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# Microbial inactivation by high pressure processing: principle, mechanism and factors responsible

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**Abstract** High-pressure processing (HPP) is a novel technology for the production of minimally processed food products with better retention of the natural aroma, fresh-like taste, additive-free, stable, convenient to use. In this regard safety of products by microbial inactivation is likely to become an important focus for food technologists from the research and industrial field. High pressure induces conformational changes in the cell membranes, cell morphology. It perturbs biochemical reactions, as well as the genetic mechanism of the microorganisms, thus ensures the reduction in the microbial count. Keeping in view the commercial demand of HPP products, the scientific literature available on the mechanism of inactivation by high pressure and intrinsic and extrinsic factors affecting the efficiency of HPP are systematically and critically analyzed in this review to develop a clear understanding of these issues. Modeling applied to study the microbial inactivation kinetics by HPP is also discussed for the benefit of interested readers.

**Keywords** Microbial inactivation · High pressure processing · Compression · Microorganism · Modelling

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## Introduction

High pressure processing (HPP), among other non-thermal methods of preservation, has gained widespread acceptance and is adopted for commercial processing of varieties of food in developed countries. It can ensure both microbial safety and shelf-life stability for various products effectively. HPP affects only non-covalent bonds as they are sensitive to pressure whereas, components accountable for retention of color attributes, volatile, non-volatile compounds, and bioactive compounds which are generally low molecular weight compounds having covalent bonds are not affected by pressure. Thus, it preserves the fresh-like attributes of foods (Huang et al., 2020; Tewari et al., 2016).

In HPP high hydrostatic pressure is applied at 100–600 MPa for commercial processes, which is immediately and evenly transmitted through-out the product (packaged or non-packaged) using a pressure transmitting medium (PTM). Along with pressure, the temperature can be increased up to 60–65 °C to reduce microbial activity (Pinto et al., 2020).

This article also briefly covers principles of HPP, typical processing steps, and key high-pressure equipment components followed by an overview of the mechanism of microorganism inactivation; and factors affecting high pressure microbial inactivation. Different kinetic models utilized for the study pattern of microbial inactivation

kinetics and their role have also explicitly been emphasized. Complied data would be beneficial for process designing, simulation, and optimization for various foods and to maintain food safety.

## HPP principle, equipment and process mechanism

### Principle

HPP is governed mainly by three basic principles as described by Yordanov and Angelova (2010). First, the Le Chatelier's principle which states that any process in equilibrium (chemical reaction, phase transition, conformational change), which is accompanied by a decrease in volume, can be enhanced by pressure (Kumar et al., 2018). Thus, HPP favors reactions that result in a volume decrease. Second is the Isostatic principle which confirms that during compression, the pressure is transmitted uniformly from all directions irrespective of the geometry of the product, thus, the product on a whole retains its shape after decompression. Figure 1 depicts the uniform transmission of pressure in all directions of food material which is packaged inside a hermetically sealed packaging material regardless of the shape of the container. This unique property of HPP has enabled the development of processes that have been successfully commercialized (Kumar et al., 2018). Third, the Principle is of microscopic ordering, which describes the enhancement of the molecular ordering of material by the increase in pressure (at constant temperature) (Yordanov and Angelova, 2010).

### Equipment and process mechanism

High pressure equipment comprises of pressure vessel and its closure, PTM, two or more pumps to generate pressure and temperature controller. Pressure vessel is the heart of HPP equipment, which is mostly forged monolithic cylindrical vessel and can be operated at the pressure in the range of 400–600 MPa depending on the internal diameter of vessel. To operate at a higher pressure range, prestressed vessel with multi-layer are available (Chavan et al., 2014). Commercially available HPP systems are batch type, semi-continuous or continuous type (Yaldagard et al., 2008). HPP involves filling with PTM, the building of pressure, pressure holding followed by decompression, as shown in Fig. 2. The pressure vessel is loaded with the product to be treated and is filled with PTM for the displacement of air if any.

Several PTM are used to transmit pressure in a vessel such as distilled water, glycol–water solution, and propylene with glycol, silicon oil, castor oil, and sodium benzoate solutions. The selection of PTM is based on the viscosity of the solution and to avoid corrosion of the vessel. Depending upon the pressure applied generally decrease in volume of distilled water up to 15% (at 600 MPa) and 2–3 °C (per 100 MPa) rise in temperature has been reported (Balakrishna et al., 2020; Balasubramanian and Balasubramaniam, 2003). Whereas in the case of other PTM i.e. oils and organic solvents due to their ability to get compressed to a higher percentage, low thermal conductivity values and lesser heat capacity, the rise in temperature is higher as compared to the distilled water. An interesting study was conducted by Balasubramanian and Balasubramaniam (2003) in which Glycol (25–75%) and 2% of sodium benzoate were used as PTM to study an apparent increase in temperature and inactivation of *B. subtilis*. The initial pressurization (759 MP/10 min.) was done at 30 °C and after pressurization, the change in temp was observed. Increase in temperature over the initial temperature was 22 °C in case of 2% sodium benzoate (minimum) and was highest i.e. 26–27 °C in 75% glycol containing 25% water; as it was dependent upon fluid properties. The inactivation of *B. subtilis* spores was highest in case of when sodium benzoate solution was used as PTM.

High pressure is usually generated by direct or indirect compression. In direct compression, PTM is pressurized

