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Polyphosphate in food systems: Their roles and applications in foods and contribution to sustainable processing practices

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ABSTRACT

Background: Polyphosphates (PolyPs) are essential not only for microbial metabolism but also as versatile agents in food science, where they play a significant role in enhancing food quality, safety, and sustainability. This review aims to investigate the multifaceted roles of PolyPs from both microbial and chemical perspectives, highlighting their importance in advancing food technologies and promoting sustainable practices.

Scope and approach: This review provides a comprehensive analysis of how polyphosphates can improve food quality and contribute to sustainable practices in food systems through microbial production, transport, and chemical additives, which are important for both food preservation. It explores the innovative applications of PolyPs in the field of food science and technology, including their use in meat, dairy, seafood, and plant-based food products, with implications for sustainable agriculture and the food industry. Additionally, the review assesses the impact of PolyPs on food product quality, including their roles in moisture retention, texture enhancement, and mineral fortification, while also addressing potential health risks and environmental impacts.

Key findings and conclusions: The review presents novel insights into the potential of microbial-derived short polyphosphates (SpolyPs) as a sustainable alternative to synthetic additives in food systems. These compounds, produced through microbial processes, offer significant benefits for enhancing food quality and extending shelf life, while aligning with green chemistry principles by reducing reliance on synthetic chemicals. Furthermore, PolyPs from chemical additives are shown to be pivotal in balancing food safety with nutritional enhancement, as their ability to chelate and stabilize essential minerals can contribute to public health by addressing micronutrient deficiencies. However, the review also underscores the need for careful management of polyphosphate use due to potential health risks associated with excessive intake, such as kidney damage and cardiovascular disease. To mitigate these risks, the development of safer, next-generation polyphosphate formulations and alternative compounds is advocated. Thus, there is a strong correlation between polyphosphate applications in food science and sustainable practices. By supporting nutrient recovery, reducing food waste, and improving environmental outcomes, PolyPs play a dual role in advancing food technology and fostering sustainability in food supply chains.

1. Introduction

PolyPs are a group of compounds formed by the polymerization of tetrahedral phosphate units. There are various structural forms, such as linear polyphosphates, cyclophosphates and ultraphosphates which have attracted considerable attention due to their ability to form stable

complexes with metal ions.

This inorganic phosphate polymer has diverse roles, ranging from energy storage and metabolic regulation to stress response and survival in microorganisms such as bacteria and yeast. In the food industry, PolyPs are extensively used to enhance food quality, preservation, and nutritional value. They improve water-holding capacity, stabilize

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emulsions, and fortify foods with essential minerals. However, their usage must be balanced to avoid potential health risks associated with excessive phosphate intake (Saia, Carrick, Buda, Regan, & Walter, 2021).

Food industry takes abundant advantages of PolyPs in order to increase food shelf life and quality. For instance, improved water-holding capacity of processed meat by polyphosphate result in juicier and more tender products. This moisture retention is important for maintaining product quality during storage and cooking, particularly in ham, sausages, and poultry (Calabrese & Riccardi, 2019; Goemaere, Glorieux, Govaert, Steen, & Fraeye, 2021; Sebranek & Bacus, 2007).

Specifically, PolyPs contribute to nutrient fortification without compromising taste or texture by chelating and stabilizing essential minerals such as calcium, magnesium, and iron. This fortification enhances the bioavailability of these minerals, making them more accessible for absorption by the body (Feng, Yang, Li, Wu, & Zhao, 2022). Such fortification can help address dietary deficiencies and improve public health outcomes by ensuring that these essential nutrients are more effectively utilized in the diet (Ranganathan, 1992; De La Fuente et al., 2004).

Despite the benefits, excessive use of PolyPs in food products can increase potential health concerns. Kidney damage, cardiovascular issues, and weakened bone due to calcium-phosphate imbalance are some of the potential consequences (Calvo & Uribarri, 2013; Kemi, Kärkkäinen, & Lamberg-Allardt, 2006).

While the potential health effects of polyphosphates are important to consumer safety, their broader implications extend to environmental sustainability, highlighting the need for a balanced approach that considers both human health and ecological impact.

Polyphosphates have long been recognized for their pivotal role in food science, not only for their direct applications in food preservation but also for their significant influence on microbial and environmental processes. In particular, their role in microbial polyphosphate metabolism extends beyond basic food preservation functions, intersecting with critical environmental and safety concerns (Hassan et al., 2024; Saia et al., 2021). These bioactive compounds are involved in complex biochemical processes that can influence the behavior of certain microorganisms within food systems, including the regulation of sulfate levels through microbial pathways (Zhang, Su, Ma, Hu, & Teng, 2021). This regulation can significantly impact both food and environmental systems (Dohan et al., 2023). In the context of a sustainable food supply chain, the management of waste and water usage in food processes involving phosphate compounds is directly linked to subsequent stages of environmental management (Saia et al., 2021). Therefore, discussing the role of phosphates in food science and technology is essential to understand their broader impact on environmental systems, particularly concerning the phosphorus cycle.

For instance, microbial polyphosphate metabolism allows phosphate recovery from the environment and it has a significant role in environmental sustainability. The enhanced biological phosphorus removal (EBPR) process in wastewater treatment plants exploits polyP-accumulating organisms (PAOs) to remove excess phosphate. Microorganisms uptake phosphate in aerobic conditions and store it as polyphosphate, which is then removed from the system during sludge wasting. This process prevents eutrophication, an environmental issue caused by excessive nutrient loading in water bodies, leading to algal blooms and hypoxia (Oehmen et al., 2007; Sun, Du, Dan, Liu, & Peng, 2021).

In addition, polyphosphates can modulate the activity of Sulfate-Reducing Bacteria (SRB), which utilize sulfate as a terminal electron acceptor to produce hydrogen sulfide (H₂S), a gas known for its toxicity and corrosiveness. By managing nutrient availability and inhibiting SRB activity, polyphosphates help to reduce the risk of H₂S formation, thereby enhancing food safety and contributing to a more sustainable approach to food production and environmental stewardship (Muyzer & Stams, 2008; Seviour, Mino, & Onuki, 2003).

The understanding and optimization of microbial polyphosphate metabolism, along with the strategic use of chemical additives, can pave the way for more sustainable practices in both environmental management and food industry applications. By promoting nutrient recovery, reducing pollution, and maintaining ecological balance, these approaches contribute to a more responsible and efficient food production system. This not only benefits the environment but also enhances the overall quality and safety of food products, aligning with the goals of sustainable food science and technology (Muyzer & Stams, 2008; Seviour et al., 2003).

The aim of this review is to explore the multifaceted roles of PolyPs produced naturally by yeast and bacteria, as well as the use of chemical additives derived from polyphosphates in improving food quality and environmental sustainability. It examines their functions in microbial metabolism and the phosphorus cycle, and highlights innovative wastewater treatment and environmental remediation strategies that leverage microbial polyphosphate metabolism.

1.1. PolyP transport and production by microbial approach

Studies of polyphosphate transport and production in microbes is essential for improving food quality and sustainability. The ability of microbes to store energy, respond to stress, and regulate vital processes through polyphosphates directly influences food preservation and stability. The understanding of how microbes manage these compounds can lead to more sustainable methods for enhancing food shelf life and environmental cleanup. The insights gained from this research connect microbial functions to practical applications, offering solutions for healthier food systems and a cleaner environment.

Specifically, phosphorus is necessary for the formation of DNA, RNA, ATP, and phospholipids, making it a key nutrient for all living organisms (Jansson, Nilsson, Modig, & Hed Vall, 2017). The ability of bacteria and yeast to synthesize, store, and degrade PolyPs is vital for their survival and functionality, especially in fluctuating environmental conditions (Jansson et al., 2017; Karl & Björkman, 2015). Microorganisms significantly influence the phosphorus cycle, a biogeochemical process that governs the movement of phosphorus through the lithosphere, hydrosphere, and biosphere.

Therefore, a microbial conversion of inorganic phosphate to organic forms and vice versa helps maintain the balance of the phosphorus cycle, supporting ecosystem productivity and sustainability. These conversions are essential for the recycling of phosphorus, making it available for plant uptake and thereby sustaining the food web. This microbial activity ensures that phosphorus remains a renewable resource within ecosystems (Martiny, Treseder, & Pusch, 2013; Paytan & McLaughlin, 2007).

Therefore, this section delves into the cellular processes and cellular pathways that enable efficient synthesis and storage of PolyP in microbial cells. Insights into these processes are crucial for optimizing biotechnological applications and enhancing the sustainability of food supply chain.

1.1.1. Role of SPolyPs in yeast and bacteria

SPolyPs are linear polymers of orthophosphate residues that are essential in yeast and bacterial cells (Albi & Serrano, 2016). Within the cell, SPolyP acts as an energy reservoir and supports ATP synthesis during periods of high metabolic demand, this function is comparable to the storage of glycogen in glucose metabolism. Not only in yeasts but also in bacteria, PolyP participates in the cellular stress response by improving survival rate under the conditions of nutrient deprivation and oxidative stress by maintaining cellular homeostasis (Kulaev & Kulaevskaya, 2000).

PolyPs are crucial biomolecules with diverse functions across various organisms, playing vital roles in cellular processes, particularly in bacteria, PolyP participates in the biofilm formation, which is essential for bacterial survival. These roles underline the evolutionary conservation

and functional versatility of PolyP across different organisms which highlights its importance in cellular physiology and pathogenicity (Seufferheld, Alvarez, & Farias, 2008). SPolyPs enhance the development and stability of biofilms by acting as a matrix and modulating the expression of biofilm-related genes, which fortifies the bacteria's ability to resist to environmental stresses and antibiotics (Choudhary et al., 2016).

In yeasts and bacteria SPolyPs binds to metal ions, helping to maintain intracellular ion balance, which is crucial for regulating enzymatic activities. This interaction stabilizes essential ions such as calcium, magnesium, and manganese, which are vital for various metabolic pathways (Saia et al., 2021; Seufferheld et al., 2008). These processes ensure cells function and adaptation to changing environmental conditions.

1.1.2. Role of large polyphosphates in yeast and bacterial cells

Large polyphosphates (LPolyPs) comprise hundreds to thousands of orthophosphate residues linked by energy-rich phosphoanhydride bonds. These molecules have a crucial role in the physiology of all the organisms, both eukaryotes and prokaryotes.

The enzymes responsible for PolyPs synthesis and degradation, such as polyphosphate kinases (PPK) and exopolyphosphatases (EPolyPs), are highly conserved across different species, highlighting the evolutionary importance of LPolyPs in cellular physiology (Erecinska, Stubbs, Miyata, Ditre, & Wilson, 1977; Neville, Roberge, & Jia, 2022).

Specifically, in yeast (for instance, *Saccharomyces cerevisiae*), LPolyPs is predominantly stored in vacuoles and mitochondria which take significant part in phosphate storage and buffering. The mechanism of action of this storage is maintaining phosphate homeostasis within the cell and providing a reservoir that can be mobilized when external phosphate level is low (Yang, Huang, Kuo, & Chiou, 2017). In vacuoles, LPolyPs participate in regulating the cytosolic concentration of free phosphate, ensuring a steady supply for various metabolic needs (Yang

et al., 2017).

On the other hand, LPolyPs participates in energy metabolism and maintains mitochondrial function under stress conditions, this capability is vital in the environments with phosphate availability fluctuation, and enables cells to adapt and maintain their metabolic balance (Sawada, Ueno, & Takeda, 2021). Moreover, large LPolyPs modulates various enzymatic activities and is essential for vacuolar functions, including pH regulation and maintaining metal ion's balance (Sawada et al., 2021).

In addition, polyP is a versatile molecule that profoundly impacts bacterial behavior, influencing everything from stress resilience to pathogenicity. In bacteria as *E. coli*, polyP is essential for enduring harsh conditions, while in *P. aeruginosa*, it governs biofilm formation and communication mechanisms, critical for its survival and infection potential (Seufferheld et al., 2008).

Disruption of polyP metabolism in pathogens such as *Salmonella enterica* and *Vibrio cholerae* leads to a significant reduction in their motility and virulence, demonstrating its role in these bacteria's ability to cause disease (Seufferheld et al., 2008).

Additionally, *Corynebacterium glutamicum* struggle to thrive in low-phosphate environments, highlighting polyP's role in nutrient acquisition and growth. These varied functions of polyP reveal its fundamental importance in bacterial survival strategies, making it a key player in the adaptability and pathogenicity of microbes (Seufferheld et al., 2008).

