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Phages for biocontrol in foods: What opportunities for *Salmonella* sp. control along the dairy food chain?

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ABSTRACT

Controlling the presence of pathogenic bacteria, such as *Salmonella* sp., in dairy products production is a burning issue since contamination with *Salmonella* can occur at any stage of the production chain. The use of *Salmonella*-phages applied as control agents has gained considerable interest. Nonetheless, *Salmonella*-phage applications specifically intended for ensuring the safety of dairy products are scarce. This review identifies recent advances in the use of *Salmonella*-phages that are or could be applied along the dairy food chain, in a farm-to-fork approach. *Salmonella*-phages can be promising tools to reduce the shedding of *Salmonella* in cattle, and to reduce and control *Salmonella* occurrence in postharvest food (such as food additives), and in food processing facilities (such as biosanitizing agents). These control measures, combined with existing methods and other biocontrol agents, constitute new opportunities to reduce *Salmonella* occurrence along the dairy food production, and consequently to alleviate the risk of *Salmonella* contamination in dairy products.

1. Introducton

The *Salmonella* genus belongs to the *Enterobacteriaceae* family. According to the latest nomenclatural system (Tindall, 2005), two species, namely *Salmonella bongori* and *S. enterica* are currently recognized. The latter is composed of six subspecies, one of which, *Salmonella enterica* ssp. *enterica*, encompasses about 2000 serovars out of the 2600 existing serovars within the genus. Some of them are strictly human pathogens (e.g. *Salmonella* Typhi), and some others are specifically associated to animals (e.g. *Salmonella* Abortusovis). Nevertheless, most are ubiquitous serovars, and pathogenic in both animals and humans and as such, they can cause zoonosis.

Among zoonotic agents investigated in the European Union, *Salmonella* usually ranks second after *Campylobacter*. Over the past decade, there have been between 87,000 and 135,000 yearly human salmonellosis cases in Europe (EFSA and ECDC, 2017, 2012). A statistically significant decrease in confirmed human salmonellosis cases was observed over the 2008–2016 period (decrease by 35%). However, during the last reported 5 years (2012–2016) the number of *Salmonella* did not decrease any further in humans. During the last reported year (2016), 9,061 human cases have been associated with 1,067 salmonellosis foodborne outbreaks, which resulted in the hospitalisation of 40% people, and in the death of 128 people (0.25% of all the foodborne cases) (EFSA and ECDC, 2017).

Eggs and egg products are the main sources of salmonellosis with a rate of 0.06 foodborne outbreaks in a population of 100,000, followed by poultry and pork meat (0.03 foodborne outbreaks in a population of 100,000) and cheese (0.01 foodborne outbreaks in a population of 100,000) (EFSA and ECDC, 2017). *Salmonella* is increasingly present in dairy cattle worldwide (Chlebicz and Slizewska, 2018; Poupée, 2016). This is particularly due to their aptitude to survive over long periods of time in the dairy environment (Taylor and Burrows, 1971). For example, *Salmonella* can survive up to one year in dry faeces, which is the main contamination vector in cattle. Even if bovine salmonellosis is a disease that remains uncontrolled, it could require epidemiologic supervision due to its clinical impact. This relates above all to asymptomatic carriers, since they are able to spread the bacteria without any symptoms. The excretion commonly occurs through faeces and, in very exceptional cases, through the milk itself (Heuchel et al., 2000). In 2014 in Europe, the most commonly reported serovar in food was *S.* Infantis, followed by *S.* Typhimurium, *S.* Enteritidis, *S.* Dublin and monophasic variants of *S.* Typhimurium. All these serovars, except for *S.* Dublin, were reported to be the most frequent amongst human cases in Europe (EFSA and ECDC, 2017). The occurrence of these major serovars seems to depend on the country, and vary in significance over time. In France for instance, during the same period, the most frequent serovar was *S.*

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Table 1
Applications of *Salmonella*-phages at primary production (listed by industry, then alphabetically by *Salmonella* serovar, and then chronologically by date of publication).

