Comprehensive REVIEWS in Food Science and Food Safety

Residential Bacteria on Surfaces in the Food Industry and Their Implications for Food Safety and Quality

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Abstract: Surface hygiene is commonly measured as a part of the quality system of food processing plants, but as the bacteria present are commonly not identified, their roles for food quality and safety are not known. Here, we review the identity of residential bacteria and characteristics relevant for survival and growth in the food industry along with potential implications for food safety and quality. Sampling after cleaning and disinfection increases the likelihood of targeting residential bacteria. The increasing use of sequencing technologies to identify bacteria has improved knowledge about the bacteria present in food premises. Overall, nonpathogenic Gram-negative bacteria, especially *Pseudomonas* spp., followed by *Enterobacteriaceae* and *Acinetobacter* spp. dominate on food processing surfaces. *Pseudomonas* spp. persistence is likely due to growth at low temperatures, biofilm formation, tolerance to biocides, and low growth requirements. Gram-positive bacteria are most frequently found in dairies and in dry production environments. The residential bacteria may end up in the final products through cross-contamination and may affect food quality. Such effects can be negative and lead to spoilage, but the bacteria may also contribute positively, as through spontaneous fermentation. Pathogenic bacteria present in food processing environments may interact with residential bacteria, resulting in both inhibitory and stimulatory effects on pathogens in multispecies biofilms. The residential bacterial population, or bacteriota, does not seem to be an important source for the transfer of antibiotic resistance genes to humans, but more knowledge is needed to verify this. If residential bacteria occur in high numbers, they may influence processes such as membrane filtration and corrosion.

Keywords: cross contamination, food quality, *Pseudomonas*, residential bacteria

Introduction

As part of their quality control systems, most food producers regularly clean and disinfect the production environments. This process removes the food, water, and microbial contaminants that accumulate on surfaces during production. The final disinfection, rinsing, and drying steps aim to reduce the number of microbes to a level that is compatible with the production of food that is safe and meets the expected sensory shelf-life. Investigations have indicated that a contamination level of less than 2.5 cfu/cm^2 after regular cleaning and disinfection is achievable in most cases and that this level is in accordance with most suggested standards (Griffith 2005). One should, however, note that although standards were given earlier (for example, the European Commission suggested an acceptable range of 0 to 10 cfu/cm^2 in their rules for establishments producing poultry in 2001; European Commission 2001), more recent regulations do not provide any general acceptability limits for surface hygiene samples as this approach is regarded to be outdated as hygiene monitoring has to be risk based. Thus, the last 10 y limits for obtaining an acceptable safety level and shelf-life are not defined by authorities and should instead be based on hazard analysis and critical control points and good manufacturing practices for each product and process. For some types of food, a permanent and stable bacteriota on surfaces is desired as part of the food production process (for example, in-house strains that are believed to contribute to fermentation processes). For others, environmental bacteria are not considered to negatively affect food quality and safety. However, the vast majority of food production processes depend on low contamination from the production environment to ensure safe, high-quality products.

At a minimum, the cleaning and disinfection process should be designed to obtain a bacterial reduction that is equal to the daily accumulation of bacteria (due to contamination and growth) and to eliminate pathogens that are introduced into the production environment. As the control processes in most cases do not aim to completely sterilize the surfaces, low numbers of bacteria commonly remain on surfaces, equipment, or machines. These bacteria may be transferred directly (such as from knives, slicers, or conveyor belts) or indirectly (as from floors or control panels) to food during the production day (Mulder and others 1978; Eisel and others 1997; Midelet and Carpentier 2002; Hinton and others

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2004; Redmond and Griffith 2004; Perez-Rodriguez and others 2008; Ferreira and others 2014). Some bacteria can be regarded as transient organisms that occur by coincidence, whereas others may establish themselves, grow, and form residential populations in food production environments. The majority of bacteria found in food processing environments after cleaning and disinfection are nonpathogenic (Mettler and Carpentier 1998; Bagge-Ravn and others 2003; Guðbjornsdottir and others 2005; Langsrud and others 2016; Møretrø and others 2016). It is common in the food industry to monitor the level of such "total counts" as a verification of the cleaning process, and many food plants have large amounts of quantitative data on the number of bacteria present on production surfaces. These bacteria, which are commonly isolated on nonselective growth media, are often referred to as the residential bacteria, background flora, total bacterial count, total viable count, heterotrophic plate count, aerobic plate count, or standard plate count (Nivens and others 2009). However, the identity of these bacteria and their impact on food quality and safety are mostly unknown.

