Meat and Muscle Biology™

# Packaging of Meats and Shelf Life: Microbial and Physiochemical Considerations‡

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**Abstract:** With the rise in the human population, the increasing amount of food waste, and the short shelf-life of raw meat products, it is evident that the animal protein sector must meet these challenges by improving the shelf-life of these meat products. Because of consumer preference for the bright red appearance of meat products, traditional overwrap and modified atmospheric packaging (MAP) technologies have remained dominant in retail display cases. However, the shelf life of overwrap tray and MAP-packaged products has not outcompeted the shelf-life provided by vacuum packaging technologies. Although traditional vacuum packaging negatively impacts color, emerging packaging technologies, such as roll stock packaging and vacuum skin packaging coupled with MAP, can maintain product color while controlling microbial growth. However, understanding the microbial ecology of meat spoilage and the ecology of the organisms prevalent in the meat products being stored in different packaging systems is critical to improving the predictability of shelf life endpoints. Therefore, the review discusses the historical and current packaging technologies that extend microbial shelf life and the corresponding microbial responses. This review will also present an overview of applications of microbiome characterization of meats transitioning from initial raw meat products to storage by different packaging approaches.

**Key words:** meat, modified atmosphere packaging, vacuum packaging, spoilage, packaging, microbial ecology
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## Introduction

In general, the shelf life of foods is defined as the time a particular food product retains its intended safety, quality, and nutritional characteristics during set storage times (Tarlak, 2023). More specifically, microbial shelf life pertains to the time frame by which the food product microbial levels remain at acceptable population levels and presumably do not contain organisms considered harmful to consumers (Tarlak, 2023). Because of the high nutrient concentrations and high water activity, meat is considered one of the most perishable foods (Odeyemi et al., 2020). The shelf life of meat and food products is particularly critical as up to one-third of human foods, approximately 1.3 billion tons, are wasted each year worldwide (FAO, 2010; Odeyemi et al., 2020; Jones et al., 2021). Causes of waste can be due to damage to the food product during any stage of processing, transport, storage, or packaging (Karanth et al., 2023).

Microbial contamination and subsequent growth can occur at any stage of food production and may result in cross-contamination as the food product moves through the production chain to retail

(Karanth et al., 2023). Fresh meat is exposed to numerous microbial contaminants during processing that can lead to the selection of subsets of organisms responsible for spoilage under specific environmental conditions, such as refrigeration and external atmosphere (Odeyemi et al., 2020). External and environmental factors are essential in determining the microbial composition and metabolic activities of the microbial contaminants on a particular meat product. For example, an oxygen atmosphere can influence the diversity of organisms in a meat product, and changing that atmosphere through some packaging barrier can, in turn, alter microbial composition (Odeyemi et al., 2020). Consequently, the basic reasoning behind the packaging of meats is to protect them from contamination, preserve color, and delay spoilage (Mondry, 1996; Brody, 1997). This review will discuss the microbial and physiochemical responses of fresh meats before and after packaging, as well as specific current packaging practices used in the meat industry to protect the meat product.

## Microbiology and Spoilage of Fresh Meat Products

### *Factors associated with microbial spoilage*

Spoilage renders meat unsuitable for human consumption due to deterioration of its odor, flavor, color, texture, or nutritive value, which subsequently leads to consumer rejection and potential safety concerns (Ercolini et al., 2006; Nychas et al., 2008; Casaburi et al., 2015). Microbial growth, lipid oxidation, and enzymatic autolysis are the 3 basic mechanisms responsible for meat spoilage (Iulietto et al., 2015). Both intrinsic and extrinsic factors contribute to the growth of spoilage microorganisms in foods (Karanth et al., 2023). Intrinsic factors include physical and chemical characteristics of the food or meat matrix, such as water activity, pH, and available nutrients (Karanth et al., 2023). For example, meat has a high water and protein content, making it a nutritious substrate with a water activity (0.99) suitable for the growth of most microorganisms (Dainty et al., 1975). Extrinsic factors involve environmental conditions the microbial population is exposed to during all production phases, including storage conditions, temperature, oxygen availability, and humidity (Karanth et al., 2023). For meat production, the relationship between intrinsic and extrinsic factors can be complex as the microbial populations on meat carcasses depend on the health of the animal at slaughter, any contamination spread during the slaughtering and processing of the carcass, and, of course, on the storage temperature and other conditions associated with storage (Nychas et al., 2008).

For red meats, the initial surface conditions of the carcass can be a critical determinant of spoilage development (Wickramasinghe et al., 2019; Karanth et al., 2023). Contamination of cattle carcasses can occur due to intestinal content, cross-contamination from hides, processing plant environment, and human and carcass-to-carcass contact (Alnajrani et al., 2018). After the initial chilling phase, a mixture of mesophiles and psychrotrophs is the primary set of organisms on the red meat carcass. In addition to temperature, other factors such as substrate availability, pH, muscle type, and storage time will dictate which bacterial species ultimately become predominant (Sofos et al., 2013). The psychrotrophs include *Pseudomonas fragi*, *P. lundensis*, *P. fluorescens*, other pseudomonads, *Acinetobacter*, and *Psychrobacter immobilis* (Dainty and Mackey, 1992; Kumar et al., 2019). Poultry skin of chilled chicken carcasses typically harbors a variety of pseudomonads, which become predominant when spoilage occurs (Arnaut-Rollier et al., 1999). Air chilling of poultry carcasses has been shown to delay the proliferation of *Pseudomonas*, but they can still become an environmental cross-contaminant from airflow (Chen et al., 2020; Belk et al., 2021). This can result in their dominance on carcasses during storage (Chen et al., 2020; Belk et al., 2021). The fat surfaces of sheep and pork may have *Brochothrix thermosphacta* and psychrotrophic Enterobacteriaceae as predominant organisms (Dainty and Mackey, 1992). Once some of these meat products are converted to ground meat, factors such as nutrient and oxygen availability can dictate the progression of spoilage microbial populations and the timing of the occurrence of spoilage (Karanth et al., 2023).