Application	*Salmonella* serovars	Phages	Phage administration	Main results obtained in the studies	References
Poultry production					
Newly hatched and vaccinated broiler chicks	Enteritidis	P1:1	Orally via feed or water	Reduction in *Salmonella* shedding using feed particles as phage delivery vehicles	(Sklar and Joerger, 2001)
One-day old broilers	Enteritidis	CNPSA1, CNPSA3 and CNPSA4	Orally	Reduction of 3.5 orders of magnitude on *Salmonella* cfu per gram of cecal content	(Fiorentin et al., 2005)
Day-of-hatch chicks	Enteritidis	CB4∅, WT45∅	Orally and cloacally	All treatments significantly reduced *Salmonella*. No persistent reduction observed.	(Andreatti Filho et al., 2007)
7- and 10-day old chickens	Enteritidis	3 phages (BP1, BP2, BP3)	Coarse spray and drinking water	Phage delivery both by coarse spray and drinking water reduced *Salmonella* intestinal colonization	(Borie et al., 2008, 2009)
One-day old broilers	Enteritidis	ΦCJ07	Feed additive	Phage therapy significantly prevented the horizontal transmission of *Salmonella* in chicken	(Lim et al., 2012)
Fertile eggs	Enteritidis	2 phages (F1055S, F12013S)	Aerosol spray	Phage treatment of challenged *Salmonella* eggs reduced the disease symptoms in chicks	(Henriques et al., 2013)
One-day old broilers	Enteritidis	NA	Feed additive	Mortality was linearly decreased with increasing phage level, and *Salmonella* concentration in the cecum was decreased with increasing levels of phage	(Kim et al., 2013)
45-day old broilers	Enteritidis	21 phages	Orally	Up to 2 log10 CFU reduction observed	(Gonçalves et al., 2014)
Newly hatched chicks	Typhimurium	Φ2.2	Orally	Considerable reduction in birds' mortality	(Berchieri et al., 1991)
36-day old broilers	Typhimurium, Hadar, Enteritidis	Φ10, Φ25, Φ151	Orally by gavage	Up to 4 log10 CFU reduction in *Salmonella* depending on the serovar and the phage	(Atterbury et al., 2007)
123-day old chickens	Typhimurium	Phage cocktail (UAB_Phi20, UAB_Phi87, UAB_Phi78)	Orally	The best reduction in *Salmonella* concentration in chicken cecum was obtained when the phage cocktail was administered 1 day before or just after bacterial infection and then again on different days post-infection	(Bardina et al., 2012)
One-day old chicks	Typhimurium	Φ st1	Intracloacal inoculation	Rapid reduction in *Salmonella* counts	(Wong et al., 2014)
Swine production					
4-week old pigs	Typhimurium	Felix 01	Oral and intramuscular inoculation	The phage treatment significantly reduced the rapid dissemination of *Salmonella* in tonsil and cecum	(Lee and Harris, 2000)
Porcine gastric juice	Typhimurium	2 phages (st104a and st104b)	In vitro challenge	st104a survived better in acidic conditions than st104b, which had become undetectable after 2 h exposure	(O'Flynn et al., 2006)
Grower pigs	Typhimurium	1 phage	Orally	Decrease in *Salmonella* shedding after phage treatment. Improving the performance of growing pigs, especially after bacterial challenge	(Gebru et al., 2010)
Market-weight swines	Typhimurium	Phage cocktail (14 wild-type phages and phage Felix O1)	Orally	Significant reduction in cecal and ileal *Salmonella* concentrations	(Wall et al., 2010)
Weaned pigs	Typhimurium	Phage cocktail	Orally	Phage treatment reduced intestinal populations of inoculated *Salmonella* in pigs compared to controls	(Callaway et al., 2011)
Small pigs	Typhimurium	Phage cocktail (14 wild-type phages)	Orally (microencapsulated phages)	Efficacy of direct feeding of microencapsulated phages for reducing *Salmonella* colonization and shedding in pigs	(Saez et al., 2011)
Other assays at primary production					
Quail breeding	Enteritidis	PSE	Oral gavage or vent lip	Oral administration was a more effective prophylactic tool for reduction of *Salmonella* shedding in poultry than vent lip administration	(Ahmadi et al., 2016)

NA: not available.

4,[5],12:i:, followed by *S*. Typhimurium, *S*. Derby, *S*. Dublin and *S*. Infantis (Lailler and Le Hello, 2016). The occurrence of some serovars tends to vary over the years. This is the case for Mbandaka (4.5 fold increase over the 2007–2012 period), Senftenberg (2.3 fold increase) and Derby serovars (2 fold decrease). The major serovars are not necessarily the same in the different food products. While Mbandaka and Enteritidis serovars appear to be involved in half of the contaminated pork meat, Dublin serovar is detected in half of the contaminated dairy products (Lailler et al., 2012).

