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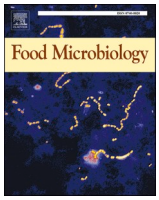

Marination increased tyramine levels in rainbow trout fillet strips packaged under modified atmosphere

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ABSTRACT

Marinades are increasingly used to manufacture raw fish products. In corresponding meats, marinating is known to have a major effect on the composition of the microbiome, but the effect of marinating on fish is not known as well. This knowledge gap prompted our study of the microbial ecology and amine formation in marinated and unmarinated modified atmosphere commercially packaged rainbow trout fillet strips. According to our findings, marination increased the maximum concentrations (7–8 log CFU/g) of psychrotrophic bacteria by one logarithmic unit and led to 5 times higher average tyramine concentrations than the corresponding unmarinated product. Instead, trimethylamine concentrations were 30 times higher in the unmarinated product than those in the marinated one. According to the 16 S rRNA sequence analyses, lactic acid bacteria (LAB) predominated in the marinated strips one day after the use-by date, whereas in the unmarinated strips *Fusobacteriaceae* and LAB were the dominating taxa. Based on the culture-dependent analysis, *Latilactobacillus fuchuensis* was the prevailing LAB in both products. Since the subset of *L. fuchuensis* strains tested was able to produce tyramine *in vitro,* we hypothesise that the use of the acidic marinade activated the production of tyrosine-decarboxylating enzymes in *L. fuchuensis* and led to the increased tyramine concentrations.

1. Introduction

Pickling and curing of fish to obtain "raw" fish preserves has been used for many years, whereas the marination of raw fish to create products intended to be cooked as such is a more contemporary or local way to process fish. Marination is commonly used to add value to raw red meat and poultry products and its effect on meat has been widely studied (Björkroth, 2005; Maxwell et al., 2018; Arcanjo et al., 2019). Marination has been shown to result in distinct changes in poultry and red meat spoilage microbiomes mainly due to the combined effect of carbohydrates and acetic acid used in the marinades (Nieminen et al., 2012). Leuconstocs are typically the prevailing spoilage LAB in these products (Björkroth et al., 2000; Nieminen et al., 2012).

Composition of fish muscle differs from red meat and poultry mainly in the amount of carbohydrates and amino acids. Fish generally contains more free amino acids and nitrogenous compounds and is not as rich in glucose as meat is (Haard, 1992; Abraha et al., 2018; Beltrán and Bellés 2019). Therefore, the effect of marinating fish may differ greatly from the corresponding effect in meat. How marinating of fish affects microbial ecology and chemical composition has been the subject of only a few studies (Kilinc and Cakli 2005; Özogul et al., 2010; Kindossi et al., 2016) and limited only to the reporting of bacterial levels, nitrogenous compounds and fatty acids. Maktabi et al. (2016) showed that marination enhanced the shelf life of rainbow trout by preventing protein degradation and delaying microbial spoilage, but the effect on the microbiome was not studied.

Since there is limited information about fish marination, we set out to study the effect of marination on the spoilage microbiome of commercially-packaged rainbow trout fillet strips. We chose rainbow trout (*Oncorhynchus mykiss*) for our study, since it is a popular food fish globally and the most significant fish in terms of production value in Finland. In addition, we studied the production of biogenic amines (BA) and trimethylamine (TMA), which play an important role as indicators of fish quality/freshness.

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2. Materials and methods

2.1. Selection of the samples and storage

The rainbow trout fillet strips were bought at local markets. Products, both unmarinated (A = 2 × 10 n, B = 2 × 5 n) and marinated strips (A = 2 × 10 n, B = 2 × 10 n), from two producers (A and B) were bought. All packages were obtained in duplicate from each production batch. One package was analysed as fresh as possible (2 days after packaging) and the other one a day after the use-by date (UBD +1). The samples were kept at 3 °C until analysis. The manufacturers had given shelf lives of 7 and 9 days for unmarinated and marinated strips, respectively. Both the unmarinated and marinated products contained 1% NaCl, acidity regulators, rapeseed oil and water. The marinades contained sucrose, organic acids (acetic acid, citric acid), spices (peppers, sugars, herbs).