Once fresh meat products reach retail distributors, other conditions can specifically contribute to shifts in the microbial compositional profiles of the fresh meat displayed for sale. Pseudomonads are the fastest-growing bacteria in retail cuts in film trays with low moisture and high oxygen permeability (Dainty and Mackay, 1992). Other microbiota include *Acinetobacter* and *Psychrobacter,* and occasionally *Broch. Thermosphacta*, if there is a build-up of carbon dioxide, which inhibits pseudomonads (Dainty and Mackey, 1992). For vacuum packaging, cuts are placed in bags made of film of low gas permeability, and the bags are evacuated, sealed, and

**Table 1.** Microorganisms associated with meat spoilage

| Microorganism | Product | Effect | Reference |
|---|---|---|---|
| *Pseudomonas spp., Ps fragi* | Ethyl esters | Sweet and fruity odor | Dainty and Mackey, 1992 |
| *Enterobacteriaceae* | Hydrogen sulfide | Putrid, sulfurous odor | Dainty and Mackey, 1992 |
| *Pseudomonas spp.* | Dimethyl sulfide | Putrid, sulfurous odor | Borch and Molin, 1989 |
| *Enterobacteriaceae, B. thermosphacta, homofermentative Lactobacillus spp.* | Acetoin/ diacetyl 3-methylbutanol | Cheesy | Borch and Molin, 1989 |
| *B. thermosphacta* and lactic acid bacteria | Acetoin Acetic acid | Buttery Pungent, vinegary | Borch and Molin, 1989 |
| *Lactobacillus sake, Shewanella putrifaciens* | Hydrogen sulfide | Greening of meat | Egan et al., 1989 |
| *Clostridium spp.* | $H_2$ and $CO_2$ | Blown pack (vacuum packaged meat) | Dainty et al., 1989 |
| *Serratia marcesens* | Prodigiosin | Red spots | Haddix and Shanks, 2018 |
| *Pseudomonas cyanacea* | | Blue color | Borch et al., 1996 |
| *Pseudomonas fluorescens* | | Fluorescence | Kumar et al., 2019 |
| *Leconostoc mesenteroides* | Dextran | Ropy slime | Cenci-Goga et al., 2020 |
| *Chromobacterium lividum* | Violacein | Greenish blue to purple color | Seitz et al., 1961 |

stored at −1°C to 0°C (Roberts et al., 2005). Tissue respiration continues inside the package and uses up any oxygen present and produces carbon dioxide, which inhibits the growth of *Pseudomonas*, *Acinetobacter*, and *Psychrobacter* and allows species of *Lactobacillus*, *Carnobacterium*, and *Leuconostoc* to become dominant (Dainty et al., 1989; Kalchayanand et al., 1989, 1993; Broda et al., 1996a, 1996b,1998a, 1998b, 1999). The main effects of spoilage bacteria are the production of off-odors and off-flavors, but discoloration, gas production, and slime production also occur (Borch et al., 1996). Some defects are caused by specific spoilage bacteria and are listed in Table 1.

## Methods for determining microorganisms associated with spoilage

The traditional methods for determining which bacteria are responsible for meat spoilage are cultural methods using nonselective media for determining total bacterial populations or selective enrichment methods followed by biochemical confirmation to identify specific organisms (Ferone et al., 2020). Nonselective media contain general nutrients required to grow a wide range of microorganisms, including water, a carbon source, a nitrogen source, and some mineral salts (Bonnet et al., 2020). A significant problem with nonselective media is that it allows the growth of many different bacterial species, which makes it challenging to identify specific organisms and their isolated effects (Bonnet et al., 2020). To isolate particular bacteria, selective media were developed to select for the growth of a desired organism, preventing the development and/or killing of nondesired organisms (Ferone et al., 2020). For example, a microorganism resistant to a particular antibiotic, such as ampicillin or tetracycline, has potential for the development of selective media for this microorganism. In that case, these antibiotics can be added to the medium to prevent the

**Table 2.** Summary of common meat packaging technologies with respect to oxygen exposure, color stability, shelf life extension, and associated microbial concerns

| Packaging Type | Oxygen Exposure | Color Stability | Shelf Life Extension | Key Microbial Concerns | Notes |
|---|---|---|---|---|---|
| Overwrap (PVC film) | High | Bright red | Short (2–5 d) | Rapid spoilage by aerobes | Preferred for appearance; poor microbial control |
| High-oxygen MAP | Moderate-High | Very bright red | Medium (10–14 d) | Lipid oxidation, premature browning | Enhances oxymyoglobin; can accelerate spoilage |
| CO-MAP | Low | Bright red | Medium-Long (14–21 days) | Misleading spoilage appearance | Banned in some countries; controversial but effective |
| Vacuum packaging | Very low | Purple color | Long (21–60+ d) | Anaerobes (Clostridium spp.) | Good for aging; unappealing color; risk of blown packs |
| Vacuum skin packaging | Very low | Purple/red mix | Long (21–30 d) | Anaerobes | Improved appearance and less purge |
| Roll stock packaging | Very low | Maintains color | Long (21+ d) | Carnobacterium, LAB | Good lipid stability; used for aging |

growth of other cells that do not possess resistance to these particular antibiotics (Ferone et al., 2020). In addition to antibiotics, other chemicals, dyes, antiseptics, sodium salts, or phages can also be used to make selective media (Bonnet et al., 2020). Once bacteria have been isolated in pure culture, they must be identified, which involves biochemical tests such as catalase testing, oxidase testing, and substrate utilization (Sandle, 2016). Time for results is the primary negative feature of cultural methods; isolation can take up to 72 h, and the actual identification of the genus can require another one to 5 d (Ferone et al., 2020). There have been numerous studies reporting on the spoilage of meats and meat products based on a comparison of viable counts of spoilage bacterial groups and the changes in their numbers during storage under various conditions (Gill and Badoni, 2002; Sakala et al., 2002; Barros-Velazquez et al., 2003; Jay et al., 2003; Venter et al., 2006; Signorini et al., 2006).