Since the dairy food chain is the third most contaminated sector after the egg and meat sectors, it is of utmost importance to try and prevent its contamination. Several strategies for *Salmonella* biocontrol have been considered (Besnard et al., 2018). The use of lytic bacteriophages (phages) appears as a promising approach for improving food safety (Endersen et al., 2014). Phages are bacterial species- (and even strain-) specific viruses, that can attack and kill a target bacterium within minutes of infection. They are self-replicating and generally only target a narrow range of bacterial strains of the same species. Phages are the most abundant entities in the biosphere, and can be isolated from several sources, including from the digestive tract of humans and animals, food, soil, water, sewage and other environment habitats (Clokie et al., 2011). Since they are species-specific and fast-replicating entities, phages provide numerous advantages and relatively few disadvantages, which can in any case be avoided by a thorough characterization of phages (Loc-Carrillo and Abedon, 2011). Despite the vast potential of phages, few studies report phage therapy against *Salmonella* in the dairy sector. Yet, *Salmonella*-phages seem quite diverse, abundant and easy to recover from the dairy farm environment (Duenas et al., 2017; Switt et al., 2013; Wongsuntornpoj et al., 2014), thus making dairy farms suitable reservoirs for isolating new *Salmonella*-phages. Commercial *Salmonella*-phage products, SalmoFresh™ (Intralytix, Inc., Baltimore, USA) and Salmonelex™ (Micreos BV, Wageningen, The Netherlands), have previously been granted the GRAS (Generally Recognized As Safe) status in the USA, and are mainly used on meat products. The commercial animal food Biotector® (CheilJedang Corporation, Republic of Korea) is also used for *Salmonella* control in poultry products. BacWash™ (Omnilytics Inc., USA), targeting *Salmonella*, can also be directly spread onto living animals and hides of livestock (Colavecchio and Goodridge, 2017). Phage-based approaches against *Salmonella* are nonetheless principally undertaken in poultry and swine productions (Carvalho et al., 2017). Despite *Salmonella* outbreaks due to contaminated dairy products, phage therapy in this sector remains poorly documented. This review strives at referencing phage-based biocontrol approaches for controlling *Salmonella* that are or could be implemented along the dairy food chain. Phage-based strategies can be applied to reduce *Salmonella* occurrence starting at primary production, by reducing *Salmonella* carriage in cattle and by decontaminating the dairy farm environment. At secondary production, phage treatments include the use of phages as food additives and sanitizing agents in dairy food processing facilities, alone or in combination with other biocontrol agents.

2. *Salmonella*-phages at dairy primary production

The literature dealing with the use of *Salmonella*-phages in dairy cattle is scarce. Three studies examined the diversity of *Salmonella* isolates and of *Salmonella*-phages on dairy farms in three different countries (Duenas et al., 2017; Switt et al., 2013; Wongsuntornpoj et al., 2014). No publication has actually described the potential use of *Salmonella*-phages as biocontrol agents in dairy cattle so far. To our knowledge, there has only been one study carried out in the dairy sector that illustrates a 2-log10 CFU reduction in *Salmonella* Typhimurium in dairy manure compost, four hours after a lytic phage cocktail has been applied (Heringa et al., 2010). This lack of data at dairy primary production is striking, given the abundant number of studies dealing with the use of *Salmonella*-phages in other animal production sectors. Poultry production is a sector in which the use of *Salmonella*-phages during poultry farming has been well documented over the last thirty years, especially when it comes to the control of Typhimurium and Enteritidis serovars (Table 1). Significant reductions of *Salmonella* cecal contents were observed in one-day-old broilers (Andreatti Filho et al., 2007; Fiorentin et al., 2005; Kim et al., 2013; Lim et al., 2012), and in 34-days-old broilers (Atterbury et al., 2007) after phage treatment. In these studies, several phages have been tested. They were mainly delivered orally to birds, alone or in combination with phage cocktails. Phage treatments also resulted in a significant decrease in mortality of newly-hatched broilers (Berchieri et al., 1991). Interestingly, in this study, when a phage-treated chicken group was placed into contact with a non-treated group, phages seemed to transfer from the treated-group to the non-treated group through faeces excretion. The most promising results in terms of *Salmonella* reduction in chickens were obtained when phages were combined with feed or delivered as feed additives (Sklar and Joerger, 2001). *Salmonella* carriage in poultry can lead to contaminated carcasses after slaughter. The proliferation of *Salmonella* is favored in the cecum and crop when feed withdrawal is carried out during the transit to the slaughterhouse (Corrier et al., 1999), which represents a critical control point before entering the secondary production stage. In this regard, a bacteriophage cocktail successfully reduced the number of *Salmonella* by 2 log10 CFU below the limit of detection in chicken cecum and crop, respectively, showing a promising use of phages for lowering the *Salmonella* risk in animals at pre-slaughter stage (Gonçalves et al., 2014).

In swine production, the efficacy of phages targeting *Salmonella* in reducing the pathogenic risk has also been described (Table 1). Oral delivery of several phages targeting *Salmonella* Typhimurium, alone or in cocktails, has been largely tested in pigs (Callaway et al., 2011; Gebru et al., 2010; Lee and Harris, 2000). These studies showed the significant and lasting efficiency of phages in reducing *Salmonella* carriage and dissemination in pig models compared to untreated animals. Phages can thus be applied to animals by oral administration mixed with livestock feed in order to lower *Salmonella* spreading to the animal's intestine. To be efficient throughout the intestinal tract, the principal requirement for phages is their resistance to the harsh acidic conditions of the animal's stomach. Acid tolerance is phage-dependent. For example, two anti-*Salmonella* phages were tested in porcine gastric juice, which had a pH of 2.5, and only one of the two phages had 10% of its population still active after 2h-exposure (O'Flynn et al., 2006). In healthy ruminants, the rumen pH is generally around 6, and can transiently drop to 5.2 a few hours after feed intake. Therefore, pH-sensitivity of phages should not be a limit to the use of phages in dairy cattle. Microencapsulation is also a means to protect phage particles (Wall et al., 2010). A microencapsulated cocktail composed of 14 anti-*Salmonella* phages, administrated to pigs by gavage or mixed with livestock feed, proved to almost eradicate *Salmonella* Typhimurium in pigs (Saez et al., 2011). It is noteworthy that, in this study, *Salmonella* shedding was significantly lower in the feed group than in the gavage group 2h and 4h after the bacterial challenge. This corroborates the promising potential of using *Salmonella*-phage directly in animal feeds. Nonetheless, investigating the impact of phage administration on animal health, and especially on the immune response, is a prerequisite to further developments of food containing phage (Capparelli et al., 2010).