1.1.3. Production of short and large polyphosphates in yeast and bacteria cells

In yeast cells (Fig. 1), Pi transport and metabolism are fundamental for maintaining cellular balance and responding to environmental changes. SPolyPs are synthesized in the cytoplasm by polyphosphate kinases (PPKs) and are transported into vacuoles, which act as major storage sites (Hothorn et al., 2009). The VTC (vacuolar transporter chaperone) complex, which includes proteins encoded by the VTC genes

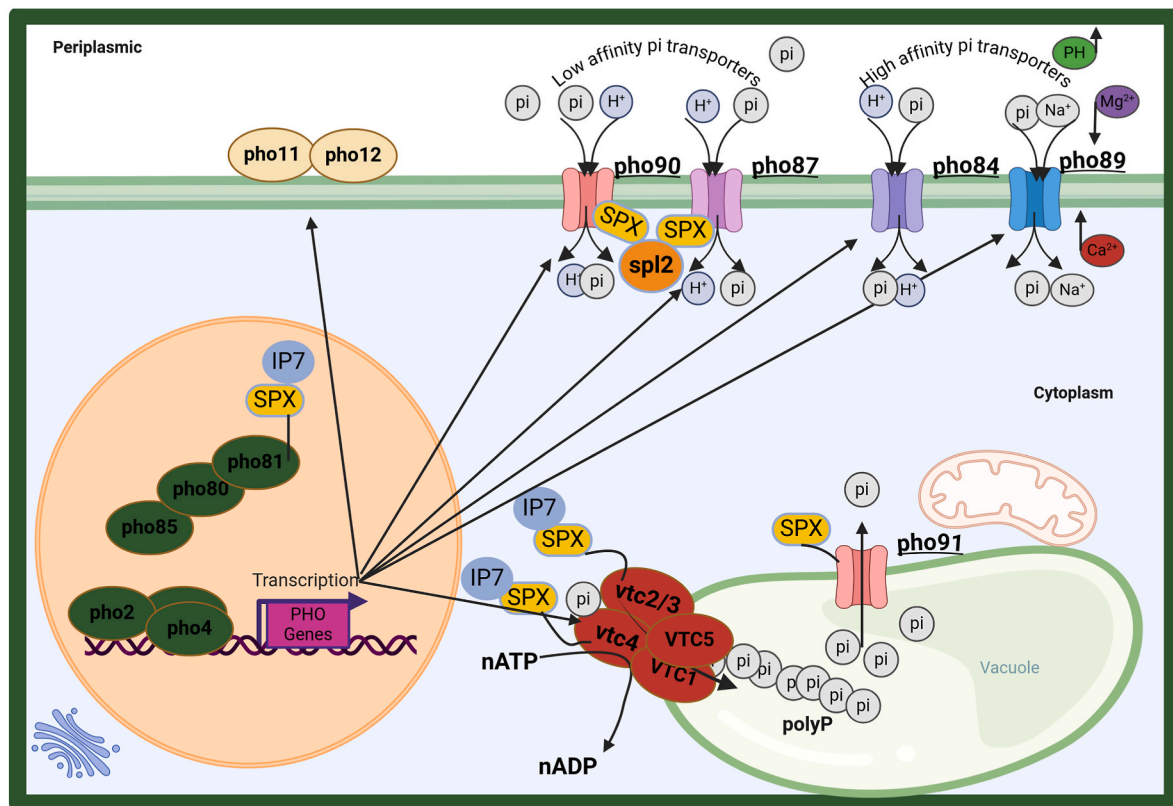


Fig. 1. Molecular mechanisms of phosphate (Pi) transport and regulation in yeast cells. It highlights the role of high and low-affinity Pi transporters, including Pho84, Pho89, Pho87, and Pho90, in the transmembrane movement of phosphate (Biorender software).

such as VTC4 and VTC2/3, manages this transport.

VTC can transfer PolyP and orthophosphate from cytosol into the vacuole, where it serves as a phosphate reserve and assists in metal ion sequestration (Gerasimaite et al., 2017; Pipercevic et al., 2023).

Hydrolysis and transfer of large PolyPs are accomplished by membrane-bound and soluble polyphosphatases such as PPK1 and PPN1. During phosphate scarcity, these polyphosphatases degrade large PolyPs to make phosphate available, which is transported back into the cytoplasm to support metabolic activities. The PHO pathway, particularly PHO5, which encodes acid phosphatase to utilize external organic phosphate sources effectively, ensures that yeast cells adapt swiftly to changing phosphate levels (Hothorn et al., 2009; Lichko, Kulakovskaya, Pestov, & Kulaev, 2006).

In bacterial cells (Fig. 2), SpolyPs are synthesized in the cytoplasm by polyphosphate kinases and can be directed to various processes within the cytosol or stored in polyphosphate granules. These granules, also known as Volutin, store PolyP and can mobilize rapidly when it is needed. The transport and compartmentalization of PolyP within bacterial cells are managed by proteins such as PPK1 and PPK2, which handle PolyP synthesis and degradation (Seviour et al., 2003).

Polyphosphate kinase 1 (PPK1) is responsible for the synthesis of long-chain PolyP, while EPolyPs such as PPX degrade PolyP to release phosphate ions. The management of large PolyPs within bacterial cells is regulated to maintain a balance between storage and mobilization, particularly under nutrient stress or during biofilm formation. The PHO regulon in bacteria, including genes like PhoA and PhoB, plays a critical role in regulating PolyP metabolism in response to phosphate availability (Rangarajan et al., 2006).

PPK1 catalyzes the polymerization of the terminal phosphate of ATP into long-chain PolyP, the process is crucial for storing energy and phosphate reserves in the PolyP structures. Conversely, PPX hydrolyzes PolyP, releasing phosphate ions that can be utilized for various metabolic activities, especially when the external phosphate sources are limited. The balance between these processes ensures that bacteria can quickly adapt to changes in environmental phosphate levels (Rangarajan et al., 2006).

The PHO regulon, including PhoA and PhoB, regulates the expression of genes involved in phosphate uptake and PolyP metabolism. PhoA

encodes alkaline phosphatase, which hydrolyzes organic phosphate compounds to release inorganic phosphate, while PhoB is a response regulator that activates the expression of PHO genes in phosphate-limiting conditions. These proteins are part of a regulatory network which is essential for bacteria to survive and adapt in diverse environments (Achbergerová & Nahálka, 2011; Marzan & Shimizu, 2011).

PolyP transport is highly organized in yeast, involving distinct pathways for short and large PolyPs. Vacuoles serve as central storage sites for both forms of PolyPs, with transporters like the VTC complex and phosphate transporters encoded by PHO genes facilitating their entry into vacuoles. The VTC complex, including proteins such as Vtc1, Vtc2, Vtc3, and Vtc4, is essential for the synthesis and transport of PolyP into the vacuoles, where it can be stored and utilized as needed (Andreeva, Trilisenko, Eldarov, & Kulakovskaya, 2015; Gerasimaite et al., 2017; Magkiriadou, Stepp, Newman, Manley, & Racki, 2024; Racki et al., 2017).

Mitochondria are responsible for the storage and regulation of large PolyPs, particularly under conditions of phosphate excess or limitation. Mitochondrial PolyP reserves are significant for energy metabolism and stress responses. The coordinated activity of polyphosphatases such as PPK1 and PPN1 ensures the dynamic regulation of PolyP levels, allowing yeast cells to adapt quickly to environmental phosphate availability (Andreeva et al., 2015; McCarthy & Downey, 2023).

In prokaryotic cells, phosphate transport (Pit) and PolyP synthesis take an important role in maintaining cellular homeostasis and responding to changes in environmental Pi levels.

There are two kinds of systems for sensing and transporting Pi in Prokaryotic cells. In the presence of low environmental concentrations of phosphate, cells typically utilize a high-affinity Phosphate-specific transport (Pst). This system consists of a periplasmic Pi binding protein (PstS), membrane proteins forming a Pi channel (PstA and PstC), and a cytoplasmic ATPase (PstB) that provides energy for Pi transport across the membrane (Rao, Gómez-García, & Kornberg, 2009). When high concentrations of Pi are available, low-affinity Phosphate inorganic transporter (Pit) system plays a significant role in Pi uptake under conditions of sufficient Pi (>4 μM). Pit function is mostly affected by the pH and metal ions presence in the environment and transports metal-phosphate complexes towards cells. Pit uses a proton-symporter

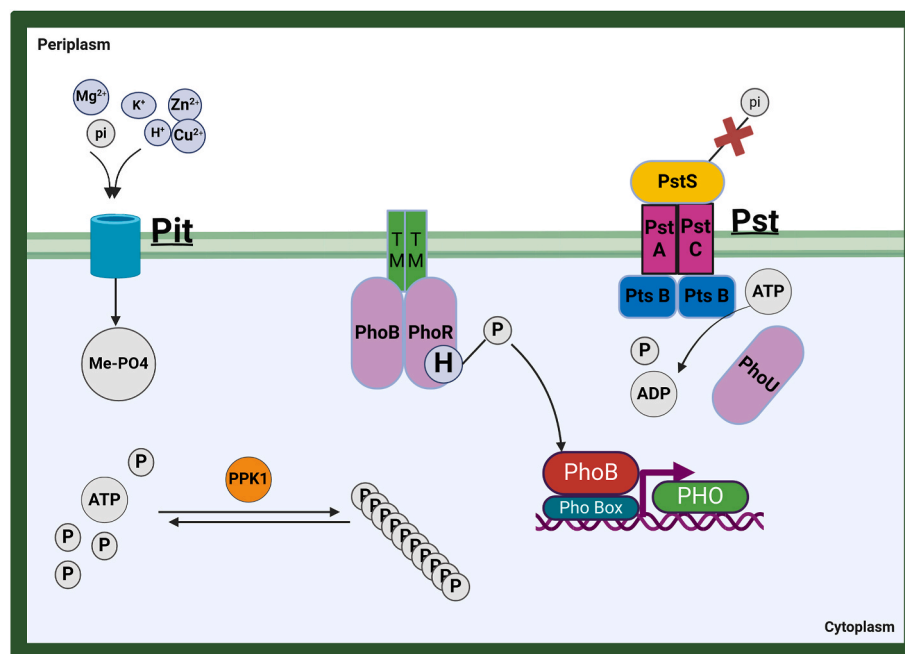


Fig. 2. Molecular mechanisms involved in phosphate (Pi) transport and regulation in prokaryotic cells, specifically focusing on the roles of the Pit and Pst systems (Biorender software).

mechanism to facilitate phosphate uptake, requiring less energy for phosphate transport [Rao et al., 2009](#)).

1.2. Phosphate transport in cells of yeasts and bacteria

The transmembrane transport of inorganic phosphate (Pi) is the initial and essential step in its cellular assimilation. Free phosphate is conveyed into the cell via specific permeases. In yeast, there are two types of transporters, the first one is the symporter of Pi and H⁺ including Pho90, Pho87 and Pho84, the second one is the symporter of Pi and Na⁺, Pho89 ([Acosta-Zaldívar et al., 2024](#); [Ogawa, DeRisi, & Brown, 2000](#); [Serra-Cardona, Petrežsélyová, Canadell, Ramos, & Ariño, 2014](#)).

In another classification, the membrane Pi transporters Pho89 and Pho84 are considered high-affinity transporters, essential for conditions with low external Pi concentrations. In contrast, Pho87 and Pho90 are low-affinity Pi transporters that function efficiently in high phosphate condition ([Ogawa et al., 2000](#); [Wykoff, Rizvi, Raser, Margolin, & O'Shea, 2007](#)).

The presence of different transport systems with high and low phosphate affinity provides flexibility for yeast phosphate metabolism in continuously changing environmental conditions. These transport systems enable yeast cells to efficiently adapt to varying phosphate levels in their environment ([Jensen, Ajua-Alemanji, & Culotta, 2003](#); [J. Zhang et al., 2022](#)). [Table 1](#) summarizes various studies evaluating the transport and synthesis of polyphosphate metabolism in yeast species.

In prokaryotic cells, at concentrations higher than 4 mM, Pi binding to PstS inhibits the histidine kinase PhoR, leading to the repression of downstream Pho-controlled gene expression, while at lower concentrations the repression on PhoR is released, allowing for the activation of the downstream response regulator PhoB, which regulates the expression of genes involved in Pi uptake and metabolism ([Chekabab, Harel, & Dozois, 2014](#)).

Intracellular Pi signaling pathway involving PhoR and PhoB confers a central role in regulating the expression of genes within the Pho regulon in response to Pi levels ([Qi, Baldwin, Muench, & Baker, 2016](#)). The

PhoU protein is involved in modulating Pi uptake by the Pst transporter and preventing high intracellular Pi toxicity in prokaryotic cells ([Qi et al., 2016](#)).

2. Correlation of intracellular polyphosphates with sustainable supply chains

The presence and function of PolyP within yeast and bacterial cells have significant implications for sustainable supply chains. These intracellular PolyPs contribute to the efficiency and sustainability of food production by enhancing microbial performance, optimizing fermentation processes, and reducing environmental impacts ([Demling, Baier, Deitert, Fees, & Blank, 2024](#)). This section explores how the intracellular roles of PolyPs in yeasts and bacteria align with the goals of a sustainable food supply chain.

In both yeast and bacterial cells, polyphosphates have a crucial role in energy storage and stress response, which are vital for efficient microbial processes. Therefore it is important to explore the essential roles of PolyPs in microbial survival and stress responses, emphasizing their impact on the efficiency and resilience of yeast and bacteria in growth and fermentation processes ([Demling et al., 2024](#); [Rashchi & Finch, 2000](#)).