Chaillou et al. (2015) have suggested that traditional culturing methods must be supplemented with molecular approaches to understand the exact species and methods of spoilage organisms. Certainly, polymerase chain reaction (PCR) assays for detecting and quantifying foodborne pathogens on meat products have been developed, optimized, and standardized for several years and now enjoy relatively routine applications in the meat industry. Applications of PCR assays for specific spoilage organisms such as pseudomonads are feasible and have been utilized over the years (Ercolini et al., 2007; Hanning et al., 2009; Morales et al., 2016). However, the onset of spoilage is unlikely to be the result of single organisms but rather the outcome of shifts and changes in microbial consortia on the meat matrix that evolve depending on changes in extrinsic and intrinsic conditions. In addition, it has been suggested that interactions among different members of these microbial populations may contribute to the onset of spoilage (Hwang et al., 2020). As a result, obtaining a composite analysis of the microbial population on a fresh meat product becomes crucial while differentiating individual members of the microbial consortia as the meat product undergoes processing and preparation for storage and, ultimately, retail presentation.

Therefore, a more comprehensive taxonomy of microbial populations is needed to characterize microbial community responses. The 16S rRNA gene sequencing and subsequent bioinformatics analysis have introduced a means to characterize entire populations from a given sample. For meat production, this has been extensively applied during the past few years for all stages of production, including live animal, processing, and retail meats (Ricke et al., 2017, 2022, 2025; Weinroth et al., 2022). In addition, taxonomic identification based on the 16S rRNA gene sequencing within samples (alpha diversity) and among samples from different sources (beta diversity) can be appraised using bioinformatic computer analyses (Ricke et al., 2017; 2025). Initially, most microbiome sequencing was based on short read sequencing (250 to 300 base pairs), which has limitations for uncovering more in-depth taxonomic identification beyond bacterial genera (Lyte et al., 2025; Olson et al., 2025). Consequently, for meat microbiology, this will only provide a certain level of taxonomic information. However, some of this has been overcome with the development of long-read sequencing technologies (complete 16S rRNA gene, 1,500 base pairs) and potential applications for animal production (Lyte et al., 2025; Olson et al., 2025). The specific technologies and opportunities for these more advanced sequencing methods for meat microbiology have been recently reviewed in detail by Olson et al. (2025) and will not be discussed in the current review.

Studies incorporating these types of analyses to identify microbial populations during processing and subsequent storage have revealed several considerations for understanding the sources of spoilage organisms in fresh meats and potential contributing factors. Using pyrosequencing, Chaillou et al. (2015) demonstrated that fresh meat products harbored microbial populations from the skin and gastrointestinal tract of the animals; however, the core psychrotrophic microbiome originated from the environment, particularly water reservoirs. Processing plant environment may be a critical factor, and there is evidence to suggest that carcass poultry microbiota diversity does vary based on plant location and the different sizes of birds processed at each respective plant (Wages et al., 2019). The temperature in the different functional rooms at a meat processing plant may also be a factor in determining the processing plant's environmental microbiome, as colder room temperatures supported a more psychrotrophic microbiome while rooms held at warmer temperatures exhibited a more diverse microbiome (Belk et al., 2022). Other environmental factors may play a role. For example, Hwang et al. (2020) noted that while psychrotrophic spoilage genera could be identified in all fresh beef samples, prevalence increased during certain months of the year. Intuitively, the various steps in processing and placement of antimicrobial treatments will influence the microbiota diversity of the carcass. Kim et al (2017) concluded that predominant

microbiome phyla abundances shift as poultry carcasses progress through the processing line and undergo antimicrobial treatments. Individual processing steps may be a factor as well. In a follow-up study, Handley et al. (2018) observed that the evisceration step highly impacted the microbial diversity of poultry carcasses. This would imply that the gastrointestinal tract's microbial composition could contribute to the carcass microbial ecology. How animals are managed before entering the processing plant may also be a factor. Along those lines, Costello et al. (2025) demonstrated that lairage time in cattle had a negative impact on the microbiome compositional profiles of the different gastrointestinal compartments of the animal when it was slaughtered, and they suggested that this could lead to potential food safety and spoilage consequences.

In summary, there is now the capability of monitoring entire microbial populations on fresh meat during processing and upon the resulting product entering storage and eventual retail markets. Based on these studies, many sources can contribute to the resulting microbial composition of raw meat products. This, in turn, can determine the timing of when spoilage initiates and how rapidly a meat product reaches a spoiled state and becomes food waste. Consequently, it is vital to delay the onset of spoilage as much as possible and protect the meat product from further cross-contamination and/or potential exposure to additional environmental contamination. The introduction of protective packaging of meat products for storage and retail purposes offers a protective barrier for fresh meats from chemical, microbial, and physical elements. It provides an extended shelf life before sale (Karanth et al., 2023). Technological packaging modifications over the years have continued to improve the management of the shelf life of meats. However, the type of packaging can also influence the microbial composition of meat products and, therefore, has to be considered when determining the extent of shelf life. In addition to being susceptible to damage and providing a route for microbial contamination, packaging materials can also be contaminated before being used on the meat product (Karanth et al., 2023).