3. *Salmonella*-phages at dairy secondary production

Many works are dedicated to proving the usefulness of phages for controlling pathogenic bacteria in food processing facilities and foods (Endersen et al., 2014; Kazi and Annapure, 2016). The use of *Salmonella*-phages in the dairy sector remains poorly documented compared to other production sectors like the meat and vegetable sectors (Table 2). Nonetheless a few applications of phages to dairy products contributed to the control of *Salmonella* occurrence. In a liquid dairy

Table 2
Salmonella-phages application at secondary production (listed by phage uses - single phage, phage cocktail, commercial solution - and then chronologically by date of publication).

Used phages	Serovars	Food type models	Main results of the studies	References
Single phages				
Phage SJ2	Enteritidis	Cheddar cheese made from raw and pasteurized milk	*S.* Enteritidis decreases by 1–2 log10 CFU cycles in raw and pasteurized milk cheeses made from milk containing phage	(Modi et al., 2001)
Phages 12, P22, 29C	Enteritidis	Chicken skin	Phages applied at a MOI of 100–1000 rapidly reduced the number of recoverable bacteria by up to 2 log10 CFU over 48 h	(Goode et al., 2003)
Variant of Felix O1 (LP) and wild -type Felix O1 (WT)	Typhimurium	Chicken frankfurters	Suppression of up to 2.1 log10 CFU were achieved with WT and LP with a significant difference between the performances of the two variants	(Whichard et al., 2003)
2 single phages and in cocktail	Typhimurium, Enteritidis	Sprout and broccoli seeds	An observed reduction of 1.37 log10 CFU in *Salmonella* on mustard seeds with a single phage, and of 1.5 log10 CFU on broccoli seeds (mixture of 2 phages)	(Pao et al., 2004)
Phage PHL 4	Enteritidis	Broiler carcass	All phage treatments reduced the *Salmonella* frequency as compared to controls	(Higgins et al., 2005)
Phage P7	Typhimurium	Raw and cooked beef meat	Host inactivation was variable and depended on the incubation conditions and food type. Significant reductions at 24 °C were achieved compared to phage-free controls	(Bigwood et al., 2008)
Phages SSP5 and SSP6	Oranienburg	Sprouting alfalfa seeds	Approximately 1 log10 CFU/g reduction of viable *Salmonella*. Development of *Salmonella* resistance to phage not evidenced in neither seed nor *in vitro* challenge trials	(Kocharunchitt et al., 2009)
Phage FO1-E2	Typhimurium	Turkey deli meat, chocolate milk, hot dogs, seafood, egg yolk	No viable cells detected following FO1-E2 application at 8 °C (> 3 log10 CFU reduction). Bacterial counts lowered by 5 logs at 15 °C in turkey deli meat and chocolate milk, and by 3 log10 CFU on hot dogs and in seafood. In egg yolk, a first effect was observed only after 2 days, but not anymore after 6 days	(Guenther et al., 2012)
Phage wksl3	Typhimurium, Enteritidis	Chicken skin	At 8 °C, about 2.5-log10 CFU reduction in bacterial cell counts	(Kang et al., 2013)
Phage P22	Typhimurium	Liquid eggs, energy drinks, whole and skimmed milk, apple juice, chicken breast and chicken mince	Reduction of 2–3 log10 CFU after 48 h at 4 °C depending on both mix of strains and specific food	(Zinno et al., 2014)
2 single phages (ΦSP-1 and ΦSP-3) and in a cocktail	Enteritidis	Chicken meat	Significant reduction in the bacterial counts at all studied temperatures	(Augustine and Bhat, 2015)
2 phages alone (PA13076 and PC2184) and in cocktail	Enteritidis	Chicken breast, pasteurized whole milk, Chinese cabbage	Better inhibitory effect at 4 °C than at 25 °C. Significant reduction of bacterial numbers in all tested foods	(Bao et al., 2015)
vB_Sal S_SJ_2 (SJ2)	Typhimurium, Enteritidis	Ground pork and liquid egg	Phage efficacy was temperature-dependent with larger reductions observed at the highest tested temperatures (21 °C)	(Hong et al., 2016)
3 phages alone (phSE-1, phSE-2 and phSE-5), and cocktails of 2 or 3 phages	Typhimurium	Bivalve	Promising choice to be used during the bivalve depuration	(Pereira et al., 2016)
2 single phages (ZCSE1 and ZCEC1)	Enterica	Chicken skin, eggs, tomatoes and meat	Observed reduction of at least 2 log10 CFU/ml depending on the phage and the food product	(El-Shibiny et al., 2017)
Phage SI1	Enteritidis	Sprouting alfalfa seeds	Reduction of 38.3 ± 3.0% of viable *Salmonella* cells was observed in the 2 h following phage treatment	(Fong et al., 2017)
Phage SE07	Enteritidis	Fruit juice, fresh eggs, beef and chicken meat	A significant reduction of *S.* Enteritidis population of at least 2 log10 CFU in all types of foods tested	(Thung et al., 2017)
Phage fmb-p1	Typhimurium, Enteritidis, Saintpaul, Agona, Miami, Anatum, Heidelberg, Paratyphi-C	Ready-to-eat duck meat	Phage treatment (~10 log10 CFU/cm^2) caused a peak reduction in *S.* Typhimurium of 4.52 log10 CFU/cm^2	(Wang et al., 2017)
Phage cocktails				
Cocktail SCPLX-1 (4 lytic phages)	Enteritidis	Fresh-cut fruits (melons, apples)	Phage mixture reduced *Salmonella* counts by approximately 3.5 log10 CFU on honeydew melon slices stored at 5 and 10 °C and by 2.5 log10 CFU on slices stored at 20 °C, which was greater than the maximal amount achieved with chemical sanitizers	(Leverentz et al., 2001)
Phage cocktail (Felix01, ΦSH17, ΦSH18, ΦSH19)	Typhimurium	Pig carcasses	Observed reduction of more than 1 log10 CFU when the ratio of phage applied was in excess of the bacterial concentration.	(Hooton et al., 2011)
Phage S16 and phage Felix-O1-E2, alone or in cocktail	Typhimurium, Newport, Enteritidis	Chocolate milk	Specific reduction of *Salmonella* by the respective phage and unhindered survival of the insensitive strain. If there was reduction, then it was complete	(Marti et al., 2013)

