Bacteriophage ecology of fermented foods: anything new under the sun?

Thomas Paillet, Eric Dugat-Bony

► To cite this version:

Thomas Paillet, Eric Dugat-Bony. Bacteriophage ecology of fermented foods: anything new under the sun?. *Current Opinion in Food Science*, 2021, 40, pp.102-111. 10.1016/j.cofs.2021.03.007 . hal-03298690

HAL Id: hal-03298690

<https://hal.inrae.fr/hal-03298690>

Submitted on 23 Jul 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Bacteriophage ecology of fermented foods: anything new under the sun?

Thomas Paillet¹, Eric Dugat-Bony^{1*}

¹UMR SayFood, INRAE, AgroParisTech, Université Paris-Saclay, Avenue Lucien Brétignières, 78850, Thiverval-Grignon, France

thomas.paillet@inrae.fr

*Corresponding author: Eric Dugat-Bony (eric.dugat-bony@inrae.fr)

Abstract

Bacteriophage ecology has raised an increasing attention over the last few years, thanks to the improvement and contributions of microscopy, comparative genomics and viral metagenomics methods. Fermented foods host dense and diverse microbial communities and, therefore, represent an ideal biotope for bacteriophages. If their occurrence in such environments has been demonstrated decades ago, data highlighting their impact on mixed communities and their ecological roles are scarce when compared to other microbial ecosystems. This review summarizes most recent knowledge into the bacteriophage diversity of fermented foods and stress evidences suggesting the impact of these entities on the dynamics of food microbial communities. The main ecological roles played by bacteriophages in microbial ecosystems are also addressed. Understanding the impact of bacteriophages in fermented foods will further help in designing adapted microbial consortia and thus providing a better control of the food fermentations.

Key-words: fermented foods; bacteriophages; microbial ecology; population dynamics.

Introduction

Fermented foods are widely consumed worldwide and encompass diverse types of products including fermented dairy products, meats, fishes, cereals, legumes, vegetables, seeds, roots and also alcoholic and non-alcoholic beverages [1]. Initially developed with the objective of extending the raw products shelf-life, they are currently also appreciated for their typical sensory properties, nutritional value and potential health benefits [2,3]. Food fermentation relies on the conversion of substrates present in the raw material (e.g. sugars, proteins, lipids) into simpler products such as lactic acid, acetic acid, alcohol, carbon dioxide, ammonia and free fatty acids, through the specific activity of microorganisms.

Fermented foods are dynamic microbial ecosystems, where the succession of several microbial groups occur in a short time, usually from days to weeks or months. This period varies according to the nutrients available in the raw material, abiotic parameters such as temperature, humidity, oxygen and osmotic pressure, and microbial interactions as well [4]. Huge efforts have been performed by the scientific community during the past decades to describe the composition and functioning of food microbial communities, helped by the recent development of several meta-omics tools [5]. It is now well-established that microbial communities of fermented foods are generally dense (e.g. $>10^9$ cells per gram of cheese [6]) and have a low diversity when compared to other microbial ecosystems such as soils [7] or oceans [8]. Bacteria from diverse phyla, e.g. *Firmicutes* (which includes lactic acid bacteria), *Actinobacteria*, *Proteobacteria* and *Bacteroidetes*, yeasts and filamentous fungi constitute the main microbial groups involved in food fermentation [9]. Through this fermentative activity, they contribute to the quality of the food products in several ways, i.e. by preventing the development of pathogens, modifying the texture, releasing aroma compounds or degrading anti-nutritional factors.

Bacteriophages (phages), viruses that infect bacterial cells, are considered as key ecological drivers in the functioning of microbial ecosystems [10]. Indeed, phage-bacterial interactions can potentially affect the balance between the different functional groups of microbes and then (re-)shape microbial communities. In the human gut, where phage particles probably do not outnumber bacteria, phages could play a transitory role in the homeostasis or the evolution of the microbiota [11]*. In food fermentations, although the presence of bacteriophages has been demonstrated around one century ago [12], only few examples of deep inventory of their diversity are available and the literature about their ecological role is even rarer.

The present review summarizes the current knowledge on the occurrence and diversity of bacteriophages in fermented foods, especially in light of the recent discoveries resulting from the analysis of viral metagenomics data, and discuss the possible ecological roles played by these biological entities in the context of this peculiar ecosystem which, ultimately, may impact the success of the fermentation process.

Current knowledge on bacteriophages' occurrence and diversity in fermented foods

Several experimental approaches have been used for enumerating bacteriophages in microbial ecosystems and exploring their diversity. Some of them require the isolation of phages, which implies as first steps to identify and cultivate susceptible bacterial hosts, while others can be applied directly on environmental samples (Figure 1).

Culture-dependent approaches

The presence of bacteriophages in fermented foods was frequently investigated by culture-dependent approaches. In practice, the main technic consists in collecting phages from a liquid sample obtained from the food product, or from a suspected reservoir in the manufacturing environment, and putting them into contact with a sensitive bacterial strain on a double-layer agar plate (for a detailed protocol, see [13]). It is also possible to directly enumerate phages to determine their initial level in food products [14], or to enrich them before isolation to enhance the probability of recovery [15].

Once isolated, phages can be further identified and characterized by applying a variety of downstream analysis. The historical classification of bacterial viruses is based on electron microscopy (EM) observations [16], and it is now progressively moving to a molecular classification. In Philippe et al., the authors used EM for the morphological characterization of phage GC1 isolated from wine musts [17]. They observed tail-less icosahedral particles, meaning that this phage did not belong to *Caudovirales* order. A further characterisation of its genomic properties determined that GC1 belongs to the *Tectiviridae* family.

In most recent articles, genome sequencing and comparative genomics were also applied to phages isolated from fermented foods. De Melo et al., made comparative genomics on 18 *Brevibacterium aurantiacum* phages isolated from cheese [18]**. They were classified into 7 distinct genomic groups based on the number of DNA tandem repeats (TRs) in each genome. They also found that 85% of phages in databases possessed such TRs. Similarly, Cheng et al., classified 7 *Propionibacterium freudenreichii* phages into two clusters, based on the nucleotide identity and coverage percentage between each genomes [15].

In most cases, such a culture-dependent approach also gives clues as to whether the isolated phage is temperate or virulent, by confronting the aspect of plaques (turbid for temperate, and usually clear for virulent [19]) and the genetic analysis of the complete genome (which usually contains an integrase when the phage is temperate).

As summarized in Table 1, both virulent and temperate phages were isolated from many fermented foods. However, surprisingly, no filamentous phages were retrieved from this type of products to date. Most of them are *Siphoviridae* and *Myoviridae* but *Podoviridae* and *Tectiviridae* were also isolated occasionally [14,17,20]. The hosts are usually members of the dominant species present in the corresponding food, such as *Leuconostoc mesenteroides* in Sauerkraut [21] or *Oenococcus oeni* in Wine [22]. For the particular case of cheese, where an abundant literature regarding phages infecting Lactic Acid Bacteria (LAB) starter cultures is

available, as reviewed previously [23,24], only a few studies described the isolation of phages infecting other important bacteria such as *Propionibacterium freudenreichii* [15], the bacteria responsible for the production of holes in Emmental-type cheese, *Brevibacterium aurantiacum* [18], a surface ripening culture used in many cheese varieties and *Enterococcus faecalis* [25,26]*.

However, in the perspective of understanding the bacteriophage ecology in fermented foods, single phage isolation suffer from the major limitation of the culture-dependent approach that is the need of a susceptible host. By definition such approach cannot accurately reflect neither the bacterial and viral diversity present in fermented foods, nor their relative abundance. It is however very efficient from a technological point of view, for example in the case where a phage is suspected to be responsible of a fermentation failure and needs to be quickly identified.