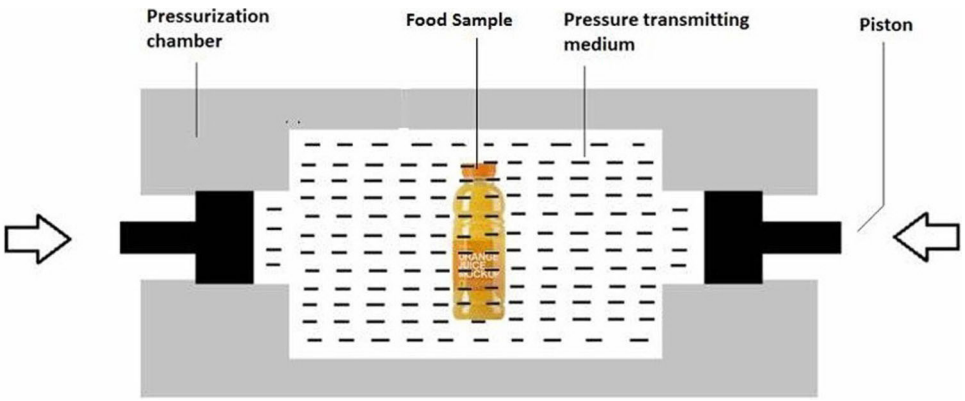


**Fig. 1** Isostatic pressurization of foods

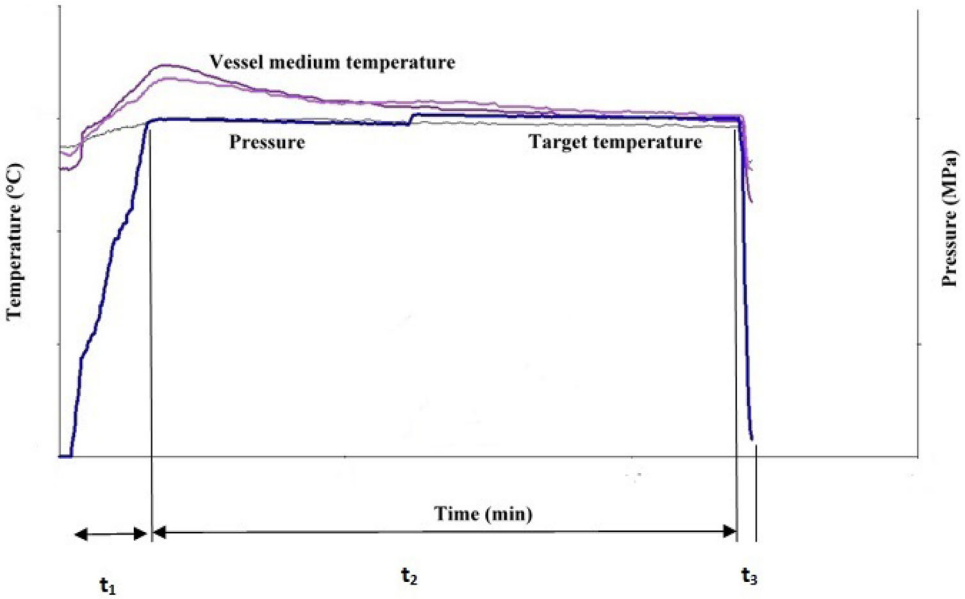


**Fig. 2** Pressure and temperature profiles during high pressure processing. $t_1$, $t_2$, $t_3$ are the come-up, holding and decompression time respectively

into the pressure vessel using a piston (Fig. 3a). It is a faster method of pressurization but limited to pilot scale or laboratory study due to the requirement to seal process fluid in between the internal surface area of high-pressure vessel and piston. Most of the industrial systems use indirect pressurization method. In indirect compression, PTM is pushed into high pressure vessel until the required pressure is achieved (Fig. 3b). After achieving the desired pressure, the piston or flow of PTM is stopped and holding the achieved pressure for the required process time followed by decompressing and removal of packaged food products (Chavan et al., 2014).

The packaging material used in HPP should be able to withstand 15–20% compression of their original volume and soon after decompression gains their original volume. When compressive forces are applied cans and glass bottles tend to fracture or deform irreversibly that is why they are not well suited as packaging material for HPP

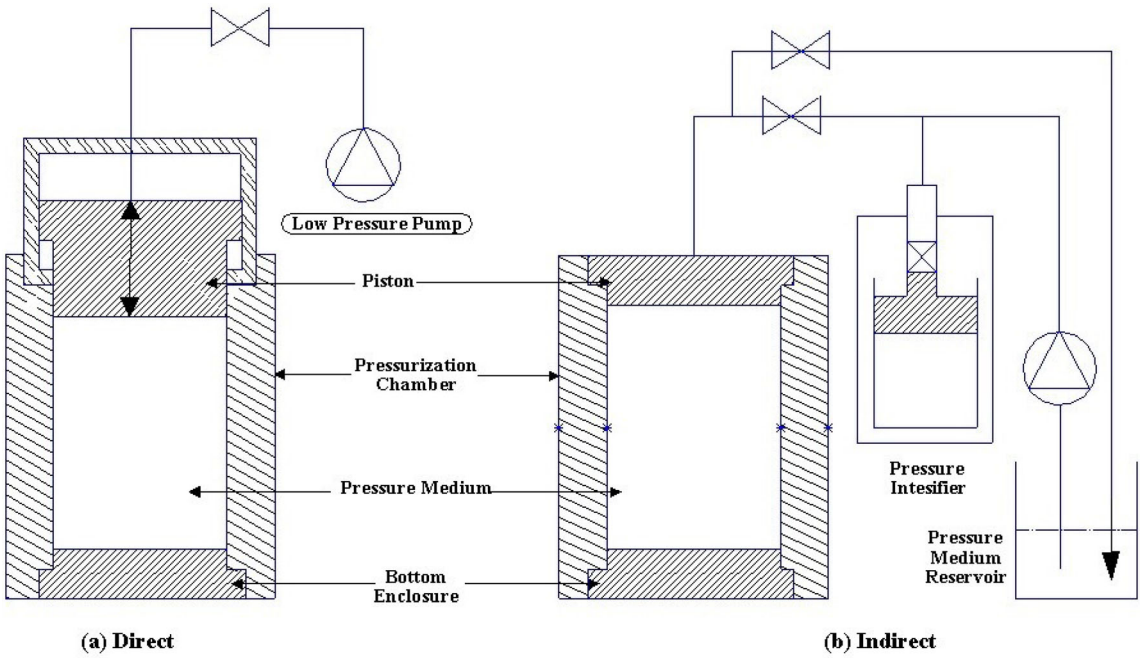


**Fig. 3** Generation of high pressure by **a** direct and **b** indirect compression of the pressure transmitting medium in high pressure processing systems

(Woldemariam and Emire, 2019). Common packaging materials used in HPP of foods are made of ethylene–vinyl alcohol and polyvinyl alcohol.

Shankar (2014) reported the cost of high pressure treated food between US$ 0.05–0.5/L or kg based on operating cost, where the former value is comparable to the thermally processed food cost. The capital cost of the commercial HPP system is high and is around 500,000 US$–2.5 million US$ depending upon size of vessel and automation (Rastogi et al., 2007). The high initial cost of HPP systems limits its use for niche products, at present, but with the advancement in technology and increase in the sale of the vessel, the cost is likely to reduce due to the rise in the sale of units from 1 to 500 and size of a pressure vessel from 25 to 500 L since 1990 to 2018.

## Microbial inactivation by HPP

High pressure treatment has a significant effect on the cellular architecture and critical functions of the microbial cell. The lethal impact of HPP on microbial population is assumed to be due to a simultaneous effect on cell membrane permeability, changes in cell morphology, altered biochemical reactions, interference in the genetic mechanism which occurs in the cell of microorganism (Yordanov and Angelova, 2010). Damage of less critical factors might not result in cell death, but multiple and simultaneous effect, less critical components or critical parameter leads to cell death (Daher et al., 2017; Rendueles et al., 2011). However, the exact mechanism triggering cell death is not known but might be due to the simultaneous action of proteins, ribosomes, and DNA (Mañas and Pagán, 2005).

To understand the effect of HPP on cell morphology, it is essential to have a clear idea about the organization and composition of the cell and its membrane. The bacterial cell wall is made up of peptidoglycans (consists of N-acetylglucosamine and N-acetylmuramic acid, and three amino acids, i.e. D-glutamic acid, D-alanine, and meso-diaminopimelic acid). Unlike plant cells, the bacterial cell lacks a nuclear membrane making the genetic material vulnerable to external factors like temperature and pressure. However, in an animal cell, the cell wall is absent, but the nuclear membrane is present (Abbot and Harker, 2004). Plant tissue of different fruits and vegetables vary in their biological functions but has a basic eukaryotic organization and consist of a nucleus, cytoplasm enclosed by a membrane, plasmalemma, and cell wall (Gonzalez and Barrett, 2010).

### Effect on the cell membrane

The cellular membrane is commonly acknowledged to be a major spot of injury in the microbes after pressure treatment (Casadei et al., 2002). The Bacterial cell membrane is a fluidic structure made up of proteins and phospholipids bilayer, which separates interior cells from the external environment. Treatment with high pressure leads to disruption of microbial cell membrane which further results in its increased permeability. Evidence of injury to the cellular membrane has been reported as the outflow of Adenosine triphosphatase (ATP) in an extracellular region or UV-absorbing substrates from microbial cells on the application of pressure or enhanced absorption of dyes [for ex. propidium iodide (PI)] which generally do not enter inside the cellular membrane of live microbial cells but can penetrate only via dead cells into genetic material, formations of buds and vesicles of lipidic origin (Patterson, 2005).