2.2. Microbial enumeration

Microbial enumeration was made for all packages. Colony counts of individual packages at the time of sampling were performed by homogenising 25 g of fish with 0.1% peptone saline (225 ml) for 1 min (Stomacher, Seward, Worthing, UK). Then, 10-fold dilutions were plated on de Man-Rogosa-Sharpe (MRS, Oxoid, Basingstoke, UK) for LAB, Long and Hammer agar (LH, Van Spreekens, 1974) for psychrotrophic bacteria and Iron agar (IA, Atlas, 2006) for total colony counts as well as H_2S-producing microorganisms (black colonies).

The plates were incubated for 5 days at 25 °C (MRS), at 20 °C (IA) and at 15 °C (LH). The MRS plates were incubated anaerobically (Anaerogen, Oxoid, Basingstoke, UK) in jars and the other plates aerobically. After the incubation period, colonies typical for the respective microbial group were counted, and the counts were transformed to log values (log CFU/g).

2.3. Physical parameters

Physical parameters were measured for all packages. Gas compositions in the MAP were measured using a gas sensor (Checkpoint, PBI Dansensor, Ringstedt, Denmark). The pH was measured from meat homogenate which prepared in microbial enumeration by an inoLab pH 720 (WTW GmbH, Weilheim, Germany) instrument.

2.4. Sensory evaluation

Sensory evaluation was performed for all "UBD +1 day packages" by a trained panel of five persons. A five-class evaluation scheme was used for odour and appearance (1 = severe defect, spoiled, 2 = clear defect, spoiled, 3 = mild defect, satisfactory, 4 = good, 5 = excellent) in which grade 3 was considered as the point of acceptability. Fresh fish stored in the freezer was used as a control. The observed deficiencies were described. The sample was considered spoiled if at least three panellists found odour or/and appearance unacceptable.

2.5. Culture-independent characterisation of the bacterial communities

Bacterial communities in fish were characterised culture-independently by sequencing the 16 S rRNA gene fragment. A total of 9 unmarinated (3 fresh, 6 UBD+1) and 15 marinated (6 fresh, 9 UBD+1) packages were analysed. DNA was extracted from 1:10 homogenate of microbial dilute as described earlier (Hultman et al., 2015).

PCR amplification of the V3–V4 region of the 16 S rRNA gene was performed in two steps. The first round of amplification was done with the primers 341F1-4 and 785R1-4, which contain partial Illumina TruSeq adapter sequences in the 5′ ends. A second PCR round was performed with full-length TruSeq P5 and Index containing P7 adapters. Details of the cycling conditions, PCR protocol and PCR-product processing were described previously (Jääskeläinen et al., 2019). Sequencing was done on the Illumina MiSeq platform at the Institute of Biotechnology, University of Helsinki, Finland. All 16 S rRNA gene sequences have been deposited in the European Nucleotide Archive (accession no. PRJEB45734). The sequences were joined with PEAR (Zhang et al., 2014) and quality trimmed using USEARCH (Edgar, 2013) fastq_filter command with fastq_maxee 1 and fastq_minlen 350 parameters. Unique sequences were identified with the VSEARCH derep_full length command. Chimeras were removed with VSEARCH uchime3_denovo and 97% OTUs clustered with the cluster_fast command. Taxonomic classification of OTUs was done using the classify.seqs command in mothur (Schloss et al., 2009) using the RDP naïve Bayesian Classifier (Wang et al., 2007) against the Silva 138 database (Quast et al., 2013) with classifier cutoff = 60.

2.6. Ribotyping-based identification of LAB cultured from fish

To identify the LAB prevailing, up to 10 colonies per sample were randomly picked from the MRS plates with measurable number of colonies, cultured from samples analysed at UBD+1 packages. Colonies A total of 252 isolates were purified, and subjected to ribotyping based on the numerical analyses of the 16 and 23 S rRNA gene HindIII restriction fragment length polymorphism patterns (ribopatterns; Vihavainen et al., 2008). In addition, 19 isolates were characterised additionally by ribotyping with EcoRI.

Ribopatterns were analysed using the BioNumerics (version 5.10; Applied Maths, Sint-Martens-Latem, Belgium) and the LAB database of the Department of Food and Environmental Hygiene, University of Helsinki, Finland, containing HindIII ribopatterns for approximately 7000 LAB, including ribopatterns of type and reference strains. Similarity among ribopatterns of the fish isolates against those in the database was determined by cluster analysis in a dendrogram using the unweighted pair group method with the arithmetic mean (UPGMA) method. Strains assigned to the same ribotype as reference strains were attributed to that species.

