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Review paper

Metabolic features of *Carnobacterium* spp. relevant to food spoilage

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Summary. Members of the genus *Carnobacterium* are psychrotolerant, facultatively anaerobic lactic acid bacteria frequently isolated from refrigerated and vacuum-packed food products of animal origin. This review explores their metabolic and physiological traits that contribute to food spoilage, with a particular focus on *C. maltaromaticum* and *C. divergens*. These species are metabolically versatile, capable of fermenting various carbohydrates and producing volatile organic compounds (VOCs) such as alcohols, ketones, aldehydes, and biogenic amines, which are strongly associated with undesirable sensory changes in meat, seafood, and dairy products. Their resilience under stress conditions, including cold temperatures, elevated pH, and modified atmosphere packaging, supports their persistence in food matrices. Proteolytic and lipolytic activities further enhance their spoilage potential by degrading proteins and fats, leading to off-odor and textural deterioration. A comprehensive understanding of the metabolic pathways and spoilage mechanisms of *Carnobacterium* spp. is essential for developing effective food preservation strategies and improving shelf-life management of perishable products.

Keywords: biogenic amines, modified atmosphere packaging (MAP), psychrotolerant bacteria, refrigerated storage, vacuum-packaged foods, volatile organic compounds (VOCs).

INTRODUCTION

Carnobacterium spp. are Gram-positive, non-spore-forming, facultatively anaerobic rods, commonly found in refrigerated and vacuum-packed (VP) animal-based food products (Hammes and Hertel 2009). Genus *Carnobacterium* belongs to the lactic acid bacteria (LAB) group that consists of over 60 genera, and those most frequently associated with food fermentation besides *Carnobacterium* include *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Pediococcus*, *Streptococcus*, *Enterococcus*, and *Weissella* (Mokoena 2017). Although typically catalase- and oxidase-negative, some strains can exhibit catalase activity in the presence of heme (Ringø et al. 2002). They exhibit fermentative metabolism, are facultatively heterofermentative, and can metabolize a broad range of carbohydrates such as glucose, fructose, mannose, ribose, and sucrose, with variability among species (Kim et al. 2009). Many strains produce acids from sugars like ribose, trehalose, and galactose, and hydrolyze substrates such as arginine and esculin, contributing to their metabolic versatility (Hammes and Hertel 2009). During fermentation, they predominantly produce L(+)-lactate, while C. pleistocenium also generates ethanol, acetic acid, and CO_2. These bacteria are psychrotolerant, able to grow at or below 0 °C, and are also halotolerant (up to 8% NaCl) and alkaliphilic, tolerating pH levels up to 9.5 (Cailliez-Grimal et al. 2014; Pikuta and Hoover 2014). Such environmental adaptability makes them particularly relevant in the spoilage of foods stored under refrigeration and VP. *C. divergens* and *C. maltaromaticum* are especially associated with meat and fish spoilage, due to their ability to grow under

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anaerobic, low-temperature, and mildly acidic-to-neutral pH conditions (5.4–6.1). Under these storage conditions, they become dominant members of the microbiota and contribute significantly to sensory degradation.

Comparative genomics revealed a high genetic diversity within the genus *Carnobacterium*, with genome sizes ranging from 2.4 to 3.6 Mb. The presence of genes involved in bacteriocin production, adaptation to cold environments, and utilization of diverse carbohydrates underlines the ecological versatility of these species. Importantly, several *Carnobacterium* genomes harbor genes encoding a V-type ATPase, which is believed to contribute to survival under cold and alkaline conditions, further supporting their dual role as potential bioprotective cultures in food and opportunistic pathogens in fish (Roh and Kim 2021).

Although typically associated with food, some strains have been reported to cause mixed infections in stressed fish and have also been isolated from human clinical samples, including pus and blood (Collins et al. 1987; Chmelař et al. 2002).

Their metabolic activity is linked to the production of volatile organic compounds (VOCs) such as 2-methylpropanal, 3-methylpropanal, 2-methylpropanol, and 3-methylpropanol, which impart a malty or spoiled aroma (Miller et al. 1974). Additionally, *Carnobacterium* spp. show a strong correlation with TVB-N (total volatile basic nitrogen) and TBARS (thiobarbituric acid-reactive substances), and a negative correlation with sensory indices like appearance, texture, and odor, further highlighting their role in food spoilage. Some species also show chitinolytic activity and the ability to utilize inulin, starch, and glycogen, supporting their adaptation and persistence in food matrices (Leisner et al. 2007; Hammes and Hertel 2009).

The aim of this review is to summarize and critically discuss the key metabolic characteristics of *Carnobacterium* species that contribute to their role in the spoilage of refrigerated and VP food products, with a focus on their fermentative pathways, production of volatile organic compounds (VOCs) (Table 1), proteolytic and lipolytic activities, and environmental adaptability.

CARNOBACTERIUM AND FOOD SAFETY

Carnobacterium species have been widely detected in a variety of processed meat and seafood products, raising concerns about their role in food spoilage and contamination. These lactic acid bacteria (LAB) are frequently associated with spoilage of cooked and cured meats, particularly terminal spoilage, and their ability to grow at refrigeration temperatures significantly impacts food safety (Samelis et al. 2006; Chenoll et al. 2007). Despite the use of food additives like ascorbic, lactic, acetic, citric, sorbic, and benzoic acids, as well as $NaNO_2$ and smoke-derived phenols, *Carnobacterium* species continue to thrive in these environments (Jørgensen et al. 2000; Dalgaard et al. 2003; Lakshmanan and Dalgaard 2004).

