzić-Vidojević et al., 2014a), as well as from one and 3-day-old Pirot cheeses (Begovic et al., 2011; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b). *Streptococcus suis/bovis* and *W. minor/viridescens* were isolated from 5-day-old salted kajmak by enrichment. The authors (Jokovic et al., 2008) considered that their low representation and appearance are, in general, the result of poor sanitary conditions during kajmak production. These species are sporadically detected in dairy products (Gobbeti et al., 2002; Golić et al., 2013; Randazzo, Vaughan, & Caggia, 2006).

2.4.2. Cheese in lambskin sacks

Cheese in lambskin or sheepskin sacks (Sir iz mišine) is a traditional food produced in the mountain regions of Dalmatia (Croatia), Bosnia and Herzegovina and Montenegro, but is also produced in Turkey and Lebanon by using different technology with the common characteristic of ripening in a sack made of animal skin (Ceylan, Caglar, & Cakmakci, 2007; Frece et al., 2016; Grbavac, 2002; Serhan, Linder, Hosri, & Fanni, 2010). Manufacturing of cheese in lambskin or sheepskin sacks has been practised in the same way for centuries and creates unique organoleptic properties, with the involvement of indigenous microorganisms. Sheepskin sacks are used for ripening, storage and transport of cheese from the mountains to the settlements of the valley (Tudor Kalit et al., 2014). The most important biochemical processes, which take place in anaerobic conditions inside of the animal skin during ripening, are proteolysis and lipolysis. These processes are responsible for the distinctive strong and piquant cheese flavor (Hayaloglu, Fox, Guven, & Cakmakci, 2007; Tudor Kalit, Kalit, Kelava, & Havranek, 2012; Yilmaz, Ahmet, & Akin, 2005).

According to data published by Frece et al. (2016), there are differences between LAB populations isolated from Croatian cheeses made from cow's and sheep's milk after ripening in lambskin sacks (Table 2). *Lactococcus lactis* subsp. *lactis* (62.2%) and *Lb. paracasei* (37.8%) were isolated from 2 to 45-day-old cow's milk cheeses while a total 52.4% of *Lactobacillus* spp., 14% *Lc. lactis* subsp. *lactis* and 33.6% *Ln. mesenteroides*, were isolated from sheep's milk cheeses (Table 2). The percentage of *Lc. lactis* subsp. *lactis* increased from 2 to 45 days of ripening of cow's milk cheeses, while at the same time the percentage of lactobacilli decreased. On the other hand, lactococci were present only in 2-day-old sheep's milk cheeses, while lactobacilli were not isolated. Similar data were reported by many authors who found lactococci in young cheeses (Begovic et al., 2011; Golić et al., 2013; Gurses & Erdogan, 2006; Edalatian, Najafi, Mortazavi, & Mayo, 2012; Jokovic, Vukasinovic, Veljovic, Tolinacki, & Topisirovic, 2011; Nikolic et al., 2008; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007, Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a). In addition, leuconostocs were found in all periods during cheese ripening (Table 2). The only identified species of lactococci and leuconostocs in Croatian sheep's milk cheeses in lambskin sacks were *Lc. lactis* subsp. *lactis* and *Ln. mesenteroides*. *Lactobacillus plantarum* was the predominant species of *Lactobacillus* in 15, 30 and 45-day-old sheep's milk cheeses while *Lb. curvatus* and *Lb. brevis* were found in 30 and 45-day-old sheep's milk cheeses,

respectively. The LAB microbiota of this group of artisanal cheeses ripened in an animal skin sack is relatively unexplored and there is a lack of information on their composition.

3. The technological properties of natural LAB isolates from WBC artisanal dairy products

3.1. Acidification and coagulation of milk

LAB play a primary role during the production of fermented dairy and nondairy products. Both raw milk and raw milk dairy products are inexhaustible sources of novel LAB strains with novel properties. Natural LAB isolates have high technological potential. Thus, many reports have described physiological and technological properties of indigenous LAB obtained from traditional dairy products (Asteri et al., 2009; Ehsani, Hashemi, Afshari, & Aminzare, 2018; Farahani, Rasooli, & Owlia, 2017; Leboš Pavunc et al., 2012; Pino et al., 2019).

Based on many years of scientific work on LAB isolated from autochthonous dairy products, the results show that the acidifying and coagulating activities of the bacterial strains varied widely, with significant differences. The strains with fast acidifying ability are crucial at the beginning of cheeses manufacturing since rapidly decreasing pH enables milk coagulation and reduction of undesirable microbiota. This refers mostly to lactococci and streptococci, which have the ability of fast conversion of lactose to L-lactate with rapid decrease of pH (Morandi & Brasca, 2012; Pisano, Deplano, Fadda, & Cosentino, 2019; Ruggirello, Dolci, & Cocolin, 2014). The acidifying and coagulation activities of 455 Lactococcus and 34 Streptococcus strains isolated from traditional raw milk dairy products were tested (Golić et al., 2013; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, b). The results showed that 17.4% of lactococci and 32.0% of streptococci were able to rapidly decrease the pH value of inoculated sterile reconstituted skim milk (RSM) (11% w/v) to 4.78-4.88 (for streptococci) and 5.17-5.28 (for lactococci), forming solid curd after 5.5 h (streptococci) and 6 h (lactococci) at optimal growth temperature (data not shown). Generally, these strains could be good candidates as primary starter cultures for the production of fermented dairy products (Hassaïne, Zadi-Karam, & Karam, 2007; Ma et al., 2011). Cogan et al. (1997) designated Lactococcus strains as good acidifiers if they lowered milk pH to below 5.3 after 6 h incubation at 30°C. We have used Lc. lactis ZGBP5-9, a fast coagulating indigenous strain, as a constituent of mixed starter culture in the production of traditional fresh cheese at small industrial scale under controlled conditions, since fresh cheese is very popular in Croatia, Bosnia and Herzegovina and Vojvodina (part of the Republic of Serbia) in the diet of the local population (Golić et al., 2013; Terzić-Vidojević et al., 2015a). It should be borne in mind that certain starter cultures are susceptible to lysis by bacteriophages, which slows down the fermentation process and leads to the low quality of the final products. One way to partially solve the problem is to use other adequate LAB strains and rotating starter cultures (Garneau & Moineau, 2011).

Streptococcus thermophilus strains are widely present in raw milk and raw milk dairy products and considered as the second most important industrial LAB species after *Lc. lactis* (Cui et al., 2016; Quigley et al., 2013). Streptococcus thermophilus strains BGVLJ1-44 and BGKMJ1-36 isolated from traditionally manufactured yogurts and sour milk were able to lower the pH of RSM to 4.80 and 4.78, respectively, after 5.5 h at 42°C (Terzic-Vidojevic et al., 2013, 2015c; unpublished data). Similar data were obtained by François et al. (2007) and Urshev et al. (2014) who examined the acidifying potential of streptococci isolated from traditional fermented milk. Two previously mentioned streptococcal strains were used in the production of a fermented probiotic drink for domestic animals and yogurt for human use as parts of mixed starter cultures (Golić et al., 2015, 2017; Veljović et al., 2017a).

On the other hand, the acidifying activity of lactobacilli and enterococci can be considered low, especially after 6 h of incubation, since they metabolize lactose more slowly than lactococci (Pisano, Deplano, Fadda, & Cosentino, 2019; Turhan & Öner, 2014). Acidifying and coagulation abilities of 443 *Lactobacillus* strains and 431 *Enterococcus* strains isolated from artisanal raw milk dairy products have been assayed (Golić et al., 2013; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, b). The results showed that only 1.6% of selected lactobacilli coagulated RSM after 7 h and 0.7% of enterococci coagulated RSM after 5 h. At the same time, the pH of RSM inoculated with lactobacilli was over 6.3 and the pH of RSM inoculated with enterococci was over 6.5 (data not shown). Further tests showed that the coagulation of RSM was due to high proteolytic activity.

3.2. Metabolism of citrate and production of aromatic compounds

The main biological activity of LAB is the conversion of sugars present in milk, fruit and vegetables by fermentation to lactic acid as the main end product. However, a small proportion of LAB has the ability to ferment

other non-carbohydrate compounds such as citrate. The utilization of citrate by LAB has a positive effect on the quality of the final dairy product since citrate can be degraded through different metabolic pathways giving various aromatic compounds, mainly diacetyl, acetoin and acetaldehyde that are responsible for the specific flavor of butter, sour cream, yogurt and different types of cheeses. Additionally, CO₂ is produced during citrate metabolism leading to the formation of small holes in Dutch-type cheeses. Several decades ago it was established that citrate metabolism is influenced by various factors such as pH and lactate concentration, culture conditions, cell density and type of LAB (Al-Naseri, Bowman, Wilson, Nilsson, & Britz, 2013; Blaya, Barzideh, & LaPointe, 2018; Medina de Figueroa, Oliver, & Benito de Cárdenas, 2001; Pretorius, Engelbrecht, & Du Toit, 2019).