2.7. Potential of tyramine production

The ability of selected (n = 20) *Latilactobacillus fuchuensis* strains (10 from marinated and 10 from unmarinated strips) to produce tyramine was determined by using broth as described by Bover-Cid and Holzapfel (1999). Precultured strains from the MRS broth were further inoculated to 0.5% (w/v) L-tyrosine di-sodium salt (Sigma-Aldrich, USA) containing broth, the pH and colour of which were monitored for 5 days at 20 °C. Cultures that had changed colour to purple and had a pH above 6.0 were considered tyramine production positive. *Carnobacterium divergens* (DSM 20623^T) and *Carnobacterium maltaromaticum* (DSM 20342^T) were used as positive controls.

2.8. LC-MS and GC-MS analysis of amines

A total of 10 unmarinated and 12 marinated samples in UBD+1 day were analysed. Biogenic amines (BAs) were analysed by LC-MS using a method by Eerola et al. (1993) converted for use with a mass selective detector. Fish samples (10 g) were homogenised with Ultra-Turrax (IKA company, Germany) and extracted twice into 10 ml of 0.4 M $HClO_4$. The supernatants were combined, 1 ml of extract was added to 300 μl of $NaHCO_3$, 200 μl of 2 M NaOH and 5 μl of 1.6 diaminohexane (internal standard). The BAs were derivatised with 1 ml of 1 g/l dansyl chloride acetone solution and incubated for 1 h at 40 °C. After filtration, the samples were diluted with acetonitrile (1:1) and analysed by using an Agilent LC and a mass-selective (MS) detector. The capillary column was a/the Luna C18 column (3 μm, 150 mm × 2.0 mm with a SecurityGuard C18 procolumn, Phenomenex Torrance, USA). The solvent in LC was a mixture of 0.1% formic acid (A) and acetonitrile (B) at a flow rate of 0.25 ml/min, started at 50% B, increased to 90% at 10 min and held until 20 min. B was decreased to 50% at 25 min and held at this rate until

the end of the program at 35 min. The sample was introduced after chromatographic separation to MS. The source parameters were as follows: voltage −4500 V, nebuliser pressure 30 psi and dry gas flow rate of 10 l ml/min at a temperature of 350 °C.

GC-MS analysis was made by the SPME Arrow system as described by Helin et al. (2015) for volatile compounds, TMA and DMA. Fish samples (10 g) were weighed in a 20 ml Headspace vial. After sealing, 250 μl of 5 M KOH was injected through the septum into the sample solution with a syringe needle in order to liberate the amines to the headspace. The solution was left to equilibrate for 5–10 min before the SPME system was inserted into the headspace of the vial.

Extraction time was 30 min at ambient temperature. Samples were analysed by Agilent 6890 N GC equipped with an Agilent 5975 C MS. The column used was Inert-Cap for Amines (30 m × 0.25 mm (i.d.), GL Sciences, Tokyo, Japan), which was connected to a deactivated fused silica retention gap (1.5 m × 0.53 mm (i.d.), Agilent Technologies, Palo Alto, USA) with a press-fit connector (BGB Analytic, Böckten, Switzerland). The oven temperature was as follows: 40 °C for 5min and then 30 °C/min to 250 °C (held 4 min). Helium (AGA, Espoo, Finland) was the carrier gas at a constant 90 kPa pressure. The injector and GC-MS transfer line temperatures were 250 °C and the ion source and quadrupole temperatures were 230 °C and 150 °C, respectively. Electron ionisation (70eV) was used and the total ion chromatogram was monitored in an m/z range of 30–200. The peak areas were calculated based on extracted ion chromatograms using base peaks, m/z 44 for dimethylamine, DMA and m/z 58 for TMA.

3. Results

3.1. Microbial enumeration

The mean initial counts of psychrotrophic bacteria were 4.3 and 5.3 CFU/g in unmarinated and marinated samples, respectively (Table 1). The average maximum counts of total psychrotrophic bacteria after cold storage until UBD+1 day were 6.3 and 7.4 CFU/g in unmarinated and marinated samples, respectively. Psychrotrophic bacterial concentrations were 2 log units higher at the end of storage than at the beginning and were one log unit higher in marinated than in unmarinated strips. Likewise, LAB counts increased as the total psychrotrophic bacteria but slightly to a higher level in the marinated product (Table 1). However, H_2S producing bacteria were detected only in unmarinated strips after storage.