***Carnobacterium* spp. presence in meat products**

Carnobacterium spp. have been widely detected in processed meats, including bacon (Shaw and Harding 1984), ham (Borch and Molin 1988; Jack et al. 1996), cooked poultry (Barakat et al. 2000), pressure-treated chicken (O'Brien and Marshall 1996), processed pork and chicken (Grant and Patterson 1991). Notably, *C. maltaromaticum* has also been detected in fermented sausages (Schillinger and Lücke 1987; Larrouture-Thiveyrat and Montel 2003), which contrasts with the typical nonaciduric environments associated with carnobacteria (Hammes and Hertel 2006). *Carnobacterium maltaromaticum* and *C. divergens* are frequently isolated from meat products stored between −1.5 °C and 2 °C, dominating microbial populations in beef, pork, lamb, and poultry. These species may comprise up to 50% of Gram-positive or LAB isolates (McMullen and Stiles 1993; Sakala et al. 2002; Jones 2004). Their prevalence is consistent across VP, aerobically stored, and modified-atmosphere packaged (MAP) meats with CO_2/N_2 ratios ranging from 10:90 to 80:20 (Shaw and Harding 1984; Grant and Patterson 1991; McMullen and Stiles 1993; Barakat et al. 2000; Sakala et al. 2002; Susiluoto et al. 2003; Jones 2004; Björkroth 2005; Laursen et al. 2005; Vihavainen et al. 2007). Other species, including *C. gallinarium* (Thornley 1957; Collins et al. 1987), *C. mobile* (Chenoll et al. 2007), and *C. viridans* (Holley et al. 2002), have also been isolated from a variety of meat products.

Psychrotrophic bacteria like *Carnobacterium* spp. can thrive at chilled temperatures, especially during carcass cutting. The primary source of contamination appears to be meat processing environments, rather than the slaughtered animals themselves. Unlike many other spoilage bacteria, *Carnobacterium* spp. have not been isolated from the gastrointestinal tract or skin of livestock such as chicken, cattle, pigs, or sheep, suggesting that processing environments are the primary source of contamination. Findings in the literature vary regarding the effectiveness of processing in eliminating *Carnobacterium* spp. For example, *C. divergens* and *C. maltaromaticum* detected on broiler carcasses were linked to airborne contamination within processing plants rather than the incoming poultry (Vihavainen et al. 2007). In contrast, other studies have reported that appropriate processing procedures can markedly reduce or even eliminate these species from raw materials (Samelis et al. 1998), indicating that the outcome depends strongly on the specific processing conditions and hygiene practices employed. Molecular techniques such as 16S rRNA gene sequencing have deepened our understanding of *Carnobacterium* presence along the pork and poultry production chains (Poirier et al. 2020).

Identical ERIC-PCR profiles of *Carnobacterium* detected in environmental samples, sheep pelts, and lamb carcasses suggest potential cross-contamination routes during processing (Mills et al. 2014). Partial 16S rRNA gene sequencing has revealed the complexity of raw beef microbiota, with *Carnobacterium* present alongside *Acinetobacter*, *Bacillus*, *Janthinobacterium*, *Lactobacillus*, *Pseudomonas*, *Psychrobacter*, and *Stenotrophomonas* (Aquilanti et al. 2016; Callahan et al. 2017; Choi et al. 2020; Yang et al. 2020). Studies on cooked ham have shown that species such as *B. thermosphacta*, *C. divergens*, *C. maltaromaticum*, *L. carnosum*, *L. gelidum*, *L. mesenteroides*, and *S. proteamaculans* persist at the end of processing, with *Brochothrix, Carnobacterium*, *Lactobacillus*, *Leuconostoc*, *Vibrio*, and *Weissella* dominating at the end of shelf life (Van Reckem et al. 2020).

Presence in dairy products

Raw milk contains a diverse microbial community that includes both beneficial bacteria with technological applications, such as lactic acid bacteria, and harmful spoilage organisms (Ercolini et al. 2009). The nutrient-rich composition and near-neutral pH of raw milk create ideal conditions for microbial proliferation. Contamination can occur through multiple pathways, including farm environments, animal feed, bedding materials, udder surfaces, and milking equipment (Von Neubeck et al. 2015; Islam et al. 2018). Initially, milk collected aseptically from heifer udders contains no bacteria, but this changes as milking frequency increases. The bacterial composition on teat skin reflects the surrounding farm environment and can be influenced by bedding materials, which are affected by feeding and housing practices. Feed sources vary in their microbial content depending on pasture conditions, supporting the growth of bacteria, yeasts, and molds. Additionally, stable dust and inadequate milking hygiene contribute to microbial contamination of teat surfaces (Frétin et al. 2018). The level of bacterial contamination in raw cow milk is determined by several interconnected factors: animal health and cleanliness, stable sanitation, pre-milking udder preparation procedures, milking techniques, proper cleaning and disinfection of milking equipment and storage tanks, appropriate milk cooling and storage practices, and personnel hygiene standards (Cempírková 2007). Dairy products, particularly cheese, represent significant reservoirs of carnobacteria. *Lactobacillus maltaromicus*, later reclassified as *Carnobacterium maltaromaticum*, was initially described by Miller et al. (1974) following its isolation from milk samples characterized by a distinct malty aroma. Among 30 French soft-ripened and red-smear cheeses made from cow, ewe, or goat milk, either raw or pasteurized, *C. maltaromaticum* was found in 10 samples, with isolates from three of them showing anti-*Listeria* activity (Cailliez-Grimal et al. 2007). In these cheeses, *C. maltaromaticum* was the predominant psychrotrophic lactic acid bacterium. It was capable of growing even under alkaline pH conditions, reaching high concentrations (10^8 to 10^9 CFU/g) during subsequent cold storage at 4 °C (Cailliez-Grimal et al. 2007). This species may also act as a potential ripening microorganism in soft cheeses (Edima 2007).