Direct detection approaches

An alternative is to detect and/or quantify phages directly in food samples or in a viral fraction extracted from food samples without *a priori* on the bacterial host(s). Several techniques are available to count or observe viruses directly in complex samples [27], such as flow cytometry [28], epifluorescence microscopy [29], nanoparticle tracking analysis [30], interferometric light microscopy [31] and electron microscopy including Scanning Electron Microscopy (SEM) [32], Transmission Electron Microscopy (TEM) [33] and cryo Electron Microscopy (cryo-EM) [34].

Only few studies used such direct approaches to characterize the phage communities of fermented foods. Dugat-Bony et al., used interferometric light microscopy to determine the phage concentration on the surface of three cheese varieties and found that it ranged from 1×10^9 to 4×10^{10} particles per gram at least [35]*. They also observed different morphotypes on Epoisses cheese with TEM, giving first indications about the complexity of phage communities present on the cheese surface.

As a complement to their metagenomic study, Park et al., used TEM on samples from shrimps, sauerkraut and kimchi, after a cesium chloride (CsCl) density gradient purification step [36]. They were able to characterize various phages morphologies, mainly *Sipho*- and *Myoviridae*.

To summarize, in the context of fermented foods, direct detection approaches can provide rapidly important ecological information such as total phage's concentration and rough elements about their diversity. However, since many bacteriophages can share similar morphological traits, techniques offering more precision are desirable to properly describe the composition of phage communities in fermented foods.

New contributions of whole metagenome sequencing and viral metagenomics

Two main categories of metagenomics approaches can be used to detect viral signals from environmental samples.

First, whole metagenome sequencing, which generates simultaneously sequences from both microbial cells and viruses, can be used to identify abundant phages present in microbial ecosystems using dedicated bioinformatic tools [37,38]. Regarding fermented foods, only two articles refer to the use of such approach for studying the composition of phage communities. In kimchi [39], the authors identified four putative phage contigs with sequence similarity with the genome of LAB-phages. In kinema, a fermented soybean product, the viral community was dominated by phages infecting *Bacillus* species. Their identity was further confirmed by taxonomic analysis, and they all had one or several well-characterized host(s) [40].

Second, viral metagenomics, or “viromics”, consist in extracting and sequencing the genomic material of the viral community selectively purified from an environmental sample (e.g. food products, natural environment, host-associated) [41]. This approach is designed to obtain a deep overview of the composition of the phage community present in a given ecosystem. Generally, only dsDNA phages are sequenced, letting a grey area regarding RNA and ssDNA phages, whose quantities and diversity are probably underestimated thus far [42]. In natural ecosystems such as ocean, or soils, numerous viral metagenomic studies targeting phages have been carried out (respectively, [43] and [44,45]). However, they are scarce when it comes to fermented foods or fermented beverages, as reviewed in [46].

Park et al. firstly analysed the metavirome of fermented shrimp, kimchi and sauerkraut [36]. Viral particles were recovered and concentrated from the food samples by using filtration and ultracentrifugation prior to viral DNA extraction and pyrosequencing. The results revealed an important diversity in phage sequences, most of which showing no significant hits in public databases, and 6 to 27 contigs >5 Kb per food sample were assembled. Major discrepancies were observed between predicted hosts and the actual bacterial diversity detected in kimchi and fermented shrimp, reflecting the fact that viral genomes of these fermented foods were poorly represented in public databases at the time of the study, so that host predictions probably failed. On the contrary, phage host predictions in sauerkraut were reliable, thanks to the availability of several phage genomes isolated in previous work [21].

The viral community from ten samples representative of Korean and Chinese kimchi was also investigated [47]. Viral concentrates were obtained through filtration and Polyethylene Glycol (PEG) concentration, and DNA was sequenced providing several thousands of contigs >500 bp per sample, and revealing a very high diversity. The phage host prediction was consistent with the bacterial diversity and, interestingly, viral community profiling was found to outperform bacterial community profiling for predicting the geographical origin of kimchi.

Recently, the first metavirome of the cheese surface was described [35] using Epoisses cheese as an example. The viral fraction was obtained according to an optimized protocol involving filtration, PEG concentration and chloroform treatment. DNA sequences were assembled into 124 viral contigs from 2.5 to 122 kb, highlighting the presence of an unexpected viral diversity in this ecosystem. The authors were able to predict a bacterial host for the most abundant ones, e.g. *Glutamicibacter*, *Lactococcus*, *Psychrobacter*, *Vibrio*,

Leuconostoc and *Halomonas*, which were previously detected as dominant bacterial genera in Epoisses cheese [48].

Overall, available data suggest that fermented foods host dense and complex phage communities, at least as diverse as bacterial ones. However, despite the growing descriptive data available regarding bacteriophages occurrence and diversity in fermented foods, there is still a gap before demonstrating that these entities play an ecological role in this environment and can impact food fermentations.

Relationships between viral and bacterial dynamics

The first step would be to determine if a relationship exists between the levels of viral and bacterial populations during the fermentation cycle. For fermented foods, few studies demonstrated such correlation.

In kimchi [39], the monitoring of the composition of bacterial and phage populations during 29 days of fermentation was achieved by using a whole metagenome sequencing approach. The relative abundance of the four putative phage contigs identified increased during the fermentation cycle, reaching ~7% of the total metagenomics sequences after 25 days. This large number of sequences was correlated to the decrease of bacterial population observed after 25 days suggesting that bacteriophages may influence the microbial community dynamics in this product.

Recently, Kong and Park used a culture media made from sterilized supernatant of dongchimi kimchi (a watery kimchi made from radish, green onions, garlic, ginger and salt) to perform co-culture of the main LAB species involved in the fermentation of this product, *i.e.* *Leuconostoc citreum*, *L. mesenteroides* and *Weissella cibaria* [49]*. They used different combinations of strains, sensitive to phages or not, and followed the dynamic of both bacterial and phage populations by culture-dependent methods over 10 days. They observed a negative relationship between the abundance of phages and the viability of their hosts, independently of the pH of the medium, demonstrating the impact of bacteriophages on the succession of LAB species during dongchimi kimchi fermentation.

Finally, Erkus et al. studied an undefined complex cheese starter culture, composed of several strains of *Lactococcus lactis* and *Leuconostoc mesenteroides* grouped in eight different genetic lineages, some of which carrying active prophages [50]. In one of the described experiment, they propagated *in vitro* the culture daily in milk during several weeks, mimicking the back-slopping procedure used in the dairy industry, and followed temperate phage population by titration and the different bacterial lineages by qPCR. The results indicated that although some strains can undergo dramatic decrease in abundance at certain stages of propagation, due to the increase in a particular phage population in the medium, the effect on the relative abundance of the genetic lineage they belong to was very limited, ensuring an overall stability of the community structure, both regarding genes and functionalities.

To summarize, there are increasing evidences that bacteriophages affect the dynamics of food microbial communities during fermentation. The impact of phage attacks on the overall structure and function of microbial communities is thought to depend on the complexity of the studied system and microdiversity seems to play an important role in the overall stability of microbial communities in fermented foods.

Ecological roles of bacteriophages

Studies elucidating the ecological roles of bacteriophages occurring in fermented foods are scarce. Thus, this section summarizes the main roles attributed to these entities regardless of the microbial ecosystem of origin. It is likely that major results observed within natural ecosystems are transferable to fermented products.

Direct regulation of bacterial populations

Bacteriophages may have several types of behaviours toward their bacterial hosts (Box 1). They can directly impact the population levels of their hosts in different ways and, consequently, the whole community structure.