3.2. Physical parameters

Only limited changes in pH were observed during storage. The pH average of the strips decreased by 0.2 units during the study period in marinated strips and remained at about the same level in unmarinated strips (Table 1). In marinated strips, the pH average was 0.4 pH units lower than in unmarinated strips at UBD+1 day. In addition, the atmospheres of the packages remained stable. Oxygen and carbon dioxide levels were about 1% and 20%, respectively, at the beginning and end of storage.

Table 1
Plate counts of bacteria, concentrations of CO_2 and O_2 and pH values of rainbow trout fillet strips at the beginning (fresh) and after storage (UBD + 1 day) at 3 °C. A total of 70 packages were studied (30 unmarinated and 40 marinated). Standard deviation is marked in parenthesis.

	Unmarinated		Marinated	
	Fresh	UBD+1	Fresh	UBD+1
Media: detected microbial group (log cfu/g)				
Long & Hammar: psychrotrofic bacteria	4.3 (0.3)	6.2 (0.3)	5.3 (0.8)	7.4 (1.1)
MRS: LAB	3.7 (0.4)	6.1 (0.3)	5.4 (0.7)	7.9 (0.8)
Iron: total colony counts	3.7 (0.2)	6.2 (0.2)	4.9 (0.8)	6.2 (1.0)
Iron: H_2S-producing bacteria	1.7 (1.7)	3.1 (3.0)	1.0 (1.3)	≤2
gas (%)				
O_2	1.1 (1.3)	0.9 (1.0)	0.7 (0.7)	0.4 (0.6)
CO_2	18.7 (2.2)	18.1 (2.9)	21.8 (4.4)	21.3 (2.0)
pH	6.4 (0.1)	6.4 (0.1)	6.2 (0.1)	6 (0.2)

3.3. Sensory evaluation

According to the sensory panel, all samples were fit for human consumption. The quality of the fresh samples was excellent (median of grades 5) and satisfactory (median of grades 3) on UBD+1 day. In the satisfactory samples, the odour of the unmarinated samples was described as fishy and pungent, while the marinated samples were recognised to mostly have the smell of marinade.

3.4. 16 S rRNA gene amplicon sequencing

The diversity of bacterial species was high in the fresh strips (Fig. 1). *Pseudomonas* OTUs represented over 20% of the sequence reads in the fresh samples, but after storage at 3 °C until UBD +1 day, the *Pseudomonas* proportion decreased to under 2%. *Flavobacterium, Psychrobacter* and *Shewanella* proportions were also higher in the fresh strips than in UBD +1 day strips. Instead, on UBD +1 day, lactobacilli became notable with and abundance of 33% and 23% in the unmarinated and marinated strips, respectively (Fig. 1). In addition, *Leuconostocs* dominated in the marinated strips and either lactobacilli or *Fusobacteriaceae* in the unmarinated strips, depending on the producer (Fig. 1S).

3.5. Identification of LAB by ribotyping

The results of ribotyping (Fig. 2) show that after storage, *L. fuchuensis* was the main LAB species detected in both types of rainbow trout fillet strips. Marination favoured *Leuconostoc gasicomitatum* and *Leuconostoc gelidum*, whereas *Lactococcus carnosus* was detected only in unmarinated rainbow trout fillet strips. The diversity of LAB was higher in the marinated strips (8 LAB species) than in the unmarinated ones (4 LAB species).