Release of metal ions was observed when pressurization of more than 300 MPa was used (Smelt, 1998), and pressure greater than 200 MPa could lead to the outflow of internal materials and ions (Abe, 2007). The greater amount of leakage of the constituents indicates a higher degree of injury to cells. The structural alterations in pressure treated cells of *Saccharomyces cerevisiae* 0–39 at 600 MPa was observed by Shimada et al. (1993) and render them incapable of surviving. The reason for these changes was reported to be the efflux of UV-absorbing substances, including amino acid pools, peptides, and metal ions. PI fluorescence was used to determine pressure mediated damage of the cytoplasmic membrane and revealed irreversible membrane damage after HPP (300–600 MPa/40 min), inactivating the majority of the population of *E. coli* (Gänzle and Vogel, 2001). A schematic diagram representing changes in cell membrane on applications of HPP is shown in Fig. 4. Increased uptake of PI from *E. coli* under various pressures was also reported by Klotz et al. (2010). Pressurization causes the perturbation in transportation and respiration due to alteration in cell membrane permeability, which leads to a lack of nutrients in cell, and finally, cell death can occur (Thakur and Nelson, 2009). Similarly, Kalagatur et al. (2018) reported HPP treatment damaged the membrane as observed by penetration of PI, which stains the dead spores of *F. graminearum* and emitted bright red fluorescence. Increasing the pressure treatment enhanced the intensity of fluorescence, indicating higher inactivation of fungal spores at increased pressure at a constant temperature of 60 °C for 30 min.

On pressurization within the phospholipid bilayer of the membrane tight packing of acyl chains occurs due to which transition of the liquid crystalline membrane to gel phase is

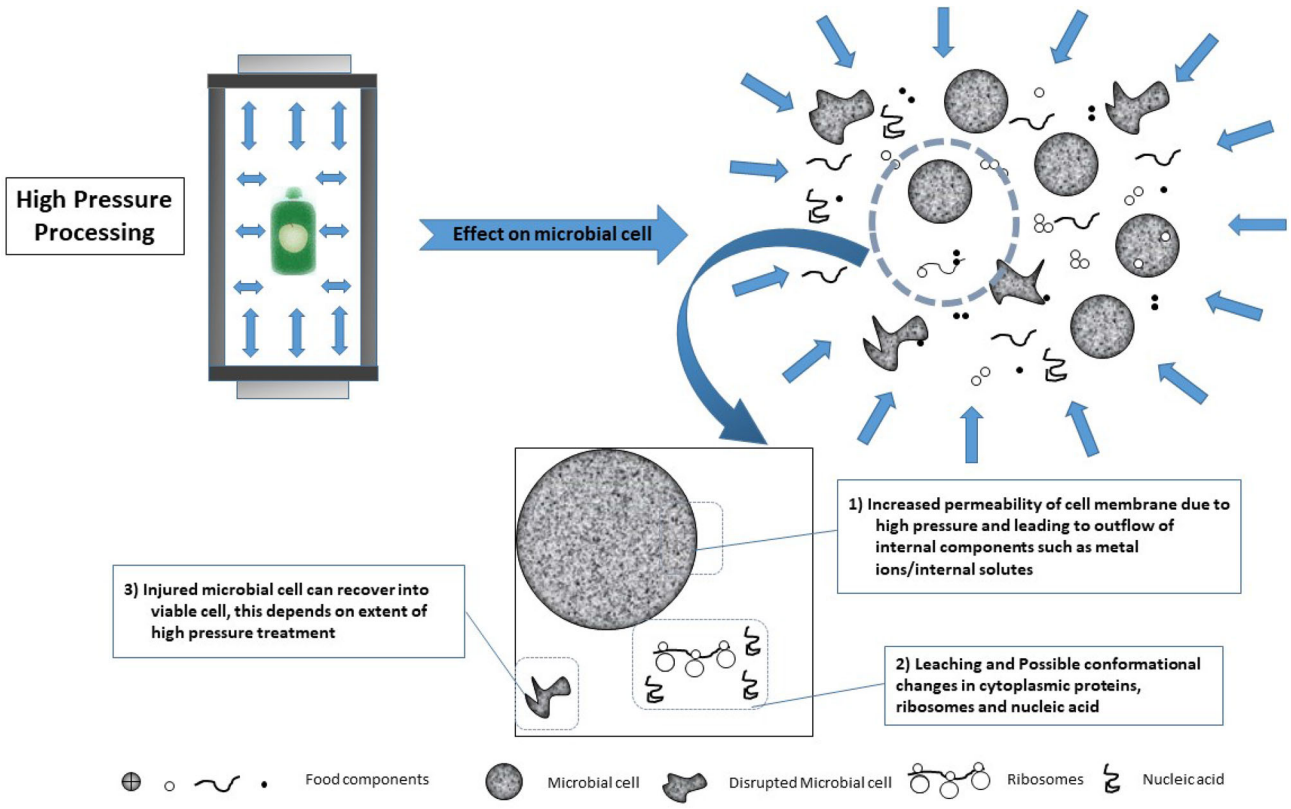


**Fig. 4** Schematic diagram representing cell membrane modification on high pressure processing

promoted. Although this phase transition might not be lethal to bacteria but it would affect the resistance to pressure treatment (Mañas and Pagán, 2005). It is also reported that cells with high fluidic membrane are more resistant to HPP treatment (Casadei et al., 2002). Although it is unclear how a membrane with more fluidic nature and phase transition is linked with cell damage. If the pressure is not sufficient to induce absolute permeability, and only the outer membrane is affected, then the membrane gets recovered after removal of a pressure (Yaldagard et al., 2008). Field Emission Scanning Electron Microscopy images of untreated whey-lime samples depicted a smooth lining of microbial cells (100 nm). In contrast, HPP treated samples showed disintegrated lining of microbial cells (1 µm) as well as leakage of cellular debris (100 nm) (Bansal et al., 2019). HPP was found to be effective in inactivating histamine forming bacteria in phosphate buffer and tuna meat slurry. Among the bacteria studied the *P. phosphoreum* was found to be more resistant, and treatment was significant to damage cell membrane and cell wall as observed using SEM (Lee et al., 2020). The effect of HPP on growth, physiology and survival of bacteria and yeast is reported by Abe (2007) in detail.

## Effect on cell morphology

Apart from the detachment of cell membrane from cell wall on pressurization (20–180 MPa), different morphological changes like increase in the length of the cell, contraction in the size of gas vacuoles, condensation of nuclear material, and cell wall contraction of microorganism were also reported to occur (Lado and Yousef, 2002). Compared to the cell membrane, the cell wall being more rigid is less affected by HPP. Reversible changes in cell morphology were also observed at low pressure, but these changes were irreversible at higher pressure, where cell death is due to membrane permeability ((Rastogi et al., 2007; Shankar, 2014; Thakur and Nelson, 2009). It was reported by Bozoglu et al. (2004) that after pressurization (350–550 MPa), damaged cells were not found but detected after getting repaired. Cells might be able to proliferate within 1–15 days, as damage caused may be reversible and could potentially recover in food on storage. Several other studies on milk, pork, and broth have reported similar results where sub-lethal damage caused to the cells were able to recover within 6 h to 4 weeks of storage (Koseki and Yamamoto, 2014).