First, phages performing a lytic cycle, which encompass professionally lytic, virulent mutant (or ex-temperate, see [51]) and temperate phages entering a lytic cycle, foster a prey-predator relationship with their host. Since bacteriophages are non-motile entities, the probability of encountering a host cell and starting infection strongly depends on the host's density. In mixed microbial communities, this means that bacteriophages kill the sensitive bacterial strain(s) with the highest density, as theorized in the Kill-the-Winner [52] and seed-bank models [53,54], while having a little impact on the total microbial biomass. This direct effect also promotes bacterial diversity since several bacterial populations sharing the same ecological niche can coexist [55] and grow in a sequential manner. Finally, it also favours the optimal utilisation of all resources present in the ecosystem, as a single dominant bacteria wouldn't have all the necessary enzymatic equipment to exploit all the available nutrients [56].

Second, temperate phages can also affect the fitness of their host when entering a lysogenic cycle. When integrated as prophages into the bacterial host genome, they can develop either a parasitic or a mutualistic interaction with their host. In complex cheese starter culture, Alexeeva et al. [57]* demonstrated the competitive advantage of *Lactococcus lactis* lysogens compared to their prophage-cured derivatives but the mechanism behind this observation was not identified. Similarly, Costantini et al. [22] observed that, among sixteen *Oenococcus oeni* strains used for malolactic fermentation in wine, the ones integrating one or several prophages in their genomes were more resistant to the predation by other oenophages.

Finally, bacteriophages which cannot enter a lysogenic cycle and are producing virions in a chronic fashion without cell lysis interact with their host through a parasitic relationship. In this case, the main expected effect would be a lower fitness of the host caused by the

energy cost required for the bacteriophage's replication but this was not studied in the context of fermented foods to our knowledge.

In addition to the regulation of the population level of their hosts, bacteriophages can also prompt substantial modifications of the bacterial transcriptome and proteome and, hence, affect their metabolism [58].

Indirect effects on non-host populations

Bacterial lysis mediated by bacteriophages is responsible for the release of organic matter into the environment. In ecology, this phenomenon is known as the "viral shunt" and it affects trophic webs by lowering bacterial biomass before it is assimilated at higher trophic levels [59]*. Bacterial lysis provides an important source of free nutrients which can support and promote the growth of other microorganisms. It has thus a large impact on microbial dynamics and densities.

For example, Fazzino et al. studied the effect of virulent bacteriophages on the mutualistic interaction between *Escherichia coli* and *Salmonella enterica* [60]**. In such cross-feeding model community, phages can have extensive indirect effects affecting the bacterial community dynamics. One of those indirect effect was the release of organic matter since the growth of *S. enterica* was stimulated by the lysis of *E. coli* by phage T7.

In fermented foods, such phenomenon is likely to occur. However, contrary to other natural ecosystems, the trophic chain is short and there is generally no upper trophic level above heterotrophic microorganisms. In this case, the role of the viral shunt encompasses probably only the release of cellular debris and intra-cellular compounds, providing additional resources for non-hosts species. In line with this suspected role, Kong & Park experimentally evidenced that a bacteriophage lysate of *Weissella cibaria* can promote the growth of *L. citreum* in kimchi fermentation [49].

Phages as bacterial evolution drivers

Bacterial viruses represent a continuous selective pressure on bacteria, driving them to evolve by selecting antiphage defence mechanisms [61]*. In response, phages adopt strategies to overcome host defence systems. This antagonistic co-evolution is a kind of perpetual arms race, referred to as the Red Queen dynamics [62]. This is due to the extremely rapid evolution and turnover of phage particles [63], increasing mutation rates in their host(s) [64], driving neither the predator nor the prey to extinction. The most prominent outcome of this interaction is ecological speciation, resulting in a high microdiversity of both hosts and phages.

Horizontal gene transfer (HGT), which refers to the incorporation by an organism of genetic material from another organism without mating, contributes to the microbial genome evolution [65]. Bacterial lysis due to the phage progeny release is accompanied by the release of intra-cellular components into the environment and especially pieces of DNA-that could be acquired by other bacteria through natural transformation [66]. HGT can also happen through transduction (generalized or specialized [67]), when a bacteriophage accidentally packages bacterial DNA and transfers it to another host.

Lysogeny has been suggested as a survival strategy when the environment contains low host densities [68]. Prophages integrated in a host bacteria are usually in a dormant state, as they don't actively replicate their genomes, while regulating bacterial genes. If some phages have evolved to insert only in highly conserved sites [69], others as transposable phages integrate themselves randomly in the host genome, possibly inactivating genes coding for essential functions and having therefore a detrimental effect on host fitness [70]. Some phages are also able to display "active lysogeny", acting as regulatory switches, as they turn off the gene by integrating in its sequence [71].

Phages can stay in lysogenic cycle for several generations. However, they are not totally inactive since the bacterial cell expresses moron genes (for "more DNA") that are not necessary for the phage cycle, and expressed during lysogeny [72,73]. A well-known example is the *stx* gene coding for shigatoxin, which is acquired by bacterial strains through lysogenic conversion, meaning the acquisition of a *stx*-positive prophage [74]. These morons are far from being all characterized, but they probably enhance bacterial fitness and expand the environmental niche of the host [75].

Conclusions

Fermented foods represent undoubtedly suitable ecosystems for the development of bacteriophages. The isolation of a large set of bacteriophages and the first viral metagenomics data shed light into the viral diversity of this type of products. However, the question of the impact of this diversity on the composition and functioning of microbial communities still remains underexplored.

The continuous improvement of sequencing techniques, with in particular the first applications of long-read sequencing for the description of metaviromes [76]**, makes it possible to envisage both the description and the monitoring of the composition of viral communities in fermented foods more easily and in a more comprehensive way.

Furthermore, synthetic microbial ecosystems offer new perspectives for investigating individual to ecosystem level microbial interactions [77]. The viral dimension of food microbial ecosystems should therefore be considered for the future design of synthetic ecology experiments with the objective of characterizing the role of bacteriophages in fermented foods.

The exploitation of this knowledge should help the food industry facing numerous challenges such as controlling phage contamination to reduce the risk of fermentation failure. Main applications are the biocontrol of pathogens [78] and spoilage bacteria [25]* but new developments could lead to finely modulate the composition of microbial communities in order to reach the desired technological properties in fermented products.

Acknowledgements

T.P. is the recipient of a doctoral fellowship from the French Ministry of Higher Education, Research and Innovation (MESRI) and the MICA department of the French National Research Institute for Agriculture, Food and Environment (INRAE). E.D-B is member of the knowledge hub SYSTEMIC which received funding from several national research funding parties in a joint action of JPI HDHL, JPI-OCEANS and FACCE-JPI launched under the ERA-NET ERA-HDHL (n° 696295). The authors thank Marie-Agnès Petit (INRAE) for her critical review of the manuscript.

Declaration of interest. None.