The biotechnological exploitation of yeasts and bacteria for producing bio-based products, including biofuels, bioplastics, and pharmaceuticals, relies heavily on the metabolic flexibility provided by intracellular polyphosphates ([Petroll, Kopp, Care, Bergquist, & Sunna, 2019](#)). These PolyPs enable microorganisms to manage phosphate reserves and maintain metabolic activity under nutrient-limited conditions, thereby enhancing yield and efficiency. For instance, the use of engineered bacterial strains with optimized PolyP metabolism can lead to more efficient bioprocesses, reducing the need for chemical inputs and minimizing waste ([Tarayre et al., 2016](#)). Polyphosphates within microbial cells can contribute to waste reduction and resource recovery in food processing and waste management. By leveraging bacteria's ability to sequester phosphate as PolyP, these waste streams can be treated biologically, recovering valuable phosphates and reducing

Table 1

Summary of studies evaluating the transport and synthesis of polyphosphate metabolism in various yeast species. The table includes details on yeast strains, growth media, polyphosphate content (% w/w), quantification methods, and publication dates.

Species	strain	medium used	% (w/w)/total polyP	PolyP Quantification	Althors
<i>S. cerevisiae</i>	VH2.200	30 mM Pi from wash water, 20 mM MgCl ₂ and 250 mM glucose pH 6.0	19.8	scPpx1p & scIpp1p	Fees, Christ, Willbold, and Blank (2023) Fees, Christ, Willbold, and Blank (2023)
<i>S. cerevisiae</i>	VH2.200baker's yeast	277.5 mM glucose, 66.6 mM KH ₂ PO ₄ , pH 6.0	0.283	scPpx1p & scIpp1p	Christ and Blank (2019)
<i>S. cerevisiae</i>	market baker's yeast	277.5 mM glucose, 66.6 mM KH ₂ PO ₄ , pH 6.0	0.272	scPpx1p & scIpp1p	Christ and Blank (2019)
<i>S. cerevisiae</i>	White beer yeast	277.5 mM glucose, 66.6 mM KH ₂ PO ₄ , pH 6.0	0.201	scPpx1p & scIpp1p	Christ and Blank (2019)
<i>S. cerevisiae</i>	Cen.pk113-7D yest	277.5 mM glucose, 66.6 mM KH ₂ PO ₄ , pH 6.0	0.056	scPpx1p & scIpp1p	Christ and Blank (2019)
<i>S. cerevisiae</i>	Port wine yeast	277.5 mM glucose, 66.6 mM KH ₂ PO ₄ , pH 6.0	0.012	scPpx1p & scIpp1p	Christ and Blank (2019)
<i>Pichia pastoris</i>	GS115	10 mM Pi, 2% glucose PH 5.8	TOTAL P 610 Mm	Acidic hydrolysis	Andreeva et al. (2018)
<i>Pichia pastoris</i>	GS116	10 mM Pi, 0.5% methanol PH 5.8	TOTAL P 370 Mm	Acidic hydrolysis	Andreeva et al. (2018)
<i>Hansenula polymorpha</i>	DL-1	10 mM Pi, 2% glucose PH 5.8	TOTAL P 353 Mm	Acidic hydrolysis	Andreeva et al. (2018)
<i>Hansenula polymorpha</i>	DL-1	10 mM Pi, 0.5% methanol PH 5.8	TOTAL P 288 Mm	Acidic hydrolysis	Andreeva et al. (2018)
<i>S. cerevisiae</i>	VKM Y-1173	glucose, 30; KH ₂ PO ₄ , 5; and MgSO ₄ , 5 Mm	0.165	Acidic hydrolysis	Breus, Ryazanova, Dmitriev, Kulakovskaya, and Kulaev (2012)
<i>S. cerevisiae</i>	CRY, CNX	YPD with 20 mM potassium phosphate	0.086	Acidic hydrolysis	Ryazanova et al. (2011)
<i>S. cerevisiae</i>	VKM Y-1173	9 mM Pi	0.171	Acidic hydrolysis	Vagabov, Trilisenko, Kulakovskaya, and Kulaev (2008b)
<i>S. cerevisiae</i>	VKM Y-1176		0.065	n. a.	Vagabov, Trilisenko, Kulakovskaya, and Kulaev (2008a)
<i>S. cerevisiae</i>	VKM Y1173	medium with the usual Pi level 9 mM	0.047	Acidic hydrolysis	Trilisenko, Vagabov, and Kulaev (2002)

environmental pollution. This approach not only mitigates waste disposal issues but also recycles nutrients back into the agricultural ecosystem, promoting a circular economy (Rashchi & Finch, 2000; Wykoff et al., 2007).

3. Polyphosphates in the food industry

PolyP are widely utilized in the food industry due to their multi-functional properties that enhance food quality, preservation, and nutritional value (Valencia, 2023).

The studies summarized in Table 2 showcase their diverse applications across various food matrices, highlighting their ability to enhance food safety and stability. Monosodium Phosphate (MSP) and Monopotassium Phosphate (MKP) are commonly used to stabilize pH, improve texture, and extend shelf life in dairy and processed foods, particularly in low-sodium options (Nogueira et al., 2018).

Disodium Phosphate (DSP) and Dipotassium Phosphate (DKP) function as emulsifiers and stabilizers in food products, improving the texture and consistency of items like cheese, puddings, and desserts. DKP also provides potassium fortification, making it ideal for non-dairy creamers and products where potassium enrichment is desired. These diphosphates align with the growing demand for plant-based and non-dairy foods, supporting sustainable and alternative food choices (Santová et al., 2024).

Trisodium Phosphate (TSP) and Tripotassium Phosphate (TKP) are powerful pH adjusters used in processed foods to control pH and improve texture. TSP is effective in maintaining moisture in meat and poultry products, while TKP is used in meat substitutes and plant-based products to enhance texture and maintain moisture. Both compounds must be balanced with environmental concerns related to phosphate runoff, as the trend towards minimizing chemical additives and finding natural alternatives gains momentum (Amaral, Silva, & Lannes, 2018).

Sodium Tripolyphosphate (STPP) and Potassium Tripolyphosphate (KTPP) are widely used as preservatives and texturizers in seafood, meats, and poultry. STPP helps retain moisture, improve texture, and extend shelf life, reducing food waste. KTPP functions similarly but is preferred where potassium enrichment is beneficial, supporting the trend towards potassium fortification and reducing sodium intake. The use of these tripolyphosphates in sustainable seafood practices is significant for environmental conservation (Gonçalves & Ribeiro, 2008; S. Q. Xu, Zhou, Peng, Zhao, & Yao, 2009).

Tetrasodium Pyrophosphate (TSPP) and Tetrapotassium Pyrophosphate (TKPP) improve texture and stabilize proteins in processed foods. TSPP is commonly found in canned seafood and baked goods, where it helps maintain firmness and prevent the formation of struvite crystals. TKPP enhances texture, stabilizes proteins, and regulates acidity in meat products, dairy alternatives, and baking applications. These pyrophosphates are vital for clean labeling and natural ingredient trends, which are influencing the reduction of synthetic additives (Delgado-Pando, Ekonomou, Stratakos, & Pintado, 2021).

Sodium Acid Pyrophosphate (SAPP) is used as a leavening agent in baked goods, controlling carbon dioxide release for consistent rising and improved texture. It also prevents discoloration in processed seafood, canned food, cooked meat, flour and bovine serum albumin products (Azimirad, Zaheri, Javaheri-Ghezeldizaj, Yekta, & Ezzati Nazhad Dolatabadi, 2023).

The trend toward reducing chemical leavening agents and finding natural alternatives is significant, with Sodium Acid Pyrophosphate (SAPP) helping to extend the shelf life of baked goods and processed potatoes, thereby reducing food waste. Sodium Hexametaphosphate (SHMP) serves as a sequestrant and stabilizer in beverages and dairy products, preventing scale formation and maintaining product clarity. It also preserves the texture of seafood and meat during processing and storage. While SHMP supports sustainability by enhancing product stability and reducing waste, there is a growing push to minimize synthetic additives, driving research into natural alternatives (Yousefi,

Table 2

Overview of key studies evaluating the applications of polyphosphates across different food matrices. The table includes details on study years, source matrices, specific polyphosphates used, and References.

Source Matrix	Studies	Name of Polyphosphate Used	References
Dairy	Modelling Ion Composition in Simulated Milk Ultrafiltrate (SMUF)	Calcium Phosphate	Gao et al. (2010)
Fermented Foods	Relating physicochemical and microbiological safety indicators during processing of <i>linguiça</i> , a Portuguese traditional dry-fermented sausage	sodium polyphosphate	Gonzales-Barron et al. (2015)
Seafood	Determination of Polyphosphates in Fish and Shrimp Muscles by Capillary Electrophoresis	disodium hydrogen phosphate	Wang, Li, and Zhang (2015)
Meat	Low-field NMR determination of water distribution in meat batters with NaCl and polyphosphate addition	disodium hydrogen phosphate, monosodium phosphate, and polyphosphates (including sodium tripolyphosphate (STP), sodium pyrophosphate (SPP) and sodium hexametaphosphate (SHMP)	Shao et al. (2016)
Meat	Effects of polyphosphates and sodium chloride on heterocyclic amines in roasted beef patties as revealed by UPLC-MS/MS	odidium tripolyphosphate (TPP) and sodium pyrophosphate (PP)	Y. Li et al. (2020)
Seafood	Detection of Polyphosphates in Seafood and Its Relevance to Food Safety	hexametaphosphate, triphosphate and orthophosphate	Panseri et al. (2020)
Meat	Influence of Phosphate Chelators on White Efflorescence Formation in Dry Fermented Sausages	Di- and polyphosphate mixture TARI S78 (mostly diphosphates, 63.6% P2O5, 21% Na+) Polyphosphate P69 (67.8% P2O5, 23% Na+)	Hilbig, Wenzel, et al. (2020)
General	Impact of sodium lactate, encapsulated or unencapsulated polyphosphates, on food matrices	sodium tripolyphosphate, and sodium acid pyrophosphate	Tenderis, Kılıç, Yalçın, and Şimşek (2020)
General	Polyphosphates as an effective vehicle for delivery of bioavailable nanoparticulate iron (III)	pyrophosphate, tripolyphosphate and hexametaphosphate	S. Li et al. (2022)
Seafood	Analysis of added phosphates in hake fillets by ion-exchange chromatography: A case study of false positives induced	di-metaphosphates, tri-metaphosphates and And Triphosphates	Teixeira and Mendes (2022)

(continued on next page)

Table 2 (continued)

Source Matrix	Studies	Name of Polyphosphate Used	References
Dairy	by nucleotides coelution Food proteins from yeast-based fermentation: Simple purification of recombinant β -lactoglobulin using polyphosphate	salt hexametaphosphate (HMP)	Hoppenreijts, Annibal, Vreeke, Boom, and Keppler (2024)

Abbasi, & Mohammadifar, 2024).

Despite the widespread use of polyphosphates, there is a need for ongoing research and innovation focused on their safety. For example, chemical modifications or the development of alternative compounds could reduce health risks associated with excessive phosphate intake, such as kidney damage or cardiovascular issues. Additionally, the environmental concerns related to phosphate runoff necessitate more sustainable practices, such as controlled usage and the development of biodegradable or less environmentally persistent alternatives.

3.1. Meat products

Polyphosphates play a significant role in enhancing the quality and safety of meat products. These compounds, when used in conjunction with sodium chloride, have been shown to markedly reduce the formation of heterocyclic amines (HCAs) during cooking processes. HCAs, which form at high temperatures, are potentially carcinogenic and pose health risks when consumed (Y. Li et al., 2020). Polyphosphates modify the chemical environment during cooking, thus reducing the formation of HCAs and potentially lowering associated health risks. This reduction is primarily achieved by altering the pH and ionic strength of the cooking medium, which influences the chemical pathways involved in HCA formation (Deng et al., 2024).

Polyphosphates significantly enhance water retention in meat products, which is crucial for maintaining their texture and juiciness. Research indicates that polyphosphates improve the water-holding capacity of meat batters by binding with water molecules. This interaction prevents water molecules from binding with metal ions, thus preserving the desired texture and juiciness of the meat (Thangavelu, Kerry, Tiwari, & McDonnell, 2019). Additionally, white efflorescence (the formation of white, powdery deposits on the surface of food products), a common quality issue in production of dry fermented sausages, can be effectively addressed using polyphosphates. These compounds reduce white efflorescence formation by complexing with divalent cations such as magnesium and calcium, which typically form complexes with lactate, leading to efflorescence. By altering the crystallization process, polyphosphates reduce visible defects (Hilbig, Hartlieb, et al., 2020; Hilbig, Wenzel, et al., 2020).

Furthermore, different pre-salting methods impact the distribution of salt and water in meat products. Varying pre-salting techniques influence the distribution of salts, affecting the texture and flavor of meat products. From a sustainability perspective, the use of polyphosphates can be seen as a green chemistry approach, as it minimizes the need for additional additives and processing steps, thereby reducing the overall environmental footprint of meat production (Herrmann et al., 2023). Advances in the development of food-grade polyphosphates also emphasize their biodegradable nature, contributing to a more sustainable food processing industry (Herrmann et al., 2023).

