Table 2. Technological properties of 40 tested *Lactococcus lactis* strains

Tested strain	Group	*t*/h						β-galactosidase activity	Proteolysis	Lipolysis
		2	4	6	8	24	48			
		pH (milk at 30 °C)								
MON101	1	6.19	5.77	5.20	4.56*	4.08	4.03	+	+	–
MON102	1	6.34	6.20	6.03	5.69	4.46*	4.21	+	+	–
MON104	1	6.28	5.94	5.31	4.58*	4.10	4.06	+	+	–
MON108	1	6.24	5.78	5.18	4.51*	4.09	4.07	+	+	–
MON111	1	6.32	6.05	5.58	4.88	4.10*	4.04	+	+	–
MON112	1	6.25	6.10	5.69	5.07	4.11*	4.03	+	+	–
MON125	3	6.39	6.31	6.26	6.18	5.28	4.17*	–	–	–
MON126	1	6.30	5.80	5.16	4.62*	4.17	4.11	+	+	–
MON127	3	6.32	6.04	5.69	5.43	4.69*	4.31	–	+	–
MON128	3	6.33	6.31	6.21	6.23	6.05	5.87	–	–	–
MON129	1	6.38	6.24	6.11	6.04	4.29*	4.12	+	+	–
MON131	3	6.34	6.26	6.18	6.13	6.04	5.85	–	–	–
MON132	1	6.25	5.97	5.61	5.37	4.62*	4.27	–	+	–
MON133	3	6.34	6.35	6.33	6.35	5.05	4.24*	–	–	–
MON136	1	6.28	5.87	5.40	5.12	4.49*	4.31	+	+	–
MON147	1	6.29	6.05	5.49	5.08	4.40*	4.16	–	+	–
MON150	3	6.30	6.09	5.96	6.67	5.12	4.76*	–	+	–
MON152	1	6.28	5.98	5.44	5.08	4.40*	4.18	–	+	–
MON153	1	6.33	6.09	5.57	5.26	4.56*	4.26	–	+	–
MON154	1	6.29	5.75	5.40	5.20	4.55*	4.29	–	+	–
MON164	1	6.18	5.45	4.60*	4.31	4.05	4.04	+	+	–
MON166	1	6.32	5.96	5.50	5.22	4.42*	4.19	+	+	–
MON167	1	6.33	5.90	5.43	5.15	4.55*	4.28	+	+	–
MON168	3	6.31	6.21	6.15	6.10	5.70	5.29	+	+	–
MON170	1	5.96	5.39	5.11	4.90*	4.30	4.13	+	+	–
MON171	3	6.27	6.16	6.09	6.03	5.61	4.62*	+	–	–
MON172	3	6.25	6.12	6.09	6.00	5.60	4.42*	+	–	–
MON174	3	6.31	6.21	6.16	6.04	5.71	5.42	+	–	–
MON185	1	6.28	5.88	5.15	4.47*	4.10	4.07	+	+	–
MON207	3	6.29	6.20	6.11	6.06	5.72	5.44	–	–	–
MON208	1	6.26	5.85	5.40	5.18	4.47*	4.22	+	+	–
MON257	3	6.38	6.29	6.29	6.23	6.24	6.13	–	–	–
MON259	3	6.40	6.30	6.28	6.20	5.24	4.32*	–	–	–
MON260	3	6.29	6.10	5.97	5.75	5.08	4.68*	+	+	–
MON265	1	6.23	5.80	5.48	5.28	4.56	4.37*	+	+	–
MON277	3	6.37	6.20	6.05	5.78	5.18	4.76*	+	–	–
MON281	1	6.24	5.88	5.41	5.19	4.50*	4.35	+	+	–
MON287	2	6.33	6.11	5.65	5.34	4.65*	4.42	+	+	–
MON288	1	6.26	5.89	5.37	5.21	4.59*	4.44	+	+	–
MON298	3	6.39	6.26	6.21	6.12	5.33	4.29*	+	–	–