378 Table 1. Selected examples describing the isolation of phages directly from fermented foods.

Fermented food	References	Phage families	Type	Host
Cheese*	[15]	7 <i>Siphoviridae</i>	Virulent	<i>Propionibacterium freudenreichii</i>
	[18]	16 <i>Siphoviridae</i>	Virulent	<i>Brevibacterium aurantiacum</i>
	[25]	1 <i>Myoviridae</i>	Virulent	<i>Enterococcus faecalis</i>
	[26]	1 <i>Siphoviridae</i>	Virulent	<i>Enterococcus faecalis</i>
Fermented Cucumber	[79]	1 <i>Siphoviridae</i>	Virulent	<i>Lactobacillus plantarum</i>
	[80]	3 <i>Siphoviridae</i> and 3 <i>Myoviridae</i>	N.D	<i>Lactobacillus brevis</i> , <i>Lactobacillus plantarum</i> , <i>Weissella paramesenteroides</i> , <i>Weissella cibaria</i>
	[81]	1 <i>Siphoviridae</i>	Virulent	<i>Pediococcus</i> sp.
Fermented Soybean	[82]	N.D	Virulent and temperate	<i>Bacillus subtilis</i>
	[83]	16 <i>Siphoviridae</i>	N.D	<i>Bacillus cereus</i>
	[84]	1 <i>Myoviridae</i>	N.D	<i>Bacillus cereus</i>
	[85]	1 <i>Siphoviridae</i> and 1 <i>Myoviridae</i>	N.D	<i>Pediococcus halophilus</i>
Kefir	[86]	2 <i>Siphoviridae</i>	N.D	<i>Lactobacillus plantarum</i>
Kimchi	[20]	1 <i>Podoviridae</i>	N.D	<i>Weissella cibaria</i>
	[49]	N.D	N.D	<i>Weissella cibaria</i> , <i>Leuconostoc citreum</i>
	[87]	1 <i>Siphoviridae</i>	N.D	<i>Lactobacillus plantarum</i>
Salami	[88]	2 <i>Podoviridae</i>	N.D	<i>Staphylococcus carnosus</i>
Sauerkraut	[89]	3 <i>Siphoviridae</i> and 3 <i>Myoviridae</i>	N.D	<i>Leuconostoc fallax</i>
	[90]	5 <i>Siphoviridae</i> and 3 <i>Myoviridae</i>	N.D	<i>Leuconostoc pseudomesenteroides</i> , <i>Leuconostoc mesenteroides</i> , <i>Leuconostoc citreum</i> , <i>Leuconostoc fallax</i> , <i>Weissella</i> sp., <i>Lactobacillus plantarum</i> , <i>Lactobacillus brevis</i>
	[21]	1 <i>Siphoviridae</i>	Virulent	<i>Leuconostoc mesenteroides</i>

	[91]	2 phages	N.D	<i>Leuconostoc mesenteroides</i>
	[92]	2 <i>Myoviridae</i> 'type 1', 5 <i>Myoviridae</i> 'type 2' and 2 <i>Siphoviridae</i>	N.D	<i>Leuconostoc mesenteroides</i> , <i>Lactobacillus plantarum</i>
Sourdough bread	[93]	9 <i>Siphoviridae</i>	3 virulent and 6 temperate	<i>Lactobacillus fermentum</i>
	[94]	1 <i>Siphoviridae</i>	Virulent	<i>Lactobacillus sanfranciscensis</i>
Wine	[95]	11 <i>Siphoviridae</i>	N.D	<i>Oenococcus oeni</i>
	[14]	<i>Siphoviridae</i> , <i>Myoviridae</i> , <i>Tectiviridae</i>	N.D	<i>Lactobacillus plantarum</i> , <i>Lactobacillus hilgardii</i> , <i>Oenococcus oeni</i>
	[22]	15 <i>Siphoviridae</i>	Temperate	<i>Oenococcus oeni</i>
	[96]	4 <i>Siphoviridae</i>	N.D	<i>Oenococcus oeni</i>
	[97]	2 <i>Siphoviridae</i>	N.D	<i>Oenococcus oeni</i>
	[98]	1 <i>Siphoviridae</i>	Virulent	<i>Oenococcus oeni</i>
	[99]	17 <i>Siphoviridae</i>	N.D	<i>Oenococcus oeni</i>
	[17]	1 <i>Tectiviridae</i>	Temperate	<i>Gluconobacter cerinus</i>
	[100]	17 <i>Siphoviridae</i>	Temperate	<i>Oenococcus oeni</i>

N.D = Not Documented.

*For cheese, no example describing the isolation of phages infecting LAB starter culture is listed since the literature on such phages is extremely abundant and already reviewed [23,24].

Figure captions

Figure 1: General methods for the study of bacteriophages in fermented foods.

387 **References**

- 388 1. Tamang JP, Cotter PD, Endo A, Han NS, Kort R, Liu SQ, Mayo B, Westerik N, Hutkins R:
389 **Fermented foods in a global age: East meets West.** *Comprehensive Reviews in Food Science*
390 *and Food Safety* 2020, **19**:184–217.
- 391 2. Marco ML, Heeney D, Binda S, Cifelli CJ, Cotter PD, Foligne B, Ganzle M, Kort R, Pasin G,
392 Pihlanto A, et al.: **Health benefits of fermented foods: microbiota and beyond.** *Curr Opin*
393 *Biotechnol* 2017, **44**:94–102.
- 394 3. Hugenholtz J: **Traditional biotechnology for new foods and beverages.** *Current Opinion in*
395 *Biotechnology* 2013, **24**:155–159.
- 396 4. Smid EJ, Lacroix C: **Microbe-microbe interactions in mixed culture food fermentations.** *Curr*
397 *Opin Biotechnol* 2013, **24**:148–154.
- 398 5. Walsh AM, Crispie F, Claesson MJ, Cotter PD: **Translating Omics to Food Microbiology.** *Annual*
399 *Review of Food Science and Technology* 2017, **8**:113–134.
- 400 6. Irlinger F, Layec S, Hélinck S, Dugat-Bony E: **Cheese rind microbial communities: diversity,**
401 **composition and origin.** *FEMS Microbiol Lett* 2015, **362**:1–11.
- 402 7. Fierer N, Breitbart M, Nulton J, Salamon P, Lozupone C, Jones R, Robeson M, Edwards RA, Felts
403 B, Rayhawk S, et al.: **Metagenomic and Small-Subunit rRNA Analyses Reveal the Genetic**
404 **Diversity of Bacteria, Archaea, Fungi, and Viruses in Soil.** *Appl Environ Microbiol* 2007,
405 **73**:7059–7066.
- 406 8. Breitbart M, Salamon P, Andresen B, Mahaffy JM, Segall AM, Mead D, Azam F, Rohwer F:
407 **Genomic analysis of uncultured marine viral communities.** *PNAS* 2002, **99**:14250–14255.
- 408 9. Tamang JP, Watanabe K, Holzapfel WH: **Review: Diversity of Microorganisms in Global**
409 **Fermented Foods and Beverages.** *Front Microbiol* 2016, **7**.
- 410 10. Koskella B, Brockhurst MA: **Bacteria–phage coevolution as a driver of ecological and**
411 **evolutionary processes in microbial communities.** *FEMS Microbiol Rev* 2014, **38**:916–931.
- 412 11. Sausset R, Petit MA, Gaboriau-Routhiau V, De Paepe M: **New insights into intestinal phages.**
413 *Mucosal Immunology* 2020, **13**:205–215.
- 414 12. Whitehead HR, Cox GA: *The Occurrence of Bacteriophage in Cultures of Lactic Streptococci: A*
415 *Preliminary Note.* Government Printer; 1935.
- 416 13. Kropinski AM, Mazzocco A, Waddell TE, Lingohr E, Johnson RP: **Enumeration of Bacteriophages**
417 **by Double Agar Overlay Plaque Assay.** In *Bacteriophages*. Edited by Clokie MRJ, Kropinski AM.
418 Humana Press; 2009:69–76.
- 419 14. Cordero-Bueso G, Moraga J, Ríos-Carrasco M, Ruiz-Muñoz M, Cantoral JM: **Bacteriophages as**
420 **an Up-and-Coming Alternative to the Use of Sulfur Dioxide in Winemaking.** *Front Microbiol*
421 2020, **10**:2931.
- 422 15. Cheng L, Marinelli LJ, Grosset N, Fitz-Gibbon ST, Bowman CA, Dang BQ, Russell DA, Jacobs-Sera
423 D, Shi B, Pellegrini M, et al.: **Complete genomic sequences of *Propionibacterium freudenreichii***