There are a number of reasons why awareness of residential bacteria in food production environments should be increased. The most obvious reason is that they may pose a threat to food quality. Traits important for survival and growth in the production environment may be related to the ability to grow on the product during storage. Often, the conditions in the food production environment are similar to those required for the product, such as similar temperature, nutrient, and stress factors (such as salt or preservatives); thus, the processing surfaces may act as reservoirs for spoilage bacteria. Second, several studies have implied that the fate of pathogens introduced to the processing environment may be affected by nonpathogenic bacteria (Giaouris and others 2015). Third, fast-growing residential bacteria bound to surfaces may have other effects in the food industry, such as influencing filtration or corroding surfaces to increase porosity. Finally, as for other ecological niches, it has been speculated that residential bacteria could play a role in the persistence and spread of antimicrobial resistance genes (Verraes and others 2013).

In this review, we define the residential bacteriota as the bacterial community able to persist over time on food production surfaces despite the use of recognized hygienic routines. We will first present the methodologies used to collect and identify the residential bacteriota, then give an overview of the literature describing the residential bacteriota in the food industry, and finally discuss the impact of residential bacteria on food quality and safety.

Methodology for Studies of Residential Bacteria

The residential bacteriota includes bacteria that are present in the same space over a long period of time, withstanding fluctuations in temperature, humidity, nutrient access, shear forces, and chemical stress. The conditions the bacteriota are exposed to lead to the selection of members with specific characteristics, but may also produce injured or stressed bacteria. If the methodology for collecting and analyzing the microbiota does not take these specific microbial and environmental factors into account, then the true residential bacteriota may not be identified. Therefore, describing the residential bacteriota is not only a matter of being able to identify a bacterial community but also requires a thorough understanding of microbial physiology, food processing, sanitation, and microbial sampling.

The methodology used to collect and analyze environmental bacteria differs significantly between studies, and it is important to be aware that bacteria identified from food production environments are not necessarily part of the residential bacteriota. For example, in a number of studies, the bacteria are isolated and identified from surfaces that are not cleaned, making it difficult to evaluate whether the bacteria are transient or residential (Licitra and others 2007; Mariani and others 2007; Vanegas and others 2009; Barbieri and others 2012; Feligini and others 2012; Schirmer and others 2013; Røder and others 2015; Dzieciol and others 2016). In some cases, sufficient methodological details are not reported, making it difficult to interpret whether a residential or sporadic flora was investigated. For example, in some investigations, it is not stated whether the microorganisms were isolated from sanitized surfaces or the sampling was performed during production (Barros and others 2007; Malek and others 2012; Bokulich and Mills 2013; De Filippis and others 2013; Ksontini and others 2013; Fox and others 2014; Cherif-Antar and others 2016; Schon and others 2016).

In this section, the main steps in the process of isolation and identification of the residential bacteriota are presented, and important factors to consider when interpreting the literature or planning investigations are discussed. An overview of the process and influencing factors is presented in Table 1.

Because of the methodological weaknesses discussed in more detail below, one would expect an over-representation in the literature of bacteria with the ability to grow in a wide temperature range, no special requirements for nutrients, characteristic colony morphology, high resistance to disinfectants, low attachment strength, the ability to be easily lysed (DNA extraction), several copies of 16S rDNA genes and good coverage in databases.

Sampling plan

The sampling plan should be based on the regular routines in the production plant, and it should be verified that these routines were followed prior to sampling. At a minimum, investigations aiming to identify the residential bacteriota should collect samples from surfaces that have been subjected to regular cleaning and disinfection. If the surfaces are always or sometimes (as on weekends) dry before productions start, the surfaces/machines should be sampled after drying. In most studies (Table 2), only one sampling visit is performed, although detection of the same bacteriota in the environment over time would provide more evidence that the bacteria are truly residential.