3.6. Tyramine production

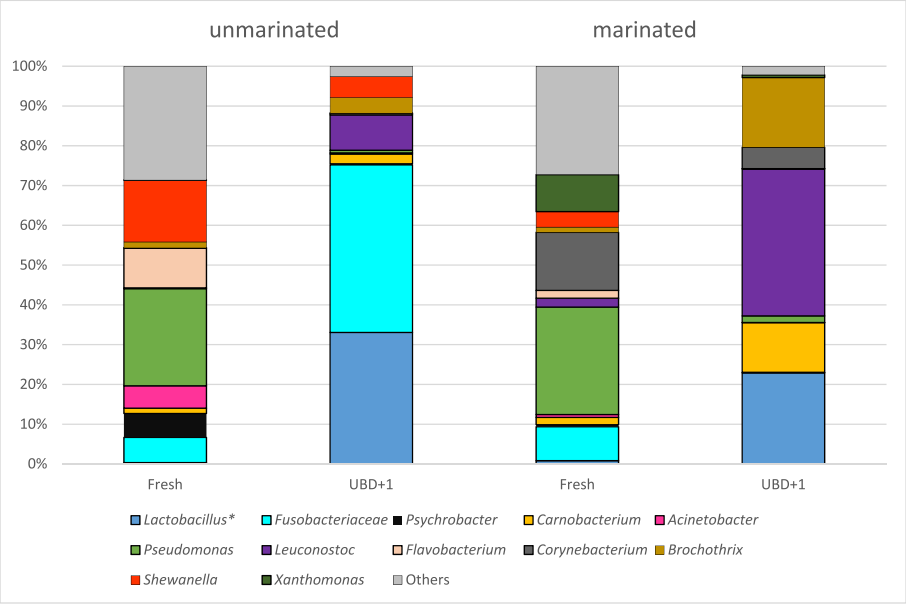
The tyrosine broth test showed 15% (3 of 20) of the tested *L. fuchuensisis* strains to be tyramine producers. One tyramine positive strain was isolated from unmarinated strips and two from marinated strips. This indicated that tyramine production is a strain-dependent feature of *L. fuchuensis* as in many other LAB.

3.7. Amines

Fig. 3 and Table 1S shows the results of amines determination using LC-MS and GC-MS. Tyramine was the most abundant biogenic amine in unmarinated and marinated rainbow trout fillet strips, with average concentrations of 5 and 25 mg/kg, respectively. Putrescine concentrations ranged from 1.5 to 5.2 mg/kg in both strip types (Table 1S). Cadaverine and spermidine concentrations were below 3 mg/kg in most of the packages. Histamine was detected in three packages of unmarinated strips (Table S1). TMA concentrations were clearly higher in unmarinated (51 mg/kg) than in marinated (2 mg/kg) strips. DMA levels were under the detection level (<1 mg/kg) in all packages.

4. Discussion

In this study, we investigated the effects of marinating on rainbow trout fillet strips. Marination increased the bacterial concentrations approximately by one log in comparison to unmarinated fillet strips (Table 1). Our results show that the effect of marination on the spoilage



* Silva 138 database is not yet updated as a reclassification of the genus *Lactobacillus*

Fig. 1. Major taxonomic groups detected in unmarinated and marinated rainbow fillet strips by 16 S rRNA gene amplicon sequence analysis at the beginning and after storage at 3 °C until UBD + one day. The figure shows the OTUs considered as genera with an incidence above 1% and average percentages above 5% are plotted. Data are expressed as the mean of 3–9 replicates of the batches.