- 424 **phages from Swiss cheese reveal greater diversity than Cutibacterium (formerly**
425 **Propionibacterium) acnes phages.** *BMC Microbiology* 2018, **18**:19.
- 426 16. International Committee on Taxonomy of Viruses, King AMQ (Eds): *Virus taxonomy:*
427 *classification and nomenclature of viruses: ninth report of the International Committee on*
428 *Taxonomy of Viruses.* Academic Press; 2012.
- 429 17. Philippe C, Krupovic M, Jaomanjaka F, Claisse O, Petrel M, Le Marrec C: **Bacteriophage GC1, a**
430 **Novel Tectivirus Infecting Gluconobacter Cerinus, an Acetic Acid Bacterium Associated with**
431 **Wine-Making.** *Viruses* 2018, **10**:39.
- 432 18. De Melo AG de, Rousseau GM, Tremblay DM, Labrie SJ, Moineau S: **DNA tandem repeats**
433 **contribute to the genetic diversity of Brevibacterium aurantiacum phages.** *Environmental*
434 *Microbiology* 2020, **22**:3413–3428.
- 435 19. Levine M: **Mutations in the temperate phage P22 and lysogeny in Salmonella.** *Virology* 1957,
436 **3**:22–41.
- 437 20. Kleppen HP, Holo H, Jeon S-R, Nes IF, Yoon S-S: **Novel Podoviridae Family Bacteriophage**
438 **Infecting Weissella cibaria Isolated from Kimchi.** *Appl Environ Microbiol* 2012, **78**:7299–7308.
- 439 21. Lu Z, Altermann E, Breidt F, Kozyavkin S: **Sequence Analysis of Leuconostoc mesenteroides**
440 **Bacteriophage Φ1-A4 Isolated from an Industrial Vegetable Fermentation.** *Appl Environ*
441 *Microbiol* 2010, **76**:1955–1966.
- 442 22. Costantini A, Doria F, Saiz J-C, Garcia-Moruno E: **Phage-host interactions analysis of newly**
443 **characterized Oenococcus oeni bacteriophages: Implications for malolactic fermentation in**
444 **wine.** *International Journal of Food Microbiology* 2017, **246**:12–19.
- 445 23. Garneau JE, Moineau S: **Bacteriophages of lactic acid bacteria and their impact on milk**
446 **fermentations.** *Microb Cell Fact* 2011, **10**:S20.
- 447 24. Brüssow H: **Phages of Dairy Bacteria.** *Annual Review of Microbiology* 2001, **55**:283–303.
- 448 25. Del Rio B, Sánchez-Llana E, Redruello B, Magadan AH, Fernández M, Martín MC, Ladero V,
449 Alvarez MA: **Enterococcus faecalis Bacteriophage 156 Is an Effective Biotechnological Tool for**
450 **Reducing the Presence of Tyramine and Putrescine in an Experimental Cheese Model.** *Front*
451 *Microbiol* 2019, **10**:566.
- 452 26. Ladero V, Gómez-Sordo C, Sánchez-Llana E, Del Rio B, Redruello B, Fernández M, Martín MC,
453 Alvarez MA: **Q69 (an E. faecalis-Infecting Bacteriophage) As a Biocontrol Agent for Reducing**
454 **Tyramine in Dairy Products.** *Front Microbiol* 2016, **7**:445.
- 455 27. Kaletta J, Pickl C, Griebler C, Klingl A, Kurmayer R, Deng L: **A rigorous assessment and**
456 **comparison of enumeration methods for environmental viruses.** *Scientific Reports* 2020,
457 **10**:18625.
- 458 28. Melo LDR, França A, Brandão A, Sillankorva S, Cerca N, Azeredo J: **Assessment of Sep1virus**
459 **interaction with stationary cultures by transcriptional and flow cytometry studies.** *FEMS*
460 *Microbiol Ecol* 2018, **94**.

- 461 29. Montañez-Izquierdo VY, Salas-Vázquez DI, Rodríguez-Jerez JJ: **Use of epifluorescence**
462 **microscopy to assess the effectiveness of phage P100 in controlling *Listeria monocytogenes***
463 **biofilms on stainless steel surfaces.** *Food Control* 2012, **23**:470–477.
- 464 30. Carr B, Siupa A, Hole P, Malloy A, Hannell C: **Nanoparticle Tracking Analysis for the rapid and**
465 **direct visualisation, sizing and counting of viruses, phage and VLPs in suspension.** *Hum Gene*
466 *Ther* 2012, **23**:A8–A9.
- 467 31. Roose-Amsaleg C, Fedala Y, Vénien-Bryan C, Garnier J, Boccara A-C, Boccara M: **Utilization of**
468 **interferometric light microscopy for the rapid analysis of virus abundance in a river.** *Res*
469 *Microbiol* 2017, **168**:413–418.
- 470 32. Linderoth NA, Simon MN, Russel M: **The Filamentous Phage pIV Multimer Visualized by**
471 **Scanning Transmission Electron Microscopy.** *Science* 1997, **278**:1635–1638.
- 472 33. Jebri S, Hmaied F, Yahya M, Ben Ammar A, Hamdi M: **Total coliphages removal by activated**
473 **sludge process and their morphological diversity by transmission electron microscopy.** *Water*
474 *Sci Technol* 2016, **74**:318–323.
- 475 34. Chaïb A, Decossas M, Philippe C, Claisse O, Lambert O, Le Marrec C: *Isolation and CryoTEM of*
476 *Phages Infecting Bacterial Wine Spoilers.* 2020.
- 477 35. Dugat-Bony E, Lossouarn J, De Paepe M, Sarthou A-S, Fedala Y, Petit M-A, Chaillou S: **Viral**
478 **metagenomic analysis of the cheese surface: A comparative study of rapid procedures for**
479 **extracting viral particles.** *Food Microbiology* 2020, **85**:103278.
- 480 36. Park E-J, Kim K-H, Abell GCJ, Kim M-S, Roh SW, Bae J-W: **Metagenomic analysis of the viral**
481 **communities in fermented foods.** *Appl Environ Microbiol* 2011, **77**:1284–1291.
- 482 37. Roux S, Enault F, Hurwitz BL, Sullivan MB: **VirSorter: mining viral signal from microbial genomic**
483 **data.** *PeerJ* 2015, **3**:e985.
- 484 38. Zheng T, Li J, Ni Y, Kang K, Misiakou M-A, Imamovic L, Chow BKC, Rode AA, Bytzer P, Sommer M,
485 et al.: **Mining, analyzing, and integrating viral signals from metagenomic data.** *Microbiome*
486 2019, **7**.
- 487 39. Jung JY, Lee SH, Kim JM, Park MS, Bae J-W, Hahn Y, Madsen EL, Jeon CO: **Metagenomic Analysis**
488 **of Kimchi, a Traditional Korean Fermented Food.** *Appl Environ Microbiol* 2011, **77**:2264–2274.
- 489 40. Kumar J, Sharma N, Kaushal G, Samurailatpam S, Sahoo D, Rai AK, Singh SP: **Metagenomic**
490 **Insights Into the Taxonomic and Functional Features of Kinema, a Traditional Fermented**
491 **Soybean Product of Sikkim Himalaya.** *Front Microbiol* 2019, **10**.
- 492 41. Edwards RA, Rohwer F: **Viral metagenomics.** *Nature Reviews Microbiology* 2005, **3**:504–510.
- 493 42. Kauffman KM, Hussain FA, Yang J, Arevalo P, Brown JM, Chang WK, VanInsberghe D, Elsherbini
494 J, Sharma RS, Cutler MB, et al.: **A major lineage of non-tailed dsDNA viruses as unrecognized**
495 **killers of marine bacteria.** *Nature* 2018, **554**:118–122.
- 496 43. Brum JR, Ignacio-Espinoza JC, Roux S, Doulier G, Acinas SG, Alberti A, Chaffron S, Cruaud C, de
497 Vargas C, Gasol JM, et al.: **Patterns and ecological drivers of ocean viral communities.** *Science*
498 2015, **348**:1261498–1261498.