3.2. Dairy products

Polyphosphates are essential in dairy products for stabilizing proteins and modifying ion composition. Sodium hexametaphosphate (SHMP) is particularly effective in this regard. Power, Fenelon, O'Mahony, and McCarthy (2019) revealed that dephosphorylation (DP) of casein reduces the viscosity of milk protein concentrate (MPC) solutions and that sodium hexametaphosphate (SHMP) interacts differently with DP-MPC and control MPC (C-MPC). SHMP sequesters calcium in C-MPC, causing micelle swelling and gelation at higher concentrations, while DP-MPC shows lower viscosity and gelation upon SHMP addition. These findings highlight the critical role of phosphate residues in maintaining micelle stability and offer strategies for controlling MPC viscosity in dairy products.

Polyphosphates help to stabilize these proteins, ensuring they replicate the functional properties of traditional dairy proteins like casein as according to Rulliere, Rondeau-Mouro, Raouche, Dufrechou, and Marchesseau (2013). In this study it was shown that ion chromatography effectively analyzed polyphosphates in aqueous solutions, while ^{31}P NMR allowed non-invasive analysis of interactions in milk and processed cheese. The study confirmed polyphosphates' role in casein solubilization and highlighted pyrophosphate's involvement in protein and calcium complexes during cheese manufacturing.

Besides that, Barth, Tormena, and Viotto (2017) investigated the effect of pH (5.2–6.8) on the hydrolysis of sodium polyphosphate in various matrices and its impact on cheese structure. Lower pH increased polyphosphate hydrolysis, with calcium accelerating this process. Milk showed higher hydrolysis rates than calcium caseinate. Lower pH led to granular cheese, while higher pH resulted in smoother textures, highlighting the need for precise pH control in cheese manufacturing.

By understanding the effects of pH on polyphosphate hydrolysis and cheese structure, manufacturers can optimize the processes to reduce waste and improve efficiency. Precise pH control can lead to better texture and quality of processed cheeses, minimizing the need for additives and reducing product spoilage. Efficient production processes and high-quality products contribute to a more sustainable dairy industry by saving resources and minimizing environmental impact.

3.3. Seafood products

Polyphosphates are approved as food additives (Regulation EC No 1129/2011), but their undeclared use is considered fraudulent. They enhance the water-holding capacity of seafood, preventing changes during commercialization. A recent study using advanced analytical techniques detected polyphosphates in various seafood products, highlighting the range of their application and the need for stringent food safety controls. Ensuring accurate labeling and detection supports sustainable practices by maintaining consumer trust and regulatory compliance, which is essential for the long-term viability of the seafood industry (Panseri et al., 2020).

Research has shown that partially replacing polyphosphates with alkaline electrolyzed water (AEW) in catfish fillets can maintain water retention, color, and texture while reducing chemical additive use. AEW treatments provided similar benefits to traditional polyphosphate treatments, suggesting that AEW can be a sustainable alternative. This reduction in polyphosphate use promotes more environmental friendly food processing practices, aligning with sustainability goals by minimizing chemical additives and their potential environmental impact (Lin, Hung, & Deng, 2020).

Another study on *Rutilus frisii kutum* (a species of fish commonly known as the Caspian kutum, native to the Caspian Sea). Demonstrated that polyphosphate treatments could delay spoilage and maintain quality during storage. By extending the shelf life of seafood, polyphosphates help reduce food waste, contributing to more sustainable food supply chains. This practice ensures that resources are used more efficiently, supporting the overall sustainability of the food industry by

reducing the environmental impact associated with food production and waste (Etemadian, Shabanpour, Sadeghi Mahoonak, Shabani, & Alami, 2011).

Their accurate detection and controlled use ensure product quality and compliance with food safety regulations, thereby preserving the natural and desirable characteristics of seafood.

3.4. Plant-based foods

Polyphosphates are important in vegetarian and vegan foods for improving texture and moisture retention. They help create the juiciness and firmness found in traditional meat products, making plant-based alternatives more satisfying. Additionally, polyphosphates enhance the stability and shelf life of these foods, ensuring they meet consumer expectations for quality. Bedin, Torricelli, Gigliano, De Leo, and Pulvirenti (2018) research aimed to develop recipes for plant-based würstel and mortadella for the Italian market, addressing the challenge of mimicking traditional textures and expanding market share. The results showed that vegan würstel and mortadella were successfully created using plant-based proteins, with tofu cubes added to mimic fat globules in mortadella. This stabilization is vital for producing alternative dairy products that have a similar texture and functionality to conventional dairy products.

4. Mechanisms of flavor impact

In this section, we discuss new insights into how polyphosphates enhance flavor in food systems and explore sustainable alternatives.

Starting with chemical additives already used in the food industry a study explored seaweed dietary fibre (SDF) as a potential alternative to phosphates in frankfurters, focusing on quality and flavor. Results showed that SDF improved cooking yield and texture, with 1.00% SDF being optimal. SDF also influenced aroma and taste, compensating for the loss of volatile flavor compounds without phosphates. These findings suggest SDF as a viable natural substitute for phosphates, aligning with consumer demand for healthier, more sustainable food options (Yuan et al., 2024).

Another study demonstrated that the use of complex phosphates (CP) and Maillard peptide complexes (MPCs) in areca nuts significantly reduced water activity (Aw), which in turn enhanced their shelf life and improved sensory attributes such as softness, pulpiness, and saltiness. The addition of phosphates was particularly effective in converting free water to bound water, thereby increasing water retention and softening the fibrous tissue (Zhu et al., 2024).

A biotechnological approach can reduce the need for synthetic additives and relies on renewable microbial processes to sustainably enhance food flavors sustainably. For instance, microorganisms such as *S. cerevisiae* and *E. coli* can be engineered to produce essential compounds like isopentenyl pyrophosphate and dimethylallyl diphosphate, which are intermediates in the biosynthesis of terpenoids and terpenes (Kirby & Keasling, 2009; Kong et al., 2023; Wu, Cheng, Cao, Qiao, & Zhao, 2019). These terpenes, including limonene can contribute significantly to the aroma, flavor, and color of various foods, highlighting the potential of phosphates produced by microorganisms.

Specifically in bacteria, limonene biosynthesis begins with the C10 unit GPP, catalyzed into L-limonene by L-limonene synthase (Yuan et al., 2024). Bacteria like *E. coli* possess the endogenous methylerythritol 4-phosphate (MEP) pathway that provides isoprene precursors necessary for limonene biosynthesis (Wu et al., 2019).

This biotechnological approach offers a sustainable solution, reducing the need for synthetic additives and relying on renewable microbial processes to maintain and improve the flavor profiles of foods (Yuan et al., 2024). Therefore, synergy among the microbial community and food ingredients promotes environmentally friendly and efficient food production practices. This aligns with sustainability goals by utilizing renewable resources to improve the overall quality and flavor

stability of food products.

5. Interaction of polyphosphates with proteins in food systems

Polyphosphates can bind to calcium ions, which are often associated with protein structures in dairy products. By sequestering these calcium ions, polyphosphates prevent the aggregation and precipitation of proteins. For example, sodium hexametaphosphate (SHMP) interacts with calcium ions in milk, stabilizing casein micelles and preventing their precipitation (Lambert & Watters, 1957; Walstra, 1990; van den Brink et al., 2016). This action is critical in preventing defects such as sedimentation in dairy products.

Polyphosphates, such as sodium hexametaphosphate (SHMP), can bind to calcium ions, which are crucial for maintaining protein structures in dairy products (Garcia, Alting, & Huppertz, 2023). In milk, calcium appears in two primary forms: ionic calcium, freely distributed throughout the liquid, and colloidal calcium phosphate (CCP), located within casein micelles (Y. Xu et al., 2016). The CCP neutralizes phosphoryl residues in proteins and stabilizes micelles by bridging caseins. Polyphosphates stabilize casein micelles by binding to calcium ions, preventing protein aggregation and precipitation, thus avoiding defects like sedimentation (Y. Xu et al., 2016).

SHMP significantly impacts the physicochemical parameters of micellar casein isolate (MCI) solutions by altering mineral equilibria and disrupting casein micelles (Power et al., 2019). Heat treatment also affects these parameters, causing pH to drop and viscosity to reduce sharply due to the hydrolysis of SHMP, which breaks down the network between SHMP and caseins (Garcia et al., 2023). During eight weeks of storage, MCI solutions with SHMP showed limited variations and good stability at both 20 °C and 40 °C, with no gelation or sedimentation (Garcia et al., 2023). Despite SHMP-induced structural changes, the stability of the solutions remained unaffected compared to those without SHMP (Garcia et al., 2023). These findings help the dairy industry better understand SHMP's effects on MCI solutions subjected to severe heat treatments, like continuous-flow or in-container sterilization, common in dairy beverage production.

Polyphosphates can stabilize proteins by binding to them or altering the ionic environment, which helps prevent denaturation and maintains the texture and functionality of food products. This is particularly important in processed cheese spreads, where the interaction between polyphosphates and proteins influences the final product's texture.

The stabilization process is also significantly affected by pH levels. Studies on processed cheese have shown that textural properties, such as hardness, cohesiveness, and relative adhesiveness, depend on the proportion and type of polyphosphates used, as well as the product's pH (Nagyová et al., 2014). For instance, a specific ratio of disodium phosphate (DSP) to tetrasodium diphosphate (TSPP) from 1:1 to 3:4 increases the hardness of the cheese when the polyphosphate content is low. This trend holds across various polyphosphates, though the absolute values differ (Nagyová et al., 2014).

Moreover, adjusting the pH of the cheese impacts its texture. Higher pH levels generally decrease hardness and cohesiveness while increasing relative adhesiveness, while lowering the pH has the opposite effect. The influence of pH adjustment on these properties highlights the careful balance needed to achieve the desired texture in processed cheese products.

In addition to traditional cheese products, recent studies have explored novel systems involving polyphosphates and proteins. For example, the phenomenon of reentrant condensation (RC), where a protein solution shifts between one- and two-phase states with changes in a single parameter, has been observed in mixtures of cola and milk (Furuki et al., 2024). At a pH of 3.2–3.6, cola induces milk condensation at specific concentrations, attributed to the interaction between polyphosphate in cola and casein in milk. This interaction demonstrates RC's potential for industrial food applications, offering insights into the behavior of proteins in contaminated environments (Furuki et al., 2024).

This cola/milk system illustrates how the concept of RC can be shifted from cell biology to industrial food production, promoting sustainable practices by optimizing protein utilization and reducing food waste (Furuki et al., 2024). Maybe, integrating RC into food science could lead to more efficient processing methods, enhancing both environmental and economic sustainability.

This transition can open new trends in utilizing uncommon compounds in food systems, providing sustainable alternatives to traditional chemical additives. This approach not only enhances food safety and quality but also supports environmentally friendly practices.

6. Phosphate and antimicrobial properties

Polyphosphates are widely recognized for their ability to inhibit bacterial growth, a property that varies with the structural length of their phosphate chains (Fusieger et al., 2022).

Notably, long-chain polyphosphates exhibit significantly higher inhibitory effects compared to their short-chain counterparts (Buňka, Salek, Kůrová, Buňková, & Lorencová, 2024; Lee, Hartman, Olson, et al., 1994; Lee, Hartman, Stahr, et al., 1994).

Even though phosphates have a mild bacteriostatic effect, Polyphosphate might have a particular inhibitory impact on gram-positive bacteria such as *Leuconostoc carnosum*, *Listeria monocytogenes*, *Staphylococcus aureus*, *Bacillus cereus*, *Bacillus stearothermophilus*, *Bacillus brevis*, *Bacillus subtilis*, *Bacillus sphaericus*, *Bacillus* sp., *Micrococcus luteus*, *Corynebacterium glutamicum* Lee, Hartman, Stahr, et al., 1994) They are also slightly effective against gram-negative bacteria including *Salmonella Typhimurium* and *E. coli* (Akhtar, Paredessabja, & Sarker, 2008).

PolyP can inhibit microorganisms growth by different mechanisms including: chelating metal ions which are required for cell division, lowering pH (PP that is acidic, like sodium acid pyrophosphate, or SPP), damaging the integrity of cell walls, and raising oxidative stress. (Feiner, 2006).

Limited research or reports may exist regarding the adverse interaction between polyphosphates and yeast. In a study conducted by Viviana Suárez et al., in 2007, it was found that phosphates with chain lengths ranging from 15 to 20 units exhibit the highest metal sequestering power and probably an inhibitory effect on yeast.

The primary inhibitory mechanism of long-chain polyphosphates is attributed to the chelation of divalent metal ions, such as Ca^{2+} and Mg^{2+} . These ions play a crucial role in forming transverse bridges among teichoic acids in the Gram-positive cell wall. By chelating these ions, long-chain polyphosphates disrupt essential physiological processes, thereby inhibiting bacterial growth (Lee, Hartman, Olson, et al., 1994). This chelation not only affects the stability of bacterial cell walls but also interferes with critical growth functions (Maier, Scherer, & Loessner, 1999).