Shimada et al. (1993) reported minor alterations in the shape of *S. cerevisiae* 0–39 after pressurization; however, transmission electron microscopy (TEM) images depicted

alterations in mitochondria and cytoplasm at 400 MPa for 10 min. Severe disruptions in inner architecture were observed at 200 MPa at – 20 °C, and the nuclear membrane was disappeared. It was reported by Park et al. (2001) that after pressurization (400 MPa or above/5 min/25 °C) of *L. viridescens* presence of nodes on cell walls was found as images of ultrastructure were obtained using SEM. On the application of TEM, the presence of cavities between the cellular membrane and the wall was seen. Kalchayanand et al. (2002) found alterations in cell wall and disruption of cell membrane integrity of *L. mesenteroides* treated at 345 MPa for 5 min at 25 °C. Conformational changes in cytoplasmic protein, ribosomes, and nucleic acid have been reported, and a direct relationship in ribosomes damage and reduction in viable cells of *E. coli* was found using SEM by Niven et al. (1999). It was also reported that stabilizing effects were observed on ribosomes structure on incubation of HPP treated cells into magnesium-rich media and concluded that loss of viable cells could be attributed to the loss of metal ions/internal solutes after cell damage along with ribosomes structure conformational changes Yang et al. (2012) observed pressure-induced (500 MPa/30 min/25 °C) inactivation of *Salmonella*, *E. coli, Shigella and S. aureus* in milk due to morphological alterations and breakdown of peptidoglycan layer. Pilavtepe-Çelik et al. (2013) reported that before pressurization, *E. coli* cells exhibited a smooth surface appearance but on exposure to pressurization of 200 MPa cells appeared bigger in size, and upon the further increase in pressure intensity to 250 MPa dimples and pinches formation was observed. In contrast, pressurization of 200–250 MPa had no significant effect on the cell surface; however, elevated pressures (300–400 MPa) resulted in a rough and cracked cell surface. Some morphological changes induced in the microorganisms by high pressure treatments are presented in Table 1.

An attempt was made by Maldonado et al. (2016) for the examination of cells after the treatment by using fluorescence material, for better understanding the mechanism of inactivation by examining the in situ microbial inactivations during pressurization, while holding pressure and depressurization. During pressurization and holding, time damage to the membrane was observed but was not detected during depressurization. When treatment was given for a longer time and at high pressure, a drop in fluorescence was observed which was more than expected. It might be due to the breakdown of ribosomes which might result in further binding of PI on the application of pressure and but might have released on the removal of pressure.

## Effect on biochemical reactions

Various biochemical reactions are required to carry out different functions to sustain life processes. These reactions result in a change in volume, and HPP favors reactions that result in a volume decrease of the solution. Apart from the cell membrane, protein and enzymes are also considered as a major target of high-pressure treatment to inactivate microorganisms (Ulmer et al., 2000).

Key enzymes such as ATP present in cell membranes are either denatured or detached from the membrane by high pressure treatment. Application of high-pressure treatment also leads to the denaturation of functional protein, which reduces the movement of proton thereby, intracellular pH gets reduced (Huang et al., 2014). Also, denaturation and unfolding of proteins lead to aggregation of proteins inside the microbes, and the process is irreversible at higher pressure (Kalagatur et al., 2018). Some of the irreversible changes at higher pressure observed due to the association of hydrophobic molecules or due to reduced volume may include dissociation of oligomeric proteins into their subunits, conformational changes of the active site (Serment-Moreno et al., 2014). It has also been stated that there exist similarities between protein denaturation kinetics and cell inactivation on HPP treatment (Mañas and Pagán, 2005). Protein biosynthesis and the number of ribosome reduction due to damage in protein structures at pressure treatment of 60 MPa and irreversible denaturation of proteins above 300 MPa pressure was reported by Abe (2007). This is attributed to dissociation of majorly uncharged ribosomes, i.e., without tRNA or mRNA accompanied by a decrease in volume of solution as observed in in vitro experiments. Moreover, on application of high pressure treatment, uptake of amino acid by microorganisms is reduced, consequently is unable to synthesize protein (Abe, 2007) eventually affecting the metabolic process of microorganisms.

The results of electrophoresis profiles revealed modifications in the cell membrane of *Salmonella typhimurium* after HPP (350–600 MPa/10 min/20 °C). Except for the major proteins OmpA and LamB, all other outer membrane proteins seem to disappeared (Ritz et al., 2000). The effects of HPP necessarily need not to be the same on the whole microorganism. It was reported that protein synthesis and gene expression were found to be influenced in between 30 and 50 MPa, and yeast nuclear membrane was affected at an approximate pressure of 100 MPa. Pressure around 400–600 MPa was effective in causing damage/alteration to cytoplasm and mitochondria (Smelt, 1998). The effect of pressure-induced on structural (reversible or irreversible modifications) and functional property of proteins and enzymes greatly depend upon the type of protein as well as the operating parameters (Tewari et al., 1999). Reduction

**Table 1** Change in morphology of microorganisms by high pressure processing

| Target microorganism | Treatment (MPa/min/°C/others) | Technique | Observation | References |
|---|---|---|---|---|
| *Saccharomyces cerevisiae* | 100–600/10/25 | SEM, TEM | Nuclear membrane affected at 100 MPa. Alteration in the structure of mitochondria and cytoplasm at 400–600 MPa | Shimada et al. (1993) |
| *Saccharomycopsis Fibuligera* CBS 2521; *Saccharomyces cerevisiae* CBS 1171 | 250/15/– | Light microscope | Average cell volume reduction by 10% after depressurization indicates transfer of mass between cell and medium due to disruption of cell membranes | Perrier-Cornet et al. (1995) |
| *L. monocytogenes* Scott A, *Salmonella typhimurium* ATCC13 311) | 150–600/10/20 | SEM | Increase in the number of pimples and swellings in the cells with increased pressure intensity | Tholozan et al. (2000) |
| *L. viridescens* | 400/5/25 | SEM, TEM | Nodes on cell walls, empty cavities between the cytoplasmic membrane and the cell wall | Park et al. (2001) |
| *L. monocytogenes* Scott A | 400/10/20/pH 5.6 citrate buffer | SEM Flow cytometry | Occurrence of buds scars on the surface of cells. Loss of membrane integrity and Reduction in membrane potential | Ritz et al. (2002) |
| *Bacillus subtilis* | 400/30/25–55 | SEM, TEM | Repeated rapid compression caused disruption of the spore surface, causing partial leakage of cellular fluid. In comparison to continuous pressurization reciprocating pressurization is more effective in inactivating spores | Furukawa et al. (2003) |
| *E. coli 0157: H7*; *S. aureus* 485 | 200-325/1/40 200-400/1/40 | SEM | Alterations in membrane integrity due to denaturation of membrane proteins and the pressure-induced phase transition of the membrane lipid bilayer | Pilavtepe-Çelik et al. (2008) |
| *Saccharmyces cerevisiae* | 600/7/21 | SEM | Perforations and release of the cell wall; scars on the surface of pressurized cells | Marx et al. (2011) |
| *E. coli* ATCC25922; *S. aureus* ATCC2921 | 500/30/25 | TEM | Cell membrane damage, cell wall rupture and chromosome DNA degradation | Yang et al. (2012) |
| *Salmonella enterica* BCRC 12947 | 350/5/25 | TEM, SEM | Cellular changes, which includes irregular shape, expanded nucleoid regions, breakdown of the peptidoglycan layer, rupture of the cell wall, and partial disintegration loss of the cell envelope | Wang et al. (2013a) |
| *Vibrio parahaemolyticus* BCRC 10806 | 300/10/25 | TEM, SEM | Bud scars on the surfaces of cells, pressure induced cell envelope and intracellular damage | Wang et al. (2013b) |
| Fungal spores (Fusarium mycotoxins) | 380/30/60 | Fluorescence microscope | Damaged membrane integrity as observed by penetration of propidium iodide | Kalagatur et al. (2018) |
| Microbial cells from whey-lime beverage | 500/10/25 | FESEM | Leakage of cellular debris due to rupture of cellular membrane induced by HPP | Bansal et al. (2019) |
| *Morganella morganii, Photobacterium phosphoreum* | | SEM | HPP induced damage to cellular membrane and cell wall | Lee et al. (2020) |

*SEM* scanning electron microscopy, *TEM* transmission electron microscopy, *FESEM* field emission scanning electron microscopy

in volume, intracellular pH, protein aggregation, and inactivation of key enzymes of microbes leads to cell death.