Sampling methodology

The sampling methodology will have a huge effect on both the level and composition of the identified bacteriota from food processing environments. The isolation and recovery of organisms will depend on a number of factors, such as the properties of the target organisms (attachment strength, injuries, stress, growth requirements), the sample site (humidity, surface material), the detachment method (mechanical forces, detergents), and recovery methodology (detachment from swabs/sponges, growth/recovery conditions for cultivation methods, DNA isolation method for methods without cultivation; Moore and Griffith 2002, 2007; Perez-Rodriguez and others 2008; Deckers and others 2010; Verran and others 2010). A universal sampling methodology that is optimal for all conditions is therefore not possible, and the methodology must be designed for the specific environment.

An important property affecting the resident bacteriota over time is surface attachment, as the bacteria would otherwise be rinsed away during production, cleaning, and disinfection. The methodology chosen for bacteria detachment will be crucial to the results, and it is important to be aware that most isolation

Table 1–Important considerations for the isolation and identification of residential bacteria.

Step	Example methodologies	Comment
Collection and transport		
1. Sampling plan	After cleaning After cleaning and disinfection After C&D and drying	Timing should be adapted to the hygienic regime of the plant, but sampling at time points where sporadic bacteria are likely to be present should be avoided, for example, recontamination after cleaning, insufficient cleaning, before drying of surfaces.
2. Collection and transport to lab	Swab sampling Contact agar	Residential bacteria may attach firmly to surfaces, and the use of physical force and/or detergents for detachment may be necessary. Neutralizers should be added to avoid inhibition. Contact agar will only reach geometrically flat surfaces and cannot be used for identification without precultivation. Selective pressure during transport should be avoided.
3. Swabs—transfer to medium		The process for detaching microbiota from swabs to medium should be optimized.
4. Identification		
4.1 Cultivation	Spreading and incubation on nutrient agar or incubation of contact plates	The residential bacteria are likely adapted/selected to grow in the environment they are collected from and may not grow under standard conditions for total counts. Factors to consider include temperature, nutrients, and selective pressure (for example, salt, sugar, acid). Selective plates will not reflect the whole microbiota but may be used to detect bacterial species present at low levels.
4.1.1 Isolation of colonies		The selection of colonies to be identified should be randomized.
4.1.2 Identification	Microbial/biochemical tests 16S rDNA sequencing Whole-genome sequencing	Extensive phenotypic/biochemical tests are necessary for identification at the species level. If the results are compared with a database, the database should include food-associated bacteria. Analysis of 16S rDNA will normally identify bacteria to the species level, while whole-genome sequencing will provide resolution to the clone level.
4.2 Direct identification	Direct sequencing techniques	Detection limits are lower than for cultivation, and no results will be obtained for niches with very low levels of bacteria. An optimized sample preparation that takes into account contaminants/inhibitors that may affect DNA isolation or PCR (for example, fat, proteins) and the fact that some environmental bacteria are difficult to lyse should be used. Dead cells may be detected by DNA-based methodologies, and the microbiota detected may be a combination of both transient and resident bacteria. Differences in 16S rDNA copy numbers may lead to a biased result. The data analyses are rather complex and personnel with experience in bioinformatics are needed.

methods will only collect a small fraction of the bacteria present on the surface, especially when the numbers of organisms are low (Griffith 2005). It is not known whether the fraction detached by swabbing or contact agar methods is representative of the microbial community in the sampling location, but it is likely that bacteria with lower attachment strengths will dominate among the collected bacteria. To sample bacteria from areas that are not flat, or if identification will be performed without cultivation, swabbing should be chosen instead of contact agar. Indeed, almost all studies on sampling food production environments to identify the microbiota have used some kind of swabbing technique (see references in Table 2).