(*continued on next page*)

Table 2 (*continued*)

Used phages	Serovars	Food type models	Main results of the studies	References
5 phages (phiSE 7, 16, 18, 36, 43)	Enteritidis	Chicken skin	Bacterial phage reduction with phage cocktail as efficient as with chemical agents	(Hungaro et al., 2013)
3-phage cocktail (UAB_Phi 20, UAB_Phi78, and UAB_Phi87)	Typhimurium, Enteritidis	Pig skin, chicken breasts, fresh eggs, and packaged lettuce	Significant reduction in all the food products, for both serovars	(Spricigo et al., 2013)
Phages fSE7, fSE8 and fSE12 fSE1C and fSE4S	Enteritidis	Raw and smoked salmon tissues	Significant reduction in bacterial counts obtained (up to 3 log10 CFU) on days 3, 6 and 10 in raw salmon samples and in smoked salmon (up to 2 log10 CFU)	(Galarce et al., 2014)
5 phages (fSE1C, fSE4S, fSE7, fSE8 and fSE12)	Enteritidis	Fresh beef, chicken, pork, salmon, turkey, processed cheese, salami, sausage, turkey ham, wiener	Two phages were up to 5 log10 CFU more stable than three phages in ten food matrices (fresh and processed) at both 4 °C and 18 °C	(Robeson et al., 2014)
10 phages	Enteritidis	Biofilms in chicken slaughter house	Observed efficiency of phages on biofilm control, depending on the type of material (glass, stainless steel, plastic)	(Garcia et al., 2017)
6-phage cocktail (JC1, S5p2, 29, 52, 1 PB, and VCA1)	Typhimurium	Workers' boots in food and feed processing plants	More than 99% reduction of *Salmonella* observed on boots	(Gong et al., 2017)
7-phage cocktail (BPS2H1, BPS7T1, BPS8H2, BPS11Q3, BPS11T1, BPS11T2, and BPS15Q2)	Enteritidis, Typhimurium, Heidelberg, Derby	Milk, liquid whole egg, chicken breasts	Complete control of *Salmonella* in foods protected by phages at all temperatures from the first day to the end of the experiment	(Han et al., 2017)
5-phage cocktail (ΦEco1, ΦEco2, ΦEco3, ΦEco4, ΦEco5)	Typhimurium	Oysters	Phages successfully reduced the concentration of *Salmonella*	(Le et al., 2017)
Phages S16 and FO1a	Infantis, Heidelberg, Newport, Enteritidis	Ground beef	Individual applications of phages and UV light decreased *Salmonella* population of approximately 1 log10 CFU/g. Combined applications of phages and UV provided an optimal decrease of 2 log10 CFU/g.	(Yeh et al., 2018)
Commercial phages				
SalmoFresh™ (Intralytix, Inc., Baltimore, MD)	Enteritidis, Heidelberg, Kentucky, Typhimurium	Turkey breast cutlets, ground turkey	Variations in efficiency depending on the serovar	(Sharma et al., 2015)
SalmoFresh™ (Intralytix, Inc., Baltimore, MD)	Enteritidis, Heidelberg, Typhimurium	Chicken breast fillets	Higher reduction rate in *Salmonella* counts achieved with surface-treated samples and storage under modified atmosphere packaging	(Sukumaran et al., 2016)
SalmoFresh™ (Intralytix, Inc., Baltimore, MD)	Newport	Whole and fresh-cut cucumbers	*Salmonella* populations were significantly lower on phage-treated cucumbers in all the tested conditions than in the non-treated cucumbers. Phage application to whole cucumbers before slicing did not reduce the transfer of *S.* Newport to fresh-cut slices	(Sharma et al., 2017)
Salmonelex™ (Micreos Food Safety, The Netherlands)	Michigan	Fresh-cut lettuce	Population reduction with Salmonelex™ treatment was similar to the reduction obtained by sodium hypochlorite and significantly higher than reductions obtained with deionized water	(Oliveira et al., 2015)
Salmonelex™ (Micreos Food Safety, The Netherlands)	Newport, Typhimurium, Thompson	Ground chicken	Phage efficacy was dependent on the type of water used to dilute the phage, *Salmonella* susceptibility to the phage, and length of treatment	(Grant et al., 2017)
Salmonelex™ (Micreos Food Safety, The Netherlands)	Enterica, Heidelberg, Newport, Enteritidis C, Se 13	Beef trim, pork, chicken, turkey	Reduction in *Salmonella* of 1 log10 CFU/g in ground beef, 0.8 log10 CFU/g in ground pork, For ground chicken and ground turkey, *Salmonella* was reduced by 1.1 log10 CFU/g in ground chicken, and 0.9 log10 CFU/g in ground turkey	(Yeh et al., 2017)