## Effect on genetic mechanism

The functionality of the genetic material depends on its enzymes, and pressure disrupts the activity of enzymes. Due to the inactivation of enzyme activity, ribosomes synthesis is reduced, which is required in replication and transcription of genetic material. This leads to the condensation of genetic material, as reported in the case of *Listeria. monocytogenes, Salmonella typhimurium,* and *L. plantarum* (Patterson, 2005), hence, affecting the functionality of nuclear material. Inactivation of intracellular enzyme and the capability of amino acids acyl-tRNA to bind m-RNA and ribosomes are sensitive to the effect of pressure.

Moreover, even small changes to amino acids may cause a change in the shape of protein (Thakur and Nelson, 2009). Covalent and hydrogen bonds are least affected by pressure as compared to electrostatic, hydrophobic, and ionic interactions. As hydrogen bonds are involved in the formation of DNA helix structure, so nucleic acids are comparatively resistant to high pressure (Patterson, 2005). But, at higher pressure, when endonuclease comes in contact with DNA, cleave DNA and lead to condensation of DNA. It is also found that in many cases, this condensation phenomenon is reversible, but if enzyme can be deactivated in the treatment, proliferation of cell can be avoided (Smelt, 1998). Epifluorescence microscopy revealed conformational changes in cytosolic protein as well as in nucleoids of *E. coli* K-12TG1 (Moussa et al., 2007). Elimination or transfer of regulatory genes related to pressure resistance affects the pressure tolerance of the strain (Robey et al., 2001). Abe (2007) reported a pressure of 50–100 MPa is sufficient to inhibit replication and transcription of microbial genetic materials.

Damage to the outer membrane is recoverable after decompression, whereas recovery of damage to the cytoplasmic membrane is difficult as RNA and protein synthesis requires energy. So, it can be concluded that the effect of HPP is multi-target in nature to cause a viable reduction of microorganisms.

## Factors affecting microbial inactivation by HPP

The food matrix plays a significant role in protecting microorganisms when high pressure is applied. Besides pressurization variables (magnitude of pressure, time, and temperature), the response of microorganisms to high pressures also depends on the composition of suspension media or food, type of microorganism, cell growth phase, pH, and water activity (Daryaei et al., 2016). Guillou and Membré (2019) developed a secondary model from published literature from 1995 to 2017 and based on known piezoresistance of three microorganisms (*Listeria monocytogenes, Staphylococcus aureus, and Salmonella enterica*) *S. aureus* was most resistant, and *S. enterica* was the least resistance. Major influencing factors were species, strain, and pH.

### Food composition

Food is a complex matrix, constituting several components in different proportions and can have a substantial influence in shielding the microorganisms to pressure. As cells stressed by pressurization might resuscitate in the presence of food matrix (Rendueles et al., 2011). The effect of the food matrix on microorganism reduction also needs to be taken into consideration before its implementation at the commercial level. Since is not necessary that in broth and food same type of reduction will be achieved while keeping all others conditions same like microorganism, pressure intensity, etc. food, might provide the shielding effects to microorganism so, keeping this in consideration, we cannot extrapolate the studies of broth directly into food system at industrial level. Proteins, carbohydrates, lipids, and metals ions can provide a shielding effect (Black et al., 2007). Microorganisms in buffers and microbiological media are more pressure-sensitive as compared to foods (Considine et al., 2008). Dogan and Erkmen (2004) studied the inactivation kinetics of *L. monocytogenes* in the pressurized broth, peach, milk, and orange juice. On pressurization, effectiveness was found to be low in milk in achieving the same reduction of *L. monocytogenes* as compared to broth and fruit juice. It was postulated that the dissimilar behaviors of microorganisms in the foods might be due to the protective effect of fat and protein in milk. A similar baroprotection of milk components to *L. innocua* 4202 was found by Black et al. (2007) and stated that HPP induced solubilization of colloidal calcium phosphate with an associated rise in the buffering capacity of milk and stabilization of the cellular membrane by $Ca^{2+}$ and $Mg^{2+}$ cations. Only 5.5 log reduction of *Lactococcus lactis* subsp. *lactis* in fresh Gouda cheese was reported by Messens et al. (1999) after HPP treatment at 400 MPa/60 min, while 7.5 log reductions of *L. lactis* subsp. *cremoris* strains in buffer suspensions were achieved by Malone et al. (2002) after HPP treatment at the pressure of 400 MPa/5 min. Although the same culture i.e., *L. lactis* was used for the preparation of cheese and pressurized for a longer duration as compared to buffer at the same level of pressurization, but still lower inactivation was obtained in cheese. The effect of pressurization on *S. aureus* in different food matrix (soybean protein, sucrose, bean oil) was studied by Gao et al. (2006), and significant reduction was obtained with an increase in the concentration of both sucrose and soybean protein. Histamine forming bacteria (*M. morganii and P. phosphoreum*) were found to be more resistant to pressure in tuna meat slurry as compared to phosphate buffer, which was indicated by lower D value of bacteria in the case of phosphate buffer (Lee et al., 2020).

It implies that mere data found in studies using buffers or synthetic media cannot be used for food commodities as they might require higher pressure treatment to attain the same degree of reduction (Patterson, 2005).

### pH

The pH of suspending media, during HPP treatment, can affect the inactivation of microorganisms. The synergistic effect of pressure and pH increased microorganism's

reduction and damage to cell membranes, and injured cells are unable to recuperate on further storage. Compression results in lowering pH as hydrogen ions increase on the ionization of water molecules. Hence, deviation from neutral pH towards low pH increases susceptibility to microbial inactivation (Alpas et al., 2000). Vegetative cells are reported to be very sensitive to pressurization treatment at low pH (Smelt, 1998).

Stewart et al. (1997) reported by altering the pH of phosphate-buffered saline (0.1 M) from 6.0 to 4.0 and HPP treatment at 353 MPa/10 min/45 °C leads to a further 3 log reduction of *L. monocytogenes* CA. Alpas et al. (2000) found a significant decrease in the reduction of eight bacterial strains by changing the pH (from 6.5 to 5.5 and to 4.5) of cell suspensions and HPP at 345 MPa for 5 min at 25–35 °C. Further addition of lactic acid (1%) or citric acid (2.1%) to the suspending medium (pH 4.5) enhanced the inactivation of pathogens by 1.2–3.9 log. *S. aureus* in different food matrix (soybean protein, sucrose, bean oil) was studied by Gao et al. (2006) at different pH was found to cause a significant reduction in *S. aureus*. Reduction in *S. aureus* was found to decrease rapidly as pH was increased. These results could be due to the interactive effect of pH and food matrix, and it was concluded that reduction was found to be quite sensitive to low and high pH, soya bean protein, and sucrose. Some of the above studies reported that bacteria are found to be sensitive to the effect of media pH (4–6).