The composition of the sampling medium will necessarily be a compromise, as it is difficult to simultaneously obtain optimal detachment from surfaces (for example, using a detergent such as Tween 20), neutralization of disinfectants (as by thiosulfate), recovery of injured organisms, and growth inhibition until analysis (Griffith 2005). Using sampling media that do not neutralize disinfectant residues may underestimate bacterial levels and favor members of the bacteriota with high intrinsic resistance. Bacteria protected from disinfectants through biofilm formation may die once they are released from the biofilm and subjected to the antibacterial agent, whereas bacteria with higher resistance will survive. However, using neutralizers is not straightforward, as different types of disinfectants need different neutralizers (Russell 2004), and their components themselves may be harmful to some bacteria, especially for those sublethally injured (Langsrud and Sundheim 1998; Sutton and others 2002), leading to both a potential underestimation of the bacterial level and a biased composition of the bacteriota. The negative effects of neutralizers on the viability of bacteria are small; in most cases, not using them would result in a larger bias. Surprisingly, fewer than half of the scientific papers on residential microbiota use neutralizers for swabs after sampling.

In addition, the storage conditions of swabs and plates between sampling and analysis are important. Introducing selection pressure may lead to biased results, for example, by promoting the growth of psychrotrophs (if stored at low temperatures) or bacteria able to grow in the presence of neutralizing agents or disinfectants. A 10-fold increase in bacterial numbers within 24 h has been reported for the chilled transport of samples from cold environments (Langsrud and others 2016). The time and temperature between sampling and further analysis are often not reported in the literature, but the time can range from "immediate analysis" (Cherif-Antar and others 2016) to "within 24 h" (Møretrø and others 2016) and the samples are stored with cooling when temperature is mentioned.

An alternative to isolating bacteria from surfaces *in situ* is to transfer the surfaces to laboratory and either isolate bacteria from the surfaces as described above or study the biofilm by microscopy (Gibson and others 1995; Guδbjornsdottir and others 2005; Moen and others 2016). Microscopic evaluation may provide more information of the spatial arrangement of bacteria and biofilm structure, but will give limited information about the identity of the microbiota and is therefore outside the scope of this review.

Cultivation

The use of different cultivation techniques, such as growth media or incubation temperatures, or the use of culture-independent sequence-based versus cultivation-based methods, can yield different results when identifying bacteria from surfaces (Brightwell and others 2006; Cherif-Antar and others 2016), and this must be considered when comparing and interpreting results from different studies. Cultivation techniques in which the growth conditions are

Table 2–Dominating residential bacteria isolated after cleaning and disinfection from food industrial surfaces.