## *Origins and historical development of meat packaging*

Packaging of meats for retail has a long history. The origin of meat packaging began with butchers cutting and wrapping meat in paper or waxed paper upon request by customers (McMillin, 2008, 2017). While some meat is still sliced in the retail store and stored in refrigerated self-service display cases, most meat is packaged in the processing plant before being displayed in retail refrigerated cases (McMillin, 2008). The lighted refrigerated meat cases, allowing consumers to handle and select their meat, required packaging that protected the contents while allowing the consumer to see the color of the product and the amount of fat. This packaging ranged from simple overwrap packaging to barrier packaging (McMillin, 2008). These forms of packaging must maintain water binding (or holding) capacity, color, microbial quality, lipid stability, nutritional value, texture, flavor, and aroma, as well as prevent spoilage deterioration (Yam et al., 2005).

An oxygen-permeable, moisture-barrier polyvinyl chloride film was developed to be stretched around polystyrene trays to display fresh meat (Brody, 2002). Customers began to associate the bright red color of pre-packaged beef displayed in these oxygen-permeable packages with freshness (Jenkins and Harrington, 1991; McMillin, 2008). Historically, this type of in-store packaging has gradually been replaced by packaging in centralized operations that produce case-ready meat (McMillin, 1994). In the United States, the 2022 National Meat Case Study revealed that 99% of turkey and 96% of chicken are case-ready. Beef is the meat most often still cut in stores, although case-ready has increased to 71% (Loria, 2022). The subsequent development was vacuum packaging, which uses negative pressure to remove the air surrounding the meat, followed by sealing in a package while maintaining the pressure (McMillin, 2017). Modified atmosphere packaging (MAP) was soon developed, which involves replacing the ambient air with gas; MAP can prevent the oxidation of oxymyoglobin to the brown colors, thus maintaining the red color that consumers have come to expect (McMillin et al., 1999; McMillin, 2017). The types of gases used include nitrogen (to prevent pack collapse), carbon dioxide (used for microbial inhibition), or carbon monoxide (to create the red pigment, carboxymyoglobin) (McMillin, 2008).

Traditional food packaging protects the product and communicates information to consumers (Ahari and Soufiani, 2021). However, traditional food packaging does not meet current demands for long-shelf-life products that can be easily transported, making alternative packaging a high priority in meat production (Ahari and Soufiani, 2021). Packaging strategies for meat products have been developed to accommodate visible qualities such as redness in fresh meats with organoleptic properties consistent with perceived freshness in a displayable package wrapping. Equally

important is creating microenvironmental conditions in the package that restrict the proliferation and metabolic activity of microorganisms capable of inducing and/or accelerating spoilage and subsequent perishability of the meat product. Most of the development of these approaches has involved altering the atmosphere in the package either through a modification of gases or vacuum packaging.

## Modified Atmosphere Packaging

### *Atmospheric gases: General concepts*

Modified atmosphere packaging has become more popular in recent years due to its ability to control food quality and safety. It offers several advantages, including improved presentation and appearance to the customer and decreasing the need to add chemical preservatives. Modified atmosphere packaging has been extensively reviewed by Kandeepan and Tahseen (2022) and will only be briefly discussed in the current review. Packaging with MAP is considered a preservation-free approach that essentially involves the alteration of the gases in the atmosphere surrounding the meat product in its respective package (Kandeepan and Tahseen, 2022). The production of MAP generally requires removing atmospheric gases by vacuum from rigid plastic trays, followed by flushing packages with the desired gas or gases for a brief period, and finally heat sealing a nonpermeable film on the tray surface.

While gas type and proportions may vary, 3 primary gases are used to achieve specific functions: oxygen, carbon dioxide, and nitrogen (Djenane and Roncales, 2018). Oxygen is employed to prevent the proliferation of anaerobic organisms and to retain meat product color. Carbon dioxide is added to inhibit microorganisms, yeasts, and molds, while nitrogen is included to prevent package deflation and is not reactive with meat pigments or absorbed by the meat (Djenane and Roncales, 2018; Kandeepan and Tahseen, 2022). While oxygen retains oxymyoglobin and the red color of meat, it can also shorten shelf life, and low concentrations of carbon monoxide can be used instead for maintaining color (McMillin, 2008; Lagerstedt et al., 2011; Nieminen et al., 2015). Carbon monoxide maintains red meat color via the formation of carboxymyoglobin, possibly due to the higher stability of carboxymyoglobin compared to oxymyoglobin ($O_2$Mb) and the stronger binding of carbon monoxide to the myoglobin iron-porphyrin site (Djenane and Roncales, 2018; Kandeepan and Tahseen, 2022).

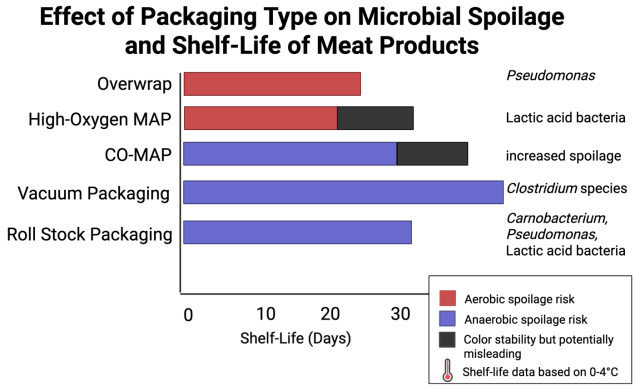


**Figure 1.** Shelf life duration and dominant microbial risks associated with various packaging types used for meat products under refrigerated storage (0–4°C). Packaging methods are compared based on their typical shelf life under industry-relevant chilling conditions and the predominant spoilage microorganisms associated with each type. Created in BioRender. Olson, E. (2025). https://BioRender.com/zuve0s6.