### Water activity ($a_w$)

Low water activity gives a shielding effect to microorganisms suspended in food, and it was illustrated that vegetative cells are sensitive to pressurization at high $a_w$ (Gao et al., 2006). The pressurization of 400 MPa resulted in higher inactivation of *L. monocytogenes* spiked in cooked ham with $a_w$ of 0.98 (Aymerich et al., 2005) while the pathogen was not significantly reduced in fermented sausages at $a_w$ of 0.90. This could be related to the bar protection derived from the lower $a_w$ of fermented sausages (0.90), as the processing treatment was the same, i.e., 400 MPa.

The presence or addition of sugar and salt also affects the $a_w$ of food commodities, which can considerably affect the microorganism inactivation rate after HPP as bar protective effects due to the presence of solutes are observed (Molina-Höppner et al., 2004; Van Opstal et al., 2003). The addition of solutes reduces the $a_w$ thereby shrinkage of cell and thickening of the cellular membrane occur, which reduces membrane permeability resulting in better survival of the microorganisms (Molina-Höppner et al., 2004). Baroprotection due to reduced $a_w$ was reported by Molina-Höppner et al. (2004) for *L. lactis* by the addition of 2–4 M sodium chloride to the suspending medium. HPP induced inactivation was also found to be inhibited by kind of solute even at similar $a_w$. Koseki and Yamamoto (2007a) reported that different concentrations of phosphate buffer (0.01 M and 0.1 M.) had a significant effect on HPP induced inactivation (400 MPa/10 min/25 °C) of *L. monocytogenes*. HPP induced inactivation was found to decrease with an increase in the saturation of suspension regardless of kind of solute (sodium chloride and sucrose).

### Temperature, pressure, compression rate, and holding time

Either very low or elevated temperature both enhances the susceptibility of microorganisms to pressure, which increases the rate of inactivation. A profile of temperature and pressure changes have been explained in an earlier section and is shown in Fig. 2. Although microorganisms exhibit resistance even at 15–30 °C, but at extreme conditions (very low and very high temperature), microorganism inactivation rate is significantly elevated in combination with pressure (Yordanov and Angelova, 2010). Donsì et al. (2007) obtained higher inactivation of *S. cerevisiae* in pineapple and orange juices at 45 °C than at 25 °C, both being treated at similar pressure conditions.

The pressure level applied to the product is the primary factor influencing its quality. The pressure level is directly proportional to the effects on the destruction of microbes and enzymes. It has been reported that biochemical reactions can start at 100 MPa, while at 300 MPa irreversible reactions begin to occur. Although high pressure, i.e., 1000 MPa, have also been studied in food applications, however, for commercial applications, the upper limit is 600 MPa (Heinz and Buckow, 2009).

It is known that compression and decompression rates could enhance the high-pressure inactivation of microorganisms. Contradictory results were obtained by different researchers regarding the effects of compression and decompression rates. Chapleau et al. (2006) obtained much higher inactivation of *Salmonella typhimurium* and *L. monocytogenes* in phosphate buffer solution for slow compression (1 MPa/s) and decompression (1 MPa/s) rates than at fast compression (10 MPa/s) and decompression (less than 2 s) rates after the application of HPP. Donsì et al. (2007) also observed a higher reduction of *S. cerevisiae* in pineapple and orange juices for slow compression rate (2.5 MPa/s) than at faster compression rates (10.5 and 25 MPa/s) during multiple pulse pressurization. Similarly, slow compression and decompression rates were reported to have increased the efficiency of high pressure for reducing spores (Syed et al., 2012). In contrast, faster compression and decompression rates were found to be more effective for the inactivation of vegetative bacterial

cells (Noma et al., 2002). The authors concluded that rapid compression and decompression rates could augment the pressure mediated damage and enhanced microbial inactivation rate. Complete inhibition of spore germination was noticed at 380 MPa of pressure and 60 °C of temperature for 30 min. HPP has effectively inhibited the spore germination and directly proportional to the pressure, temperature, and pressure-holding time (Kalagatur et al., 2018).

### Type and age of microorganism

Vegetative and pathogenic microorganisms are effectively inactivated by exposure to 200–600 MPa (Balasubramaniam and Farkas, 2008). Gram-positive bacteria, compared to gram-negative bacteria, are more resistant to pressurization due to the presence of rigid teichoic acid in its cell wall (Silhavy et al., 2010). Bacteria were reported to be more resistant to high pressures than yeast. Molds and yeast are easily inactivated at 25 °C using 300–400 MPa for a few minutes except yeast ascopores as they require elevated pressures for inactivation (Palou et al., 2002). It is also reported by Pilavtepe-Çelik et al. (2013) that rod shape bacteria (*E. coli*) are more resistant than slender rod shape bacteria (*P. aeruginosa*) whereas maximum resistance is exhibited by cocci (*S. aureus*). Variations in resistance to pressure might be attributed to enormous structural variations. Spores inactivation requires high pressure in combination with moderate temperatures due to their high resistance as compared to vegetative microorganisms. Nonproteolytic type B spores (spore-forming pathogens) are highly insensitive to HPP (Balasubramaniam and Farkas, 2008) as they can retain dipicolinic acid or it could be due to the thickness and structure of the bacterial spore coat. For the inactivation of spores, two-step exposure treatment is found to be more effective. In the first step, HPP treatment is given at low pressure to germinate the spores. Pressure triggers the germination process in spores, and volume reduction on compression (according to Le Chatelier's principle) ultimately increases the solvation of spore's component. The germination eases out inactivation (100–300 MPa) by rendering spores more sensitive to HPP (Yaldagard et al., 2008). In the second step, high-pressure treatment is suggested to inactivates the spores. Pressure and heat also act synergistically to inactivate spores without germination. On the application of pressure at a higher temperature, the cortexlytic enzymes present in bacterial spores get inactivated directly and eliminating the step of spore germination (Landfeld et al., 2011). Inactivation of bacterial spores by HPP has been studied in detail comparative to fungal spores (Kalagatur et al., 2018). In the life cycle of microorganisms, cells in the proliferating phase are less resistant to high pressure than in stationery and lag phases (Yordanov and Angelova, 2010).

It was reported by Rong et al. (2018) that HPP could alter the spoilage process of Oysters when observed during storage at chilled conditions. As in fresh, spoiled, and HPP treated spoiled oyster samples, different microorganism dominance was observed at phylum, class, order, family, and genus level. Similarly, Cruz-Romero et al. (2008) reported the influence of HPP on differences in microbiota, whereas Prapaiwong et al. (2009) could not found differences in the microbiological ecology of treated and untreated oyster samples.

## Kinetics modeling of microbial inactivation

The study of kinetic modeling helps optimize the process parameters for efficient processing and prediction of the effects of HPP on nutritional composition, microorganism reduction, and shelf life of the product (Smelt et al., 2002). Apart from processing conditions, the microbial inactivation rate and their resistance is affected by the composition of the medium and kind of microorganisms and have shown significant variation. Therefore, it is important to predict the death behavior accurately for the foodborne and resistant microbial groups present in the food.