Presence in seafood

Carnobacterium spp. are also emerging as important seafood spoilage bacteria (Jaffrès et al. 2009; Noseda et al. 2012). They have been shown to dominate the microbiota of peeled brown shrimp stored at 4 °C by day 7 (Calliauw et al. 2016) and rapidly spoil cooked tropical shrimp (Macé et al. 2014). *Carnobacterium maltaromaticum* represents a significant spoilage microorganism in seafood products, particularly shrimp, with its spoilage potential being highly dependent on storage conditions and packaging methods. *Carnobacterium maltoaromaticum* demonstrates the ability to produce off-odor compounds in shrimp (Dabadé et al. 2015) and generates volatile compounds such as ammonia and other TVB-N compounds that contribute to spoilage in both cooked cold-water shrimp (*Pandalus borealis*) and tropical shrimp species (Laursen et al. 2005; Jaffrès et al. 2011; Macé et al. 2014). The spoilage activity of *C. maltaromaticum* exhibits temperature-dependent characteristics, with studies showing that while *Pseudomonas psychrophila* produces significantly higher amounts of TVB-N and demonstrates faster growth rates at temperatures ranging from 0 to 15 °C, *C. maltaromaticum* exhibits superior growth rates at elevated temperatures such as 28 °C. The competitive advantage of *C. maltaromaticum* becomes particularly pronounced under oxygen-limited conditions due to its high resistance to CO_2 and anaerobic environments (Alfaro and Hernandez 2013), allowing it to outcompete aerobic spoilage bacteria in MAP or VP systems. However, in air-stored products, its spoilage impact is diminished in the presence of more active aerobic spoilers such as *Pseudomonas* sp. This packaging-dependent spoilage behavior has been demonstrated in comparative studies, where *C. maltaromaticum* showed reduced spoilage activity compared to *Pseudomonas fragi* in air-stored meat products (Ercolini et al. 2010; Casaburi et al. 2011), while emerging as the dominant spoiler in modified atmosphere packaged cooked tropical shrimp compared to other bacterial species (Macé et al. 2014). Both Laursen et al. (2005) and Noseda et al. (2012) concluded that right before the expiration date of MAP seafood, the predominant microorganisms isolated were Gram-positive bacteria, specifically *C. maltaromaticum*, *C. divergens*, and *B. thermosphacta*. A multiplex real-time quantitative PCR (qPCR) method was developed and validated for the specific detection and quantification of

C. maltaromaticum and *C. divergens* in cold-smoked salmon. This assay enables rapid and accurate monitoring of these species in seafood products, offering an efficient alternative to conventional culture-dependent techniques (Le Rhun et al. 2021).

Presence in other foods

In a study investigating bacterial eggshell penetration and whole egg contamination, *Carnobacterium* sp. was among seven bacterial strains tested for their ability to invade and persist within eggs. Using both an agar-filled egg model and intact eggs, *Carnobacterium* was shown to penetrate eggshells and survive within whole eggs, achieving a 17.5% contamination rate, second only to *Salmonella enteritidis* (De Reu et al. 2006). *Carnobacterium divergens* MB421, isolated from fermented green olives, exhibited strong probiotic characteristics, including tolerance to bile salts (up to 1%), gastric juice (pH 2.2), and salt concentrations up to 7%. It showed antimicrobial activity against several pathogenic bacteria and was capable of fermenting various carbohydrates and producing significant amounts of organic acids. These properties suggest its potential use as a starter culture in fermented foods and as a viable probiotic candidate (Saeed et al. 2023). In the study investigating LAB in flour-based fermentations, *Carnobacterium* spp. was identified among the isolates from wheat flour dough. These findings demonstrate that wheat flour supports a more diverse LAB community, including *Carnobacterium*, which may contribute to the fermentation process and affect the dough's biochemical properties, such as acidification and antimicrobial activity (Kleib et al. 2023).

ROLE OF *CARNOBACTERIUM* SPP. IN FOOD SPOILAGE

Meat spoilage is a complex and multifaceted process driven by a combination of chemical and biological factors, resulting in the deterioration of meat to a state unfit for human consumption (Gram et al. 2002). The nutrient-rich composition of meat, its favorable pH (5.5–6.5), and high moisture content create an ideal environment for microbial growth. Spoilage is not solely the result of lipid oxidation or enzymatic reactions but is heavily influenced by microbial activity (Nychas et al. 2007, 2008; Doulgeraki et al. 2012). Key contributors to spoilage include microbial species selected under specific environmental and storage conditions. Factors such as the animal's physiological state at slaughter, processing, transportation, preservation, and storage conditions significantly influence the microbial quality of raw meat (Nychas et al. 2008). Packaging and temperature are particularly critical, refrigeration favors psychrotrophic microorganisms, and the presence or absence of oxygen influences microbial dynamics and spoilage potential (Nychas et al. 2007, 2008; Doulgeraki et al. 2012). A limited number of microbial species are primarily responsible for spoilage. These include both Gram-positive and Gram-negative bacteria, which, through aerobic or anaerobic metabolism, produce spoilage compounds such as esters, ketones, aldehydes, sulfur compounds, amines, and volatile fatty acids (Dainty et al. 1985; Lambert et al. 1991; Kakouri and Nychas 1994).

Among the dominant spoilage organisms are LAB, notably *Carnobacterium* spp., which frequently prevail in VP and MAP meat and seafood (Leisner et al. 2007). LAB, including *Carnobacterium*, are often involved in the terminal spoilage of cooked and cured meats (Samelis et al. 2006; Chenoll et al. 2007). These bacteria are psychrotrophic, capable of surviving and proliferating at low temperatures, and have been implicated in the spoilage of refrigerated chicken under aerobic conditions (Liang et al. 2012), raw salmon in MAP (Macé et al. 2013), and cooked shrimp, producing off-odors such as cheese/feet, or fermented smells (Jaffrès et al. 2011). In MAP poultry products, spoilage is largely attributed to Gram-positive bacteria like *B. thermosphacta* and LAB, including *Carnobacterium*, *Lactococcus*, *Lactobacillus*, and *Leuconostoc* (Barakat et al. 2000; Koort et al. 2005; Säde et al. 2013). Environmental and packaging factors significantly affect microbial selection: for instance, *C. divergens* is suppressed in MAP with high O_2 (20–40%) and 40% CO_2, while it thrives under aerobic storage (Ercolini et al. 2011). The growth of *C. funditum* is similarly inhibited by oxygen (Franzmann et al. 1991). Seasonal factors further influence the prevalence of *Carnobacterium*. In warm climates, mesophilic LAB such as *Carnobacterium* spp., *L. sakei*, *L. curvatus*, and *Weissella* spp. are more frequently associated with spoilage (Ercolini et al. 2009, 2011; Doulgeraki et al. 2010, 2012). *Carnobacterium* was found to dominate beef samples collected in July (Hwang et al. 2020).