matrix, such as pasteurized milk spiked with *Salmonella*, pathogenic cells were successfully controlled, and their occurrence was reduced in the presence of single phages and phage cocktails, when tested at different temperatures and for extended periods of time (Bao et al., 2015; Han et al., 2017; Zinno et al., 2014). Phages could be pre-added to the dairy matrix as "food additives" instead of being used as a post-treatment in dairy products, which are very sensitive to cross- and secondary contamination (Han et al., 2017).

Anti-*Salmonella* phages were also efficient when applied to contaminated goat cheese (Jorquera et al., 2015). *Salmonella* did not survive in Cheddar cheese made from pasteurized milk in the presence of phage SJ2 (Modi et al., 2001). However, *Salmonella* could still be observed in raw milk Cheddar cheese but with a 2-log10 CFU reduction compared to the control cheese. The food matrix has an impact on the accessibility of target bacteria to phage depending on the structure of the matrix that could impair or favor phage diffusion (Ly-Chatain, 2014). For example, whey proteins can limit the adsorption of phages to bacteria (Gill et al., 2006). When associated to fat globules in raw milk, target bacteria can also form clusters that protect them from phage attack, while in heat-treated milk, bacterial agglutination does not occur (O'Flaherty et al., 2005).

A major drawback of the use of phage is the possible apparition of bacteriophage-insensitive mutants (BIMs). In chocolate milk spiked with 3 log10 CFU/mL of *Salmonella* Typhimurium and treated with 8.4 log10 PFU/g of the Felix-like phage F01-E2, BIMs were detected after 6 days at 15 °C (Guenther et al., 2012). The apparition of BIMs can be prevented by the use of phage cocktails as demonstrated in chocolate milk spiked with three different *Salmonella enterica* serovars and treated with a combination of phage F01-E2 and phage S16 (Marti et al., 2013). No BIMs were detected even after a 6-day period storage at 6.5 °C. Even if at this temperature the apparition of BIMs after a longer storage period could still be assumed, these studies demonstrate that the use of phages against *Salmonella* is promising, and needs to be further investigated and applied to the diversity of dairy products that exists worldwide.

4. New strategies for improving the efficacy of *Salmonella*-phages

At primary production, the viability of phages administered orally to animals can be affected by several factors such as environmental conditions (temperature, pH …), and physical and chemical stresses encountered while passing through the gastro-intestinal tract (O'Flynn et al., 2006). Similarly, industry specific conditions could be serious obstacles to phage effectiveness during food processing, because of the reduction induced in the phage titer. To address this issue, some strategies have been developed to allow a better distribution of phages using new administration routes in animals and applications in food products.