After 24 h of incubation, the pH of milk decreased to: pH<4.65 (group 1), pH=4.65 (group 2) and pH>4.65 (group 3)
*coagulation

substances and others (*21*,*58*). Within our study none of the lactococci showed any activity against the Gram-negative indicator bacteria (*Enterobacter* spp., *Pseudomonas* spp. and *Serratia* spp.). According to Rodríguez *et al.* (*59*), LAB bacteriocins are generally inactive against Gram-negative bacteria due to their resistance conferred by the outer membrane. The test strains were also less effective in reducing the growth of two *Listeria* spp. strains (DSM 15675 and DSM 20649), which may be related to the production of organic acids or hydrogen peroxide. However,

seven of the 40 *Lactococcus* strains were able to inhibit the growth of *Staphylococcus aureus* strains and isolates (DSM 1104, DSM 20231 and SA17) (Table 3). Nevertheless, characterising these strains for antibacterial compounds using the agar well diffusion assay, no inhibition zone could be observed. Similar results were reported by Ammor *et al.*

Table 3. Antimicrobial activity of 40 tested *Lactococcus lactis* strains

Tested strain	Group	*Staphylococcus aureus*			*Listeria* spp.		*Escherichia* spp.		*Enterobacter* spp.		*Serratia* spp.		*Pseudomonas* spp.	
		DSM 1104	DSM 20231	SA17	DSM 15675	DSM 20649	EC7	EC9	DSM 30053	EN3	DSM 4487	EN1	DSM 1117	DSM 50090
MON101	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON102	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON104	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON108	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON111	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON112	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON125	3	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON126	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON127	3	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON128	3	–	+	–	(+)	(+)	–	–	–	–	–	–	–	–
MON129	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON131	3	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON132	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON133	3	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON136	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON147	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON150	3	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON152	1	–	–	(+)	(+)	(+)	–	–	–	–	–	–	–	–
MON153	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON154	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON164	1	–	–	+	(+)	(+)	–	–	–	–	–	–	–	–
MON166	1	(+)	(+)	+	(+)	(+)	–	–	–	–	–	–	–	–
MON167	1	(+)	(+)	+	(+)	(+)	–	–	–	–	–	–	–	–
MON168	3	(+)	(+)	+	(+)	(+)	–	–	–	–	–	–	–	–
MON170	1	–	(+)	+	(+)	(+)	–	–	–	–	–	–	–	–
MON171	3	+	(+)	+	(+)	(+)	–	–	–	–	–	–	–	–
MON172	3	+	(+)	+	(+)	(+)	–	–	–	–	–	–	–	–
MON174	3	(+)	+	+	(+)	(+)	–	–	–	–	–	–	–	–
MON185	1	–	–	+	(+)	(+)	–	–	–	–	–	–	–	–
MON207	3	(+)	+	+	(+)	(+)	–	–	–	–	–	–	–	–
MON208	1	–	(+)	+	(+)	(+)	–	–	–	–	–	–	–	–
MON257	3	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON259	3	–	–	(+)	(+)	(+)	–	–	–	–	–	–	–	–
MON260	3	(+)	–	+	(+)	(+)	–	–	–	–	–	–	–	–
MON265	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON277	3	(+)	–	+	(+)	(+)	–	–	–	–	–	–	–	–
MON281	1	–	–	–	(+)	(+)	–	–	–	–	–	–	–	–
MON287	2	–	–	+	(+)	(+)	–	–	–	–	–	–	–	–
MON288	1	–	–	+	(+)	(+)	–	–	–	–	–	–	–	–
MON298	3	–	–	+	(+)	(+)	–	–	–	–	–	–	–	–

After 24 h of incubation, the pH of milk decreased to: pH<4.65 (group 1), pH=4.65 (group 2) and pH>4.65 (group 3); DSM=Deutsche Sammlung von Mikroorganismen (German Collection of Microorganisms); SA17, EC7, EC9, EN3 and EN1=isolates from Montenegrin dairy products; –=no inhibition, *i.e.* growth like the control, (+)=weak inhibition, *i.e.* growth between that of the control and no growth, +=total inhibition, *i.e.* no growth

(*60*), as they could only detect antimicrobial activity on agar but not in the cell-free supernatant fluids. These authors had several hypotheses for this phenomenon such as the adsorption of bacteriocin-like substances by filters, their attachment to the cell wall or the inability of the strains to produce inhibitors in liquid cultures (*60*).