## Kinetic data analysis

### Pulse pressurization

A single cycle of HPP consists of three steps: pressurization, pressure-hold, and depressurization period, each exerting different effects on the microbial activity. The inactivation rate in the dynamic period has been described in terms of pulse effect values and the isobaric–isothermal holding period by a standard kinetic model. Pressurization and depressurization effects are additive. Based on this assumption 3-stage effect was simplified to a 2-stage as shown in Fig. 5, and can be quantified in term of pulse-effect (PE) by Ramaswamy et al. (2003) and computed using (Eq. 1):

$$PE = Log_{10}(N_0) - Log_{10}(N_{PE}) \quad (1)$$

where $N_0$ is the initial microorganism number in the control samples and $N_{PE}$, the number of survival microbial cells after single pulse pressure treatment. Analogous to the

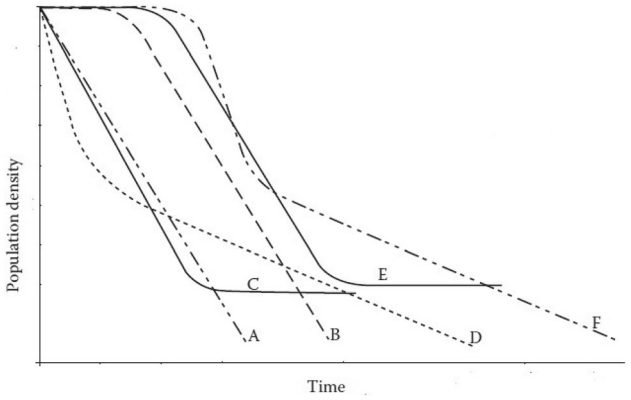


**Fig. 5** Representation of six different shapes of survival curves: (A) log-linear, (B) survival with shoulder, (C) survival with tail, (D) biphasic, (E) survival with shoulder and tail, and (F) biphasic with shoulder

decimal reduction time in thermal processing, $N_D$ value was calculated as ($1/PE$), which signifies the number of pulses requisite to attain 90% reduction in the microorganism count.

The reduction in the count by pulse pressurization is due to the development of cavitation in the cell as an outcome of quick pressurization and depressurization during HPP, leading to physical alterations in the cell wall and, finally, loss of cell integrity resulting in cell death (Hiremath and Ramaswamy, 2012). The magnitude of depressurization is reported to have a greater effect than pressurization on the cell wall. The physical disruptions are reliant on the magnitude of the process treatment given (Ramaswamy et al., 2003). The escalation in pressure come up time provides extra period to the microorganisms being exposed to stress developed during pressurization, which increased the extent of inactivation. Additional to pressure treatment, at a higher temperature, the inactivation rate of the bacterial cell increases, which could can be due to thermal damage, therefore, aiding the disruptions initiated by the pressure effect (Chakraborty et al., 2015). Some of the findings of the researchers in which the separate effect of single pulse pressurization, from the pressure-hold time, has been studied and has been summarized in Table 2.

## Isobaric inactivation kinetics

### Log-linear models

During the isobaric process for inactivating microorganisms very often follows a monophasic first-order kinetic model, the best-known primary survival model (Eq. 4; Table 3). It is assumed that the D value calculated with this model has a log-linear temperature dependence or, the temperature effect on the exponential rate constant ($k = 1/D$) follows the Arrhenius equation (Eq. 2).

$$\mathrm{Ln}k = \mathrm{Ln}k_{ref,T} + \frac{E_a}{R}\left[\frac{1}{T_{ref}} - \frac{1}{T}\right] \quad (2)$$

The sensitivity of $k$ (microbial inactivation rate) to pressure at a particular temperature can be calculated as activation volume ($V_a$,) by employing the Eyring Eq. (3).

$$\mathrm{Ln}k = \mathrm{Ln}k_{ref,P} + \frac{V_a}{RT}\left[P_{ref} - P\right] \quad (3)$$

Apart from the first-order kinetic model, the biphasic model is usually used to show the existence of two distinct sub-populations having variable sensitivities (pressure sensitive and pressure-resistant) at isobaric conditions; where each population exhibits distinct first-order microbial inactivation. In Eq. (5) f corresponds to the sensitive fraction of the population, (1 − f) represents the fraction of the resistant population, $k_{max1}$ and $k_{max2}$ are the inactivation rates of the two distinct populations, respectively (Lee et al., 2001). The major drawback of this model was reported by Campanella and Peleg (2001) that variations in the microbial inactivation rate might be due to changes in the food matrix instead affected by variant populations.

### Nonlinear kinetic models

Although first-order kinetics model is commonly used to depict the inactivation rate of microorganisms using high pressure processing, variations from linear behavior have been stated by researchers (Buzrul et al., 2008; Rendueles et al., 2011), and precise outcomes are obtained on the inclusion of curvature in the fit (Klotz et al., 2007). After pressure treatment, microbial inactivation curves of different shapes have been described, i.e., curves with shoulders, curves with tails, and sigmoidal curves (Fig. 5). Non-linearity of the semi-logarithmic survival curve might be due to the variations in defense and repair mechanism of subpopulations against the lethal agents (Bevilacqua et al., 2015). To describe the nonlinear behavior of curve survival curves, several models have been postulated. The detailed discussion of some of these models has been done by Buckow et al. (2009) and Serment-Moreno et al. (2015). The Weibull model was reported to be most simple, flexible, and found to fit the experimental data better than other functions. Table 3 reviews the several kinetic models used

**Table 2** PE values for different microorganisms in food samples

| Sample | Microorganisms | Treatment conditions (MPa/°C) | CUT/DCT > in (min/min) | Maximum PE values at highest treatment (log values) | References |
|---|---|---|---|---|---|
| Apple juice | *E. coli* (29055) | 150–400/25 | 0.5–3/< 15 s | 8 | Ramaswamy et al. (2003) |
| Fish slurry | *E. coli* (O157:H7); *L. monocytogenes* (Scott A) | 250–400/ 20–25/ | 0.5–3/15 s | 0.68; 0.27 | Ramaswamy et al. (2008) |
| Mango juice | *E. coli* (O157:H7); *L. monocytogenes* (Scott A) | 250–550/ 20–23 | 1–3/< 20 s | 3.5<br>0.12 | Hiremath and Ramaswamy (2012) |
| Black tiger shrimp | *E. coli* ATCC 11775 | 300–600/27 | 1.5/< 10 s | 2.17 | Pavuluri and Kaur (2014) |
| Mango pulp | Natural microflora; Aerobic mesophiles; Yeast & mold; Coliforms; Lactic acid bacteria; Psychrotrophs | 100–600/30 | 0.30–1.62/ < 10 s | 1.62; 2.70;4.24; 5.23; 4.59; 2.88 | Kaushik et al. (2015) |
| Black tiger shrimp | Aerobic mesophiles; Psychrotrophs; *E. coli*, *S.aureus* | 300–600/27 | 0.35–1.5/< 10 s | 1.32; 1.37; 1.72; 1.40 | Kaur and Rao (2017) |

*PE* pulse effect, *CUT* come up time, *DCT* decompression time

to describe the microbial inactivation rate obtained after pressurization.

During extrapolative microbial experiments, modeling of microorganism's growth has been studied by several researchers in a variety of food matrix (Pilavtepe-Çelik et al., 2009; Slongo et al., 2009). Basak et al. (2002) studied the destruction kinetics of *Leuconostoc mesenteroides* and *S. cerevisiae* using first-order kinetics for orange juice. A quasi-chemical model was used to describe the inactivation of *S. aureus, E. coli, and L. monocytogenes* in food samples i.e. bread, turkey meat, ham, and cheese by Doona et al. (2005). Chen and Hoover (2003) reported that a better fit of data of *Yersinia enterocolitica* inactivation was obtained using Weibull and log-logistic models in comparison to linear and modified Gompertz models for the selected bacterium. Guan et al. (2005), in the case of UHT treated milk observed tailing in all curves of *Salmonella typhimurium* pressurized from 350 to 600 MPa and sigmoidal survival curves when pressurized at 500–600 MPa. Modeling results indicated that the log-logistic model produced the best fit to data. Slongo et al. (2009) used modified Gompertz and logistic models to fit experimental data obtained for the microbial load in HPP treated ham and concluded that these models could be successfully used to predict the shelf life of HPP treated products. During all these studies, only the effect of processing conditions was taken into account. An extension towards the influence of environmental and processing factors like temperature, pH, water activity, recovery conditions, food structure, and composition on the extent of the microbial inactivation is necessary.