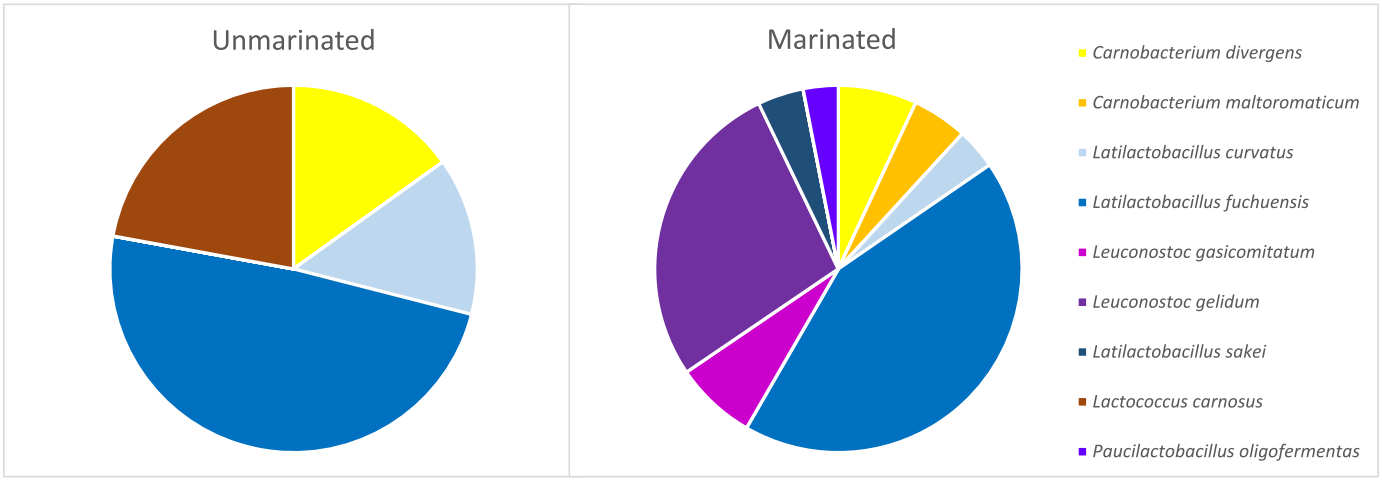


Fig. 2. Proportions of isolates (n = 252) derived from marinated and unmarinated rainbow trout fillet strips assigned to species using numerical analysis of ribotype patterns. The packages were stored at 3 °C until the use-by date (UBD) +1 day.

microbiome of rainbow trout, especially the increased LAB counts and prevailing leuconostocs, followed along the same lines as the previously described changes in meat (Vihavainen and Björkroth, 2009; Nieminen et al., 2012). In the current study, many Gram-negative bacteria, such as *Flavobacterium, Pseudomonas*, *Psychrobacter*, and *Shewanella*, were not competitive either in marinated or unmarinated MAP strips according to the 16 S rRNA gene amplicon sequence analyses (Fig. 1). However, in addition to lactobacilli, *Fusobacterium* was the dominative species in unmarinated strips. Marination increased the proportion of LAB (Fig. 1) and especially leuconostocs were more abundant in the marinated products. *Leuconostoc gasicomitatum* has been commonly detected in marinated meat products (Vihavainen and Björkroth, 2009) and it has been associated with gaseous spoilage in marinated broiler meat (Björkroth et al., 2000). Thus, the biochemical differences between fish and meat were not dramatically reflected in the species diversity detected in the marinated fish.

Amines have a significant role in the quality of the fish concerned. A major aspect in fish spoilage is the formation of TMA, causing the typical fishy odour of spoiled fish. In our study, average TMA levels in unmarinated rainbow trout fillet strips reached levels of 510 mg/100 g, which exceeds the typical point of rejection (10–15 mg/100 g) by sensory panels (Dalgaard et al., 1993). In marinated rainbow trout fillet strips, TMA levels were approximately 30 times lower. Many Gram-negative bacteria produce TMA (Gram and Huss, 2000), and in our study the higher TMA levels detected in the unmarinated strips could be due to the growth of Gram-negative bacteria. Instead, BAs were formed in marinated rainbow trout strips. The formation of a BA requires the availability of a precursor amino acid and the presence of amino acid decarboxylases from microorganisms. An important factor is also the level of activation of the decarboxylative pathway, which is affected by several physiological reasons (Barbieri et al., 2019). The formation of BAs can be a protective mechanism against acidic

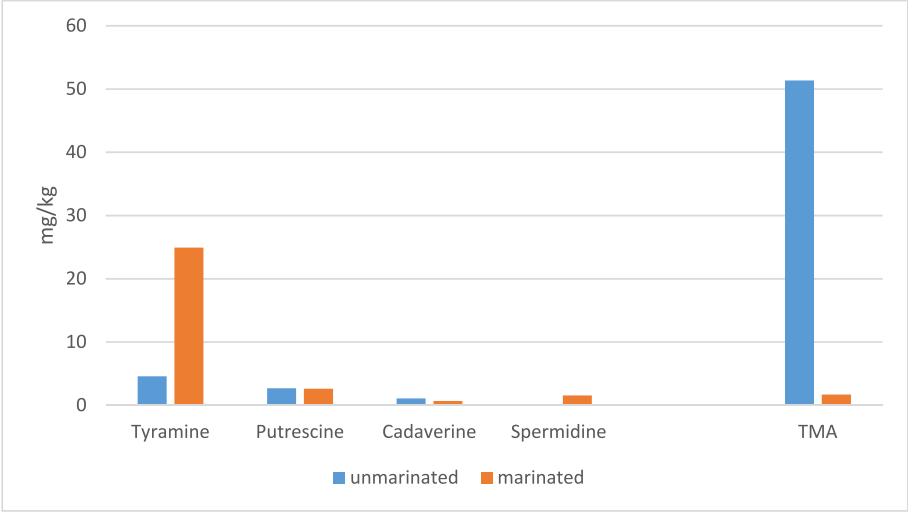


Fig. 3. Amine concentrations (mg amine/kg fish) in unmarinated and marinated rainbow trout fillet strips after storage (UBD+1) at 3 °C measured using GC-MS (DMA, TMA) and LC-MS (BA). Concentrations are the average of samples (10n and 12n of unmarinated and marinated, respectively). Variation between samples is shown in Table S1.