7. Correlation of polyphosphates with the phosphorus cycle and food supply chain

In this topic, we focus on phosphorus cycling. Polyphosphates, particularly in EBPR systems, are important for maintaining sustainable food chains by ensuring the efficient use of phosphorus, an essential nutrient (Saunders, Oehmen, Blackall, Yuan, & Keller, 2003). These systems leverage PAOs, which facilitate phosphorus recycling through their cyclic release and uptake of phosphorus. This process not only supports environmental sustainability by reducing nutrient pollution but also enhances food security by maintaining soil fertility and productivity. Understanding the role of polyphosphates in these systems can lead to innovative strategies for sustainable agriculture and food production (Chen et al., 2022; Saad et al., 2016).

The removal of phosphates from wastewater is critical to preventing environmental issues such as eutrophication, which can lead to excessive herbaceous growth on streets or pavements and complications from over-fertilization. On average, 99.5% of phosphates and 76% of total

phosphorus are removed, highlighting the efficiency of current wastewater treatment technologies (Egea-Corbacho Lopera, Gutiérrez Ruiz, & Quiroga Alonso, 2019). These removal processes are essential in industries like food production and farming, which are significant contributors to the phosphate load in wastewater. Effective phosphate management supports the sustainability of the food supply chain by reducing the environmental impact of agricultural runoff and industrial waste, thereby ensuring that the surrounding ecosystems remain balanced and productive. Given their effectiveness in wastewater treatment, phosphates hold significant potential for application across various food production sectors, including dairy, meat, seafood, and plant-based foods (W. Li et al., 2024).

In dairy production, PolyPs are utilized to stabilize proteins and improve texture, which is crucial for products like cheese and yogurt. The correlation between polyphosphate use and the phosphorus cycle ensures that dairy wastewater is treated efficiently, reducing environmental impact while supporting sustainable dairy farming practices (Singh et al., 2024). Efficient EBPR and recycling in dairy processing plants help to maintain the nutrient balance in agricultural systems (Chang et al., 2023).

In the meat industry, PolyPs are employed to enhance the water-holding capacity of meat products, improving quality and shelf life. The integration of PAOs in meat processing wastewater treatment ensures that phosphorus is effectively removed and recycled, reducing eutrophication risks and promoting a more sustainable meat supply chain. This practice not only benefits the environment but also aligns with sustainable meat production goals (W. Li et al., 2024).

Seafood processing generates wastewater with high phosphorus content, necessitating efficient treatment methods. The application of PAOs in seafood wastewater treatment systems facilitates the removal and recycling of phosphorus, supporting sustainable aquaculture practices (Y. Zhang et al., 2024). By mitigating the environmental impact of phosphorus discharge, these systems help maintain the health of aquatic ecosystems, which is crucial for the sustainability of seafood supplies (Paytan & McLaughlin, 2007).

In plant-based food production, PolyPs are used to enhance the texture and stability of products like plant-based meats and dairy alternatives. The role of organophosphate esters (OPEs) in treating wastewater from these production processes ensures that phosphorus is efficiently managed and recycled (W. Li et al., 2024; Tian & Wang, 2020).

The food industry generates significant amounts of wastewater rich in phosphorus, necessitating effective treatment methods to prevent environmental pollution and enable resource recovery. PAOs in EBPR systems are instrumental in treating this wastewater, converting waste into valuable resources. By integrating PolyPs and PAOs, the food industry can enhance water quality, recycle phosphorus efficiently, and support sustainable practices, thereby reducing the environmental impact and contributing to a circular economy (Oehmen et al., 2007). Additionally, ongoing studies on yeast and bacterial polyphosphate transport mechanisms are crucial, as they provide insights into optimizing phosphorus uptake and release processes, thereby enhancing the efficiency of phosphorus recycling in diverse environmental conditions (Oehmen et al., 2007; Petriglieri et al., 2021).

The integration of PolyPs and PAOs across various food sectors underscores their importance in maintaining a sustainable food chain. By ensuring efficient phosphorus recycling and reducing environmental impact, these systems contribute to the overall goal of sustainable food production and environmental management (Oehmen et al., 2007).

8. Positive and negative aspects of PolyPs in food and human health

PolyP play significant roles in food processing and human health, with both beneficial and adverse impacts as described in Fig. 3.

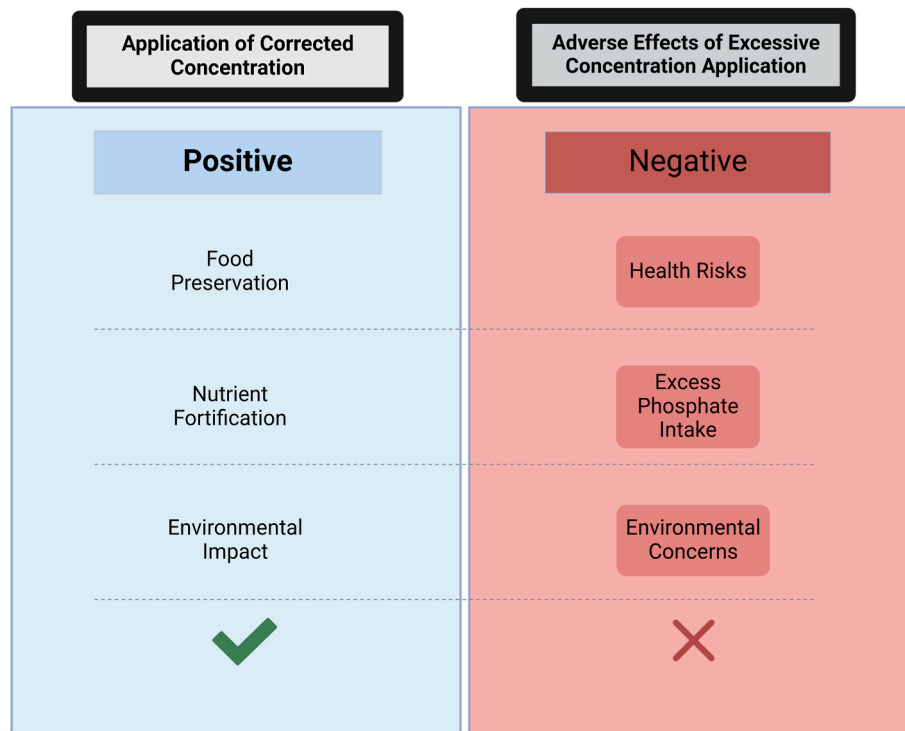


Fig. 3. This diagram contrasts the outcomes of applying polyphosphates at corrected versus excessive concentrations in food products. On the left, the application of corrected concentrations results in positive effects, including improved food preservation, nutrient fortification, and beneficial environmental impact. On the right, the adverse effects of excessive concentration application are highlighted, including health risks, excessive phosphate intake, and negative environmental concerns (Biorender software).

8.1. Positive aspects

PolyPs are widely used in food preservation and quality improvement. They enhance the water-holding capacity of processed meats, leading to improved juiciness and texture in products such as ham, sausages, and poultry. This moisture retention is essential for maintaining product quality during storage and cooking (O'Mahony et al., 2016). In dairy products, PolyPs act as stabilizers, preventing separation in creams and dressings and improving texture in cheese. Their ability to stabilize minerals in beverages also enhances the nutritional value of these products (Lukáčová et al., 2008). Additionally, PolyPs contribute to nutrient fortification by chelating minerals and making them more bioavailable. This fortification can help address deficiencies in essential minerals such as calcium, magnesium, and iron, contributing to better public health outcomes (Lee et al., 2017). In functional foods, PolyPs are used to encapsulate sensitive nutrients and probiotics, protecting them during processing and storage, ensuring their viability and health benefits (Rao et al., 2009).

8.2. Negative aspects

Excessive dietary intake of phosphates can pose significant health risks, particularly affecting kidney and cardiovascular health. High phosphate consumption has been linked to kidney calcification and nephropathy, with chronic exposure causing notable renal damage in both humans and animals (EFSA Panel on Food Additives and Flavourings (FAF) et al., 2019). Additionally, evidence suggests a potential association between high phosphate intake and increased risk of cardiovascular diseases. Human studies indicate that consuming more than 3000 mg of phosphates per day can impair renal function, especially in those with pre-existing kidney conditions (EFSA Panel on Food Additives and Flavourings (FAF) et al., 2019).

The gastrointestinal effects of high phosphate intake are also concerning. Consumption above 2000 mg/day can lead to discomfort, such

as soft stools or diarrhea, while significantly higher doses used for bowel cleansing act as strong cathartic agents. Regulatory measures are necessary to manage phosphate levels in food additives, particularly to protect vulnerable groups like infants, toddlers, and individuals with renal issues who are at risk of exceeding the acceptable daily intake (ADI) and experiencing adverse health effects (EFSA Panel on Food Additives and Flavourings (FAF) et al., 2019).

Phosphates in food supplements are an additional concern, as intake estimates suggest that people may exceed the proposed ADI, highlighting the need for potential revisions in the permitted levels of these additives. Continuous monitoring and re-evaluation of the safety of phosphates in food and supplements are essential to ensure consumer safety (EFSA Panel on Food Additives and Flavourings (FAF) et al., 2019). PolyPs offer significant benefits in food preservation, quality improvement, and nutrient fortification, their use must be carefully managed to avoid potential health risks. Ensuring appropriate usage levels and clear labeling can help maximize the benefits while minimizing the drawbacks associated with PolyPs in food products.

9. Prospective and challenges of polyphosphate utilization in food and environmental sustainability

9.1. Prospective

The use of PolyPs in food processing holds significant potential for enhancing food quality and nutritional value. Additionally, their ability to fortify foods with essential minerals like calcium, magnesium, and iron can address nutritional deficiencies and promote public health. Future innovations may explore more efficient and targeted fortification techniques, leveraging PolyPs to deliver specific health benefits in functional foods and nutraceuticals.

The role of PAOs in EBPR processes presents a promising avenue for improving wastewater treatment technologies. By optimizing the conditions for PAO activity, wastewater treatment plants can achieve more

effective phosphate removal, reducing the risk of eutrophication in water bodies. Advancements in microbial engineering and bioreactor design could enhance the efficiency of these processes, making wastewater treatment more sustainable and environmentally friendly. Furthermore, integrating polyphosphate metabolism with nutrient recovery systems could provide a valuable source of reclaimed phosphorus for agricultural use, promoting a circular economy.

PolyPs have potential applications in environmental remediation, particularly in mitigating sulfate contamination. By managing the availability of nutrients through polyphosphate metabolism, the growth of sulfate-reducing bacteria (SRB) and the production of hydrogen sulfide (H₂S) can be controlled (Bagheri Novair, Biglari Quchan Atigh, Asgari Lajayer, Shu, & Price, 2024). This approach could be integrated into broader bioremediation strategies to address contamination in industrial and natural environments. Research into the interactions between PolyPs and other environmental pollutants could uncover new methods for detoxifying contaminated sites and restoring ecological balance.

9.2. Challenges

Despite their benefits, the use of PolyPs in food products raises health and safety concerns.

While previous studies have provided important insights into how PolyPs work in microbes, they tend to focus heavily on the biological and chemical aspects, leaving some crucial areas underexplored. For instance, there's limited information on the specific types of PolyPs found inside yeast and bacterial cells, and whether these particular forms have unique benefits that could be applied directly in food science. Additionally, the potential for using these PolyPs in sustainable food processing hasn't been fully investigated. Addressing these gaps is essential for translating the basic science into practical, sustainable applications in the food industry.

Excessive consumption of PolyPs can lead to imbalances in phosphate metabolism, potentially causing kidney damage, cardiovascular issues, and weakened bone health. Regulatory agencies must establish and enforce guidelines to ensure safe levels of polyphosphate use in food products. Ongoing research is needed to better understand the long-term health effects of polyphosphate consumption and to develop safer alternatives or complementary strategies for achieving similar food quality improvements.

The industrial use of PolyPs must be carefully managed to balance their benefits with potential environmental impacts. For example, the overuse of PolyPs in agriculture and food processing could lead to phosphate run-off and subsequent eutrophication of water bodies. Developing more sustainable practices for polyphosphate application, including precision agriculture techniques and controlled-release formulations, can help mitigate these risks. Additionally, the integration of polyphosphate management with broader sustainability initiatives, such as the reduction of waste and the promotion of resource recovery, is essential for minimizing environmental impact.

Implementing advanced polyphosphate-based technologies in food processing and environmental management faces technical and economic barriers. The development and scaling of efficient polyphosphate recovery and recycling systems require significant investment in research and infrastructure. Additionally, optimizing microbial polyphosphate metabolism for industrial applications involves complex genetic and metabolic engineering challenges. Collaboration between industry, academia, and government agencies is necessary to overcome these barriers and to translate scientific advancements into practical, cost-effective solutions.