Brochothrix thermosphacta and *Carnobacterium* spp. exhibit moderate tuna fish spoilage potential, characterized by the production of butter/caramel-like odors (Silbande et al. 2018). Some *C. maltaromaticum* strains have been implicated in spoilage phenomena, such as textural degradation of salmon fillets (Morzel et al. 1997). The expression of spoilage traits is further influenced by environmental factors. For instance, essential oils have exhibited antimicrobial effects against several spoilage-associated species, including *L. sakei*, *L. curvatus*, *C. maltaromaticum*, *B. thermosphacta*, *P. fluorescens*, and *Serratia liquefaciens* (Ouattara et al. 1997). Notably, oregano essential oil has been shown to modulate glucose metabolism pathways in lactic acid bacteria, thereby altering the production of spoilage-related metabolites (Nychas et al. 1998; Skandamis and Nychas 2001).

Among dairy products, surface mold-ripened soft cheeses made from unpasteurized milk, such as Brie, have been shown to support substantial microbial growth. The relatively high surface pH of Brie cheese (pH 6.8–7.6) facilitates the proliferation of these bacteria, with populations reaching concentrations of 10^8 to 10^9 CFU/g. Furthermore, *C. divergens* and *C. maltaromaticum* are prominent members of the LAB community present in the curd of mozzarella cheese produced using unpasteurized milk (Morea et al. 1999). Lipolytic or proteolytic activity is observed at low temperatures in several genera present in minor abundance, including *Arthrobacter* spp. and *Carnobacterium* spp. In a study by Vithanage et al. (2014) examining the extracellular protease activity of psychrotrophic bacterial populations in raw milk, approximately half of the bacterial isolates demonstrated proteolytic capabilities. Isolates of *Carnobacterium* consistently produced biofilms at 10 °C or 4 °C making them the most prevalent bacteria among high total bacterial count raw milk samples and this confirms elevated bacterial counts can result from biofilms and poor hygiene in the milk processing environment (Hahne et al. 2019).

Carnobacterium spp. are widely studied for their potential as bioprotective cultures, valued for their ability to enhance shelf life without negatively impacting sensory qualities. Among them, *C. maltaromaticum* strains KOPRI 25789 and MMF-32 have demonstrated notable antimicrobial activity, primarily through bacteriocin production, effectively inhibiting *Listeria monocytogenes* and various Gram-negative bacteria in cold-smoked salmon (Darbandi et al. 2021). However, antimicrobial efficacy is not solely dependent on bacteriocin synthesis, as both bacteriocin-producing and non-producing strains have shown inhibitory capabilities (Nilsson et al. 1999). Bacteria of this genus exhibit three key bioprotective mechanisms: competition, exclusion, and displacement. Their ability to produce antimicrobial substances, secrete enzymes, and express adhesion proteins on the cell surface enables carnobacteria to inhibit pathogenic and opportunistic bacteria. Genomic features are central to this activity, as an extensive secretome and proteome equip carnobacteria to quickly colonize niches and outcompete other microorganisms (Leisner et al. 2007).

Carnobacterium species exhibit antimicrobial properties against various foodborne pathogens and spoilage microorganisms, including *Listeria* (Danielski et al. 2022), *Salmonella* (Hu et al. 2019), *Serratia* spp., *Pseudomonas* spp. (Zhang et al. 2019), *Campylobacter* spp. (Smialek et al. 2018), *Pseudomonas fluorescens*, *Brochothrix thermosphacta* (Cavalari et al. 2019), and *Enterobacteriaceae* (Imazaki et al. 2014) across seafood, meat, and dairy applications. These characteristics demonstrate *Carnobacterium*'s capacity to enhance food safety measures (Koutsoumanis et al. 2021). Additionally, *Carnobacterium* shows promise for use in plant-based food systems (Agriopoulou et al. 2020), and plant-based food items (Geeraerts et al. 2020). Research conducted by González-Gragera et al. (2024) highlights the significant promise of integrating piscicolin CM22, a newly identified bacteriocin produced by a cold-tolerant *C. maltaromaticum* strain, into edible coatings (ECs) made from chitosan and fish gelatin to improve the quality and safety of fish products. The results show that these ECs notably enhanced microbiological properties and prolonged the storage life of fresh fish maintained at both 4 °C and 8 °C temperatures. Furthermore, chitosan-derived ECs provided pH stabilization and improved color preservation, thus maintaining the sensory and functional characteristics of the fish products.

METABOLIC PROCESSES AND PRODUCTS OF *CARNOBACTERIUM* SPP. DURING MEAT SPOILAGE

Metabolic processes

In contrast to the extensive metabolic knowledge accumulated for lactococci and lactobacilli in recent years, metabolism of *Carnobacterium* spp. remains relatively understudied. These bacteria demonstrate strong aerobic growth capabilities, with *C. maltaromaticus* showing a 10-fold increase in growth yield when heme is supplemented to aerobically cultured cells (Meisel et al. 1994). Under these conditions, functional cytochromes of both b and d types become detectable, similar to the cytochrome induction observed in lactococci and enterococci (Sijpesteijn 1970; Ritchey and Seely 1976). The presence of *cydAB* genes encoding cytochrome oxidase (bd) in *Lactococcus lactis* (Gaudu et al. 2002) suggests that when heme is accessible, *C. maltaromaticum* possesses respiratory metabolic potential and displays catalase activity. This catalase property is shared among all *Carnobacterium* species (Ringø et al. 2002), with the exception of *C. pleistocenium*, which has not been examined for this characteristic. Respiratory metabolism correlates with enhanced oxygen consumption, decreased lactate production, and elevated acetoin and CO_2 generation.