environments (KoesslerHankes and Sheppard, 1928), because decarboxylation of amino acids is coupled with an electrogenic antiport system and it has been shown that the transcription of many decarboxylase genes is induced by low pH (Pereira et al., 2009; Marcobal et al., 2012; Romano et al., 2012; Romano et al., 2014; Perez et al., 2015). In our study, the pH-lowering effect of marinating (Table 1) could be the reason for the higher tyramine levels in marinated rainbow strips even though the change in pH was only approximately two decimals (Fig. 3). In addition, as a consequence of the added glucose, marinating resulted in higher LAB amounts (Table 1), predominating by *L. fuchuensis* (Fig. 2), compared to the ones in the unmarinated fish. Thus, the growing LAB community had also produced organic acids likely to promote the need to upscale metabolism related to the tolerance of the acidifying environment. As such the level of glucose has not been found to play a major role in tyramine production in the related species *Latilactobacillus curvatus* (Straub et al., 1994; Bover-Cid et al., 2008).

Decarboxylase activity has been described also in Gram-positive microbial groups, such as staphylococci, *Bacillus* spp. and, especially, LAB, that are considered as the most efficient tyramine producers (Barbieri et al., 2019). The most common species/genera in marinated strips on UBD +1 day were leuconostocs, lactobacilli, *Brochothrix thermotosphacta* and *Carnobacterium*, in order of diminishing abundance according to the 16 S rRNA gene amplicon sequence analyses (Fig. 1). Decarboxylases have not been identified in the *B. thermosphacta* genomes (Stanborough et al., 2017) and only few leuconostocs (*Barbieri* et al., 2019) can form biogenic amines, whereas some *Latilactobacillus* species, like *L. curvatus* (Bover-Cid and Holzapfel, 1999; Barbieri et al., 2019) and carnobacteria are commonly known to produce tyramine from tyrosine (Curiel et al., 2011; Barbieri et al., 2019).

Tyramine production can either be species dependent, as in *Enterococcus* spp. (Leisner et al., 1994; Ladero et al., 2012), or strain dependent, as in *Latilactobacillus* (Coton and Coton 2009). In our study, *L. fuchuensis* was the predominating LAB species and tyramine the main BA detected. The capability of *L. fuchuensis* to produce tyramine had not been studied previously, but our results indicate that some strains can convert tyrosine to tyramine *in vitro*. It is therefore likely that the tyrosine we observed in the marinated strips was produced by *Latilactobacillus* and/or *Carnobacterium*.

BAs have both toxicological and spoilage implications. The toxicological level of BA varies, but a maximum total BA level of 750–900 mg/kg has been proposed (Ladero et al., 2010). The use of more than a single BA has been used as a quality indicator for fish freshness. Histamine and cadaverine concentrations were low and detected in only some samples in our study (Table S1). Chytire et al. (2004) reported that cadaverine and histamine were produced only in the late time of storage and are therefore not suitable as freshness indicators for rainbow trout. Instead, putrescine and tyramine that are commonly detected, as in our study, could be used as potential freshness indicators for rainbow trout (Chytire et al., 2004).

The acceptability range of BAs as a freshness indicator has been proposed as 15–20 μg/g (Baixas-Nogueras et al., 2005). In our study, the sum of average BAs was 8 μg/g and 30 μg/g in unmarinated and marinated rainbow strips, respectively. The levels were below toxicological implications, but the freshness level was exceeded in the marinated strips. Since marination effectively masks other odours, it could cause a quality risk for consumers.

In conclusion, our study of the microbiological quality and amine content of packaged rainbow trout fillet strips indicated that marination may enrich both the concentration of LAB and formation of tyramine, while TMA is the main potential spoilage agent in the unmarinated strips.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fm.2022.104099.

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