Public perception and acceptance of PolyPs in food and environmental applications can influence their widespread adoption. Transparent communication about the benefits and risks associated with PolyPs is crucial for gaining consumer trust. Educational initiatives that highlight the role of PolyPs in improving food quality and

environmental sustainability can help address misconceptions and promote informed decision-making. Engaging stakeholders, including consumers, industry professionals, and policymakers, in the development and implementation of polyphosphate technologies can foster a collaborative approach to address these challenges. The utilization of PolyPs in food processing and environmental management presents significant opportunities for enhancing quality, sustainability, and public health. However, addressing the associated challenges requires a balanced and informed approach. By advancing research, optimizing technologies, and fostering collaboration, the potential benefits of PolyPs can be realized while mitigating risks and promoting a sustainable future.

10. Conclusion

The widespread use of polyphosphates necessitates a balanced approach, particularly in light of emerging concerns regarding their impact on human health. High dietary phosphate intake has been increasingly associated with adverse health outcomes, including renal dysfunction, cardiovascular disease, and disrupted calcium homeostasis. These potential risks call for a more judicious application of polyphosphates within the food industry, guided by rigorous scientific assessment and regulatory oversight.

The development of next-generation polyphosphate formulations, with improved safety profiles, alongside the exploration of alternative compounds, represents a forward-looking strategy to mitigate these risks while retaining the functional benefits that polyphosphates offer.

A promising area of research lies in the characterization and application of SpolyPs produced through microbial approaches. These compounds, synthesized by yeast and bacteria, offer a natural and potentially safer alternative to chemically synthesized polyphosphates.

Understanding the specific properties of these microbial polyphosphates, particularly their role in energy storage and stress response in microorganisms, could lead to innovative applications in food systems. Such research could uncover new ways to enhance food quality and shelf life while reducing the reliance on synthetic additives.

Additionally, the sustainable production of these SpolyPs through microbial processes aligns with the broader goals of reducing environmental impact and promoting green chemistry in food production.

From a sustainability perspective, polyphosphates also offer potential in reducing environmental impact through their role in microbial processes that support nutrient recycling and waste reduction. Their application in wastewater treatment, for example, helps mitigate environmental issues such as eutrophication by enabling efficient phosphorus recovery and recycling. This not only supports environmental health but also contributes to the sustainability of food production systems by closing nutrient loops and reducing the dependency on chemical fertilizers.

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Declarations

Conflict of interest, the authors declare no conflict of interest.

Data availability

No data was used for the research described in the article.

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References

- Achbergerová, L., & Nahálka, J. (2011). Polyphosphate—an ancient energy source and active metabolic regulator. *Microbial Cell Factories*, *10*(1), 63. <https://doi.org/10.1186/1475-2859-10-63>
- Acosta-Zaldívar, M., Qi, W., Mishra, A., Roy, U., King, W. R., Patton-Vogt, J., et al. (2024). *Candida albicans*' inorganic phosphate transport and evolutionary adaptation to phosphate scarcity. <https://doi.org/10.1101/2024.01.29.577887>.
- Akhtar, S., Paredessabja, D., & Sarker, M. (2008). Inhibitory effects of polyphosphates on *Clostridium perfringens* growth, sporulation and spore outgrowth. *Food Microbiology*, *25*(6), 802–808. <https://doi.org/10.1016/j.fm.2008.04.006>
- Albi, T., & Serrano, A. (2016). Inorganic polyphosphate in the microbial world. Emerging roles for a multifaceted biopolymer. *World Journal of Microbiology and Biotechnology*, *32*(2), 27. <https://doi.org/10.1007/s11274-015-1983-2>
- Amaral, A. B., Silva, M. V. da, & Lannes, S. C. da S. (2018). Lipid oxidation in meat: Mechanisms and protective factors – a review. *Food Science and Technology*, *38*, 1–15. <https://doi.org/10.1590/15190011832518>
- Andreeva, N., Ryazanova, L., Zvonarev, A., Trilisenko, L., Kulakovskaya, T., & Eldarov, M. (2018). Inorganic polyphosphate in methylotrophic yeasts. *Applied Microbiology and Biotechnology*, *102*(12), 5235–5244. <https://doi.org/10.1007/s00253-018-9008-3>
- Andreeva, N., Trilisenko, L., Eldarov, M., & Kulakovskaya, T. (2015). Polyphosphatase PPN1 of *Saccharomyces cerevisiae*: Switching of exopolyphosphatase and endopolyphosphatase activities. *PLoS One*, *10*(3), Article e0119594. <https://doi.org/10.1371/journal.pone.0119594>
- Azimirad, M., Zaheri, M., Javaheri-Ghezeldizaj, F., Yekta, R., & Ezzati Nazhad Dolatabadi, J. (2023). Probing binding mode between sodium acid pyrophosphate and albumin: Multi-spectroscopic and molecular docking analysis. *Journal of Biomolecular Structure and Dynamics*, 1–8. <https://doi.org/10.1080/07391102.2023.2272197>
- Bagheri Novair, S., Biglari Quchan Atigh, Z., Asgari Lajayer, B., Shu, W., & Price, G. W. (2024). The role of sulphate-reducing bacteria (SRB) in bioremediation of sulphate-rich wastewater: Focus on the source of electron donors. *Process Safety and Environmental Protection*, *184*, 190–207. <https://doi.org/10.1016/j.psep.2024.01.103>
- Barth, A. P., Tormena, C. F., & Viotto, W. H. (2017). pH influences hydrolysis of sodium polyphosphate in dairy matrices and the structure of processed cheese. *Journal of Dairy Science*, *100*(11), 8735–8743. <https://doi.org/10.3168/jds.2017-12764>
- Bedin, E., Torricelli, C., Gigliano, S., De Leo, R., & Pulvirenti, A. (2018). Vegan foods: Mimit meat products in the Italian market. *International Journal of Gastronomy and Food Science*, *13*, 1–9. <https://doi.org/10.1016/j.ijgfs.2018.04.003>
- Breus, N. A., Ryazanova, L. P., Dmitriev, V. V., Kulakovskaya, T. V., & Kulaev, I. S. (2012). Accumulation of phosphate and polyphosphate by *Cryptococcus humicola* and *Saccharomyces cerevisiae* in the absence of nitrogen. *FEMS Yeast Research*, *12*(6), 617–624. <https://doi.org/10.1111/j.1567-1364.2012.00812.x>
- Buňka, F., Salek, R. N., Kúrová, V., Buňková, L., & Lorencová, E. (2024). The impact of phosphate- and citrate-based emulsifying salts on processed cheese techno-functional properties: A review. *International Dairy Journal*, *106031*. <https://doi.org/10.1016/j.idairyj.2024.106031>
- Calabrese, I., & Riccardi, G. (2019). Effectiveness of changes in diet composition on reducing the incidence of cardiovascular disease. *Current Cardiology Reports*, *21*(9), 88. <https://doi.org/10.1007/s11886-019-1176-y>
- Calvo, M. S., & Uribarri, J. (2013). Public health impact of dietary phosphorus excess on bone and cardiovascular health in the general population. *The American Journal of Clinical Nutrition*, *98*(1), 6–15. <https://doi.org/10.3945/ajcn.112.053934>
- Chang, Y.-L., Nagarajan, D., Chen, J.-H., Yen Chen, C., Wu, Y.-J., Whang, L.-M., et al. (2023). Microalgae-bacteria consortia for the treatment of raw dairy manure wastewater using a novel two-stage process: Process optimization and bacterial community analysis. *Chemical Engineering Journal*, *473*, Article 145388. <https://doi.org/10.1016/j.cej.2023.145388>
- Chekabab, S. M., Harel, J., & Dozois, C. M. (2014). Interplay between genetic regulation of phosphate homeostasis and bacterial virulence. *Virulence*, *5*(8), 786–793. <https://doi.org/10.4161/viru.29307>
- Chen, L., Chen, H., Hu, Z., Tian, Y., Wang, C., Xie, P., et al. (2022). Carbon uptake bioenergetics of PAOs and GAOs in full-scale enhanced biological phosphorus removal systems. *Water Research*, *216*, Article 118258. <https://doi.org/10.1016/j.watres.2022.118258>
- Choudhary, D. K., Kasotia, A., Jain, S., Vaishnav, A., Kumari, S., Sharma, K. P., et al. (2016). Bacterial-mediated tolerance and resistance to plants under abiotic and biotic stresses. *Journal of Plant Growth Regulation*, *35*(1), 276–300. <https://doi.org/10.1007/s00344-015-9521-x>
- Christ, J. J., & Blank, L. M. (2019). *Saccharomyces cerevisiae* containing 28% polyphosphate and production of a polyphosphate-rich yeast extract thereof. *FEMS Yeast Research*, *19*(3), Article foz011. <https://doi.org/10.1093/femsyr/foz011>
- Delgado-Pando, G., Ekonomou, S. I., Stratakos, A. C., & Pintado, T. (2021). Clean label alternatives in meat products. *Foods*, *10*(7), 1615. <https://doi.org/10.3390/foods10071615>
- Demling, P., Baier, M., Deitert, A., Fees, J., & Blank, L. M. (2024). Biotechnological polyphosphate as an opportunity to contribute to the circularization of the phosphate economy. *Current Opinion in Biotechnology*, *87*, Article 103107. <https://doi.org/10.1016/j.copbio.2024.103107>
- Deng, P., Teng, S., Zhou, Y., Liu, Y., Liao, B., Ren, X., et al. (2024). Effects of basic amino acids on heterocyclic amines and quality characteristics of fried beef patties at low NaCl level. *Meat Science*, *215*, Article 109541. <https://doi.org/10.1016/j.meatsci.2024.109541>
- Dohan, S., Mathias, P. B., Armel, Z. N., Delwendé, I. K., Gnankambary, Z., & Papoba, M. S. (2023). Potential of biogas and organic fertilizers production through anaerobic digestion of slaughterhouse waste in ouagadougou, Burkina Faso. *International Journal of Agriculture and Biosciences*, *12*(1), 27–30. <https://doi.org/10.47278/journal.ijab.2022.041>
- Egea-Corbacho Lopera, A., Gutiérrez Ruiz, S., & Quiroga Alonso, J. M. (2019). Removal of emerging contaminants from wastewater using reverse osmosis for its subsequent reuse: Pilot plant. *Journal of Water Process Engineering*, *29*, Article 100800. <https://doi.org/10.1016/j.jwpe.2019.100800>
- Erecinska, M., Stubbs, M., Miyata, Y., Ditre, C. M., & Wilson, D. F. (1977). Regulation of cellular metabolism by intracellular phosphate. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*, *462*(1), 20–35. [https://doi.org/10.1016/0005-2728\(77\)90186-4](https://doi.org/10.1016/0005-2728(77)90186-4)
- Etemadian, Y., Shabanpour, B., Sadeghi Mahoonak, A. R., Shabani, A., & Alami, M. (2011). Cryoprotective effects of polyphosphates on *Rutilus frisii kutum* fillets during ice storage. *Food Chemistry*, *129*(4), 1544–1551. <https://doi.org/10.1016/j.foodchem.2011.06.005>
- Fees, J., Christ, J. J., Willbold, S., & Blank, L. M. (2023). Biotechnological production of polyphosphate from industrial wash water. *Biotechnology and Bioengineering*, *120*(2), 456–464. <https://doi.org/10.1002/bit.28274>
- Feng, Y., Yang, Y., Li, S., Wu, H., & Zhao, T. (2022). Enrichment and delivery of bioavailable zinc by microalgae polyphosphate nanoparticles. *Lebensmittel-Wissenschaft & Technologie*, *167*, Article 113818. <https://doi.org/10.1016/j.lwt.2022.113818>
- Furuki, T., Nobeyama, T., Suetaka, S., Matsui, R., Fukuoka, T., Arai, M., et al. (2024). Reentrant condensation of a multicomponent cola/milk system induced by polyphosphate. *Food Chemistry X*, *21*, Article 101165. <https://doi.org/10.1016/j.fochx.2024.101165>
- Gao, R., Van Halsema, F. E. D., Temminghoff, E. J. M., Van Leeuwen, H. P., Van Valenbergh, H. J. F., Eisner, M. D., et al. (2010). Modelling ion composition in simulated milk ultrafiltrate (SMUF). I: Influence of calcium phosphate precipitation. *Food Chemistry*, *122*(3), 700–709. <https://doi.org/10.1016/j.foodchem.2010.03.040>
- García, A., Alting, A., & Huppertz, T. (2023). Effect of sodium hexametaphosphate on heat-induced changes in micellar casein isolate solutions. *International Dairy Journal*, *140*, Article 105583. <https://doi.org/10.1016/j.idairyj.2023.105583>
- Gerasimaite, R., Pavlovic, I., Capolicchio, S., Hofer, A., Schmidt, A., Jessen, H. J., et al. (2017). Inositol pyrophosphate specificity of the SPX-dependent polyphosphate polymerase VTC. *ACS Chemical Biology*, *12*(3), 648–653. <https://doi.org/10.1021/acscmbio.7b00026>
- Goemaere, O., Glorieux, S., Govaert, M., Steen, L., & Fraeye, I. (2021). Phosphate elimination in emulsified meat products: Impact of protein-based ingredients on quality characteristics. *Foods*, *10*(4), 882. <https://doi.org/10.3390/foods10040882>
- Gonçalves, A. A., & Ribeiro, J. L. D. (2008). Do phosphates improve the seafood quality? Reality and legislation. *Pan-American Journal of Aquatic Sciences*, *3*(3), 237–247.
- Gonzales-Barron, U., Cadavez, V., Pereira, A. P., Gomes, A., Araújo, J. P., Saavedra, M. J., et al. (2015). Relating physicochemical and microbiological safety indicators during processing of linguica, a Portuguese traditional dry-fermented sausage. *Food Research International*, *78*, 50–61. <https://doi.org/10.1016/j.foodres.2015.11.007>
- Hassan, S. A., Abbas, M., Zia, S., Maan, A. A., Khan, M. K. I., Hassoun, A., et al. (2024). An appealing review of industrial and nutraceutical applications of pistachio waste. *Critical Reviews in Food Science and Nutrition*, *64*(10), 3103–3121. <https://doi.org/10.1080/10408398.2022.2130158>
- Herrmann, K. R., Fees, J., Christ, J. J., Hofmann, L., Block, C., Herzberg, D., et al. (2023). Biotechnological production of food-grade polyphosphate from deoiled seeds and bran. *EFB Bioeconomy Journal*, *3*, Article 100048. <https://doi.org/10.1016/j.bioeco.2023.100048>
- Hilbig, J., Hartlieb, K., Herrmann, K., Weiss, J., & Gibis, M. (2020a). Influence of phosphates and pH value on white efflorescence formation on dry fermented sausages. *European Food Research and Technology*, *246*(3), 471–484. <https://doi.org/10.1007/s00217-019-03415-9>
- Hilbig, J., Wenzel, H., Herrmann, K., Weiss, J., & Gibis, M. (2020b). Effects of combined measures to minimize white efflorescence formation on dry fermented sausages co-extruded with alginate casings. *Journal of Food Science*, *85*(8), 2350–2357. <https://doi.org/10.1111/1750-3841.15333>
- Hoppenreijls, L. J. G., Annibal, A., Vreeke, G. J. C., Boom, R. M., & Keppler, J. K. (2024). Food proteins from yeast-based precision fermentation: Simple purification of recombinant β -lactoglobulin using polyphosphate. *Food Research International*, *176*, Article 113801. <https://doi.org/10.1016/j.foodres.2023.113801>
- Hothorn, M., Neumann, H., Lenherr, E. D., Wehner, M., Rybin, V., Hassa, P. O., et al. (2009). Catalytic core of a membrane-associated eukaryotic polyphosphate polymerase. *Science*, *324*(5926), 513–516. <https://doi.org/10.1126/science.1168120>
- Jansson, J., Nilsson, J., Modig, F., & Hed Vall, G. (2017). Commitment to sustainability in small and medium-sized enterprises: The influence of strategic orientations and management values. *Business Strategy and the Environment*, *26*(1), 69–83. <https://doi.org/10.1002/bse.1901>