Understanding gene expression under different atmospheric conditions provides insight into microbial metabolic adaptations. Although no significant differential expression of genes related to general metabolic pathways was detected by metatranscriptomic analysis under MAP conditions, including CO_2/O_2 and CO_2/N_2 environments, specific stress responses were observed. For instance, genes encoding superoxide dismutase and organic hydrogen peroxide resistance proteins were upregulated under CO_2/O_2 conditions, suggesting a cellular response to oxidative stress (Madamanchi and Runge 2007; Li et al. 2013). Despite the lack of significant transcriptomic changes, metabolic activity remained evident across both atmospheric environments. The most abundantly expressed proteins belonged to enzymes involved in glycolysis, indicating a strong glycolytic flux. Previous research has shown that *C. divergens* is homofermentative, as it lacks phosphoketolase, an essential enzyme for heterolactic fermentation (Höll et al. 2020). Nevertheless, transcriptomic data indicate that pyruvate-derived metabolic byproducts such as ethanol (via ethanol dehydrogenase), acetate (via acetate kinase), formate (via formate acetyltransferase), and CO_2 (via pyruvate dehydrogenase) are produced under both CO_2/O_2 and CO_2/N_2 conditions. This suggests a metabolic flexibility, with the production of compounds typically associated with heterofermentative pathways even in the absence of phosphoketolase. Prior studies have indicated that growth conditions and pyruvate availability influence metabolite formation (Bartowsky and Henschke 2004), and aerobic conditions in particular have been shown to enhance these metabolic processes, notably in *C. maltaromaticum* (Casaburi et al. 2011). Carnobacteria exhibit facultatively heterofermentative carbohydrate metabolism, fermenting both hexoses and pentoses. Excluding *C. pleistocenium*, hexoses are converted to L(+)-lactate, while also producing CO_2, acetate, and ethanol. Furthermore, formate is produced under anaerobic conditions (Borch and Molin 1989) and acetoin under aerobic conditions. Pentose metabolism yields L(+)-lactate, acetate, and ethanol (Holzapfel and Gerber 1983). Glucose processing occurs through the glycolytic pathway (De Bruyn et al. 1987, 1988). In Group I species, approximately 75% of lactate production is derived from glucose, with less than 10% originating from formate and acetate, while the remaining products presumably stem from endogenous substrates in nutrient-rich media (Hammes and Hertel 2009). Group II species show distinct patterns, with *C. pleistocenium* producing ethanol, acetate, and CO_2 without lactate formation from carbohydrate fermentation. This metabolic profile excludes this species from the physiological definition of lactic acid bacteria, suggesting metabolism resembling the Embden-Meyerhof pathway in yeast. Similarly, *C. funditum* and *C. alterfunditum* do not generate lactate from glycerol, producing exclusively formate, ethanol, and acetate. Certain species or strains demonstrate polysaccharide hydrolysis and fermentation capabilities. Inulin utilization occurs in *C. divergens*, *C. gallinarum*, and specific *C. maltaromaticum* strains. Amylolytic activity is documented through starch utilization in *C. pleistocenium* and glycogen utilization in *C. mobile* and *C. gallinarum*. The presence of starch in plant materials and subsequently in fish intestinal tracts may reflect adaptation of *Carnobacterium* to that ecological niche (Hammes and Hertel 2009). *C. maltaromaticum* utilizes two distinct pathways for lactose and galactose metabolism: the Tagatose-6-phosphate (Tagatose-6P) pathway and the Leloir pathway. Some strains possess genes encoding one or both pathways, while others lack these genes entirely. The Tagatose-6P pathway is typically encoded by the *lac* gene cluster (e.g., *lacA-G*), and is involved in the phosphoenolpyruvate phosphotransferase system (PTS)-mediated uptake and phosphorylation of lactose or galactose, followed by enzymatic degradation. The Leloir pathway, on the other hand, includes genes like *galK*, *galT*, *galE*, and *galM*, which sequentially convert galactose into glucose-6-phosphate (Iskandar et al. 2016). Genomic comparisons across multiple *C. maltaromaticum* strains showed that these metabolic genes are variably located on chromosomes and megaplasmids, and often exhibit signs of horizontal gene transfer, duplication, and genomic rearrangement. In particular, the *C. maltoaromaticum* exhibits the highest intraspecific heterogeneity among the LAB analyzed, a finding that correlates with its previously reported high genetic diversity (Rahman et al. 2014). These findings suggest that the evolutionary adaptation of lactose metabolism in *C. maltaromaticum* has been shaped by environmental pressures, particularly in dairy environments, where lactose is a primary carbon source (Iskandar et al. 2016).