- 499 44. Adriaenssens EM, Van Zyl L, De Maayer P, Rubagotti E, Rybicki E, Tuffin M, Cowan DA:
500 **Metagenomic analysis of the viral community in Namib Desert hypoliths: Metaviromics of**
501 **Namib hypoliths.** *Environ Microbiol* 2015, **17**:480–495.
- 502 45. Scola V, Ramond J-B, Frossard A, Zablocki O, Adriaenssens EM, Johnson RM, Seely M, Cowan
503 DA: **Namib Desert Soil Microbial Community Diversity, Assembly, and Function Along a**
504 **Natural Xeric Gradient.** *Microb Ecol* 2018, **75**:193–203.
- 505 46. Ledormand P, Desmasures N, Dalmasso M: **Phage community involvement in fermented**
506 **beverages: an open door to technological advances?** *Crit Rev Food Sci Nutr* 2020,
507 doi:10.1080/10408398.2020.1790497.
- 508 47. Jung M-J, Kim M-S, Yun J-H, Lee J-Y, Kim PS, Lee H-W, Ha J-H, Roh SW, Bae J-W: **Viral**
509 **community predicts the geographical origin of fermented vegetable foods more precisely**
510 **than bacterial community.** *Food Microbiology* 2018, **76**:319–327.
- 511 48. Dugat-Bony E, GARNIER L, Denonfoux J, Ferreira S, Sarthou A-S, Bonnarne P, Irlinger F:
512 **Highlighting the microbial diversity of 12 French cheese varieties.** *International Journal of*
513 *Food Microbiology* 2016, **238**:265–273.
- 514 49. Kong S-J, Park J-H: **Effect of Bacteriophages on Viability and Growth of Co-cultivated Weissella**
515 **and Leuconostoc in Kimchi Fermentation.** *J Microbiol Biotechnol* 2019, **29**:558–561.
- 516 50. Erkus O, de Jager VC, Spus M, van Alen-Boerrigter IJ, van Rijswijck IM, Hazelwood L, Janssen
517 PW, van Hijum SA, Kleerebezem M, Smid EJ: **Multifactorial diversity sustains microbial**
518 **community stability.** *The ISME Journal* 2013, **7**:2126–2136.
- 519 51. Chopin A, Bolotin A, Sorokin A, Ehrlich SD, Chopin M-C: **Analysis of six prophages in**
520 **Lactococcus lactis IL1403: different genetic structure of temperate and virulent phage**
521 **populations.** *Nucleic Acids Research* 2001, **29**:644–651.
- 522 52. Thingstad TF: **Elements of a theory for the mechanisms controlling abundance, diversity, and**
523 **biogeochemical role of lytic bacterial viruses in aquatic systems.** *Limnology and Oceanography*
524 2000, **45**:1320–1328.
- 525 53. Breitbart M, Rohwer F: **Here a virus, there a virus, everywhere the same virus?** *Trends in*
526 *Microbiology* 2005, **13**:278–284.
- 527 54. Brum JR, Ignacio-Espinoza JC, Roux S, Doulcier G, Acinas SG, Alberti A, Chaffron S, Cruaud C,
528 Vargas C de, Gasol JM, et al.: **Patterns and ecological drivers of ocean viral communities.**
529 *Science* 2015, **348**.
- 530 55. Shapiro OH, Kushmaro A, Brenner A: **Bacteriophage predation regulates microbial abundance**
531 **and diversity in a full-scale bioreactor treating industrial wastewater.** *The ISME Journal* 2010,
532 **4**:327–336.
- 533 56. Rodriguez-Valera F, Martin-Cuadrado A-B, Rodriguez-Brito B, Pasić L, Thingstad TF, Rohwer F,
534 Mira A: **Explaining microbial population genomics through phage predation.** *Nat Rev Microbiol*
535 2009, **7**:828–836.
- 536 57. Alexeeva S, Guerra Martínez JA, Spus M, Smid EJ: **Spontaneously induced prophages are**
537 **abundant in a naturally evolved bacterial starter culture and deliver competitive advantage**
538 **to the host.** *BMC Microbiol* 2018, **18**:120.

- 539 58. Fernández L, Rodríguez A, García P: **Phage or foe: an insight into the impact of viral predation**
540 **on microbial communities**. *The ISME Journal* 2018, **12**:1171–1179.
- 541 59. Burmeister AR, Abedon ST, Turner PE: **Bacteriophage Ecology**. In *Reference Module in Life*
542 *Sciences*. . Elsevier; 2019:B9780128096338907000.
- 543 60. Fazzino L, Anisman J, Chacón JM, Heineman RH, Harcombe WR: **Lytic bacteriophage have**
544 **diverse indirect effects in a synthetic cross-feeding community**. *The ISME Journal* 2020,
545 **14**:123–134.
- 546 61. Hampton HG, Watson BNJ, Fineran PC: **The arms race between bacteria and their phage foes**.
547 *Nature* 2020, **577**:327–336.
- 548 62. Lythgoe KA, Read AF: **Catching the Red Queen? The advice of the Rose**. *Trends in Ecology &*
549 *Evolution* 1998, **13**:473–474.
- 550 63. Stern A, Sorek R: **The phage-host arms-race: Shaping the evolution of microbes**. *Bioessays*
551 2011, **33**:43–51.
- 552 64. Paterson S, Vogwill T, Buckling A, Benmayor R, Spiers AJ, Thomson NR, Quail M, Smith F, Walker
553 D, Libberton B, et al.: **Antagonistic coevolution accelerates molecular evolution**. *Nature* 2010,
554 **464**:275–278.
- 555 65. Touchon M, Moura de Sousa JA, Rocha EP: **Embracing the enemy: the diversification of**
556 **microbial gene repertoires by phage-mediated horizontal gene transfer**. *Curr Opin Microbiol*
557 2017, **38**:66–73.
- 558 66. Keen EC, Bliskovsky VV, Malagon F, Baker JD, Prince JS, Klaus JS, Adhya SL: **Novel**
559 **“Superspreader” Bacteriophages Promote Horizontal Gene Transfer by Transformation**. *mBio*
560 2017, **8**.
- 561 67. Braga LPP, Soucy SM, Amgarten DE, da Silva AM, Setubal JC: **Bacterial Diversification in the**
562 **Light of the Interactions with Phages: The Genetic Symbionts and Their Role in Ecological**
563 **Speciation**. *Front Ecol Evol* 2018, **6**.
- 564 68. Fuhrman JA: **Marine viruses and their biogeochemical and ecological effects**. *Nature* 1999,
565 **399**:541–548.
- 566 69. Bobay L-M, Rocha EPC, Touchon M: **The Adaptation of Temperate Bacteriophages to Their**
567 **Host Genomes**. *Molecular Biology and Evolution* 2013, **30**:737–751.
- 568 70. Toussaint A, Rice PA: **Transposable phages, DNA reorganization and transfer**. *Current Opinion*
569 *in Microbiology* 2017, **38**:88–94.
- 570 71. Feiner R, Argov T, Rabinovich L, Sigal N, Borovok I, Herskovits AA: **A new perspective on**
571 **lysogeny: prophages as active regulatory switches of bacteria**. *Nat Rev Microbiol* 2015,
572 **13**:641–650.
- 573 72. Brüssow H, Canchaya C, Hardt W-D: **Phages and the Evolution of Bacterial Pathogens: from**
574 **Genomic Rearrangements to Lysogenic Conversion**. *Microbiol Mol Biol Rev* 2004, **68**:560–602.