- Jensen, L. T., Ajua-Alemanji, M., & Culotta, V. C. (2003). The *Saccharomyces cerevisiae* high affinity phosphate transporter encoded by PHO84 also functions in manganese homeostasis. *Journal of Biological Chemistry*, 278(43), 42036–42040. <https://doi.org/10.1074/jbc.M307413200>
- Karl, D. M., & Björkman, K. M. (2015). Dynamics of dissolved organic phosphorus. In *Biogeochemistry of marine dissolved organic matter* (pp. 233–334). Elsevier. <https://doi.org/10.1016/B978-0-12-405940-5.00005-4>
- Kemi, V. E., Kärkkäinen, M. U. M., & Lamberg-Allardt, C. J. E. (2006). High phosphorus intakes acutely and negatively affect Ca and bone metabolism in a dose-dependent manner in healthy young females. *British Journal of Nutrition*, 96(3), 545–552. <https://doi.org/10.1079/BJN20061838>
- Kirby, J., & Keasling, J. D. (2009). Biosynthesis of plant isoprenoids: Perspectives for microbial engineering. *Annual Review of Plant Biology*, 60(1), 335–355. <https://doi.org/10.1146/annurev.arplant.043008.091955>
- Kong, X., Wu, Y., Yu, W., Liu, Y., Li, J., Du, G., et al. (2023). Efficient synthesis of limonene in *Saccharomyces cerevisiae* using combinatorial metabolic engineering strategies. *Journal of Agricultural and Food Chemistry*, 71(20), 7752–7764. <https://doi.org/10.1021/acs.jafc.3c02076>
- Kulaev, I., & Kulakovskaya, T. (2000). Polyphosphate and phosphate pump. *Annual Review of Microbiology*, 54(1), 709–734. <https://doi.org/10.1146/annurev.micro.54.1.709>
- Lee, R. M., Hartman, P. A., Olson, D. G., & Williams, F. D. (1994a). Bactericidal and bacteriolytic effects of selected food-grade phosphates, using *Staphylococcus aureus* as a model system. *Journal of Food Protection*, 57(4), 276–283. <https://doi.org/10.4315/0362-028X-57.4.276>
- Lee, R. M., Hartman, P. A., Stahr, H. M., Olson, D. G., & Williams, F. D. (1994b). Antibacterial mechanism of long-chain polyphosphates in *Staphylococcus aureus*. *Journal of Food Protection*, 57(4), 289–294. <https://doi.org/10.4315/0362-028X-57.4.289>
- Li, W., Chen, J., Bie, Q., Chen, X., Huang, Y., Zhang, K., et al. (2024). Exploring organophosphate ester contamination and distribution in food: A meta-analysis. *Food Chemistry*, 456, Article 140035. <https://doi.org/10.1016/j.foodchem.2024.140035>
- Li, S., Guo, T., Guo, W., Cui, X., Zeng, M., & Wu, H. (2022). Polyphosphates as an effective vehicle for delivery of bioavailable nanoparticulate iron(III). *Food Chemistry*, 373, Article 131477. <https://doi.org/10.1016/j.foodchem.2021.131477>
- Li, Y., He, J., Quan, W., He, Z., Qin, F., Tao, G., et al. (2020). Effects of polyphosphates and sodium chloride on heterocyclic amines in roasted beef patties as revealed by UPLC-MS/MS. *Food Chemistry*, 326, Article 127016. <https://doi.org/10.1016/j.foodchem.2020.127016>
- Lichko, L., Kulakovskaya, T., Pestov, N., & Kulaev, I. (2006). Inorganic polyphosphates and exopolyphosphates in cell compartments of the yeast *Saccharomyces cerevisiae* under inactivation of *PPX1* and *PPN1* genes. *Bioscience Reports*, 26(1), 45–54. <https://doi.org/10.1007/s10540-006-9003-2>
- Lin, H.-M., Hung, Y.-C., & Deng, S.-G. (2020). Effect of partial replacement of polyphosphate with alkaline electrolyzed water (AEW) on the quality of catfish filets. *Food Control*, 112, Article 107117. <https://doi.org/10.1016/j.foodcont.2020.107117>
- Magkiriadou, S., Stepp, W. L., Newman, D. K., Manley, S., & Racki, L. R. (2024). Polyphosphate affects cytoplasmic and chromosomal dynamics in nitrogen-starved *Pseudomonas aeruginosa*. *Proceedings of the National Academy of Sciences*, 121(15), Article e2313004121. <https://doi.org/10.1073/pnas.2313004121>
- Maier, S. K., Scherer, S., & Loessner, M. J. (1999). Long-chain polyphosphate causes cell lysis and inhibits *Bacillus cereus* septum formation, which is dependent on divalent cations. *Applied and Environmental Microbiology*, 65(9), 3942–3949. <https://doi.org/10.1128/AEM.65.9.3942-3949.1999>
- Martiny, A. C., Treseder, K., & Pusch, G. (2013). Phylogenetic conservatism of functional traits in microorganisms. *The ISME Journal*, 7(4), 830–838. <https://doi.org/10.1038/ismej.2012.160>
- Marzan, L., & Shimizu, K. (2011). Metabolic regulation of *Escherichia coli* and its *phoB* and *phoR* genes knockout mutants under phosphate and nitrogen limitations as well as at acidic condition. *Microbial Cell Factories*, 10(1), 39. <https://doi.org/10.1186/1475-2859-10-39>
- McCarthy, L., & Downey, M. (2023). The emerging landscape of eukaryotic polyphosphatases. *FEBS Letters*, 597(11), 1447–1461. <https://doi.org/10.1002/1873-3468.14584>
- Muyzer, G., & Stams, A. J. M. (2008). The ecology and biotechnology of sulphate-reducing bacteria. *Nature Reviews Microbiology*, 6(6), 441–454. <https://doi.org/10.1038/nrmicro1892>
- Nagyová, G., Buňka, F., Salek, R. N., Černíková, M., Mančík, P., Grüber, T., et al. (2014). Use of sodium polyphosphates with different linear lengths in the production of spreadable processed cheese. *Journal of Dairy Science*, 97(1), 111–122. <https://doi.org/10.3168/jds.2013-7210>
- Neville, N., Roberge, N., & Jia, Z. (2022). Polyphosphate kinase 2 (PPK2) enzymes: Structure, function, and roles in bacterial physiology and virulence. *International Journal of Molecular Sciences*, 23(2), 670. <https://doi.org/10.3390/ijms23020670>
- Nogueira, E. B., Costa-Lima, B. R. C., Torres, F., Regazone, A. V., Melo, L., Franco, R. M., et al. (2018). Effect of potassium-based emulsifying salts on the sensory and physicochemical parameters of low-sodium spreadable processed cheese. *International Journal of Dairy Technology*, 71(3), 717–722. <https://doi.org/10.1111/1471-0307.12519>
- Oehmen, A., Lemos, P., Carvalho, G., Yuan, Z., Keller, J., Blackall, L., et al. (2007). Advances in enhanced biological phosphorus removal: From micro to macro scale. *Water Research*, 41(11), 2271–2300. <https://doi.org/10.1016/j.watres.2007.02.030>
- Ogawa, N., DeRisi, J., & Brown, P. O. (2000). New components of a system for phosphate accumulation and polyphosphate metabolism in *Saccharomyces cerevisiae* revealed by genomic expression analysis. *Molecular Biology of the Cell*, 11(12), 4309–4321. <https://doi.org/10.1091/mbc.11.12.4309>
- Panseri, S., Arioli, F., Biolatti, C., Mosconi, G., Pavlovic, R., & Chiesa, L. M. (2020). Detection of polyphosphates in seafood and its relevance toward food safety. *Food Chemistry*, 332, Article 127397. <https://doi.org/10.1016/j.foodchem.2020.127397>
- Paytan, A., & McLaughlin, K. (2007). The oceanic phosphorus cycle. *Chemical Reviews*, 107(2), 563–576. <https://doi.org/10.1021/cr0503613>
- Petriglieri, F., Singleton, C., Peces, M., Petersen, J. F., Nierychlo, M., & Nielsen, P. H. (2021). “*Candidatus* Dechloromonas phosphoritropha” and “*Ca. D.* phosphorivorans”. *Novel Polyphosphate Accumulating Organisms Abundant in Wastewater Treatment Systems*. *The ISME Journal*, 15(12), 3605–3614. <https://doi.org/10.1038/s41396-021-01029-2>
- Petroll, K., Kopp, D., Care, A., Bergquist, P. L., & Sunna, A. (2019). Tools and strategies for constructing cell-free enzyme pathways. *Biotechnology Advances*, 37(1), 91–108. <https://doi.org/10.1016/j.biotechadv.2018.11.007>
- Piperčević, J., Kohl, B., Gerasimaite, R., Comte-Miserez, V., Hostachy, S., Müntener, T., et al. (2023). Inositol pyrophosphates activate the vacuolar transport chaperone complex in yeast by disrupting a homotypic SPX domain interaction. *Nature Communications*, 14(1), 2645. <https://doi.org/10.1038/s41467-023-38315-w>
- Power, O. M., Fenelon, M. A., O'Mahony, J. A., & McCarthy, N. A. (2019). Dephosphorylation of caseins in milk protein concentrate alters their interactions with sodium hexametaphosphate. *Food Chemistry*, 271, 136–141. <https://doi.org/10.1016/j.foodchem.2018.07.086>
- Qi, W., Baldwin, S. A., Muench, S. P., & Baker, A. (2016). Pi sensing and signalling: From prokaryotic to eukaryotic cells. *Biochemical Society Transactions*, 44(3), 766–773. <https://doi.org/10.1042/BST20160026>
- Racki, L. R., Tocheva, E. I., Dieterle, M. G., Sullivan, M. C., Jensen, G. J., & Newman, D. K. (2017). Polyphosphate granule biogenesis is temporally and functionally tied to cell cycle exit during starvation in *Pseudomonas aeruginosa*. *Proceedings of the National Academy of Sciences*, 114(12). <https://doi.org/10.1073/pnas.1615575114>
- Ranganathan, S. (1992). Fortification of common salt with iron: Use of polyphosphate stabilisers. *Food Chemistry*, 45(4), 263–267. [https://doi.org/10.1016/0308-8146\(92\)90158-X](https://doi.org/10.1016/0308-8146(92)90158-X)
- Rangarajan, E. S., Nadeau, G., Li, Y., Wagner, J., Hung, M.-N., Schrag, J. D., et al. (2006). The structure of the exopolyphosphatase (PPX) from *Escherichia coli* O157:H7 suggests a binding mode for long polyphosphate chains. *Journal of Molecular Biology*, 359(5), 1249–1260. <https://doi.org/10.1016/j.jmb.2006.04.031>
- Rao, N. N., Gómez-García, M. R., & Kornberg, A. (2009). Inorganic polyphosphate: Essential for growth and survival. *Annual Review of Biochemistry*, 78(1), 605–647. <https://doi.org/10.1146/annurev.biochem.77.083007.093039>
- Rashchi, F., & Finch, J. A. (2000). Polyphosphates: A review their chemistry and application with particular reference to mineral processing. *Minerals Engineering*, 13(10–11), 1019–1035. [https://doi.org/10.1016/S0892-6875\(00\)00087-X](https://doi.org/10.1016/S0892-6875(00)00087-X)
- Rulliere, C., Rondeau-Mouro, C., Raouche, S., Dufrechou, M., & Marchesau, S. (2013). Studies of polyphosphate composition and their interaction with dairy matrices by ion chromatography and 31P NMR spectroscopy. *International Dairy Journal*, 28(2), 102–108. <https://doi.org/10.1016/j.idairyj.2012.09.005>
- Ryazanova, L., Andreeva, N., Kulakovskaya, T., Valiakmetov, A., Yashin, V., Vagabov, V., et al. (2011). The early stage of polyphosphate accumulation in *saccharomyces cerevisiae*: Comparative study by extraction and DAPI staining. *Advances in Bioscience and Biotechnology*, 2(4), 293–297. <https://doi.org/10.4236/abb.2011.24042>
- Saad, S. A., Welles, L., Abbas, B., Lopez-Vazquez, C. M., Van Loosdrecht, M. C. M., & Brdjanovic, D. (2016). Denitrification of nitrate and nitrite by ‘*Candidatus* Accumulibacter phosphatis’ clade IC. *Water Research*, 105, 97–109. <https://doi.org/10.1016/j.watres.2016.08.061>
- Saia, S. M., Carrick, H. J., Buda, A. R., Regan, J. M., & Walter, M. T. (2021). Critical review of polyphosphate and polyphosphate accumulating organisms for agricultural water quality management. *Environmental Science and Technology*, 55(5), 2722–2742. <https://doi.org/10.1021/acs.est.0c03566>
- Šantová, K., Salek, R. N., Kúrová, V., Mížera, A., Lapčíková, B., Vincová, A., et al. (2024). Potassium-based emulsifying salts in processed cheese: A rheological, textural, tribological and thermal approach. *Journal of Dairy Science*, S0022030224009263. <https://doi.org/10.3168/jds.2024-24939>
- Saunders, A. M., Oehmen, A., Blackall, L. L., Yuan, Z., & Keller, J. (2003). The effect of GAOs (glycogen accumulating organisms) on anaerobic carbon requirements in full-scale Australian EBPR (enhanced biological phosphorus removal) plants. *Water Science and Technology*, 47(11), 37–43. <https://doi.org/10.2166/wst.2003.0584>
- Sawada, N., Ueno, S., & Takeda, K. (2021). Regulation of inorganic polyphosphate is required for proper vacuolar proteolysis in fission yeast. *Journal of Biological Chemistry*, 297(1), Article 100891. <https://doi.org/10.1016/j.jbc.2021.100891>
- Sebraneck, J. G., & Bacus, J. N. (2007). Cured meat products without direct addition of nitrate or nitrite: What are the issues? *Meat Science*, 77(1), 136–147. <https://doi.org/10.1016/j.meatsci.2007.03.025>
- Serra-Cardona, A., Petrežsélyová, S., Canadell, D., Ramos, J., & Ariño, J. (2014). Coregulated expression of the Na⁺/phosphate Pho89 transporter and Ena1 Na⁺-ATPase allows their functional coupling under high-pH stress. *Molecular and Cellular Biology*, 34(24), 4420–4435. <https://doi.org/10.1128/MCB.01089-14>
- Seufferheld, M. J., Alvarez, H. M., & Farias, M. E. (2008). Role of polyphosphates in microbial adaptation to extreme environments. *Applied and Environmental Microbiology*, 74(19), 5867–5874. <https://doi.org/10.1128/AEM.00501-08>
- Seviour, R. J., Mino, T., & Onuki, M. (2003). The microbiology of biological phosphorus removal in activated sludge systems. *FEMS Microbiology Reviews*, 27(1), 99–127. [https://doi.org/10.1016/S0168-6445\(03\)00021-4](https://doi.org/10.1016/S0168-6445(03)00021-4)