Among LAB, Lc. lactis subsp. lactis biovar. diacetylactis and several Leuconostoc species are the best flavor producers (Farahani, Rasooli, & Owlia, 2017). However, other LAB can produce various volatile compounds which contribute to the flavor formation of certain dairy products (Cuffia, Bergamini, Wolf, Hynes, & Perotti, 2017). As we previously reported, many dairy products manufactured in rural regions of WBC are made from raw milk without the addition of starter cultures. The richness of microbiota diversity, primarily LAB, in such dairy products, contributes to their exceptionally intense flavor. Citrate utilization, and diacetyl and acetoin production by a total of 1458 LAB strains have been examined (Golić et al., 2013; Terzic-Vidojevic, Vukasinovic, Veliovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic et al., 2009a; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, b, 2015b) (Table 3). A large number of leuconostocs (72.5%) utilized citrate as a carbon source, followed by lactococci (55.5%), then lactobacilli (42.9%), pediococci (39.1%) and enterococci (35.4%). On the other hand, the highest number of strains that produced diacetyl were enterococci (25.5%) while 56.7% of examined lactobacilli showed a positive reaction to acetoin production (Table 3). The results indicate that the most important representatives of LAB-flavor producers were Lb. plantarum, Lc. lactis subsp. lactis, E. faecium, E. faecalis, E. durans, Ln. mesenteroides, S. thermophilus and P. pentosaceus (Golić et al., 2013; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic et al., 2009a; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, b, 2015b). Data given by Garabal, Rodriguez-Alonso, and Centeno (2008) showed that the facultatively heterofermentative lactobacilli produced the largest amounts of diacetyl-acetoin in milk, while leuconostocs produced the lowest amounts of diacetyl-acetoin in acidified milk, Cavanagh et al. (2015) reported that Lc. lactis subsp. lactis biovar. diacetylactis (Lc. lactis subsp. lactiscit) has the ability to ferment citrate, while Lc. lactis subsp. cremoris does not. Production of aromatic carbonyl compounds has been considered strain-specific characteristic (Franciosi, Settanni, Cavazza, & Poznanski, 2009). The same authors reported that certain LAB strains had the ability to produce different (high, medium or low) levels of diacetyl, while one S. thermophilus strain, three E. faecalis strains, four Lc. lactis subsp. lactis strains and six Lc. lactis subsp. cremoris strains did not.

Table 3

Detailed characterization of the technological properties of indigenous LAB isolates provided new knowledge on the technological capacity of natural isolates from WBC artisanal products. Moreover, the obtained data are very useful in the formulation of novel starter cultures for production of dairy products resembling the traditional WBC dairy products. For this purpose, several flavor-producing natural isolates from WBC artisanal dairy products were selected for formulation of mixed starter cultures for production of yogurt, two types of cheeses and sour cream (Table 4).

Table 4

3.3. Proteolytic activity

In view of the great importance of the proteolytic system of natural LAB isolates that enables the growth of starter and NSLAB in protein-rich media, detailed biochemical, genetic and physiological characterization of proteolytic features of LAB strains was performed. The proteolytic activity of 1029 LAB strains isolated from various homemade dairy products manufactured in different geographical regions of WBC was studied (Terzic-Vidojevic et al., 2009c, d, 2013, 2014a, b; 2015b; Veljovic et al., 2007). Results showed that about 25% of all isolated LAB strains were able to completely degrade β-casein (Table 3). Literature data revealed that the highest proteolytic activity was found in lactocci from Manchego cheeses (Nieto-Arribas, Seseña, Poveda, Palop, & Cabezas, 2009) while significant proteolytic activity was reported in lactobacilli from traditional Pecorino Sardo cheese and goat's milk from different Algerian breeds (Badis, Guetarni, Moussa Boudjema, Henni, & Kihal, 2004; Madrau et al., 2006).

In parallel with proteolytic activity, analysis of the *prt* genes in natural isolates revealed the presence of novel *prt* genes in various species. The *prtP* and *prtM* genes in *Lc. lactis* were found to be necessary for the

synthesis of an active form of the PrtP proteinase (de Vos, Vos, de Haard, & Boerrigter, 1989; Haandrikman, Kok, & Venema, 1991). A PrtP proteinase similar to lactococcal PrtP proteinase was for the first time identified in *Lb. paracasei* BGHN14 (formerly *Lb. casei* HN14), a natural isolate from homemade hard cheese traditionally manufactured in a household in a Montenegro seaside village (Kojic, Fira, Banina, & Topisirovic, 1991). Moreover, the same proteinase was identified in all natural *Lb. paracasei* isolates from WBC artisanal products that exhibite proteolytic activity (Kojic, Fira, Bojovic, Banina, & Topisirovic, 1995). In addition, our results revealed the presence of a *prtP* gene similar to that found in lactococci and *Lb. paracasei* in proteolytically active natural isolates of *Lb. plantarum* (Strahinic, Kojic, Tolinacki, Fira, & Topisirovic, 2010). The results showed that the strain *Lb. plantarum* BGSJ3-18 (natural isolate obtained from the semi-hard homemade white cheese produced in Sjenica, Pester plateau, Serbia) contained the catalytic domain of the *prtP* gene, as well as *prtP–prtM* intergenic region. This region showed more than 95% sequence identity to the *prtP* gene regions present in *Lb. paracasei*, *Lb. casei* and *Lc. lactis* (Strahinic, Kojic, Tolinacki, Fira, & Topisirovic, 2010). The PrtP proteinase of *Lb. plantarum* BGVL2a-18 strain, isolated from Vlasina raw goat's milk cheese (Vlasina Lake, Serbia), showed the ability to degrade α, β and κ-casein, similarly to the PrtP proteinase of *Lc. lactic* SK11 (Terzic-Vidojevic et al., 2013; de Vos, Vos, de Haard, & Boerrigter, 1989).

In the following years, many different cell envelope associated proteinases (CEPs) were identified, since they had been detected in several LAB species including PrtB from Lb. bulgaricus (Gilbert et al., 1996), PrtH from Lb. helveticus (Pederson, Mileski, Weimer, & Steele, 1999), PrtR from Lb. rhamnosus BGT10 (Paštar et al., 2006) and PrtS from S. thermophilus (Fernandez-Espla, Garault, Monnet, & Rul, 2000). The studies on natural LAB isolates from the WBC region showed even greater diversity of the prt genes, particularly among mesophilic lactobacilli, e.g. the strain with the highest proteolytic activity, Lb. zeae LMG17315, harbours catalytic domains of three different proteinase genes highly similar to the prtP and the prtR genes that were previously characterized in other species (Vukotić et al., 2016; Paštar et al., 2006). In general, the results obtained from diverse natural LAB isolates suggest that the observed diversity of CEPs in mesophilic lactobacilli could be the result of horizontal gene transfer (HGT), since the loss and acquisition of genes was documented as one of the important characteristics of the LAB genom's evolution (Makarova & Koonin, 2007). The main driving force for the acquisition of proteinase genes in these bacteria was most likely their adaptation for growth in protein-rich habitats, since they represent the regular microbiota of milk and dairy products. Moreover, concerning the regulation of production of proteinases in LAB, the medium-dependent regulation of divergently oriented promoters of the prtM and prtP genes was reported, revealing that the production of proteinases is regulated by the concentration of oligopeptides and amino acids in the growth medium, supporting the previously hypothesized evolutionary adaptation of LAB for growth in protein-rich niches (Marugg et al., 1995; Miladinov, Kuipers, & Topisirovic, 2001a; Paštar et al., 2006).

Finaly, thermophilic strains of lactobacilli, particularly *Lb. helveticus*, have intense proteolytic activity (Fira et al., 2001), also reported by de Candia et al. (2007) after examining the proteolytic activity of natural starter cultures in Mozzarella cheeses. For example, *Lb. helveticus* BGTRM7-58 isolated from artisanal Travnik sweet cream completely degraded ß-casein (Terzić-Vidojević et al., 2014b). The proteolytic system of *Lb. helveticus* was of particular interest, since several varieties of proteinase PrtH were detected in different strains (Griffiths & Tellez, 2013). Beside PrtH and PrtH2 genes which were most common in the majority of the *Lb. helveticus* strains, additional putative genes designated as PrtH3, PrtH4 and PrtH5 were detected in particular strains. This diversity, as well as the presence of more than one proteinase genes in many strains, can give an explanation for the generally high proteolytic activity of *Lb. helveticus*. Together with previously mentioned data concerning the mesophilic LAB strains, these results demonstrate the value of research on natural isolates from different ecological niches as the best way to elucidate the diversity of proteolytic systems among these microorganisms.

4. Autochthonous dairy isolates of LAB: a natural source of probiotic features

4.1. Bacteriocins production

Considerable knowledge has been accumulated in the last two decades by the characterization of natural isolates of LAB as bacteriocin-like producers. It was shown that about 19.5% of tested LAB strains exhibited antimicrobial activity against one to five indicator strains (Golić et al., 2013; Nikolic et al., 2008; Terzic-Vidojevic et al., 2009a; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, b; Veljovic et al., 2007). The analysis of 1467 natural LAB isolates from WBC showed that the most numerous producers of antimicrobial compounds of a proteinaceous nature are enterococci (37.3%) and lactococci (30.3%) (Table 3) (Golić et al., 2013; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-

Vidojevic et al., 2009a; Terzic-Vidojevic, Lozo, & Topisirovic, 2009b; Terzic-Vidojevic et al., 2013, 2014a, b). The highest number of LAB bacteriocin-like producers were isolated from cheeses in the regions of Zlatar Mountain (Serbia) and Vlasina Lake (Serbia), 34.4% and 34.2%, respectively (Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Terzic-Vidojevic et al., 2013; Veljović et al., 2007). The authors Veljovic et al. (2007) reported that the strain *Lc. lactis* subsp. *lactis* BGZLM1-24, isolated from raw milk in the region of Zlatar Mountain (Serbia), produced nisin-like antimicrobial substance significant for the food industry as a commercial biopreservative (Delves-Broughton, 1990; Henning, Metz, & Hammes, 1986).