4.1. Improving the delivery of Salmonella-phages

Encapsulation is a method that consists in incorporating and protecting phage particles within a coating structure. Different materials can be applied in the coated microsphere such as alginate (Colom et al., 2017; Wall et al., 2010) or combinations of several substances such as chitosan and alginate (Ma et al., 2008), alginate and whey proteins (Tang et al., 2013). Formulation techniques should be selected according to their physical and chemical properties in order to be effective in the core protection and the phage stability, and no aggregation should occur. Another essential property is the microparticle ability to release the beneficial phages. Several encapsulation methods are known and have already been reviewed (Malik et al., 2017). Other encapsulation methods have also been well documented such as freeze drying (Colom et al., 2015), spray drying (Leung et al., 2017), extrusion and gelation (Ma et al., 2008; Tang et al., 2013), precipitation and polymerization (Hathaway et al., 2015), and the use of liposomes (Balcão et al., 2014; Colom et al., 2015). When placed in simulated gastric or intestinal fluid, in bile salt, and during cold and room temperature storage, the stability and viability of microencapsulated *Salmonella*-phages were improved in comparison to non-encapsulated phages (Ma et al., 2008; Tang et al., 2013; Zhang et al., 2010). A recent study focused on alginate-Ca^{2+} matrixes to improve the viability and release of *Salmonella* phage f3αSE in a water flow system simulating the bath used in the poultry industry (Soto et al., 2018). At pH 3, almost 81% of the microencapsulated phages were still active whereas no non-encapsulated phage was recovered. In the water flow system, microencapsulated phage detection lasted 100 more hours than for non-encapsulated phages.

In swine and broiler models, the efficiency of the microencapsulation of *Salmonella*-phages was confirmed in terms of viability and persistence of phages (Colom et al., 2015, 2017; Saez et al., 2011). These improved delivery modes could be investigated in rumen digestive models to reduce *Salmonella* shedding in dairy cattle.

4.2. Phages in food bioactive packaging

The use of phages in bioactive packaging has emerged as a promising approach to inhibit pathogen survival and growth in the packaged food environment. Anti-*Listeria monocytogenes* and anti-*Escherichia coli* effects of lytic phage cocktails free or immobilized into packaging materials to control and prevent the bacterial contamination of fresh seeds and vegetables, and ready-to-eat meat have already been tested with success (Lone et al., 2016). Several packaging materials such as cellulose membranes, paper coated with encapsulated phage or impregnated with phage suspension, poly lactic acid film with phage xanthan coatings on the surface, can be used to immobilize phages (Lone et al., 2016; Radford et al., 2017). In chilled meat trays, absorbent food pads containing phages successfully reduced *Salmonella* Typhimurium contamination *in vitro* (Gouvêa et al., 2016).

4.3. Salmonella-phage endolysins

Phage endolysins are peptidoglycan hydrolases that play a role in host lysis after phage replication within the infected cell. At the end of phage replication, phage holin proteins enable the endolysins to cross the cytoplasmic membrane and to access the cell wall for the release of new virions. The interest in endolysins, as potential biocontrol agents, has been growing over the past decade as their lytic activity on the peptidoglycan is also effective from outside the bacterial cells, at least with respect to Gram-positive bacteria which do not carry an outer membrane (for review (Bai et al., 2016; Schmelcher and Loessner, 2016)). In the case of Gram-negative bacteria, the outer membrane prevents the contact between free endolysins and the peptidoglycan. This is the reason why literature on endolysins targeting Gram-negative bacteria and especially *Salmonella* is scarce. Only a few *Salmonella* phage endolysins have been described so far, and have shown to be efficient against Gram-negative bacteria thanks to their muralytic activity (Legotsky et al., 2014; Li et al., 2016; Walmagh et al., 2012, 2013), especially when used in combination with different outer membrane permeabilizers such as EDTA, and citric and malic acids (Lim et al., 2012; Oliveira et al., 2014). A Salmonella phage endolysin has recently proved to exhibit an enzymatic activity exceeding that of all other endolysins previously characterized (Rodriguez-Rubio et al., 2016). This emphasizes the promising potential of phage endolysins as biocontrol agents against *Salmonella*, especially in dairy products where they have been successfully applied against other pathogens such as *Listeria monocytogenes* in fresh cheese (Van Tassell et al., 2017).

To improve endolysin bactericidal effect towards Gram-negative bacteria, modified endolysins, named Artilysins, have also been developed. These engineered enzymes combining an endolysin and lipopolysaccharide (LPS)-destabilizing peptides showed promising results against *Pseudomonas aeruginosa* with a reduction of up to 5 log CFU/ml,

but still had a limited efficiency against *Salmonella* Typhimurium (< 1 logCFU/ml reduction), and thus require further improvement (Briers et al., 2014).

4.4. Associating Salmonella-phages to other antibacterial agents

As mentioned above, the main limitations to the use of phages as biocontrol agents are their decreased activity in food matrices and the development of different types of mechanisms that confer bacterial resistance to phages (Rios et al., 2016), including the selection of BIMs. In order to enhance antibacterial activity of phages, alternative strategies consisting in combining phages or their lysins and chemical and/or physical agents have been investigated.

Few examples are available in the literature as regards the association of phages and physical hurdle. In ground beef inoculated with a mix of four *Salmonella* strains, *Salmonella* populations decreased from 3.52 to 2.29 log10 CFU/g when treated with 9 log10 PFU/ml of phages S16 and FO1a. Exposing samples to UV light at 254 nm led to similar results (2.37 log10 CFU/g), while combining UV light and phages reduced *Salmonella* populations to 1.55 log10 CFU/g (Yeh et al., 2018).