Depending on the gas mixtures, different microbial populations can flourish (Figure 1). For example, carbon dioxide at 20% is often included with high (80%) oxygen in MAP systems to specifically limit Gram-negative aerobic spoilage species belonging to *Pseudomonas* (Djenane and Roncales, 2018). However, other spoilage organisms can proliferate as gas mixtures are altered in MAP packaging. Nieminen et al. (2015) compared 4 combinations of carbon dioxide, oxygen, nitrogen, and carbon monoxide to evaluate the lactic acid populations after storage in the respective gas mixtures. They reported that a high concentration of carbon dioxide was selected for *Lactobacillus* sp., versus high concentrations of oxygen that supported *Leuconostoc* species. In contrast, an 80% nitrogen−20% carbon dioxide mixture preferentially supported *Lactococcus* sp. In addition to these primary MAP gases, several inert filler gases, such as the noble gases argon, helium, neon, and xenon, have also been employed in MAP packaging and are considered essentially nonreactive (Djenane and Roncales, 2018; Kandeepan and Tahseen, 2022). Two of the more distinctive MAP types, commonly referred to as high-oxygen (HI-OX) and carbon monoxide (CO-MAP), will be discussed in the following sections.

### *HI-OX MAP packaging*

High-oxygen MAP uses a gas composition of 60 to 80% oxygen with 20 to 30% carbon dioxide to reduce myoglobin oxidation and support a consumer-desirable bright cherry-red color (Djenane and Roncales, 2018). Furthermore, the concentration of carbon dioxide

provides an antimicrobial effect against the growth of Gram-negative spoilage bacteria, thus promoting product shelf life (Djenane and Roncales, 2018). Other advantages have been identified. For example, packaging minced beef with a HI-OX atmosphere has also been shown to maintain low levels of the metabolite cadaverine (Thamsborg et al., 2023). Cadaverine, a biogenic amine produced via decarboxylation of lysine, has been suggested as a potential chemical indicator of spoilage (Thamsborg et al., 2023). However, there are multiple concerns with the use of HI-OX packaging. Lipid and protein oxidation can be accelerated by a higher oxygen concentration, leading to the production of volatile off-flavors and aromas as well as decreased tenderness (Jakobsen and Bertelsen, 2000; Lindahl et al., 2010; Vierck et al., 2020). Additionally, premature browning may occur during cooking, causing a cooked color before reaching the required temperature to reduce pathogenic bacteria to safe levels (Hague et al., 1994).

In addition, HI-OX MAP packaging can alter microbial compositional profiles during storage compared to other forms of packaging. Cauchie et al. (2020) compared food wrap film wrapped versus 30% carbon dioxide/70% oxygen MAP-packed minced pork meat samples from different food companies using 16S rRNA gene sequencing. Following sample microbiome profiles over storage time, they identified 12 dominant genera in the MAP samples versus 7 in the food-wrapped samples, with *Pseudomonas* being more prevalent in the food-wrapped microbial populations versus *Brochothrix* in MAP samples. This led them to speculate that *Brochothrix* may have replaced *Pseudomonas* under MAP conditions. They also concluded that bacterial diversity should be considered as a function of food company source, batch variation, and the storage conditions used for a particular product (Cauchie et al., 2020).

The type of microbiota in the meat product may also influence the oxygen levels in packages using a HI-OX atmosphere. Kolbeck et al. (2019) have suggested that oxygen levels in high HI-OX MAP packages can be reduced over time due to the metabolic activities of the meat spoilage microbiota, leading to amino acid conversion and detectable sensory changes indicative of spoilage. To demonstrate this, Kolbeck et al. (2019) grew meat spoilage bacteria *Brochothrix thermosphacta* and 4 lactic acid bacteria using a meat simulation model containing an atmosphere of 70% oxygen and 30% carbon dioxide. Based on oxygen uptake rates for atmospheric and dissolved oxygen, all bacterial strains could consume oxygen and produce carbon dioxide. Based on genomic analyses, Kolback et al. (2019) concluded that none of the test strains possessed a citric acid cycle but could still potentially form a respiratory chain without the citric acid cycle to couple fermentation with respiration by regeneration of NADH. The authors concluded that the oxygen consumption capability possessed by the bacterial strains may be a competitive advantage for these spoilage bacteria.

### *Carbon monoxide MAP packaging*

Carbon monoxide is an anaerobic alternative to HI-OX, which typically uses a gas composition of approximately 0.4% carbon monoxide, 40 to 60% carbon dioxide, and a balance of nitrogen (Sørheim et al., 1999). Carbon monoxide MAP provides a bright red color with high stability due to the formation of carboxymyoglobin (De Santos et al., 2007). Although the low carbon monoxide concentration does not have antimicrobial properties alone, it creates an anaerobic environment contributing to an extended shelf life (Brooks et al., 2008). Despite this, the use of carbon monoxide for MAP has been debated due to its potential toxicity and ability to mask visible spoilage, and it remains controversial in several countries (Djenane and Roncales, 2018). Although spoilage can also be assessed through odor, this does not occur until after the consumer has purchased and opened the package. However, these issues have been addressed by studies that found that 0.4% carbon monoxide is not likely to be toxic (Sørheim et al., 1997; Watts et al., 1978) or mask visible spoilage (Eilert, 2005; Van Rooyen et al., 2017).