- 575 73. Tsao Y-F, Taylor VL, Kala S, Bondy-Denomy J, Khan AN, Bona D, Cattoir V, Lory S, Davidson AR,
576 Maxwell KL: **Phage Morons Play an Important Role in Pseudomonas aeruginosa Phenotypes.**
577 *Journal of Bacteriology* 2018, **200**.
- 578 74. Davis BM, Kimsey HH, Kane AV, Waldor MK: **A satellite phage-encoded antirepressor induces**
579 **repressor aggregation and cholera toxin gene transfer.** *EMBO J* 2002, **21**:4240–4249.
- 580 75. Taylor VL, Fitzpatrick AD, Islam Z, Maxwell KL: **Chapter One - The Diverse Impacts of Phage**
581 **Morons on Bacterial Fitness and Virulence.** In *Advances in Virus Research*. Edited by Kielian M,
582 Mettenleiter TC, Roossinck MJ. Academic Press; 2019:1–31.
- 583 76. Beaulaurier J, Luo E, Eppley JM, Uyl PD, Dai X, Burger A, Turner DJ, Pendleton M, Juul S,
584 Harrington E, et al.: **Assembly-free single-molecule sequencing recovers complete virus**
585 **genomes from natural microbial communities.** *Genome Res* 2020, doi:10.1101/gr.251686.119.
- 586 77. Shetty SA, Smidt H, de Vos WM: **Reconstructing functional networks in the human intestinal**
587 **tract using synthetic microbiomes.** *Current Opinion in Biotechnology* 2019, **58**:146–154.
- 588 78. El Haddad L, Roy J-P, Khalil GE, St-Gelais D, Champagne CP, Labrie S, Moineau S: **Efficacy of two**
589 **Staphylococcus aureus phage cocktails in cheese production.** *Int J Food Microbiol* 2016, **217**:7–
590 13.
- 591 79. Lu Z, Breidt F, Fleming HP, Altermann E, Klaenhammer TR: **Isolation and characterization of a**
592 **Lactobacillus plantarum bacteriophage, ΦJL-1, from a cucumber fermentation.** *International*
593 *Journal of Food Microbiology* 2003, **84**:225–235.
- 594 80. Lu Z, Pérez-Díaz IM, Hayes JS, Breidt F: **Bacteriophage Ecology in a Commercial Cucumber**
595 **Fermentation.** *Appl Environ Microbiol* 2012, **78**:8571–8578.
- 596 81. Yoon S-S, Barrangou-Pouey R, Breidt F, Fleming HP: **Detection and characterization of a lytic**
597 **Pediococcus bacteriophage from the fermenting cucumber brine.** *J Microbiol Biotechnol* 2007,
598 **17**:262–270.
- 599 82. Nagai T, Yamasaki F: **Bacillus subtilis (natto) Bacteriophages Isolated in Japan.** *FSTR* 2009,
600 **15**:293–298.
- 601 83. Oh H, Seo DJ, Jeon SB, Park H, Jeong S, Chun HS, Oh M, Choi C: **Isolation and Characterization**
602 **of Bacillus cereus Bacteriophages from Foods and Soil.** *Food Environ Virol* 2017, **9**:260–269.
- 603 84. Shin H, Bandara N, Shin E, Ryu S, Kim K: **Prevalence of Bacillus cereus bacteriophages in**
604 **fermented foods and characterization of phage JBP901.** *Research in Microbiology* 2011,
605 **162**:791–797.
- 606 85. Uchida K, Kanbe C: **OCCURRENCE OF BACTERIOPHAGES LYTIC FOR PEDIOCOCCUS**
607 **HALOPHILUS, A HALOPHILIC LACTIC-ACID BACTERIUM, IN SOY SAUCE FERMENTATION.** *The*
608 *Journal of General and Applied Microbiology* 1993, **39**:429–437.
- 609 86. Antoni GD, Zago M, Vasek O, Giraffa G, Carminati D, Marcó MB, Reinheimer J, Suárez V:
610 **Lactobacillus plantarum bacteriophages isolated from Kefir grains: phenotypic and molecular**
611 **characterization.** *Journal of Dairy Research* 2010, **77**:7–12.

- 612 87. Yoon S-S, Kim J-W, Breidt F, Fleming HP: **Characterization of a lytic *Lactobacillus plantarum***
613 **bacteriophage and molecular cloning of a lysin gene in *Escherichia coli***. *International Journal*
614 *of Food Microbiology* 2001, **65**:63–74.
- 615 88. Bruttin A, Marchesini B, Moreton RS, Sozzi T: ***Staphylococcus carnosus* bacteriophages isolated**
616 **from salami factories in Germany and Italy**. *Journal of Applied Bacteriology* 1992, **73**:401–406.
- 617 89. Barrangou R, Yoon S-S, Frederick Breidt J, Fleming HP, Klaenhammer TR: **Characterization of Six**
618 ***Leuconostoc fallax* Bacteriophages Isolated from an Industrial Sauerkraut Fermentation**. *Appl*
619 *Environ Microbiol* 2002, **68**:5452–5458.
- 620 90. Lu Z, Breidt F, Plengvidhya V, Fleming HP: **Bacteriophage Ecology in Commercial Sauerkraut**
621 **Fermentations**. *Applied and Environmental Microbiology* 2003, **69**:3192–3202.
- 622 91. Mudgal P, Breidt F, Lubkin SR, Sandeep KP: **Quantifying the Significance of Phage Attack on**
623 **Starter Cultures: a Mechanistic Model for Population Dynamics of Phage and Their Hosts**
624 **Isolated from Fermenting Sauerkraut**. *Appl Environ Microbiol* 2006, **72**:3908–3915.
- 625 92. Yoon SS, Barrangou-Pouey R, Breidt F, Klaenhammer TR, Fleming HP: **Isolation and**
626 **Characterization of Bacteriophages from Fermenting Sauerkraut**. *Appl Environ Microbiol* 2002,
627 **68**:973–976.
- 628 93. Foschino R, Picozzi C, Galli A: **Comparative study of nine *Lactobacillus fermentum***
629 **bacteriophages**. *Journal of Applied Microbiology* 2001, **91**:394–403.
- 630 94. Foschino R, Venturelli E, Picozzi C: **Isolation and characterization of a virulent *Lactobacillus***
631 ***sanfranciscensis* bacteriophage and its impact on microbial population in sourdough**. *Curr*
632 *Microbiol* 2005, **51**:413–418.
- 633 95. Arendt EK, Hammes WP: **Isolation and characterization of *Leuconostoc oenos* phages from**
634 **German wines**. *Appl Microbiol Biotechnol* 1992, **37**:643–646.
- 635 96. Davis C, Silveira NF, Fleet GH: **Occurrence and properties of bacteriophages of *Leuconostoc***
636 ***oenos* in Australian wines**. *Applied and Environmental Microbiology* 1985, **50**:872–876.
- 637 97. Henick-Kling T, Lee TH, Nicholas DJD: **Characterization of the lytic activity of bacteriophages of**
638 ***Leuconostoc oenos* isolated from wine**. *Journal of Applied Bacteriology* 1986, **61**:525–534.
- 639 98. Jaomanjaka F, Claisse O, Blanche-Barbat M, Petrel M, Ballestra P, Marrec CL: **Characterization**
640 **of a new virulent phage infecting the lactic acid bacterium *Oenococcus oeni***. *Food*
641 *Microbiology* 2016, **54**:167–177.
- 642 99. Nel L, Wingfield BD, Van der Meer LJ, Van Vuuren HJJ: **Isolation and characterization of**
643 ***Leuconostoc oenos* bacteriophages from wine and sugarcane**. *FEMS Microbiol Lett* 1987,
644 **44**:63–67.
- 645 100. Santos R, Vieira G, Santos MA, Paveia H: **Characterization of temperate bacteriophages of**
646 ***Leuconostoc oenos* and evidence for two prophage attachment sites in the genome of starter**
647 **strain PSU-1**. *Journal of Applied Bacteriology* 1996, **81**:383–392.