The association of phages with various chemicals has been reported for the control of pathogenic bacteria at laboratory scale and in food matrices. The application of organic acids and phages/lysins is mainly documented, and gives variable results. In the study of Yeh et al. (2018), *Salmonella* populations in ground beef, obtained by combining phages and 5% lactic acid (2.46 log10 CFU/g) or 400 ppm peroxyacetic acid (2.07 log10 CFU/g), were not significantly different from those obtained when applying phages alone. The combination of endolysins with weak organic acids, such as citric and malic acids used as food preservatives, has proven to broaden the lysin antibacterial effect toward *Salmonella* (Oliveira et al., 2014), as already mentioned in the current review. In fresh fruits and vegetables contaminated with a five-strain cocktail of *Salmonella enterica*, the most effective treatment was the combination of SalmoFresh™ phage cocktail and levulinic acid (Magnone et al., 2013). Though, it is important to note the need to carefully plan and execute multiple hurdle approaches, as some phages can be impaired by other antimicrobial agents. For example, peroxyacetic acid (100 ppm) and chlorine (5 ppm) completely inactivated the commercial *Salmonella* lytic phage preparation SalmoFresh™ at 4 °C (Sukumaran et al., 2015).

Technologies based on the association of phages and essential oil have some potential that deserves to be further investigated for the control of pathogenic bacteria. For example, a phage cocktail composed of 8 lytic phages active against *Escherichia coli* was used at MOI levels of 1, 10 and 100 either alone or combined with 0.5% trans-cinnamaldehyde to control the growth of *E.coli* O157:H7 on the surface of leaves of green vegetables. At 23 and 37 °C, green vegetables treatment resulted in a decrease of *E. coli* of at least 1 log10 CFU after 24 h whatever the MOI. The highest levels of time, temperature and MOI generated the highest levels of inactivation and no surviving *E. coli* cells were detected at 37 °C with low levels of inoculation (ca. 4 log10 CFU/leaf). The combination of phages and *trans*-cinnamaldehyde resulted in a complete inhibition at all temperatures including at 4 and 8 °C, and at inoculum levels (4, 5 and 6 log10 CFU/leaf) visible after 1 h and 24 h (Viazis et al., 2011).

Some authors investigated the efficacy of combinations of phages and bacteriocins or bacteriocin-producing strains. Some attempts were made to control *Listeria monocytogenes* in ready-to-eat sliced pork ham using phage P100 and nisin (Figueiredo and Almeida, 2017), but phage P100 was at its highest level of efficiency when used as the sole individual treatment, which indicates a possible antagonism between the two treatments. Phages and partially purified bacteriocin or bacteriocin-producing strains were tested to control *Clostridium perfringens* (Heo et al., 2018) in Brain Heart Infusion broth at 37 °C. Combining phages and bacteriocin led to a synergistic effect compared to the individual treatments, and to an eradication of *C. perfringens* when phages were used together with the bacteriocin-producing strain. Here again the efficacy tends to vary depending on the matrix, the target bacterium and the associated agents. This reinforces the fact that each association should be validated according to its intended use. These results on other pathogenic bacteria are promising and similar strategies could be implemented for the control of *Salmonella* occurrence along the dairy food chain.

5. Conclusion

This review makes evident that many published works dealing with anti-*Salmonella* phages were performed with *Salmonella* strains of Typhimurium or Enteritidis serovars, which are of utmost importance in food products. To our knowledge, only one study reported phage activity against *S.* Infantis, the most common serovar in Europe (Yeh et al., 2018). No phage study were carried out with *S.* Dublin strains, even though it is the major serovar found in dairy products in Europe (Lailler et al., 2012). Considering the host specificity of phages, it would presumably be necessary to improve knowledge regarding anti-*Salmonella* phage potential against the most important serovars of the dairy sector.

The effective control of *Salmonella* along the dairy food chain is of utmost importance to reduce foodborne outbreaks worldwide. Phage applications have gained much interest as biocontrol agents against this pathogenic bacteria, and can be used in a 'farm to fork' approach. Some intrinsic factors can nevertheless lead to variations in the efficacy of phages, and improvements are needed to optimize *Salmonella*-phage treatments, especially in the dairy sector. Including the use of phages in multiple hurdle technology, i.e. the combination of multiple methods for ensuring food safety (Singh and Shalini, 2016), has already proven to be potentially interesting. Combining biocontrol techniques especially appears as an attractive alternative for the control of pathogenic bacteria, because biological entities are seen as more acceptable by consumers than chemical additives when it comes to the agri-food sector. Thus, the ecological impact of the addition of phages to microbial communities on the whole ecosystem, such as foods, is to be evaluated along with the collection of more data regarding phage communities which are lacking at the moment. Further research in this area still remains to be carried out.

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