The most studied bacteriocins are those from LAB belonging to genus *Lactococcus*. Lactococcin A was produced by strain Lc. lactis subsp. lactis biovar. diacetylactis BGS50 isolated from artisanal butter starter culture (Kojic, Strahinic, & Topisirovic, 2005). Lactococcin B was detected in strain Lc. lactis subsp. lactis BGIS29 isolated from artisanal white cheese, from Ilijaš, Bosnia and Herzegovina (Miladinov, Kojic, Arsenijevic, Lozo, & Topisirovic, 2001b) and lactococcin A and lactococcin B, as products of *Lactococcus* sp. BGKF, were isolated from home-made kefir (Kojic, Lozo, Begovic, Jovcic, & Topisirovic, 2007). However, among lactococcal strains with bacteriocin activity isolated from semi-hard homemade cheese from Zabrde, in the region of Boka Kotorska bay, Montenegro, all isolates were lactococcin B producers except strain Lc. lactis subsp. lactis BGMN1-5 which produces two different bacteriocins designated as LsbA and LsbB (Kojic, Strahinic, Fira, Joycic, & Topisirovic, 2006). Further research on LsbB, a Class II leaderless bacteriocin revealed a novel mechanism of bacteriocin activity, including Zn-dependent metallopeptidase, responsible for sensitivity to this bacteriocin in target cells. This is an example of how artisanal products could be source of new bacteriocins, with a novel mechanism of action where membrane-bound peptidase is involved in bacteriocin sensitivity in target cells (Uzelac et al., 2013, 2015). An extensive study that implied an evaluation of LAB and yeast diversity in traditional white pickled and fresh soft cheeses from the mountain regions of Serbia and lowland regions of Croatia (Golić et al., 2013) was the source of the new bacteriocin producing strain Lc. lactis subsp. lactis biovar, diacetylactis (Lc. lactis subsp. lactiscit) BGBU1-4. This strain was isolated from a 3-day-old traditional semi-hard cheese made from mixed cow (20%) and sheep (80%) milks and produced without the use of starter cultures in a household in the village of Buzina, located on Beljanica Mountain in Eastern Serbia. New leaderless bacteriocin lactolisterin BU, produced by BGBU1-4, has a broad activity spectrum against many species of Gram-positive bacteria, including important food spoilage and foodborne pathogens, such as Listeria monocytogenes, Staphylococcus aureus, Bacillus spp. and Streptococcus spp. (Cirkovic et al., 2016; Lozo et al., 2017; Madi et al., 2016). Interestingly, mannose phosphotransferase (Man-PTS) is not a receptor for the activity of this antilisterial strain as it usually is for other bacteriocins belonging to subclass IIa (Diep, Skaugen, Salehian, Holo, & Nes, 2007; Lozo et al., 2017), so further research to determine the mechanism of action is needed. Bacteriocin producing strains are not only important as food biopreservatives when they are part of starter cultures but could have a beneficial effect for final users as a type of functional food. For this purpose, the effect of lactolisterin BU was examined in applying BGBU1-4 for treatment of listeriosis in Wistar rats where different modulation of early immunological response was determined in comparison with another tested strain, Lactobacillus salivarius BGHO1 (Lukić et al., 2017).

Isolation of different *Lactobacillus* strains from artisanal products is more frequent because they are a more robust and more diverse group of LAB. Strains belonging to species *Lb. paracasei* subsp. *paracasei* are usually isolated from diverse products and often they were bacteriocin producers (Kojic et al., 2010; Lozo, Vukasinovic, Strahinic, & Topisirovic, 2004; Lozo et al., 2007; Tolinački et al., 2010; Veljovic et al., 2007). A common feature for all of these bacteriocins is a narrow inhibitory spectrum that limits their potential application. However, investigations of these bacteriocins are interesting from a scientific point of view, allowing characterization of new antimicrobials with novel mechanisms of action or types of distribution and evolution. Natural isolate *Lb. paracasei* subsp. *paracasei* BGSJ2-8, which originated from the homemade semi-hard white cheese traditionally manufactured in one Serbian household (Sjenica, Pester Plateau), harbors a few interesting features, e.g. bacteriocin and proteinase production, as well as aggregation phenotype (Lozo et al., 2007). Sequencing of the bacteriocin genes revealed the presence of two bacteriocins, BacSJ and acidocin 8912 (Kojic et al., 2010).

It is known that enterococcal strains have the ability to produce enterocins, ribosomally synthesized antimicrobial peptides that generally belong to the Class II bacteriocins (Franz, Van Belkum, Holzapfel, Abriouel, & Gálvez, 2007). Enterocins are active against a wide range of spoilage and foodborne pathogens including *Listeria monocytogenes* (Foulquié-Moreno, Sarantinopoulos, Tsakalidou, & DeVuyst, 2006; Giraffa, 2002, 2003). Ten dairy enterococci that synthesized enterocins showed antimicrobial activity against foodborne pathogens such as *L. monocytogenes* and *St. aureus*. The broadest spectrum of antimicrobial activity was detected in *E. faecalis* strains BGPT1-10P and BGPT1-78 (Veljovic et al., 2009). Moreover, *E. durans* strains BGGO8-25, BGGO8-26, BGGO9-30, BGRE2-40, BGVL2a-53 and BGTRK10-45 showed inhibitory effect on *E. faecalis* BG221 (Golić et

al., 2013; Popović et al., 2018; Terzić-Vidojević et al., 2014a, b, 2015b; Veljović et al., 2014). *E. faecium* strain BGPAS1-3 isolated from raw milk cheese manufactured in the region of Pale, Bosnia and Herzegovina, (Terzić-Vidojević et al., 2015b) showed inhibitory effect on *L. monocytogenes* ATCC 19111, *Acinetobacter baumannii* 6077/12, *Chromobacterium violaceum* CV026, *E. faecalis* BG221, *Bacillus subtilis* 168 and *Erwinia carotovora* (Popović et al., 2019a; Popović, 2019b). In addition, *E. faecium* strain BGZLM1-5 isolated from raw milk in the region of Zlatar Mountain, Serbia, inhibited the growth of *L. monocytogenes* ATCC 19111 and *E. faecalis* BG221 (Popović, 2019b; Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Veljovic et al., 2007). Both enterococcal strains are good candidates for further study and eventual application in the food industry, agriculture and pharmacy.

4.2. Aggregation ability

Aggregation of bacterial cells is defined as their ability to form clearly visible snow flake or sand-like particles of cell-aggregates, that gravitate to the bottom of the tube, forming a precipitate and clear supernatant. Aggregation ability is rare phenotype among LAB. During two decades of investigation of LAB from various artisanal dairy products we detected only 2.7% of LAB strains that possessed the ability to aggregate (Table 3). The most numerous LAB strains in which aggregation phenotype was scored belonged to *Enterococcus* and *Lactobacillus* genera.

The complexity of the mechanisms and components involved in cell aggregation and adherence, the species specificity, environmental dependence and contribution to multiple functional probiotic roles are the reasons for the poor knowledge of the specific biological role of aggregation factors. Different LAB genera possess various mechanisms of aggregation. Eleven Lactobacillus strains with aggregation ability (Agg+) were tested: Lb. paracasei subsp. paracasei BGSJ2-8, (from artisanal semi-hard cheese, Sjenica, southwestern Serbia), Lb. paracasei strains BGGR2-68 and BGGR2-82 (from artisanal semi-hard cheese, Zakurjaj village, Nikšić, Montenegro), Lb. casei/paracasei strains BGDP1-84 and BGDP9-38 strains (from artisanal semi-hard cheese. Šumarak village, Deliblatska Peščara, Serbia), Lb. casei/paracasei strains BGNJ1-3, BGNJ1-61, BGNJ1-64 and BGNJ1-70 (from artisanal semi-hard cheese, Njeguši village, Cetinje, Montenegro), Lb. paracasei BGZLS30-6 (from artisanal semi-hard cheese, Zlatar Mountain, Serbia) and Lb. paracasei BGAR75 (from artisanal semi-hard cheese, Aranđelovac, Serbia) (Lozo et al., 2007; Miljkovic et al., 2015, 2016a; Nikolic et al., 2008; Nikolic, Jovcic, Kojic, & Topisirovic, 2010; Veljovic et al., 2007). Based on the level of aggregation and the appearance of the aggregates formed, aggregation strains can be classified into three main groups: with fast, medium and slow aggregating ability or into groups of those forming large, medium or small aggregates wherein a direct correlation between the aggregation kinetics and the type of the aggregates formed could be established (Miljković, 2016b). Comparative analysis of the binding ability of the selected Lactobacillus Agg⁺ strains to the components of extracellular matrix (ECM) showed a wide range of binding capacities to collagen, varying from the intensive to complete lack of interaction, while two strains (BGGR2-68 and BGGR2-82) showed the ability to bind even to plastics (biofilms production). Deletion analysis of lactobacilli aggregation factor (AggLb) revealed that, depending on the presence of different domains, AggLb aggregation factor can be switched from aggregation ability and collagen binding to biofilm formation ability (Miljkovic et al., 2016a).

Aggregation of lactococci is also a phenomenon that was intensively studied in the last decade. A strong auto-aggregation phenotype was detected in three natural isolates: *Lc. lactis* subsp. *lactis* BGKP1 (from artisanal white semi-hard cheese, Randera village, Kopaonik Mountain, Serbia) and *Lc. lactis* subsp. lactis BGBM50 (from artisanal white semi-hard cheese, Žanjice village, Montenegro) expressing AggL aggregation factor (Kojic et al., 2011; Mirkovic et al., 2015), and *Lc. raffinolactis* BGTRK10-1 (from artisanal kajmak, Travnik, Vlašić Muntain, Bosnia and Herzegovina) expressing AggLr aggregation factor (Miljkovic et al., 2018). It is interesting that the *aggL* gene encoding AggL aggregation factor is located on plasmids while *aggLr* gene is located on the chromosome (Miljkovic et al., 2018).