Although carbon monoxide cannot mask spoilage, it still inaccurately presents freshness and shelf life through its high color stability and redness beyond the marked shelf life, as seen in the study by Jayasingh et al. (2001). Carbon monoxide and HI-OX have been used for MAP in the meat industry. However, CO-MAP is restricted in other countries, such as the European Union, and thus requires researchers and processors to pursue other alternative packaging technologies (European Commission, Health and Consumer Protection Directorate General, 2001; Djenane and Roncales, 2018). Numerous studies on red meat products have been conducted to determine the utility and potential of CO-MAP-based packaging and to establish best practices for its application (Djenane and Roncales, 2018). Despite some promising attributes of CO-MAP, Djenane and Roncales (2018) concluded that research must continue to

overcome regulatory concerns and public perceptions for widespread international adaptation of CO-MAP to occur. Other gases have also been explored for their ability to stabilize quality attributes in meats—for example, a study from Z.-C. Wang et al. (2018) found that tilapia filets increased in quality attributes and color stability when packaged with 0.4% nitric oxide (NO). To date, few studies have evaluated the efficacy of NO-MAP for red meats. However, a recent pilot study suggests that NO-MAP may also effectively promote the redness of ground beef (Carpenter et al., 2024).

### MAP bag concept

Another recent advance in the use of MAP packaging is to seal a traditional overwrapped tray packed raw meat product within a MAP bag containing an oxygen scavenger and filled with a Tri-Gas mixture (19.6% carbon dioxide, 0.4% carbon monoxide, balanced with nitrogen) during the dark storage period (21 days) of the raw meat products life before retail display (Weinroth et al., 2019). Weinroth et al. (2019) reported the microbiota of ground beef packaged using the MAP bag concept paired with a 5-d retail display. Using amplicon sequencing of the V4 region of the 16S rRNA gene, Weinroth et al. (2019) reported that the phyla Firmicutes (97.3%; *Leuconostocaceae, Lactobacillales, Lactobacillaceae, Streptococcaceae*) and Proteobacteria (2.2%; *Enterobacteriaceae, Pseudomonaceae, Pasteurellaceae, Bradyhizobiaceae, Sphingomonadaceae*) dominated the microbiota of tray packs that had been maintained in MAP bags during 21 days of dark storage and were eliminated during a 5-d retail display period.

## Vacuum Packaging

Vacuum packaging has existed in the meat industry for several decades, beginning with primal cuts and cured meats (McMillin, 2008). Vacuum packaging has remained a viable and reliable packaging technology due to the atmospheric transition from aerobic to anaerobic within the packaging, limiting spoilage-specific microorganisms such as *Pseudomonas* and *Carnobacterium* spp., which have been highly associated with the spoilage of meat and poultry products (Jay et al., 2003; Laursen et al., 2005; Ercolini et al., 2007). Vacuum packaging has typically been used within the confines of the red meat industry throughout processing and final consumer packaging, extending the life of beef primal to 28 wks (Small et al., 2012; Youssef et al., 2014) and consumer cuts to as much as 28 and 21 d compared with the 10- to 14-d shelf life of MAP when stored under low refrigeration temperatures, < 8°C (Jeremiah et al., 2001; Figure 1).

Due to the lack of oxygen, the oxymyoglobin changes to deoxymyoglobin, changing the color of the meat from bright red to purple (McMillin, 2008). In addition, the anaerobic atmosphere induced by the vacuum packaging increases the release of purge that rests in the folds of the vacuum packaging (Li et al., 2012). Thus, consumer preference has deterred the market from solely relying on vacuum packaging (Salvage, 2014). However, more recently, the market has demonstrated an increased trend in using roll stock and vacuum skin packaging systems in the meat market. Vacuum packaging has also been used for wet aging, the process in which aging subprimal in vacuum packaging under refrigeration increases the tenderness, juiciness, and flavor of the fresh beef or meat product (Eastwood et al., 2016; Barker et al., 2023).

### Roll stock packaging

Roll stock packaging, also referred to as form and fill packaging, involves 2 layers of films made of various materials, including ethylene vinyl alcohol, polyvinylidene, di-chloride, nylon, amorphous polyethylene terephthalate, and polyolefins (North American Meat Institute, n.d.; Pauer et al., 2020; Kaiser et al., 2017; Dixon, 2011). Roll stock packaging has become popular for beef products such as ground beef and steaks (Reyes et al., 2022; Smith et al., 2021; Hanlon et al., 2021). Vacuum roll stock packaging has been demonstrated to retain color in terms of objective and subjective lightness ($L^*$) and redness ($a^*$) of individually packaged beef strip loins (IMPS 180) compared to those packaged with polyvinyl chloride overwrap (Reyes et al., 2022). Lipid oxidation was less prevalent among vacuum roll stock packaged steaks than those packed in overwrap (Reyes et al., 2022). These results are in congruence with the findings by Smith et al. (2021). Smith et al. (2021) determined regardless of roll stock barrier films (oxygen transmission rate 0.4 cc/m$^2$/24 h or 0.2 cc/m$^2$/24 h) used in packaging fresh ground beef trimmings, there was no effect on the surface color redness ($a^*$), yellowness ($b^*$), chroma, or hue and no impact on the lipid oxidation throughout a 21-d simulated retail display period. Additionally, Hanlon et al. (2021) described the microbiota of roll stock packaged strip loin steaks (IMPS 180) as primarily being comprised

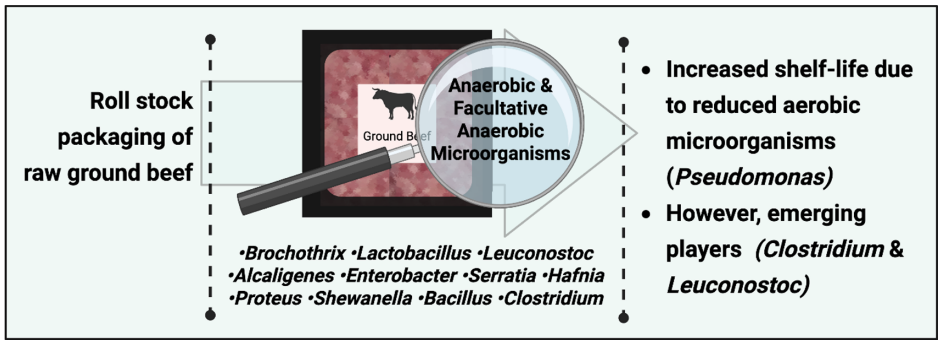


**Figure 2.** Dominant microbial risks associated with roll stock packaging of ground beef. Created in BioRender. Dittoe, D. (2025). https://BioRender.com/dy7ifdt.

of *Carnobacterium* (51.65%), *Pseudomonas* (22.88%), *Lactobacillus* (22.74%), and *Leuconostoc* (2.29%) after retail display (23 d, Figure 2).