The development of linear and nonlinear models has simplified the calculation of microbial inactivation rate under different processing conditions, but still, more attention is required, particularly on the effect of food structure and composition (Koseki and Yamamoto, 2007b). This would enable food producers to have an overall view on the influence of their processing conditions on microbial survival, and hence, to assess performances of their processes accurately.

Ensuring the safety of the product after HPP by microbial inactivation is a matter of prime importance in the food processing sector. Various possible mechanisms for microbial inactivation by HPP such as induced conformational changes in the cell membrane, cell morphology, and perturbs biochemical reactions, as well as a genetic mechanism of the microorganisms, have been discussed in detail and critically analyzed. Studies on various factors affecting microbial inactivation have also been compared comprehensively and depicted in tabular form along with microbial inactivation kinetic modeling to develop a better

**Table 3** Mathematical equations describing microbial inactivation by high pressure processing

| Kinetic model | Mathematical representation | Eq. | Pathogen | Medium/Sample | Treatment (MPa/min/ °C) | References |
|---|---|---|---|---|---|---|
| First order Kinetics | $\mathrm{Log}\left(\frac{N_t}{N_0}\right) = -\frac{t}{D}$ | 4 | *E. coli* 29055 | Apple juice | 150–400/ 0–80/25 | Ramaswamy et al. (2003) |
| | | | *E. coli* | Broth, milk, peach, orange juice | 300–700/ 0–24/25 | Dogan and Erkmen (2004) |
| | | | *E. coli* O157:H7<br>*L. monocytogenes* Scott A | Fish slurry | 250–400/ 0–60/ 20–25 | Ramaswamy et al. (2008) |
| | | | *Morganella morganii, Photobacterium phosphoreum* | Phosphate buffer and tuna meat slurry | | Lee et al. (2020) |
| Biphasic model | $\mathrm{Log}(N_t) = \mathrm{Log}\ (N_o) + \mathrm{Log}\ (f.e^{-k1.t}_{max} + (1\text{-}f).e^{-k2.t}_{max})$ | 5 | *E. coli* | Carrot juice | 150–600/ 0–60/5–45 | van Opstal et al. (2005) |
| | | | *E. coli* | KOH Buffer | 150–600/ 0–60/5–45 | |
| | | | *L. monocytogenes* | RTE cooked meat products | 300–800/ 0.1–15/15 | Hereu et al. (2012) |
| Log-logistic equation | $\log(N_t) = \log(N_0) + \frac{\omega-\alpha}{1+e^{\frac{4\sigma(\tau-log t)}{\omega-\alpha}}} - \frac{\omega-\alpha}{1+e^{4\sigma(\tau+\sigma)/(\omega-\alpha)}}$ | 6 | *L. monocytogenes* Scott A | Whole Milk | 400–500/ 0–120/ 22–50 | Chen and Hoover (2003) |
| | | | *L. innocua* CDW47 | Peptone water | 138–345/ 5–30/ 25–50 | Buzrul and Alpas (2004) |
| Modified Gompertz model | $\log(N_t) = \log(N_0) + Ce^{-e^{BM}} - Ce^{-e^{-B(t-M)}}$ | 6 | *Salmonella typhimurium* DT 104 | Whole milk | 350–600/ 0–30/21 | Guan et al. (2005) |
| | | | *Salmonella typhimurium* | Tryptone soy broth | 200–350/ 0–50/ 15–45 | Erkmen (2009) |
| Weibull | $\log(N_t) = \log(N_0) - \left(\frac{t}{\delta}\right)^{\beta}$ | 7 | *V. vulnificus; V. parahaemolyticus* | Oysters | 276–379/ 1–15/– | Hu et al. (2005) |
| | | | *S. aureus* | Carrot juice, Peptone water | 200–400/ 5–40/40 | Pilavtepe-Celik et al. (2009) |
| | | | *Lactobacillus plantarum* | Mandarin Juice | 0–450/1/15, 30, 45 | Carreño et al. (2011) |
| | | | *Escherichia coli* P36, *Listeria innocua* ATCC 51742, and *Salmonella typhimurium* WG49 | Wheatgrass juice | 400–600/ 1–3/11 | Ali et al. (2019) |
| Log linear | $\log(N_t) = \log(N_0) - \frac{k_{max}.t}{\mathrm{Ln}(10)}$ | 8 | *L. monocytogenes* | RTE cooked meat products | 300–800/ 0.1–15/15 | Hereu et al. (2012) |

**Table 3** continued

| Kinetic model | Mathematical representation | Eq. | Pathogen | Medium/Sample | Treatment (MPa/min/°C) | References |
|---|---|---|---|---|---|---|
| | | | *Escherichia coli* P36, *Listeria innocua* ATCC 51742, and *Salmonella typhimurium* WG49 | Wheatgrass juice | 400–600/1–3/11 | Ali et al. (2019) |
| Log linear with tail | $Log(N_t) = \log\left[\left(10^{\log(N_0)} - 10^{\log(N_{res})}\right).e^{-kmax.t} + 10^{\log(N_{res})}\right]$ | 9 | *L. monocytogenes* | RTE cooked meat products | 300–800/0.1–15/15 | Hereu et al. (2012) |
| | | | *Escherichia coli* P36, *Listeria innocua* ATCC 51742, and *Salmonella typhimurium* WG49 | Wheatgrass juice | 400–600/1–3/11 | Ali et al. (2019) |
| Log- linear with shoulder and tail | $\log(N_t) = Log\left[\left(\frac{\left(10^{\log(N_0)} - 10^{\log(N_{res})}\right)e^{-kmaxt}}{1 + \left(e^{kmax.S_l} - 1\right).e^{-kmaxt}}\right) + 10^{\log(N_{res})}\right]$ | 10 | *L. monocytogenes* | RTE cooked meat products | 300–800/0.1–15/15 | Hereu et al. (2012) |
| Ratkowsky's square root model | $\sqrt{k_{max}} = b.(P - P_{max})$ | 11 | *E. coli* | Trypticase soy broth | 200–400/1–30/15 | Koseki and Yamamoto (2007b) |

$N_t$ is the number of surviving microorganisms following pressure treatment for time t (min); $N_0$ is the initial number of microorganisms with no pressure treatment; $k$ is the reaction rate constant ($min^{-1}$); D = decimal reduction time; $\delta$ is a scale factor; p is a shape factor; $k_{max}$ the maximum specific inactivation rate ($min^{-1}$); $N_{res}$ the residual population density (Log CFU/g) that characterize tailing of inactivation kinetics; $S_l$ being the degree of freedom; b is constant, $P_{min}$ is minimum pressure for microbial inactivation; α is the upper asymptote (Log CFU/mL); ω is lower asymptote (Log CFU/mL), σ is the maximum rate of inactivation (Log (CFU/mL)/Log min); τ is the Log(time) to the maximum rate of inactivation (Log(min))

understanding. HPP promises as a potential process for valued food products while retaining food quality and safety.

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**Compliance with ethical standards**

**Conflict of interest** Authors have no competing interests to declare.

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