Fourteen out of 636 dairy *Enterococus* isolates examined (Terzić-Vidojević et al., 2015b) showed the ability to form large cell aggregates. All enterococcal aggregation positive strains were isolated from artisanal homemade cow's milk cheeses produced in households of the Golija and Valjevo Mountains regions of the Republic of Serbia. Genes encoding enterococcal aggregation factor (AggE) are located on plasmids of similar size in all selected strains (Veljović et al., 2017b).

No particular difference was observed in aggregation ability or in the size of aggregates formed between lactobacilli, lactococci and enterococci snowflake-forming collagen-binding aggregation factor (SFCBAF) expressing strains, indicating that the domain structure rather than the amino acid sequence is crucial for expressing the function of the aggregation factors. The highest differences were observed among selected

aggregation-positive strains of lactobacilli, for which it has been shown that they possess aggregation factors that do not belong to the SFCBAF type/family (Miljković, 2016b).

4.3. Exopolysaccharide production

It has been reported that the surface polysaccharides of lactobacilli interact with other microorganisms as well as with the intestinal mucosa and intestinal epithelial cells (IEC) (Castro-Bravo, Wells, Margolles, & Ruas-Madiedo, 2018; Živković et al., 2016). The most important feature for the interaction of probiotic strains with the host is the ability of gut colonization, including resistance to the harsh condition of the gastrointestinal tract (GIT) and adhesion to IEC (Nishiyama, Sugiyama, & Mukai, 2016). Our previous results revealed that dairy isolates mainly survive passage through GIT conditions when applied in a food matrix, e.g. milk (Nikolic et al., 2012; Soković Bajić et al., 2019; Uroić et al., 2014). It has been previously reported that the use of food carriers to protect the probiotic bacteria through GIT transit favors their survival due to a buffering effect (Ranadheera, Baines, & Adams, 2010). This could indicate that natural dairy isolates are less adapted to the GIT environment. However, some dairy isolates belonging to Lactococcus spp., Lactobacillus spp. and particularly Enterococcus spp. successfully survive the rigorous GIT conditions without food matrix protection (Popović et al., 2018; Uroić et al., 2014) indicating that acid and bile resistance are highly strain-dependent (Nikolic et al., 2012). Taking into account different EPS polymers, it seems that the polymer itself was not digested during GIT transit. This has been reported for other purified EPS synthesized by LAB and bifidobacteria, which are stable in harsh conditions probably due to their intrinsic resistance to acid hydrolysis (Nikolic et al., 2012; Salazar et al., 2009). The capability of EPS surrounding the producing bacteria to deal with the harsh conditions of the upper part of the gut tract seems to be both polymer and strain dependent. EPS-producing Lb. paraplantarum BGCG11 (formerly Lb. casei CG11) was isolated from a traditional Montenegrin soft white cheese homemade from raw milk (Kojic et al., 1992). It did not have increased survival abilities in comparison to its non-ropy derivatives, as also occurred for the EPS-producing Lb. delbrueckii subsp. lactis 193 and 193+ strains, nor for Bifidobacterium longum NB667 and 667Co (Burns et al., 2011; Nikolic et al., 2012). In contrast, the EPS layer surrounding several Bifidobacterium animalis subsp. lactis strains were effective in maintaining the number and viability of bacterial cells after simulated GIT transit (de los Reyes-Gavilán et al., 2011). We can speculate that an EPS's physicochemical characteristics, intrinsic to each polymer type, must account for its biological, technological and protective abilities (Ruas-Madiedo, Abraham, Mozzi, & de los Reyes-Gavilán, 2008).

However, the natural EPS-producing strain *Lb. paracasei* subsp. *paracasei* BGSJ2-8 (Lozo et al., 2007) as well as the strains *Lb. rhamnosus* DR20, *Lb. acidophilus* HN017 and *Bifidobacterium lactis* DR10, had a two to three times higher degree of adhesion to human intestinal HT29-MTX cells compared to their adhesion to human intestinal Caco-2 cells (Gopal, Prasad, Smart, & Gill, 2001; Živković et al., 2016). It is possible that the mucin present on the surface of HT29-MTX participates in the interaction with the EPS of the bacterial cell surface. Interestingly, the EPS-producing natural *Lb. paraplantarum* BGCG11 isolate exhibits lower adhesion ability to IEC compared to its non-EPS-producing derivatives, implying that the adhesion of bacteria to IEC is better in the absence of cell surface polysaccharides due to better exposure of bacterial cell surface proteins to the adhesins on eukaryotic cells (Nikolic et al., 2012, Živković et al., 2016). Hence, it could be inferred that the adhesion to IEC is strain-dependent and the result of differences in physicochemical and/or structural characteristics of the EPS polymers, as well as of the surface characteristics of the strains (Ruas-Madiedo, Gueimonde, Margolles, de los Reyes-Gavilán, & Salminen, 2006).

In addition, neutralization of the negative effects of pathogens such as *Clostridium difficile* might also be explained by other mechanisms including: i) induction of mucus production, ii) increased production of tightjunction proteins, reinforcing the epithelial membrane barrier, iii) production of antimicrobial factors, and iv) stimulation of the innate immune response (Gareau, Sherman, & Walker, 2010; Golić et al., 2017; Liévin-Le Moal & Servin, 2014; Soković Bajić et al., 2019; Zivkovic et al., 2015). Interestingly, our results revealed that EPS-CG11 produced by the natural isolate *Lb. paraplantarum* BGCG11 could be an effective macromolecule in the protection of HT29-MTX cells from pathogen-induced lysis (Zivkovic et al., 2015).

Besides the antimicrobial potential of high molecular weight EPS, it was demonstrated that EPS-CG11 successfully alleviated inflammatory pain in Wistar rats. The antihyperalgesic and antiedematous effects of EPS-CG11 were studied in a rat inflammation model by injection of carrageenan into the hind paw. The results revealed that the intraperitoneal administration of EPS-CG11 decreased pain sensations (mechanical hyperalgesia) in a dose-dependent manner (Dinić et al., 2018). The results are in accordance with the literature data, where the polysaccharide extracts from lichens and seaweeds were reported to alleviate inflammatory pain in mice by suppressing the production of interleukin (IL)-1 β and/or tumor necrosis factor (TNF)- α (Chaves et al., 2013; Córdova et al., 2013). Similar to the results of Córdova et al. (2013), EPS-CG11 caused down regulation of IL-1 β

and inducible nitric oxide synthase (iNOS) mRNA levels in the paw tissue of EPS CG11/carrageenan treated rats, while the levels of TNF- α and IL-6 mRNAs were not changed compared to the controls (Dinić et al., 2018).

4.4. Other benefits of LAB to human health

The adhesion of probiotic strains to IEC provides several important abilities: the colonization of intestinal mucosa, persistence in the intestine, the competitive exclusion of pathogenic microorganisms, and immunomodulation (Muñoz-Provencio et al., 2009; Nishiyama, Sugiyama, & Mukai, 2016). Literature data show that different lactobacilli species are capable of reducing the adhesion of diverse enteropathogens to IEC (García-Cayuela et al., 2014). Our previous results revealed that natural LAB isolates have a strong ability to decrease the association of Escherichia coli ATCC 25922, Salmonella Enteritidis 654/7E and L. monocytogenes ATCC19111 to IEC (Veljović et al., 2017a; Zivkovic et al., 2015, Živković et al., 2016). The role of various cell-surface proteins in adhesion of probiotic LAB strains to the host has been reported (Nishiyama, Sugiyama, & Mukai, 2016). Our results obtained with human Caco-2 and HT29-MTX intestinal epithelial cells expressing morphologically and functionally differentiated characteristics resembling that of mature enterocytes revealed that natural isolates of LAB exert significantly higher adhesion to Caco-2 cells than to HT29-MTX (Uroić et al., 2014). At the same time, our results revealed the high ability of enterococcal dairy isolates to bind to HT29-MTX epithelial cells and mucin (Popović et al., 2018). The results for pathogen exclusion indicated that adhesion of E. coli ATCC 25922 and Salmonella Enteritidis 654/7E to HT29-MTX was reduced in the presence of ten natural enterococci strains isolated in the region of WBC. The adhesion rate of Salmonella Enteritidis 654/7E to the HT29-MTX cells was reduced in co-incubation with E. durans strains BGGO8-25, BGGO8-30 and BGGO9-30 (Popović et al., 2018; Terzić-Vidojević et al., 2014a). Moreover, live or heat-killed natural isolate E. faecium BGPAS1-3 strongly inhibited adhesion of L. monocytogenes ATCC19111 to differentiated Caco-2 cells during competition, exclusion, and displacement. Although live and heat-killed BGPAS1-3 have been shown to reduce the adhesion of L. monocytogenes ATCC19111, none of the fractions had the ability to reduce the invasion of L. monocytogenes ATCC19111 in Caco-2 cells (Popović et al., 2019a; Popović, 2019b).

Besides the general health-promoting effects of probiotics, their roles in various diseases have also been documented (Rajilić-Stojanović, Dimitrijević-Branković, & Golić, 2019). It was reported that the anti-inflammatory, antioxidant and immunomodulatory effects of probiotics could be related to their effect on diabetes attenuation (Mihailović et al., 2017). The treatment of streptozotocin-induced diabetic rats with natural isolate *Lb. paraplantarum* BGCG11 ameliorated the effect of diabetes on redox balance in the liver and kidneys, reduced the DNA damage level, lowered the level of inflammatory mediators and attenuated the fibrotic process.