These bacteria also possess the ability to degrade proteins. Genomic analysis has revealed that *C. maltaromaticum* and *C. divergens* possess conserved oligopeptide transporter systems (OppABCDF, DtpT) and intracellular peptidases, enabling them to efficiently import and degrade peptides derived from food proteins (Dallagnol et al. 2021). Experimental studies on *C. maltaromaticum* strains growing in raw fish protein extracts showed significant degradation of soluble proteins (up to ~137 mg/100 mL) and accumulation of free amino acids, confirming their active proteolysis during spoilage. This enhances their capacity to generate free amino acids that can be further converted into spoilage metabolites. Carnobacteria exhibited moderate degradation of fish sarcoplasmic proteins (≤73%), leading to the release of small peptides and free amino acids, with alanine, glycine, asparagine, and arginine showing the greatest increases in concentration (Dallagnol et al. 2021). Recent genomic analyses have revealed that *C. maltaromaticum* and *C. divergens* possess homologs of PrtB, a cell envelope-associated protease (CEP) commonly associated with dairy lactic acid bacteria such as *Lactobacillus delbrueckii subsp. bulgaricus (Iskandar et al. 2017)*. These proteases enable the extracellular degradation of proteins into peptides, which are subsequently internalized via oligopeptide transport systems (OppABCDF and DtpT) and hydrolyzed further by intracellular peptidases. This proteolytic system appears to be conserved in *C. maltaromaticum* and *C. divergens*, but not in all *Carnobacterium* strains, suggesting a selective advantage in protein-rich environments such as meat, fish, and dairy products. The ability to exploit environmental proteins for amino acid acquisition likely contributes to their success in refrigerated foods and plays a critical role in spoilage through the release of volatile nitrogenous compounds, off-odors, and degradation of texture and sensory quality. Arginine hydrolysis provides an additional source of adenosine triphosphate (ATP), and most members of the genus *Carnobacterium* are capable of it, though it is absent in *C. viridans* and *C. maltaromaticum* (Laursen et al. 2005). In addition, genes associated with the arginine deaminase pathway are expressed. This pathway contributes to energy generation via substrate-level phosphorylation and plays a role in microenvironmental pH regulation, further supporting adaptation to varying environmental conditions (Höll et al. 2020). These findings emphasize the metabolic versatility of *Carnobacterium* spp., especially *C. divergens*, under MAP, and highlight how specific metabolic routes help sustain cellular function and adaptation under stress.

Carnobacteria also produce lipases, which are considered secondary spoilage factors. This activity has been observed on olive oil/Tween-80 agar at both 20 °C and 4 °C, indicating their ability to break down fats, generate flavor compounds, and contribute to rancidity (Casaburi et al. 2011). Also, it has been reported that they are able to hydrolyze tributyrin, indicating lipolytic activity (Papon and Talon 1988). *Carnobacterium divergens* and *C. maltaromaticum* did not inhibit the oxidation of linoleic acid during growth (Talon et al. 2000), suggesting that these species are unlikely to protect meat products from quality deterioration caused by lipid oxidation.

Carnobacterium spp. do not produce DNases or RNases and no nuclease activity has been associated with them (Palevich et al. 2024). Some species, such as *C. viridans* and *C. divergens*, produce hydrogen peroxide, which reacts with myoglobin in VP cooked cured Bologna sausage, causing an undesirable green discoloration (Borch and Molin 1989; Holley et al. 2002; Peirson et al. 2003). Despite this, the specific enzymes responsible for hydrogen peroxide production remain unidentified (Remenant et al. 2015) (Fig. 1).

Metabolic products

Fresh raw meat is characterized by a distinctive sensory profile, including a bloody, metallic, and salty taste and an aroma similar to blood serum (Joo and Kim 2011). These attributes are largely driven by VOCs, which contribute significantly to meat aroma due to their high vapor pressures at room temperature (Carter 2010). VOCs encompass a broad range of chemical classes—fatty acids, hydrocarbons, aldehydes, ketones, alcohols, esters, benzenoids, terpenoids, and various nitrogen- and sulfur-containing compounds (Estévez et al. 2003; Rivas-Cañedo et al. 2009). In addition to being key contributors to aroma, some VOCs can serve as species-specific markers in meat (Rødbotten et al. 2004; Wood et al. 2004; Rota and Schieberle 2006). Sensory evaluations have further expanded the olfactory descriptors associated with raw meat (Ercolini et al. 2010; Casaburi et al. 2011; La Storia et al. 2012). *Carnobacterium* spp. are known contributors to VOC production during chilled storage under aerobic, VP, or MAP conditions. These bacteria synthesize alcohols via metabolic routes including amino acid catabolism, proteolysis, aldehyde reduction from lipid oxidation, and methyl ketone