- Shao, J.-H., Deng, Y.-M., Jia, N., Li, R.-R., Cao, J.-X., Liu, D.-Y., et al. (2016). Low-field NMR determination of water distribution in meat batters with NaCl and polyphosphate addition. *Food Chemistry*, 200, 308–314. <https://doi.org/10.1016/j.foodchem.2016.01.013>
- Singh, V., Pandit, C., Roy, A., Pandit, S., Rai, A. K., Rani, A., et al. (2024). Degradation of food dyes via biological methods: A state-of-the-art review. *Bioresource Technology Reports*, 25, Article 101780. <https://doi.org/10.1016/j.biteb.2024.101780>
- Sun, T., Du, R., Dan, Q., Liu, Y., & Peng, Y. (2021). Rapidly achieving partial nitrification of municipal wastewater in enhanced biological phosphorus removal (EBPR) reactor: Effect of heterotrophs proliferation and microbial interactions. *Bioresource Technology*, 340, Article 125712. <https://doi.org/10.1016/j.biortech.2021.125712>
- Tarayre, C., De Clercq, L., Charlier, R., Michels, E., Meers, E., Camargo-Valero, M., et al. (2016). New perspectives for the design of sustainable bioprocesses for phosphorus recovery from waste. *Bioresource Technology*, 206, 264–274. <https://doi.org/10.1016/j.biortech.2016.01.091>
- Teixeira, B., & Mendes, R. (2022). Analysis of added phosphates in hake fillets by ion-exchange chromatography: A case study of false positives induced by nucleotides coelution. *Food Chemistry*, 368, Article 130841. <https://doi.org/10.1016/j.foodchem.2021.130841>
- Tenderis, B., Kılıç, B., Yalçın, H., & Şimşek, A. (2020). Impact of sodium lactate, encapsulated or unencapsulated polyphosphates and their combinations on Salmonella Typhimurium, Escherichia coli O157:H7 and Staphylococcus aureus growth in cooked ground beef. *International Journal of Food Microbiology*, 321, Article 108560. <https://doi.org/10.1016/j.ijfoodmicro.2020.108560>
- Thangavelu, K. P., Kerry, J. P., Tiwari, B. K., & McDonnell, C. K. (2019). Novel processing technologies and ingredient strategies for the reduction of phosphate additives in processed meat. *Trends in Food Science & Technology*, 94, 43–53. <https://doi.org/10.1016/j.tifs.2019.10.001>
- Tian, L., & Wang, L. (2020). A meta-analysis of microbial community structures and associated metabolic potential of municipal wastewater treatment plants in global scope. *Environmental Pollution*, 263, Article 114598. <https://doi.org/10.1016/j.envpol.2020.114598>
- Trilisenko, L. V., Vagabov, V. M., & Kulaev, I. S. (2002). [No title found]. *Biochemistry (Moscow)*, 67(5), 592–596. <https://doi.org/10.1023/A:1015510631271>
- Vagabov, V. M., Trilisenko, L. V., Kulakovskaya, E. V., & Kulaev, I. S. (2008a). Study of the content of inorganic polyphosphates in *Saccharomyces cerevisiae* grown on different carbon sources with different O₂ concentrations in the medium. *Microbiology*, 77(5), 541–546. <https://doi.org/10.1134/S0026261708050056>
- Vagabov, V. M., Trilisenko, L. V., Kulakovskaya, T. V., & Kulaev, I. S. (2008b). Effect of a carbon source on polyphosphate accumulation in *Saccharomyces cerevisiae*. *FEMS Yeast Research*, 8(6), 877–882. <https://doi.org/10.1111/j.1567-1364.2008.00420.x>
- Valencia, G. A. (Ed.). (2023). *Natural additives in foods*. Springer International Publishing. <https://doi.org/10.1007/978-3-031-17346-2>
- Wang, L., Li, J., & Zhang, L. (2015). Determination of polyphosphates in fish and shrimp muscles by capillary electrophoresis with indirect UV detection after phosphatase inhibition using high pressure pretreatment. *Food Chemistry*, 185, 349–354. <https://doi.org/10.1016/j.foodchem.2015.04.008>
- Wu, J., Cheng, S., Cao, J., Qiao, J., & Zhao, G.-R. (2019). Systematic optimization of limonene production in engineered *Escherichia coli*. *Journal of Agricultural and Food Chemistry*, 67(25), 7087–7097. <https://doi.org/10.1021/acs.jafc.9b01427>
- Wykoff, D. D., Rizvi, A. H., Raser, J. M., Margolin, B., & O'Shea, E. K. (2007). Positive feedback regulates switching of phosphate transporters in *S. cerevisiae*. *Molecular Cell*, 27(6), 1005–1013. <https://doi.org/10.1016/j.molcel.2007.07.022>
- Xu, Y., Liu, D., Yang, H., Zhang, J., Liu, X., Regenstein, J. M., et al. (2016). Effect of calcium sequestration by ion-exchange treatment on the dissociation of casein micelles in model milk protein concentrates. *Food Hydrocolloids*, 60, 59–66. <https://doi.org/10.1016/j.foodhyd.2016.03.026>
- Xu, S. Q., Zhou, G. H., Peng, Z. Q., Zhao, L. Y., & Yao, R. (2009). The influence of polyphosphate marination on simmental beef shear value and ultrastructure. *Journal of Muscle Foods*, 20(1), 101–116. <https://doi.org/10.1111/j.1745-4573.2008.00136.x>
- Yang, S.-Y., Huang, T.-K., Kuo, H.-F., & Chiou, T.-J. (2017). Role of vacuoles in phosphorus storage and remobilization. *Journal of Experimental Botany*. <https://doi.org/10.1093/jxb/erw481>. erw481.
- EFSA Panel on Food Additives and Flavourings (FAF), Younes, M., Aquilina, G., Castle, L., Engel, K., Fowler, P., Frutos Fernandez, M. J., et al. (2019). Re-evaluation of phosphoric acid–phosphates – di-, tri- and polyphosphates (E 338–341, E 343, E 450–452) as food additives and the safety of proposed extension of use. *EFSA Journal*, 17(6). <https://doi.org/10.2903/j.efsa.2019.5674>
- Yousefi, N., Abbasi, S., & Mohammadifar, M. A. (2024). Prevention of thermal gelation in concentrated whey protein isolate dispersions by using H₂O₂ and SHMP. *International Dairy Journal*, 155, Article 105942. <https://doi.org/10.1016/j.idairyj.2024.105942>
- Yuan, D., Liang, X., Kong, B., Xia, X., Cao, C., Zhang, H., et al. (2024). Influence of seaweed dietary fibre as a potential alternative to phosphates on the quality profiles and flavour attributes of frankfurters. *Meat Science*, 213, Article 109511. <https://doi.org/10.1016/j.meatsci.2024.109511>
- Zhang, Y., Qiu, X., Luo, J., Li, H., How, S.-W., Wu, D., et al. (2024). A review of the phosphorus removal of polyphosphate-accumulating organisms in natural and engineered systems. *The Science of the Total Environment*, 912, Article 169103. <https://doi.org/10.1016/j.scitotenv.2023.169103>
- Zhang, J., Shen, Y., Chen, W., Bai, B., Ji, X., & Chi, Y. (2022). Systematic identification and expression analysis of the sorghum Pht1 gene family reveals several new members encoding high-affinity phosphate transporters. *International Journal of Molecular Sciences*, 23(22), Article 13855. <https://doi.org/10.3390/ijms232213855>
- Zhang, J., Su, J., Ma, C., Hu, X., & Teng, H. H. (2021). Periphytic microbial response to environmental phosphate (P) bioavailability and its relevance to P management in paddy fields. *Applied and Environmental Microbiology*, 87(20), Article e01201. <https://doi.org/10.1128/AEM.01201-21>
- Zhu, M., Yao, Y., Li, J., Zhang, F., Yu, J., Zhou, T., et al. (2024). Reducing water activity and softening texture of Areca catechu L. by phosphates and Maillard peptides and their improvement on flavor. *Food Bioscience*, 57, Article 103554. <https://doi.org/10.1016/j.fbio.2023.103554>