The most exciting effect of probiotics is their ability to influence the gut-brain axis. It was previously shown that lactobacilli can produce γ -amino butyric acid (GABA), the major inhibitory neurotransmitter in the mammalian central nervous system, known for its hypotensive, tranquilizing, diuretic, antidiabetic, and stress management effects (Cho, Chang, & Chang, 2007; Dhakal, Bajpai, & Baek, 2012; Lebeer, Vanderleyden, & De Keersmaecker, 2008; Li & Cao, 2010). Our recent results revealed that *Lb. brevis* BGZLS10-17 and BGZLS30, natural isolates from artisanal Zlatar cheese (Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, & Topisirovic, 2007; Veljovic et al., 2007), represent good GABA producers with strong probiotic activity (Soković Bajić et al., 2019). The highest amount of GABA (6.4 ± 0.2 mg mL⁻¹ [62 ± 1.94 mM] in 1% monosodium glutamate) was produced by the isolate *Lb. brevis* BGZLS10-17 after 48 h of culture. In comparison, the strain *Lb. paracasei* NFRI 7415, isolated from traditional fermented tuna-sushi in Japan, produced a similar amount (60 mM) after 6 days of culture (Komatsuzaki, Shima, Kawamoto, Momose, & Kimura, 2005). The GABA-containing supernatant of BGZLS10-17 significantly decreased the production of IL-8, alleviated inflammation caused by IL-1 β and stimulated the expression of tight junction proteins and transforming growth factor (TGF)- β cytokine. It can be concluded that GABA produced by strain BGZLS10-17 exhibits immunosuppressive activity and strengthens the intestinal epithelial barrier's integrity (Soković Bajić et al., 2019).

The protective role of *E. faecium* BGPAS1-3 by an indirect mode of action was demonstrated by infection of differentiated Caco-2 cells with *L. monocytogenes* ATCC19111 (Popović et al., 2019a). *L. monocytogenes* ATCC19111 infection of Caco-2 cells strongly decreased claudin expression. On the other hand, treatment of uninfected differentiated Caco-2 cells with live or heat-killed BGPAS1-3 strongly stimulated the expression of claudin. Interestingly, heat-killed BGPAS1-3 stimulated the expression of claudin, regardless of whether it had been administered before or after *L. monocytogenes* ATCC19111 infection. One of the most interesting effects of *Enterococcus* spp. as probiotics is their ability to modulate the immune system through the induction of cytokine secretion by epithelial cells in a strain-specific manner (Castro et al., 2016b). It has been shown that *L. monocytogenes* ATCC19111 increased proinflammatory *IL-8* mRNA expression. However, live or heat-killed *E. faecium* BGPAS1-3 cells decreased the level of *IL-8* mRNA. Furthermore, live or heat-killed

BGPAS1-3 treatments of Caco-2 cells before *L. monocytogenes* ATCC19111 infection decreased the level of *IL-8* mRNA expression in comparison with treatment with *L. monocytogenes* ATCC19111 alone (Popović et al., 2019a).

5. Probiotics in aquaculture - is there a place for natural LAB dairy isolates?

Although supplementation with LAB as probiotics for humans and terrestrial animals already has a strong foundation in practice, the use of LAB for aquatic animals is still in its infancy. This refers to the application to animals in rearing facilities, including both extensive, pond rearing and intensive rearing in closed recirculating systems. Due to the crowding of a high number of fish in a small area, artificial fish breeding is confronted with numerous obstacles. These include uncontrolled growth of bacterial pathogens and parasites (Kujawa et al., 2016; Ljubobratović et al., 2015; Southgate, 2019) and difficulties associated with the development of the fish's swim bladder (Chatan, 1989). Most of these problems arise in the early stage of fish development, which represents a bottleneck in artificial fish rearing. As a result, fish growth is retarded and mortalities are high, leading to significant economic losses in fish hatcheries (China & Holzman, 2014; Rehman, Gora, Ahmad, & Rasool, 2017). Though swim bladder inflation is mostly linked to technological issues and the high velocity of water in recirculating systems, numerous attempts have been made to address the other two problems by application of antimicrobials and by various feed enrichment and modification methods.

Probiotics make the most preferable solution, given their possibility to directly and indirectly, via immune system stimulation, combat infections, as demonstrated for land animals (Markowiak & Śliżewska, 2018). Furthermore, probiotic bacteria might aid the digestive processes in larval fish (De Schrijver & Ollevier, 2000; Taoka, Maeda, Jo, & Sakata, 2007). Hence, selection of an appropriate probiotic agent, which must be both safe for humans and effective in fish in terms of direct regulation of growth of opportunistic pathogens, represents a significant challenge. Some LAB were shown to be pathogenic to fish, e.g. *Lc. garvieae* and *Streptococcus iniae* (Eldar & Ghittino, 1999). Among LAB, lactobacilli represent the safest option, since most lactobacilli strains possess qualified presumption of safety (QPS) status and investigation of their effects in other hosts aside from humans and livestock is highly encouraged by European authorities (EFSA, 2018). Application of lactobacilli would also prevent eventual zoonotic infections in staff working in fish hatcheries.

So far, there are several reports of LAB applications to fish in experimental settings. Water application of LAB was performed in several studies, correlating with improved fish immune response and reduction of pathogen growth (Jahangiri & Esteban, 2018). Though this method of LAB supplementation would allow for wider control of pathogen growth, including on the surfaces of rearing units, the other two pathways represent more economically sustainable alternatives, considering the number of probiotic bacteria needed to be added to exert a specific activity. Both live and inert feed can act as delivery vectors for probiotic bacteria, which would activate fish immunity (Nayak, 2010), regulate microbiota composition (Akbar et al., 2014) and/or take part in food digestion inside the fish gut (De Schrijver & Ollevier, 2000; Taoka, Maeda, Jo, & Sakata, 2007). However, LAB have a low ability to survive inside the fish digestive tract. Furthermore, *Artemia*, which is the most commonly used live feedingin commercial hatcheries (Treece, 2000), is recommended to be offered to larval fish early after hatching of nauplii, in order to retain its full caloric value (Merchie, 1996). Since newly hatched nauplii are not capable of probiotic ingestion (Qin, 2008), their potential to deliver probiotics to fish is low.

Considering these facts, targeting the biochemical profile of live and inert feed by probiotics might be more efficient in terms of improvement of fish health. Only a few studies have demonstrated the ability of bacteria to alter the biochemical profile of live prey (Hamsah, Widanarni, Alimuddin, Yuhana, & Zairin, 2017; Lobo et al., 2018). Though live food has close to the optimal balance of nutrients needed to support larval development, the study performed by our group has demonstrated that modification of the Artemia live food's nutritive profile with lactobacilli improved the growth rate of gradually weaned pike-perch (Ljubobratovic et al., 2020; Lukic et al., 2020). This was presumably related to elevation of the lipid content of the Artemia nauplii which satisfies the energetic demands of young fish larvae prior to swim bladder inflation. Inert feed is generally poorly accepted by larval fish partly due to the lower quality of nutrients as opposed to live food (García-Ortega, Huisman, Sorgeloos, & Verreth, 2007). Therefore, the effect of modification of inert feed composition by probiotics would have a higher impact on larval fish in comparison to live food. Investigation of the probiotic properties of selected natural isolates from Lactobacillus genera and their application in aquaculture showed that Lb. paracasei subsp. paracasei BGHN14 (isolated from homemade hard cheese traditionally manufactured in the coastal region of Montenegro) in combination with Lb. rhamnosus BGT10 drastically reduced neutral lipid amounts on the surface of granular fish feed (Lukic et al., 2019; Nikolic, Tolinacki, Fira, Golic, & Topisirovic, 2009; Vukotic et al., 2015). This correlated with improved skeletal differentiation in suddenly early-weaned larval fish (Ljubobratovic et al., 2020).

Our research has demonstrated the ability of *Lb. reuteri* BGGO6-55 (originating from artisanal white brined cow's milk cheese, Golija Mountain, Serbia), in combination with *Lb. salivarius* BGHO1 to control the growth of *Flavobacterium* spp. in *Artemia* live food, which translated to lower *Flavobacterium* spp. levels in larval fish (Busarcevic et al., 2008; Ljubobratović et al., 2017; Lukić et al., 2017; Terzić-Vidojević et al., 2014a). On the other hand, alteration of the nutritive profile of ingested feed changes the availability of nutrients for potential pathogens in fish or in fish rearing units. Furthermore, improvement of consumption of inert feed by larval fish lowers the amount of undigested feed, which serves as a substrate for bacterial growth inside the rearing water (Wold et al., 2014). In support of this view, our results showed that alteration of inert feed's nutritive profile in a manner that correlated with increased feed utilization by larval fish reduced the count of *Vibrio* spp. in suddenly-weaned fish (Ljubobratovic et al., 2020; Lukic et al., 2019).

Considering the above facts, we assume that LAB, particularly natural isolates of lactobacilli, might be successfully applied in fish larviculture, which is the critical time point in fish farming. Future research in this respect should be directed towards further manipulation of live and inert feed biochemical composition by lactobacilli in order to attain maximal benefits for fish growth. This would allow efficient and cost-effective larval fish production.

6. Conclusions

Based on the data presented in this review, it can be concluded that Western Balkan Countries region harbors a vast variety of traditional, spontaneously fermented dairy products manufactured in specific ecological localities, while these products harbor a rich diversity of LAB with unique technological and health-promoting properties. The market share of the artisanal fermented food products in Europe is growing, while consumers recognized the gastronomic quality, and healthy food status. However, the tightened European legislation on food safety, resulting in lower production flexibility, may interfere with the traditional manufacturing and consecutively lead to disappearance of regional and artisan fermented products and their associated microbiota. In order to raise the public awareness on the importance of artisanal products in human diet, the aim of this review was to summarize the main types of artisanal dairy products manufactured in WBC and to highlight the importance of their associated LAB that may have strong impact on general human health, as well as on specific health conditions such as diabetes, inflammatory pain, gut-brain axis etc.