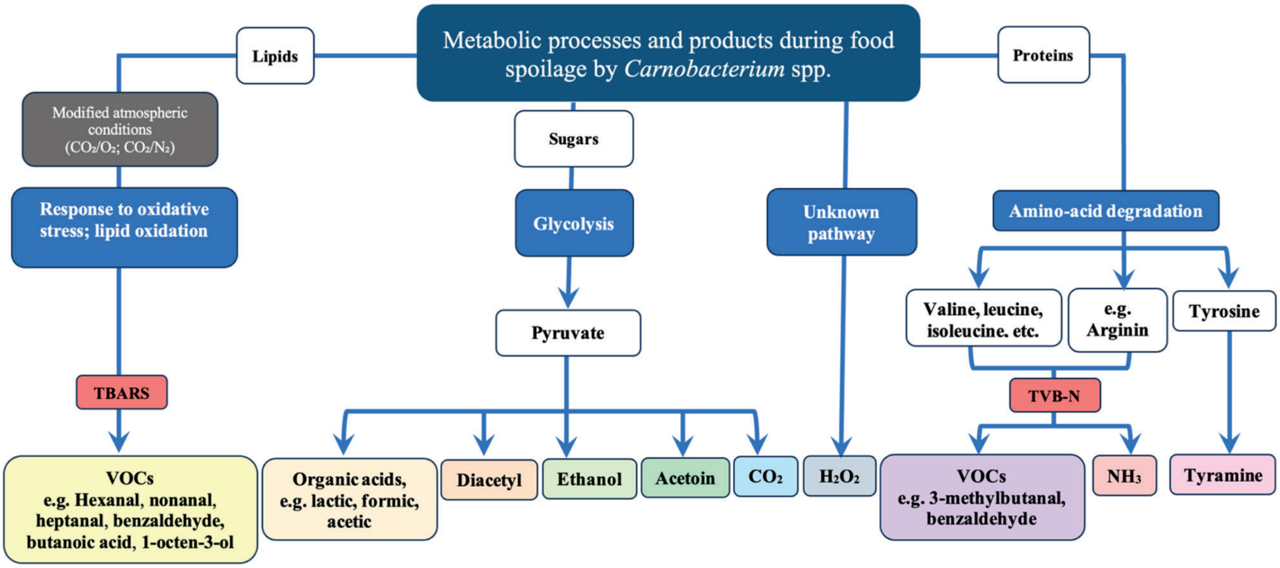
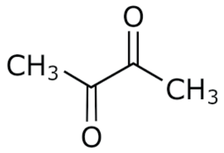
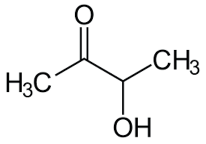
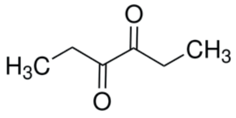
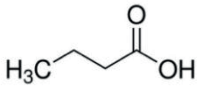
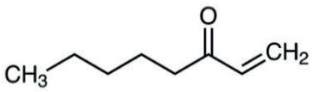
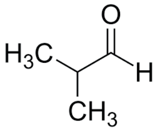
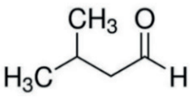
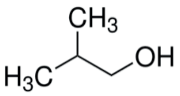
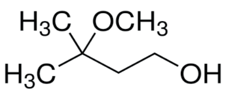
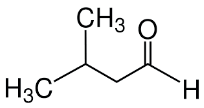
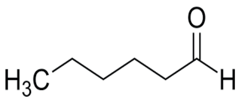
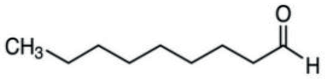
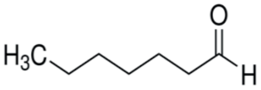
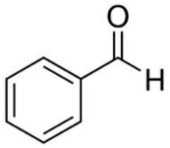
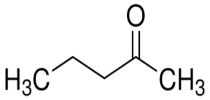
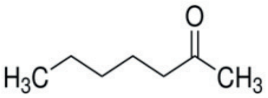
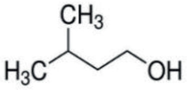
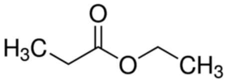
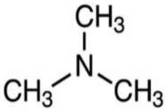
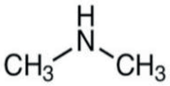


Fig. 1. Metabolic processes and products during food spoilage by *Carnobacterium* spp. (TBARS – thiobarbituric acid-reactive substances; VOCs – volatile organic compounds: TVB-N – total volatile basic nitrogen).

Table 1. Volatile organic compounds produced by *Carnobacterium* spp.

Volatile organic compound (VOC)		Characteristic smell	Common Food Sources	References
Diacetyl (2,3-butanedione)		Buttery, popcorn-like, creamy	Butter, cheese, spoiled meat/fish	Joffraud et al. 2001
Acetoin (3-hydroxy-2-butanone)		Mildly buttery, creamy	Dairy, spoiled meat	Dainty et al. 1989
2,3-Pentanedione		Caramel-like	Smoked or cooked meat	Odeyemi et al. 2018
Butanoic acid		Rancid butter, sweaty, sour milk	Spoiled dairy or meat	Jones 2004
1-Octen-3-ol		Mushroom-like, earthy	Meats, dairy, spoiled fish	Leisner et al. 1995
2-methylpropanal		Sharp, bitter, slightly fruity (aldehydic)	Beer (as an off-flavor), fermented dairy, aged cheese, oxidized fats	Miller et al. 1974
3-methylpropanal		Sweet, nutty, fruity, slightly cheesy	Fermented foods, ripened cheese, cured meats, wine	Miller et al. 1974
2-methylpropanol		Sharp, alcoholic, mildly fruity	Beer, wine, fermented fruits, sourdough	Miller et al. 1974
3-methylpropanol		Cheesy, fruity, alcoholic	Aged cheese, fermented soy, beer, sour milk	Miller et al. 1974
3-methylbutanal		Malty, nutty, cheesy, fruity	Aged cheese, fermented meats, beer, chocolate	Ramírez and Cava 2007
hexanal		Green, grassy, fatty, rancid in high concentrations	Fresh meats, dairy, oxidized fats, vegetables	Ramírez and Cava 2007

Volatile organic compound (VOC)		Characteristic smell	Common Food Sources	References
nonanal		Floral, citrus-like, fatty	Cooked meats, dairy products, fruits, vegetable oils	Ramírez and Cava 2007
heptanal		Fatty, oily, green, citrus	Animal fats, dairy, roasted meat, nuts	Ramírez and Cava 2007
benzaldehyde		Almond-like, nutty, sweet	Almonds, cherries, apricot kernels, some dairy products	Muriel et al. 2004
2-pentanone		Sweet, fruity, solvent-like	Cooked meat, cheese, some fruits	Tan et al. 2020
2-heptanone		Fruity, banana-like, blue cheese	Blue cheese, ripened cheeses, cooked meats, some fruits	Tan et al. 2020
isopentyl alcohol		Alcoholic, banana, fuel oil	Fermented beverages, cheeses, soy sauce, overripe fruits	Tan et al. 2020
ethyl propanoate		Fruity, pineapple, rum	Pineapple, strawberries, fermented dairy, baked goods	Tan et al. 2020
trimethylamine		Fishy, ammonia-like	Spoiled fish, seafood, some cheeses	Prabhakar et al. 2021
dimethylamine		Fishy, ammoniacal, unpleasant	Spoiled meats, fish, fermented protein-rich foods, aged cheeses, meat extracts	Prabhakar et al. 2021