Table 4. Safety evaluation of 40 tested *Lactococcus lactis* strains

Tested strain	Group	Biogenic amine gene			Antimicrobial susceptibility								
					MIC/(μg/mL)								
		HDC	TDC	ODC	AMP	VAN	GEN	KAN	STR	ERY	CLI	TET	CHL
MON101	1	–	–	–	0.5	0.5	4	16	128*	0.25	0.5	0.5	4
MON102	1	–	–	–	0.5	0.5	8	16	128*	0.25	0.5	0.5	4
MON104	1	–	–	–	0.5	0.5	4	16	64*	0.25	0.25	0.5	4
MON108	1	–	–	–	0.5	0.5	4	16	64*	0.25	0.5	0.5	4
MON111	1	–	–	–	0.5	0.5	8	16	128*	0.25	0.25	0.5	4
MON112	1	–	–	–	0.5	0.5	4	16	64*	0.25	0.25	0.5	4
MON125	3	–	–	–	0.5	0.5	2	8	32	0.25	0.12	0.25	4
MON126	1	–	–	–	0.5	0.5	4	8	32	0.25	0.25	0.25	4
MON127	3	–	–	–	0.5	0.5	4	8	32	0.25	0.25	0.25	4
MON128	3	–	–	–	0.5	0.5	4	8	32	0.25	0.25	0.25	4
MON129	1	–	–	–	0.5	0.5	2	8	256*	0.25	0.12	0.25	4
MON131	3	–	–	–	0.5	0.5	4	8	32	0.25	0.25	0.25	4
MON132	1	–	–	–	0.5	0.5	2	8	32	0.25	0.12	0.25	4
MON133	3	–	–	–	0.5	0.5	4	16	32	0.25	0.12	0.25	4
MON136	1	–	–	–	0.25	0.5	2	8	16	0.25	0.06	0.5	8
MON147	1	–	–	–	0.25	0.5	2	4	16	0.25	0.12	0.25	4
MON150	3	–	–	–	0.25	0.5	1	4	32	0.25	0.06	0.5	2
MON152	1	–	–	–	0.5	0.5	2	4	32	0.25	0.12	0.5	4
MON153	1	–	–	–	0.25	0.5	2	16	16	0.25	0.12	0.5	4
MON154	1	–	–	–	0.25	0.5	2	8	32	0.25	0.12	0.5	4
MON164	1	–	–	+	0.5	0.5	2	8	32	0.25	0.06	0.5	4
MON166	1	–	–	–	0.5	0.5	4	16	16	0.25	0.06	0.5	8
MON167	1	–	–	–	0.25	0.5	4	16	32	0.25	0.25	0.5	8
MON168	3	–	–	–	0.5	0.5	2	8	32	0.25	0.12	0.5	4
MON170	1	–	–	–	0.5	0.5	2	8	32	0.25	0.06	0.5	8
MON171	3	–	–	–	0.5	0.5	4	16	64*	2*	0.25	0.5	8
MON172	3	–	–	–	0.5	0.5	2	8	32	0.25	0.06	0.5	8
MON174	3	–	–	–	0.5	1.0	1	4	128*	2*	0.12	0.5	4
MON185	1	–	–	–	0.25	0.5	2	4	16	0.25	0.06	0.25	8
MON207	3	–	–	–	0.5	0.5	2	8	32	0.25	0.06	0.5	8
MON208	1	–	–	–	0.5	0.5	2	4	16	0.25	0.06	0.5	8
MON257	3	–	–	–	0.5	0.5	2	4	32	0.25	0.06	0.25	8
MON259	3	–	–	–	0.25	0.5	2	8	32	0.25	0.06	0.5	4
MON260	3	–	–	–	0.5	0.5	4	16	64*	0.25	0.12	0.5	4
MON265	1	–	–	–	0.25	0.5	4	16	16	0.25	0.06	0.5	4
MON277	3	–	–	–	0.5	0.5	4	16	64*	0.25	0.12	0.5	4
MON281	1	–	–	–	0.25	0.5	4	8	32	0.25	0.12	0.5	4
MON287	2	–	–	–	0.5	0.5	4	16	64*	0.25	0.06	1	8
MON288	1	–	–	–	0.25	0.5	4	16	64*	0.25	0.06	0.5	4
MON298	3	–	–	+	0.25	0.5	2	8	64*	0.25	0.12	0.5	4