As shown in this review, each LAB strain has its own specific features so we can safely say that each strain, introduced into the human and animal organism through a varied diet, as part of the gut microbiota, in its own way brings certain benefits to that organism. Our findings and those of many other authors illustrate the importance of the research on natural isolates of LAB as a valuable source of strains with novel properties, since they can provide deeper and more complete insight into the functioning and organization of the comprehensive metabolic system in these bacteria and their impact on human and animal health. In addition, natural LAB isolates originating from artisanal dairy products with probiotic potential could be good candidates for designing innovative starter and adjunct cultures for production of novel, functional dairy foods. Although the therapeutic potential of probiotics in the management of various metabolic or autoimmune diseases and other pathological states associated with inflammation should not be neglected, the probiotic efficacy of each particular strain in specific diseases needs to be proven in clinical trials in line with the Food and Agriculture Organisation of the United Nations (FAO), World Health Organisation (WHO) criteria, and European Food Safety Authority (EFSA) recommendations.

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Conflict of Interest Statement

The authors declare that they have no conflicts of interest.

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Table 1
List of locations in Western Balkan Countries and dairy products used for the survey of LAB population.

Region and altitude of artisanal dairy product sampling	Type and number of artisanal dairy product	Reference
Serbia, surroundings of Belgrade (Sopot, Mali Mokri Lug), 70-200 m; Zaječar, 130 m; Niš, 190 m; Ivanjica, 450 m, Divčibare, 900 m	Fresh white cheeses (10 samples from each location)	Pešić-Mikulec and Jovanović (2005)
Serbia, Zlatar Mountain, 1200 m and 700 m	White semi-hard raw cow's milk cheeses (1 sample during 60 days of ripening and 1 sample 90 days old)	Terzic-Vidojevic, Vukasinovic, Veljovic, Ostojic, and Topisirovic (2007); Terzic- Vidojevic et al. (2009a)
Serbia, surroundings of Aranđelovac (500 m)	Soft-white brined heat-treated goat's milk cheeses (3 samples 5 days old)	Nikolic et al. (2008)
Serbia, middle-height mountainous region, central region and Zlatibor Mountain, between 500 and 1400m	Cooked cow's milk kajmaks (3 samples 5, 7 and 40 days old; 2 samples 1 month old; 1 sample 7 months old)	Jokovic et al. (2008)
Serbia, Stara Planina Mountain, 400-1400 m	White semi-hard raw bovine milk cheeses (5 samples 1-3 days old) and white raw cow's milk cheeses (2 samples 4 days and 8 months old)	Begovic et al. (2011); Terzic-Vidojevic Lozo, and Topisirovic (2009b)
Serbia, Radan Mountain, 800 m	White mixed raw cow's and ewes' milk cheese (1 sample during 120 days of ripening)	Jokovic, Vukasinovic, Veljovic, Tolinacki, and Topisirovic (2011)
Serbia, mountain Lake Vlasina, 1200 m	White raw goat's milk cheeses (2 samples 5 and 15 days old)	Terzic-Vidojevic et al. (2013)
Serbia, the South Morava, 250 m and mountainous region of Eastern Serbia, 800-1300 m	White pickled raw cow's milk cheeses (6 samples 1-10 days old)	Golić et al. (2013)
Serbia, Golija Mountain, 1000 m	White brined cooked cow's milk cheeses (6 samples 15 days old, 1 sample 20 days old) and white pickled raw cow's milk cheeses (2 samples 10 days old, 1 sample 60 days old)	Golić et al. (2013); Terzić-Vidojević et al. (2014a);

Table 1 continued

Region and altitude of artisanal dairy product sampling	Type and number of artisanal dairy product	Reference
Croatia, Vukovar region (100 m)	Fresh raw sheep's milk cheese "Karakačanski skakutanac" (11 samples 1-3 days old)	Pogačić et al. (2011)
Croatia, Prigorje, Bilogorsko-Podravska region, Zagorje, 90-500 m	Fresh raw cow's milk cheeses (9 samples 2-3 days old)	Golić et al. (2013)
Croatia, different areas in the Istrian region, 300 m	Hard raw ewes' milk cheeses (Istrian cheese) (7 samples during 120 days of ripening)	Mrkonjić Fuka, Engel, Skelin, Redžepović, and Schloter (2010); Skelin et al. (2012)
Croatia, Istrian Peninsula, 300 m	Hard raw ewes' milk cheeses (Istrian, Krcki and Paski cheese) (6 samples during 90 days of ripening)	Mrkonjić Fuka et al. (2013)
Croatia, Knin, 200 m	Cheese in lambskin sacks (Sir iz mišine) from raw cow's milk (3 samples during 45 days of ripening) and from sheep's milk (3 samples during 45 days of ripening)	Frece et al. (2016)
Slovenia, Karst plateau, 200-600 m	Hard raw ewes' milk cheese (Karst cheese-10 samples)	Čanžek Majhenič, Mohar Lorberg, and Rogelj (2007)
Slovenia, Tolmin, 200 m	Hard raw cow's milk cheese (Tolminc cheese-1 sample)	Čanžek Majhenič, Rogelj, and Perko (2005)
Bosnia and Herzegovina, mountainous region near Travnik town, 500 m	Young raw cow's milk cheeses (4 samples 2 days old), sweet creams from raw cow's milk (4 samples 2 days old) and sweet kajmaks from cooked cow's milk (4 samples 2 days old)	Terzić-Vidojević et al. (2014b)
North Macedonia, Peshtani, Mariovo region, 900 m	Beaten raw ewes' milk cheese (2 samples during 45 days of ripening)	Levkov and Kakurinov (2012)

Table 1 continued

Region and altitude of artisanal dairy product sampling	Type and number of artisanal dairy product	Reference
North Macedonia, five different regions, no additional data	White brined raw ewes' milk cheese (5 samples 10 and 90 days old).	Mojsova et al. (2013)
North Macedonia, Peshtani, Mariovo region, 900 m	Beaten raw ewes' milk cheese (10 samples)	Levkov, Srbinovska, and Gjorgovska (2014)
North Macedonia, Mariovo region (southern part of North Macedonia, 1000 m); Debar and Gostivar (western part of North Macedonia), 400-600 m, and Shtip and Kriva Palanka (eastern part of North Macedonia), 300- 650 m	Beaten raw ewes' milk cheese (2 samples during different stages of productions) and white brined raw ewes' milk cheese (4 samples during 90-100 days of ripening).	Levkov, Mojsova, Nastova, Srbinovska, and Gjorgovska (2017)

Table 2

LAB isolated from hard cheeses and other types of WBC dairy products.

d cheeses (five sa					Reference Mrkonjić Fuka, Engel, Skelin,
e of LAB genera (Engel, Skelin,
Last	log CFU/g)				Redžepović, and Schloter (2010)
Last					
	ococcus spp. lactis subsp. s)	Enterococcus spp.	Leuconostoc spp.	Streptococcus spp.	
5.4-6	5.9	4.6-6.9	ND	ND	
6.3-7	7.9	6.2-7.4	ND	ND	
eeses (two samples	s)				Mrkonjić Fuka et al (2013)
Prevalence of LAB genera (% of OTUs)					
c1; Lacte crum ^{c2} ; (Lc. iscisc ³ ; vorus ^{c4}) ^c		Enterococcus spp.	Leuconostoc spp./ Weissella spp. (Ln. mesenteroides; W. paramesenteroides) ^{e,f}	Streptococcus spp.	
	.3	1.5-1.6	ND ^{e,f}	0-13.3	
	91.7	5.9-45.2	0.1-2.4° 0-0.2 ^f	0.3-38.8	
	36.5	7.1-42.7	0-1.4° 0-0.6 ^f	0.3-40.3	
	eeses (two samples e of LAB genera (illus spp. / c1; Lacte urumc2; (Lc. viscisc3; vorusc4)c 4 0-97 .2c2 NDc4	illus spp. / c1;	6.3-7.9 6.2-7.4 eeses (two samples) e of LAB genera (% of OTUs) fillus spp. /- c1;	6.3-7.9 6.2-7.4 ND eeses (two samples) e of LAB genera (% of OTUs) fillus spp. // c1;	6.3-7.9 6.2-7.4 ND ND eeses (two samples) e of LAB genera (% of OTUs) illus spp. / cl: Lactococcus spp. (Lc. lactis) iscisciscis; voruscisciscisciscis voruscisciscisciscisciscisciscisciscisciscis

Table 2 continued

	Cheese					Reference
	Krcki cheeses (two s	Mrkonjić Fuka et al. (2013)				
Ripening period	Prevalence of LAB	genera (% of OTUs)				
Ripening period	Lactobacillus spp. (Lb acidipiscis)	Lactococcus spp. (Lc. lactis)	Enterococcus spp.	Leuconostoc spp./ Weissella spp. (Ln. mesenteroides; W. hellenica) ^{e,f}	Streptococcus spp./ Pediococcus spp. (P. pentosaceus) ^{g,h}	
0 day	ND	95.6-98.7	0.3-0.9	0-0.04e; 0-0.4f	0.08-0.14g; NDh	
45 days	ND	64.7-98.8	0.3-0.6	0-1e; NDf	0.04-23.3g; NDh,	
90 days	0-3.0	83.4-99.2	0.3-0.4	$ND^{e,f}$	0.1-6.0 ^g ; 0-2.1 ^h	
	Paski cheeses (two s	amples)				Mrkonjić Fuka et al. (2013)
	Prevalence of LAB					
Ripening period	Lactobacillus spp. (Lb. casei/ paracasei ^{c1} Lb. plantarum ^{c2} Lb. brevis ^{c3}) ^c	Lactococcus spp. (Lc. lactis ^{d1} ; Lc. raffinolactis ^{d2}) ^d	Enterococcus spp.	Leuconostoc spp. (Ln. mesenteroides ^{e1} Ln. citreum ^{e2}) ^e	Streptococcus spp./ Pediococcus spp. (P.pentosaceus) ^g ,	
0 day	ND ^{c1,c2,c3}	9.4-33.3 ^{d1} 0-0.04 ^{d2}	0-39.7	0-0.1 ^{e1} ; ND ^{e2}	2.9-6.2 ^g ; ND ^h	
45 days	0-0.1 ^{c1} ; ND ^{c2} 0-0.1 ^{c3}	38.1-39.5 ^{d1} ND ^{d2}	0-0.1	1.4-8.1 ^{e1} ; 0.1-0.2 ^{e2}	2.4-2.7 ^g ; ND ^h	
90 days	0.1-0.3 ^{c1} ; 0-0.04 ^{c2} ND ^{c3}	11.4-36.8 ^{d1} 0-0.1 ^{d2}	0-0.1	1.5-14.8 ^{e1} ; 0.4-1.6 ^{e2}	1.2-2.6 ^g ; 0-0.04 ^h	