Box1: definitions of the different bacteriophage types according to (Hobbs & Abedon, 2016).

Professionally lytic: Phage that is both obligately lytic and not recently descended from a temperate ancestor

Virulent mutant (ex-temperate): Clear temperate phage mutant that can form plaques even on lysogens (i.e. bacteria hosting a prophage) formed by the phage wild-type parent

Temperate phage: Description of a phage that is able to display lysogenic cycles (under the form of a prophage) or lytic cycle according to specific environmental and host parameters.

Filamentous phage: Phage whose productive infection is chronic (may or may not be a temperate phage)

Authors declare no conflict of interest.

Figure 1

Table 1. Selected examples describing the isolation of phages directly from fermented foods.

Fermented food	References	Phage families	Type	Host
Cheese*	(Cheng <i>et al.</i> , 2018)	7 <i>Siphoviridae</i>	Virulent	<i>Propionibacterium freudenreichii</i>
	(De Melo <i>et al.</i> , 2020)	16 <i>Siphoviridae</i>	Virulent	<i>Brevibacterium aurantiacum</i>
	(Del Rio <i>et al.</i> , 2019)	1 <i>Myoviridae</i>	Virulent	<i>Enterococcus faecalis</i>
	(Ladero <i>et al.</i> , 2016)	1 <i>Siphoviridae</i>	Virulent	<i>Enterococcus faecalis</i>
Fermented Cucumber	(Lu <i>et al.</i> , 2003a)	1 <i>Siphoviridae</i>	Virulent	<i>Lactobacillus plantarum</i>
	(Lu <i>et al.</i> , 2012)	3 <i>Siphoviridae</i> and 3 <i>Myoviridae</i>	N.D	<i>Lactobacillus brevis</i> , <i>Lactobacillus plantarum</i> , <i>Weissella paramesenteroides</i> , <i>Weissella cibaria</i>
	(Yoon <i>et al.</i> , 2007)	1 <i>Siphoviridae</i>	Virulent	<i>Pediococcus</i> sp.
Fermented Soybean	(Nagai & Yamasaki, 2009)	N.D	Virulent and temperate	<i>Bacillus subtilis</i>
	(Oh <i>et al.</i> , 2017)	16 <i>Siphoviridae</i>	N.D	<i>Bacillus cereus</i>
	(Shin <i>et al.</i> , 2011)	1 <i>Myoviridae</i>	N.D	<i>Bacillus cereus</i>
	(Uchida & Kanbe, 1993)	1 <i>Siphoviridae</i> and 1 <i>Myoviridae</i>	N.D	<i>Pediococcus halophilus</i>
Kefir	(Antoni <i>et al.</i> , 2010)	2 <i>Siphoviridae</i>	N.D	<i>Lactobacillus plantarum</i>
Kimchi	(Kleppen <i>et al.</i> , 2012)	1 <i>Podoviridae</i>	N.D	<i>Weissella cibaria</i>
	(Kong & Park, 2019)	N.D	N.D	<i>Weissella cibaria</i> , <i>Leuconostoc citreum</i>
	(Yoon <i>et al.</i> , 2001)	1 <i>Siphoviridae</i>	N.D	<i>Lactobacillus plantarum</i>
Salami	(Bruttin <i>et al.</i> , 1992)	2 <i>Podoviridae</i>	N.D	<i>Staphylococcus carnosus</i>
Sauerkraut	(Barrangou <i>et al.</i> , 2002)	3 <i>Siphoviridae</i> and 3 <i>Myoviridae</i>	N.D	<i>Leuconostoc fallax</i>
	(Lu <i>et al.</i> , 2003b)	5 <i>Siphoviridae</i> and 3 <i>Myoviridae</i>	N.D	<i>Leuconostoc pseudomesenteroides</i> , <i>Leuconostoc mesenteroides</i> , <i>Leuconostoc citreum</i> , <i>Leuconostoc fallax</i> , <i>Weissella</i> sp.,

				<i>Lactobacillus plantarum</i> , <i>Lactobacillus brevis</i>
	(Lu <i>et al.</i> , 2010)	1 <i>Siphoviridae</i>	Virulent	<i>Leuconostoc mesenteroides</i>
	(Mudgal <i>et al.</i> , 2006)	2 phages	N.D	<i>Leuconostoc mesenteroides</i>
	(Yoon <i>et al.</i> , 2002)	2 <i>Myoviridae</i> 'type 1', 5 <i>Myoviridae</i> 'type 2' and 2 <i>Siphoviridae</i>	N.D	<i>Leuconostoc mesenteroides</i> , <i>Lactobacillus plantarum</i>
Sourdough bread	(Foschino <i>et al.</i> , 2001)	9 <i>Siphoviridae</i>	3 virulent and 6 temperate	<i>Lactobacillus fermentum</i>
	(Foschino <i>et al.</i> , 2005)	1 <i>Siphoviridae</i>	Virulent	<i>Lactobacillus sanfranciscensis</i>
Wine	(Arendt & Hammes, 1992)	11 <i>Siphoviridae</i>	N.D	<i>Oenococcus oeni</i>
	(Cordero-Bueso <i>et al.</i> , 2020)	<i>Siphoviridae</i> , <i>Myoviridae</i> , <i>Tectiviridae</i>	N.D	<i>Lactobacillus plantarum</i> , <i>Lactobacillus hilgardii</i> , <i>Oenococcus oeni</i>
	(Costantini <i>et al.</i> , 2017)	15 <i>Siphoviridae</i>	Temperate	<i>Oenococcus oeni</i>
	(Davis <i>et al.</i> , 1985)	4 <i>Siphoviridae</i>	N.D	<i>Oenococcus oeni</i>
	(Henick-Kling <i>et al.</i> , 1986)	2 <i>Siphoviridae</i>	N.D	<i>Oenococcus oeni</i>
	(Jaomanjaka <i>et al.</i> , 2016)	1 <i>Siphoviridae</i>	Virulent	<i>Oenococcus oeni</i>
	(Nel <i>et al.</i> , 1987)	17 <i>Siphoviridae</i>	N.D	<i>Oenococcus oeni</i>
	(Philippe <i>et al.</i> , 2018)	1 <i>Tectiviridae</i>	Temperate	<i>Gluconobacter cerinus</i>
	(Santos <i>et al.</i> , 1996)	17 <i>Siphoviridae</i>	Temperate	<i>Oenococcus oeni</i>

N.D = Not Documented.

*For cheese, no example describing the isolation of phages infecting LAB starter culture is listed since the literature on such phages is extremely abundant and already reviewed (Brüssow, 2001; Garneau & Moineau, 2011).

Highlights

- Food fermentations are driven by microbial communities
- Bacteriophages have an impact on the dynamic of food microbial communities
- The precise roles of bacteriophages in fermented foods remain to be characterized