## Vacuum skin packaging

Vacuum skin packaging, an extended vacuum packaging technology, has become more popular in recent years due to improved consumer perception, longer shelf life, and reduced purge production (Vázquez et al., 2004; Paramithiotis et al., 2009; Łopacka et al., 2016). Vacuum skin packaging consists of 2 film layers with a hard tray, and the product is presented between the 2 layers of film. The top layer is vacuum sealed tightly around the meat product to avoid film wrinkles, reducing oil and water exudates (Lagerstedt et al., 2011; Vázquez et al., 2004).

To overcome the individual quality hurdles presented by MAP (increased lipid oxidation rate) and vacuum skin packaging (purple color of meat due to anaerobic conditions), Łopacka et al. (2016) investigated the combination of MAP and vacuum skin packaging combined by using a two-film system, an inner oxygen-permeable vacuum skin film and outer barrier film where the MAP gas mixture (80% oxygen, 20% carbon dioxide) is used (Cryovac® Darfresh® Bloom). Łopacka et al. (2016) determined that the use of the combined vacuum skin–MAP system maintained color (CIE $L^*a^*b^*$) and reduced lipid oxidation compared to beef strip loin (*M. longissimus lumborum*) steaks, but increased myoglobin oxidation compared to vacuum skin-packed steaks. Drip loss and tenderness (Warner-Bratzler shear force) were not impacted by either packaging type or combination (Łopacka et al., 2016). Ultimately, Łopacka et al. (2016) concluded that using vacuum skin packages coupled with MAP may overcome the negative quality attributes presented by individual packaging technologies.

## Wet aging

Wet aging of subprimals has existed in the retail and food service landscape for over half a century (Campbell et al., 2001; Oreskovich et al., 1988; Parrish et al., 1991; Sitz et al., 2006). The current review will briefly discuss the advancements in vacuum packaging for wet aging. More recently, there has been an interest in individually aged food service steaks versus the traditional vacuum-packaged subprimals (Eastwood et al., 2016; Barker et al., 2023). Eastwood et al. (2016) investigated quality characteristics and consumer preferences of 5 different subprimal types (beef ribeye: IMPS 112A, strip loin: IMPS 180, top sirloin butt: IMPS 184, tenderloin: IMPS 189, and short loin: IMPS 174) aged as subprimal or aged as individually vacuum-packaged steaks. Individually aged ribeye and strip loin steaks had lower APC and LAB (aerobic plate count and lactic acid bacteria) bacterial populations than the corresponding aged subprimals (approximately 2 Log10 CFU/cm$^2$ reduction), with individual top sirloin butt steaks having lower LAB bacterial populations than the corresponding aged primal (~1 $Log_{10}$ CFU/cm$^2$) (Eastwood et al., 2016). Individually vacuum-packaged steak aging decreased redness ($a^*$ 19.57 versus 20.96) overall, decreased yellowness in the individually vacuum-packaged aged tenderloin and top sirloin butt steaks compared to those aged subprimal, less purge (score and weight) of vacuum-packaged individual steaks, and no difference in tenderness (Warner-Bratzler shear force evaluation). Among the consumer panelists, there was no difference in the overall liking, flavor, juiciness, tenderness liking, and tenderness level perceived of the ribeye, short loin, tenderloin, or top sirloin butt (Eastwood et al., 2016). There was an increased overall liking, flavor, juiciness, and tenderness liking of the individually vacuum-packed strip loin steaks compared to the corresponding wet-aged subprimal (Eastwood et al., 2016).

More recently, Barker et al. (2023) investigated the specific flavor development of individually rolled stock vacuum-packed beef steaks during extended wet aging and determined optimal times to age without off-flavor development. Strip loins (IMPS 180), top sirloin butts (IMPS 184), and paired tenderloins (IMPS 189A) from USDA low-choice were wet-aged as subprimal for 28 d (Barker et al., 2023). On day 28, individual steaks were fabricated, vacuum roll stock packaged, and aged to 28, 35, 42, 49, and 56 d. Barker (2023) determined through trained consumer panels that over time, specifically, by day 42, the positively associated attributes, beef flavor, buttery, and brown/roasted, decreased in score at day 49, and the negatively associated flavors, fishy, sour, liver-like, and oxidized) were increased at day 42. Umami flavors and overall juiciness and tenderness did not differ over the 56-d aging period (Barker et al., 2023). Barker (2023) also investigated the volatile organic compounds (VOCs) produced when wet again and used discriminant functional analysis to describe the change in flavor and VOCs as aging progressed (day 28 to 56). Ultimately, Barker et al. (2023) suggested that as aging increases beyond day 42, off-flavors become more present and mask the positive flavor-associated VOCs produced later during the wet aging. Barker et al. (2023) concluded that the optimal individual wet aging of steaks in roll stock packaging is 49 d, potentially extending aging to 49 d.