Table 2 continued

	Cheese					Reference
Ripening period	Beaten cheeses (two	Levkov and Kakurinov (2012)				
rapening period	Prevalence of LAB g	genera (log CFU/g)				
	Lactobacillus spp.	Lactococcus spp.	Enterococcus spp.	Leuconostoc spp.	Streptococcus spp.	_
0 day	7.9-8.2	7.9-8.4	No data	No data	No data	
45 days	6.7-6.5	6.7-6.7	No data	No data	No data	
	Salted kajmaks (six	samples obtained fro	om cooked milk)			Jokovic et al. (2008)
Dinaning pariod	Prevalence of LAB	genera				
Ripening period	Lactobacillus spp. (19.5%)	Lactococcus spp. (8.3%)	Enterococcus spp. (29.2%)	Leuconostoc spp./ Weissella spp. (42.1%)	Streptococcus spp. (0.9%)	
5 days ⁱ	No data	Lc. lactis (3%) Lc. raffinolactis (16%)	E. faecium (24%) E. faecalis (4%)	Ln. mesenteroides (51%) W. minor/ viridescens (0.5%)	S. thermophilus (0.5%) S. suis/bovis (1%)	
7 days ^j	No data	Lc. lactis (13%)	No data	Ln. mesenteroides (87%)	No data	
30 days ⁱ	No data	Lc. garvieae (3%)	E. faecium (30%) E. faecalis (2%)	Ln. mesenteroides (65%)	No data	
30 days ^j	Lb. plantarum (2%) Lb. curvatus (2%)	Lc. lactis (6%)	E. faecium (16%) E. faecalis (4%)	Ln. mesenteroides (70%)	No data	

Table 2 continued

	Dairy product				1.6	Reference
Ripening period	Salted kajmaks (six	samples obtained fro	m cooked milk)			Jokovic et al. (2008)
rapening period	Prevalence of LAB §	genera				
40 days	Lb. plantarum (38%) Lactobacillus spp. (6%)	No data	E. faecium (43%)	Ln. mesenteroides (13%)	No data	
7 months ^j	Lb. kefiri (28%) Lb. plantarum (16%) Lb. paracasei (15%) Lb. kefiranofaciens (5%)	No data	E. faecium (23%) E. faecalis (10%)	Ln. mesenteroides (2%) Ln. lactis (1%)	No data	
	Unsalted (sweet) kaj	maks (four samples	obtained from cooked	d milk)		Terzić-Vidojević et al. (2014b)
Ripening period	Prevalence of LAB §	genera		•		
	Lactobacillus spp. (8.9%)	Lactococcus spp. (42.8%)	Enterococcus spp. (15.2%)	Leuconostoc spp. (31.3%)	Streptococcus spp. (1.8%)	
2 days	Lb. casei (100%)	Lc. lactis (97.9%) Lc. raffinolactis (2.1%)	E. durans (64.7%) E. faecium (5.9%) E. faecalis (5.9%) E. italicus (5.9%) Enterococcus spp. (17.6%)	Ln. mesenteroides (68.6%); Ln. pseudomesenteroides (22.8%) Ln. lactis (8.6%)	S. mitis (100%)	

Table 2 continued

	Dairy product					Reference
Ripening period	Unsalted (sweet) cre	Terzić-Vidojević et al. (2014b)				
Ripelling period	Prevalence of LAB	genera				
	Lactobacillus spp. (20.0%)	Lactococcus spp. (44.9%)	Enterococcus spp. (30.3%)	Leuconostoc spp. (4.2%)	Streptococcus spp. (0.6%)	
2 days	Lb. casei (93.8%) Lb. plantarum (3.1%) Lb. helveticus (3.1%)	Lc. lactis (98.6%) Lc. garvieae (1.4%)	Enterococcus spp. (66%) E. faecalis (22%) E. durans (6%) E. faecium (6%)	Ln. mesenteroides (100%)	S. thermophilus (100%)	
	Cheeses in lambskir	sacks from cow's mi	lk "Sir iz mišine" (th	ree samples)		Frece et al. (2016)
Ripening period	Prevalence of LAB					
r - 2r	Lb paracasei (37.8%)	Lc. lactis subsp. lactis (62.2%)	Enterococcus spp.	Leuconostoc spp.	Streptococcus spp.	
2 days	42.1%	57.9%	No data	No data	No data	
15 days	38.2%	61.8%	No data	No data	No data	
30 days	36.4%	63.6%	No data	No data	No data	
45 days	34.2%	65.8%	No data	No data	No data	

Table 2 continued

	Dairy product				Reference		
Ripening period	Cheeses in lambskii	Cheeses in lambskin sacks from sheep's milk "Sir iz mišine" (three samples)					
Kipening period	Prevalence of LAB	genera					
	Lactobacillus spp. (52.4%)	Lactococcus spp. (14%)	Enterococcus spp.	Leuconostoc spp. (33.6%)	Streptococcus spp.		
2 days	No data	Lc. lactis subsp. lactis (100%) ^k	No data	Ln. mesenteroides (100%) ^k	No data		
15 days	Lb. plantarum (51.4%) ¹ Lb. curvatus (48.6%) ¹	No data	No data	Ln. mesenteroides (100%) ^l	No data		
30 days	Lb. plantarum (100%) ^m	No data	No data	Ln. mesenteroides (100%) ^m	No data		
45 days	Lb. plantarum (69.2%) ⁿ Lb. brevis (30.8%) ⁿ	No data	No data	Ln. mesenteroides (100%) ⁿ	No data		

ND: No detected; CFU: Colony forming units; OUT: Operational taxonomical units.

Table 3

^a Isolation on MRS, anaerobically at 42°C.

^b Isolation on MRS, anaerobically at 30°C.

^c Lactobacillus spp.

d Lactococcus spp.

^eLeuconostoc spp.

^f Weissella spp.

g Non dairy Streptococcus spp.

^h Pediococcus spp.

ⁱLAB from kajmaks making in the same household (middle-height mountainous region, Serbia).

^jLAB from kajmaks making in the same household (central region, Serbia).

^k Ratio between lactococci and leuconostocs in 2-day-old cheese = 60.6%: 39.4%.

¹Ratio between lactobacilli and leuconostocs in 15-day-old cheese = 68.6% : 31.4%.

 $^{^{\}rm m}$ Ratio between lactobacilli and leuconostocs in 30-day-old cheese = 61.1% : 38.9%.

ⁿ Ratio between lactobacilli and leuconostocs in 45-day-old cheese = 74.4% : 25.6%.

Utilization of citrate and production of diacetyl and acetoin, proteolytic activity, production of bacteriocin-like compounds and aggregation ability of the main LAB groups isolated from WBC artisanal raw milk dairy products.

Group of LAB	Citrate utilization ^a	Diacetyl production ^a	Acetoin production ^a	Proteolytic active LAB ^a	Bacteriocin-like producers ^a	Aggregation ability ^a
Lactobacilli	159/371 (42.9%)	110/461 (23.96%)	132/233 (56.7%)	138/335 (41.2%)	45/516 (8.7%)	13/516 (2.5%)
Lactococci	146/263 (55.5%)	26/293 (8.9%)	30/244 (12.3%)	112/234 (49.0%)	87/287 (30.3%)	5/287 (1.7%)
Enterococci	118/333 (35.4%)	100/392 (25.5%)	94/235 (40.0%)	11/211 (4.4%)	150/402 (37.3%)	19/402 (4.7%)
Leuconostocs	116/160 (72.5%)	28/255 (11.0%)	9/160 (5.6%)	0/249	4/236 (1.7%)	3/236 (1.3%)
Streptococci	1/33 (3.0%)	4/34 (11.8%)	13/33 (39.4%)	NT	0/12	0/12
Pedococci	9/23 (39.1%)	0/23	0/23	NT	0/14	0/14
Total	549/1183 (46.4%)	268/1458 (18.4%)	278/928 (30.0%)	261/1029 (25.4%)	286/1467 (19.5%)	40/1467 (2.7%)

NT: No tested.

Note: LAB isolates were assayed for the proteolytic activity described by Kojic et al. (2001). The degradation of β -casein was analyzed on 12.5% sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE). The level of β -casein degradation was quantified by ImageQuant software (Molecular Dynamics GmbH, Krefeld, Germany).

Table 4

LAB strains isolated from WBC artisanal dairy products that generate aromatic carbonyl compounds when they are part of mixed starter cultures.