After 24 h of incubation, the pH of milk decreased to: pH<4.65 (group 1), pH=4.65 (group 2) and pH>4.65 (group 3); MIC=minimum inhibitory concentration; HDC=histidine decarboxylase, TDC=tyrosine decarboxylase, ODC=ornithine decarboxylase; AMP=ampicillin, VAN=vancomycin, GEN=gentamicin, KAN=kanamycin, STR=streptomycin, ERY=erythromycin, CLI=clindamycin, TET=tetracycline, CHL=chloramphenicol; *resistant according to EFSA (*61*)

The biogenic amines most commonly found in fermented dairy products are histamine and tyramine, but putrescine is also frequently detected (*62*). Thus, PCR was used to amplify fragments of genes coding for HDC, TDC and ODC. While no amplicons for HDC and TDC could be observed, two strains were positive for ODC (Table 4). The PCR products of these strains were subjected to sequencing for confirmation. The obtained sequences verified the result as they corresponded to fragments of the ODC gene, detected in *Oenoccocus oeni* strains (GenBank accession no. FR751075.1-FR751079.1) (*27*). According to Ladero *et al.* (*63*), *L. lactis* is one of the main putrescine producers in cheese. However, only *L. lactis* strains producing putrescine by the agmatine deiminase (AgDI) pathway and not by the ornithine decarboxylase (ODC) pathway have been described (*63*). Although some *L. lactis* strains have been reported as potential histamine or tyramine formers (*64*), none of the relevant genes was found within our study. Similarly, Priyadarshani and Rakshit (*64*) could not observe any histamine and tyramine formation in their tested *L. lactis* strains.

Using the cut-off values of EFSA (*61*) to distinguish resistant from susceptible strains, all lactococci were susceptible to the tested antibiotics except for streptomycin and erythromycin (Table 4). While only two strains slightly exceeded the cut-off value of erythromycin, approximately one third of the investigated strains can be classified as resistant to streptomycin according to EFSA (*61*). However, the typical MIC distribution for wild type organisms covers three to five adjacent 2-fold dilution steps surrounding the modal MIC (*65*). This applies to the streptomycin MIC distribution obtained within our study (Table 4). As a wild type organism is defined as a strain which does not harbour acquired resistance to the examined antibiotic (*66*), the higher streptomycin MICs might be natural in *L. lactis*. High streptomycin MIC values for lactococci were also observed by Fernández *et al.* (*8*), Toomey *et al.* (*67*) and Rodríguez-Alonso *et al.* (*68*). Nevertheless, the possibility of the presence of antibiotic resistance genes should not be ignored and needs further investigations. For instance, a decreased susceptibility to erythromycin due to a multidrug transporter encoded by the gene *mdt*-(A) was shown in *L. lactis* (*69*). Otherwise the erythromycin-resistance gene *erm*(B) could likewise be responsible for the higher MIC values of the two *Lactococcus* strains, as this gene was also found in intermediate-level resistant (2–16 μg/mL) *L. garviae* isolates (*70*).

Conclusions

Our study suggests that 11 (27.5 %) of the 40 tested *Lactococcus lactis* ssp. *lactis* strains have a potential to be used as starter cultures for the production of traditional Montenegrin cheese. Of course, further studies such as an investigation of antimicrobial resistance determinants have to be done to assure the innocuousness of these strains. For a successful application of these well characterised lactococci in dairy industry, it is also necessary to determine the biochemical reactions that take place during fermentation and ripening of the product due to the activity of these bacteria. Thus, after inoculating milk with these strains, changes of microbial, physical, chemical and sensory characteristics during fermentation and ripening of cheese as well as the final product should be monitored.

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