reduction (García et al. 1991; Borch et al. 1996; Beck et al. 2004). For example, *C. maltaromaticum* produces 2,3-butanedione (diacetyl) and 2,3-pentanedione, which contribute buttery aromas to cold-smoked salmon (Joffraud et al. 2001; Odeyemi et al. 2018). The genus also generates aldehydes such as 3-methylbutanal, hexanal, nonanal, heptanal, and benzaldehyde, all of which are associated with spoilage due to their low odor thresholds (Muriel et al. 2004; Ramírez and Cava 2007). Afzal et al. (2012) described two biosynthetic routes for 3-methylbutanal production in *C. maltaromaticum* LMA 28: a direct route via α-ketoacid decarboxylase (KADC) and an indirect oxidative route via α-ketoacid dehydrogenase (KADH), both confirmed through enzymatic assays and genetic analysis. The partial reduction in 3-methylbutanal upon KADH inhibition indicates both pathways function *in vivo*, highlighting the strain's metabolic adaptability and its role in cheese aroma development. Ketones such as acetoin (3-hydroxy-2-butanone) are also significant metabolites produced by *C. maltaromaticum*, *B. thermosphacta*, and *Lactobacillus* spp. via glucose catabolism (Ardö 2006). Acetoin has a detection threshold of 800 mg/L (Belitz and Grosch 1982) and imparts creamy, dairy-like notes (Dainty et al. 1989). A study of 45 *Carnobacterium* strains revealed that 80% of strains produced acetoin under both air and vacuum conditions (Leisner et al. 1995). Among volatile fatty acids, butanoic acid, frequently detected in both air- and VP meat, is strongly linked to spoilage, primarily due to the activity of *Carnobacterium* spp. and *B. thermosphacta* (Leisner et al. 1995; Jones 2004). Casaburi et al. (2011) observed that meat stored in air exhibited a more diverse VOC profile than vacuum-stored samples, illustrating how packaging affects microbial metabolism and spoilage dynamics. In addition to VOCs, *C. divergens* and *C. maltaromaticum* are notable for producing tyramine, a biogenic amine formed via tyrosine decarboxylation (Straub et al. 1995). Tyramine is not volatile but poses toxicological concerns, especially in individuals with monoamine oxidase (MAO) deficiencies, due to its potential to trigger hypertensive crises and migraines (McCabe 1986) (Fig. 2). Its formation is influenced by strain-specific traits, storage conditions, and precursor availability (Leisner et al. 1994; Bover-Cid and Holzapfel 1999; Masson et al. 1999; Laursen et al. 2005), with high levels observed in *C. divergens* under low-pH, glucose-rich conditions, effects that can be mitigated by NaCl (Masson et al. 1999).

Spoilage-related metabolites are also formed through enzymatic pathways such as transamination, decarboxylation, and reduction of branched-chain amino acids (valine, leucine, isoleucine), leading to low-threshold, malodorous compounds (Leisner et al. 2007). In seafood products like shrimp, *Carnobacterium* can degrade arginine to ammonia, contributing to unpleasant off-odors (Laursen et al. 2005).

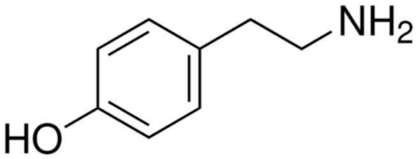


Fig. 2. Tyramine structural formula.

Interestingly, while *C. maltaromaticum* is capable of producing a broad range of VOCs, sensory panels have not consistently reported negative effects on meat quality, suggesting that not all strains necessarily compromise sensory properties (Casaburi et al. 2011; Pothakos et al. 2015). Recent multi-omics studies have shed further light on *Carnobacterium*'s role in spoilage. In VP beef, microbiome and metabolome analyses revealed a decline in overall bacterial diversity and a rise in LAB, including *Carnobacterium*, especially in samples with pH between 5.4 and 6.1 (Rodriguez-Caturla et al. 2025). This microbial shift correlated with elevated levels of spoilage-associated VOCs, including alcohols (e.g., 1-propanol, 2-methylpropanol) and ketones (e.g., 2-nonanone, 2-octanone, 2-heptanone). In high-pressure processed (HPP) baby clams treated at 400 MPa, *Carnobacterium* was one of the dominant genera associated with extended shelf life, reduced spoilage compounds (e.g., trimethylamine), and favorable sensory outcomes, unlike control samples dominated by *Aeromonas*, *Shewanella*, and *Pseudomonas* (Palamae et al. 2025). Nevertheless, the spoilage potential of *Carnobacterium* remains evident. In cold-stored sturgeon fillets, *Carnobacterium* abundance positively correlated with chemical spoilage markers such as TVB-N and TBARS, as well as VOCs like 2-pentanone, 2-heptanone, isopentyl alcohol, and ethyl propanoate, compounds associated with off-odors and quality deterioration (Prabhakar et al. 2021; Tan et al. 2022). These findings were supported by a decline in sensory attributes including appearance, texture, and odor, affirming the genus' significant contribution to quality degradation during refrigerated storage.

CONCLUSION

Carnobacterium spp., particularly *C. maltaromaticum* and *C. divergens*, play a significant role in the spoilage of refrigerated and VP food products due to their remarkable metabolic adaptability and environmental tolerance. These psychrotolerant LAB thrive under cold, anaerobic, and modified atmosphere conditions, where they contribute to quality degradation through the production of volatile organic compounds, biogenic amines, proteases, and lipases. Their metabolic activities result in the formation of off-odors, discoloration, textural changes, and elevated spoilage markers such as TVB-N and TBARS in meat, seafood, and dairy products.

Although some strains exhibit antimicrobial properties and are explored for biopreservative use, their spoilage potential underlines the importance of strain-level characterization and targeted control strategies. Their dual role is shaped by strain-specific traits and environmental conditions, including packaging, temperature, and nutrient availability. Further investigation into their genomics, metabolic pathways, and interactions with other microbiota is essential for improving food safety and extending shelf life in chilled and packaged foods.

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