Dairy product	LAB strain as part of starter culture	Citrate utilizatin	Acetoin production	Reference
Yogurt	Streptococcus thermophilus BGKMJ1-36	_	+	Unpublished data
White brined cheese	Lactobacillus plantarum BGVL2a-18 Lactococcus lactis BGVL2-8	++	+ -	Golić et al. (2013);
White soft	Lactobacillus plantarum BGGO7-29	±	+	Terzic-Vidojevic et al. (2013, 2014b,
cheese without ripening	Lactococcus lactis BGTRK4-21	+	±	2015c)
Sour cream	Lactococcus lactis subsp. lactis biovar. diacetylactis BGTRK10-2	+	_	

^a Number of isolates which gave a positive reaction/total number of tested isolates.

Lactococcus lactis subsp. cremoris BGTRM1-22	_	+
Leuconostoc mesenteroides. subsp. cremoris BGTRS1-2	_	+

BGTRS1-2 +: Positive reaction; -: Negative reaction; ±: Weak reaction.

Figure legends

Fig. 1. LAB isolated from WBC white brined cheeses: 1) Zlatar cheese BGZLS^a, 2) Zlatar cheese BGNV^a, 3) Radan cheeses BGGJ^a, 4) Golija cheeses BGGO^b, 5) Vlasina cheeses BGVL^b, 6) Bukuljac cheeses BGAR^c, 7) Pirot cheeses BGPT^b, 8) Cheeses from South Morava region (BGAL and BGLE)^b and Eastern Serbia region (BGVL, BGBU and BGRE)^b.

Note: a LAB from one sample of cheese followed during ripening.

- ^b LAB from cheeses of different ripening periods making in different households.
- ^c Three samples from three different batches of the same household.
- **Fig. 2.** The prevalence of certain LAB species isolated from WBC white brined cheeses (%): 1) Zlatar cheese BGZLS^a, 2) Zlatar cheese BGNV^a, 3) Radan cheeses BGGJ^{a,d}, 4) Golija cheeses BGGO^b, 5) Vlasina cheeses BGVL^b, 6) Bukuljac cheeses BGAR^c, 7) Pirot cheeses BGPT^{b,e}, 8) Cheeses from South Morava region (BGAL and BGLE)^b and Eastern Serbia region (BGVL, BGBU and BGRE)^b.

Note: a LAB from one sample of cheese followed during ripening.

- ^b LAB from cheeses of different ripening periods making in different households.
- ^c Three samples from three different batches of the same household.
- ^d 6.6% are unidentified LAB strains.
- e 1.9% are unidentified LAB strains.
- **Fig. 3.** Groups of LAB (A) and the prevalence of certain LAB species (B) isolated from WBC fresh cheeses: 1) Serbian fresh cheeses (Sopot, Mali Mokri Lug, Zaječar, Niš, Ivanjica and Divčibare regions)^a, 2) Karakačanski skakutanac cheeses^b, 3) Croatian fresh cheeses (Prigorje, Zagorje and Bilogorsko-Podravska regions)^a, 4) Travnik young cheeses^c.

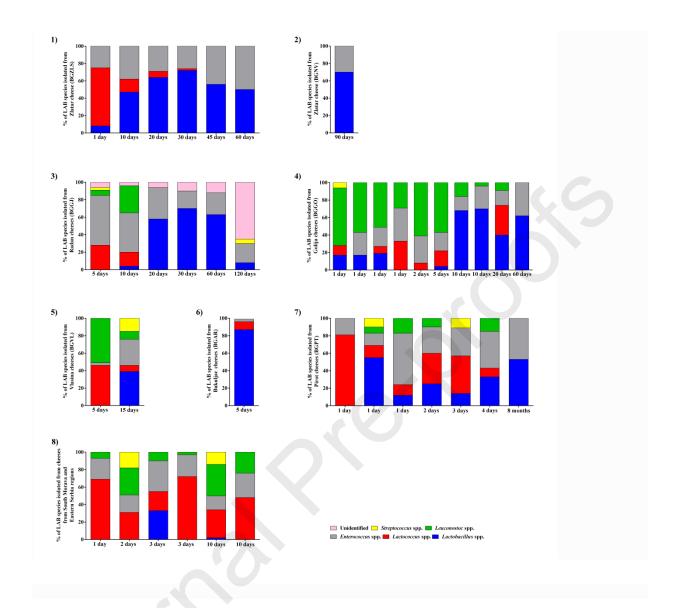
Note: a LAB from cheeses making in different households.

- ^b Eleven samples from eleven different batches of the same farm.
- ^c Four samples from four different batches of the same household.
- ^d No data on percentage of certain LAB species.

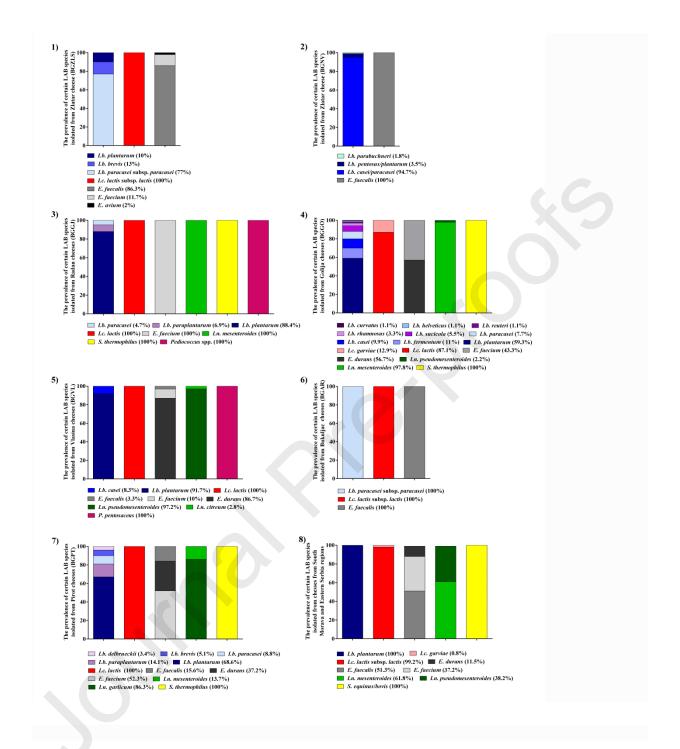
Author contributions

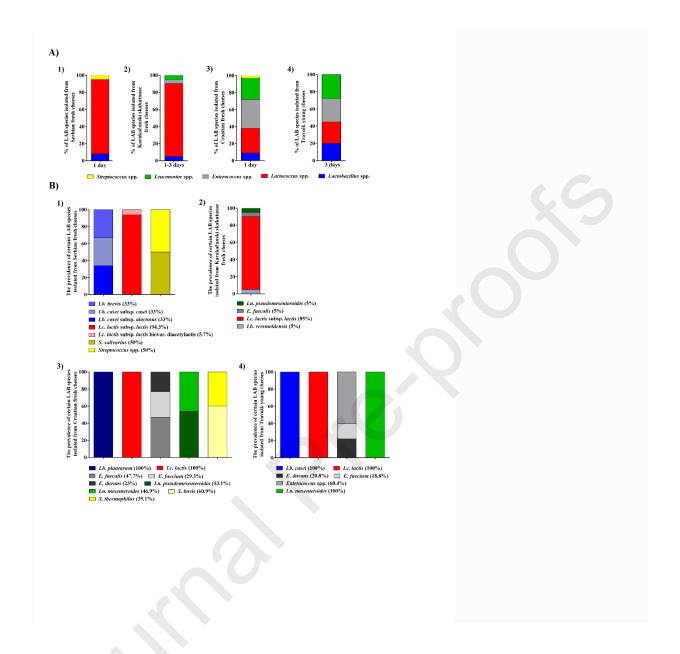
All authors contributed to the study conception and design. Amarela Terzić-Vidojević had the idea for the article. Amarela Terzić-Vidojević, Katarina Veljović, Maja Tolinački, Đorđe Fira and Nikola Popović performed the literature search and data analysis for part of manuscript related to diversity of lactic acid bacteria and their certain technological properties. Milica Živković, Jelena Lozo, Marija Miljković and Nataša Golić performed the literature search and data analysis for part of manuscript related to certain probiotic properties. Jovanka Lukić performed the literature search and data analysis for part of manuscript related to probiotics in aquaculture. Branko Jovčić, Ivana Strahinić, Jelena Begović, Milan Kojić, Ljubiša Topisirović and Nataša Golić drafted and critically revised the work.

Journal Pre-proofs

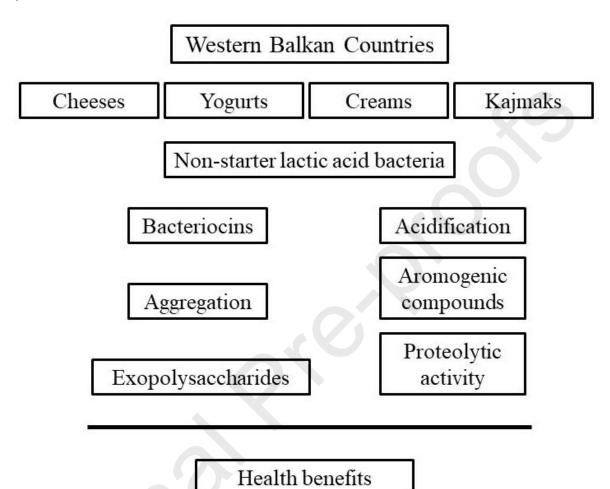


Journal Pre-proofs





Graphical abstract



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Lactic acid bacteria from artisanal dairy products of the Western Balkan were tested. White brined, fresh and hard cheeses, yogurt, cream and kajmak were analyzed.

Over 3000 isolates were characterized and 28 species were identified. Many strains had one, two or more probiotic properties.