### *Emerging spoilage microorganisms in vacuum-packaged meat*

Although vacuum packaging has increased the shelf life of meat products by removing the oxygen in the atmosphere, psychrophilic anaerobic specific spoilage microorganisms (SSO) belonging to the *Enterobacteriaceae* family and the *Clostridium* spp. are a primary spoilage concern, resulting in blown packages of raw meat (De Filippis et al., 2019; Lavieri and Williams, 2014; Mansur et al., 2019; Chaillou et al., 2015; Hultman et al., 2015; Dorn-in et al., 2018, Figure 1). Specifically, these have occurred in primal cuts of raw beef, venison, and lamb, pre-cooked turkey and roast beef, and sous vide (food cooked in an impermeable vacuum bag and stored at refrigeration temperatures (Broda et al., 1996a; Kalinowski and Tompkin, 1999). The first blown packaging of vacuum-packaged raw beef was reported in 1989 in the United States and the United Kingdom (Kalchayanand et al., 1989; Dainty et al., 1989). Blown packaging was also detected in New Zealand (Broda et al., 2000) and Ireland (Byrne et al., 2009).

Chilled vacuum-packaged meat and meat products' SSOs primarily include *Streptococcus* spp., *Brochothrix* spp., *Psychrobacter* spp., and *Acinetobacter* spp. (Stellato et al., 2016; Chaillou et al., 2015; Hultman et al., 2015). In addition, a range of Clostridial species (*Clostridium estertheticum, Cl. Algidicarnis, Cl. Frgidicarnis, Cl. Gasigenes, Cl. Frigoris,* and *Cl. bowmanni*) and *Enterobacteriaceae* have been identified as SSO in chilled vacuum-packaged meat (André et al., 2017; Zhang et al., 2019; Brightwell et al., 2007). Only *Cl. estertheticum* subsp. *estertheticum* and subsp. *laramiense* (formally *Cl.* Laramie) and *Cl. gasigenes* result in blown packages, with *Cl. estertheticum* being the main causative agent of blown packs (Brightwell and Clemens, 2012). With impermeable vacuum packaging, *Cl. estertheticum* contamination occurs most likely during harvest from the soil and feces brought in on the animal's hide or through equipment (Boerema et al., 2003). Using an enrichment-based PCR, Boerema et al. (2003) surveyed a New Zealand meat processing plant where *Cl. estertheticum* and *Cl. gasigenes* were detected in soil, feces, and hide samples. A combination of factors that include an increase in ambient temperature (−1.5 to 1 or 4°C), an increase in muscle pH (5.5 to 6.0), steam vacuuming and hot water washing carcass, hot deboning, and heat treatment for shrink vacuum packs may activate Clostridial spores (Bell et al., 2001; Mills et al., 2014; Moschonas et al., 2011; Reid et al., 2017). The initial contamination of 1 spore of *Cl. estertheticum* has been demonstrated to be sufficient to cause blown packs with 10 spores per $cm^2$ capable of reducing the shelf life of vacuum-packaged meat from 60 to 70 d to 44 d at −1.5°C (Clemens et al, 2010; James and James, 2002). As such, 100 spores per $cm^2$ have been determined to be the critical number for vacuum-packaged meat (Silva et al., 2016). *Clostridium estertheticum* has also demonstrated the ability to outcompete other SSOs that use glucose, such as *Leuconostoc mesenteroides*, in vacuum-packaged meat (Yang et al., 2011).

## Conclusions and Future Directions

Considerable technological advances have been accomplished over the years in packaging for meat products. However, microbial populations in meat and their relationship to shelf life remain elusive. In general, microbial ecology characterizes microbial

communities and individual relationships with each other and their respective environment (Mony et al., 2020). Traditional microbial methods based on culturing have primarily identified types of supposed spoilage bacteria. Challenge testing using monocultures of these spoilage organisms has also been implemented to attempt to establish a relationship between the candidate organism and the onset of spoilage. The introduction of 16S rRNA gene sequencing for meat production systems has revealed that spoilage is a more complex process involving entire consortia of organisms at different stages in the meat production cycle. Intuitively, the core community of microorganisms associated with meat would be the main source of spoilage bacteria. However, as various extrinsic and intrinsic factors are introduced via packaging, MAP, or vacuum atmospheres, selection occurs, and certain organisms become more predominant.

Continued research applying 16S rRNA gene sequencing to characterize the microbiome of meat during the various stages of spoilage should provide a more comprehensive approach to developing a more detailed description of microbial-driven spoilage ecology. However, it is also possible that taxonomic identification of members of microbial communities alone will not be sufficient to delineate the potential interactions occurring among the organisms within the microbial community as the meat product begins to enter a spoilage state. Understanding taxonomic and functional diversity allows linking organisms within a microbial community with their corresponding responses to the environmental factors that drive the ecosystem (Cook et al., 2025). This will require more than just 16S rRNA gene sequencing. A combination of multi-omic approaches involving metagenomics, proteomics, metabolomics, and transcriptomics to follow the progression of meat spoilage from fresh meat to the endpoint of shelf life will not only identify the key organisms but differentiate their contribution(s) to the complex characteristics associated with a "spoiled" meat product (Chatman et al, 2024; Ricke et al., 2025). Developing a better understanding of the meat microbial compositional profiles would, in turn, help to optimize packaging materials to maximize shelf life and potentially lead to the design of sensors targeting key spoilage microorganisms as early indicators of meat product deterioration.

### Declaration of Competing Interest

Authors have no conflicts of interest.

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### Author Contribution

Conceptualization: DKD, JFL, SCR; Data curation: Not applicable; Formal analysis: Not applicable; Funding acquisition: None required; Investigation Methodology: Not applicable; Project administration: DKD, JFL, SCR; Resources: Not applicable; Software: EGO; Supervision: DKD, JFL, SCR; Validation: DKD, CAO, JFL, EGO, SCR; Visualization: EGO; Writing – original draft: DKD, CAO, JFL, EGO, SCR; Writing – review & editing: DKD, CAO, JFL, EGO, SCR.

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