Pseudomonas	*Acinetobacter*	*Enterobacteriaceae*	*Aeromonas (A)* /*Shewanella (S)*	*Bacillus/Paenibacillus (P)*	*Staphylococcus*	Lactic acid bacteria (LAB)	Yeast	Other genera >10% *Enterobacteriaceae* (EB) genera LAB genera	Plants	Samples[a]	Environment	Approach[b]	Reference
Meat and poultry processing													
84[c]								Culturing: *Pseudomonas* 84%, *Microbacterium* 11%, EB: *Serratia* 4% Non-culturing: *Pseudomonas* 13%, *Sphingomonas* 65%, alfa-proteobacterium 22%	1	5	Meat processing, conveyor belt	C/NC	(Brightwell and others 2006)
								EB: *Yersinia* (dominant)	1	10/36	Meat processing	NC	(Hultman and others 2015)
								EB: *Serratia*	1	3	Poultry processing, floor	C	(Møretrø and others 2006)
								EB: *Serratia, Enterobacter, Citrobacter* LAB: *Aerococcus* (dominant)	1	19/20	Meat abattoir	C	(Møretrø and others 2013)
								EB: *Enterobacter, Kluyvera*	1	-	Meat processing, coupons 8 weeks	C	(Mettler and Carpentier 1998)
			A					EB: *Hafnia, Citrobacter, Klebsiella*	4	17	Meat processing, chips/coupons	C	(Hood and Zottola 1997)
5		2	A:3 S:1	28	31	1		*Micrococcus* 11% EB: *Serratia, Pantoea* LAB: *Lactococcus*	1	21/26	Meat processing	C	(Marouani-Gadri and others 2009)
								Brochothrix >10%, *Psychrobacter* >10% LAB: *Lactococcus, Streptococcus, Carnobacterium*	10	20	Large meat processing plants	NC	(Stellato and others 2016)
								Brochothrix >10%, *Psychrobacter* >10% LAB: *Streptococcus, Carnobacterium*	10	20	Small meat processing plants	NC	(Stellato and others 2016)
Fish and seafood processing													
28	8			7	5	6	9	*Neisseriaceae* 11%, *Alcaligenes* 10%, LAB: no genus information	1	-	Smoke house salmon I	C	(Bagge-Ravn and others 2003)
23	11	8				8	41	EB: no genus information LAB: no genus information	1	-	Smoke house salmon II	C	(Bagge-Ravn and others 2003)
23	6				17		12	*Neisseriaceae* 10%	1	-	Caviar Processing	C	(Bagge-Ravn and others 2003)
23	11					7	27	*Vibrio* 11%	1	-	Semi-processed herring	C	(Bagge-Ravn and others 2003)
69	2	2						EB: *Serratia* 2%	1	3	Salmon processing plant A	C	(Langsrud and others 2016)
23	35		A: 3 S: 3		1	4		*Rhodococcus* 18% LAB: *Carnobacterium*	1	4	Salmon processing plant B	C	(Langsrud and others 2016)
46	4	19						EB: *Serratia* 15%, *Rahnella* 4%, *Providencia* 2%, *Hafnia* 2%	1	3	Salmon processing plant C	C	(Langsrud and others 2016)
19	11	27	A:6					*Micrococcus* 14%, coryneforms 11%	1	20	Fish processing	C	(Guðbjornsdottir and others 2005)
66	1	4	A:13				10		1	16	Shrimp processing	C	(Guðbjornsdottir and others 2005)
56	10	6	S:7 A:3					EB: *Yersinia, Serratia, Morganella*	1	42	Salmon processing plant B	C	(Møretrø and others 2016)
54	4	4	S:12		2	<1		*Psychrobacter* 15%, EB: *Morganella; Yersinia* LAB: *Lactobacillus*	1	45	Salmon processing plant H	C	(Møretrø and others 2016)

(*Continued*)

Table 2–Continued.

Pseudomonas	*Acinetobacter*	*Enterobacteriaceae*	*/Shewanella (S)*	*Aeromonas (A)*	*Bacillus/Paenibacillus (P)*	*Staphylococcus*	Lactic acid bacteria (LAB)	Yeast	Other genera >10% *Enterobacteriaceae* (EB) genera LAB genera	Plants	Samples[a]	Environment	Approach[b]	Reference
Dairies														
									EB: *Klebsiella* LAB: *Enterococcus*	4	12	Dairies, disinfecting footbaths (chlorine)	C	(Langsrud, Seifert et al. 2006)
		31		38	14		2		EB: *Shigella* 12%, *Escherichia* 11%, *Enterobacter* 9%	1	9	Dairy pasteurization lines	C	(Sharma and Anand 2002)
>25					Ca *25*	Ca *20*			LAB: *Lactococcus* ca. 10%, *Enterococcus* ca. 10%	1	1	Milking machine	C	(Teixeira and others 2005)
										1	-	Milk processing	C	(Mettler and Carpentier 1998)
									LAB: *Streptococcus* (dominant) (starter), *Lactococcus* (starter), *Lactobacillus*	1	9	Dairy, cheese production	C/NC	(Calasso and others 2016)
			A, S						*Psychrobacter* LAB: *Streptococcus*	1	15	Dairy, cheese production	NC	(Stellato and others 2015)
8		31		23		15			EB: *Klebsiella* LAB: *Lactococcus, Lactobacillus*	4	-	Membranes, dairies	C	(Tang and others 2009)
									LAB (dominant): *Lactobacillus, Leuconostoc*	10	>100	Wooden vats for cheese, cleaned	C	(Didienne and others 2012)
			A						EB: *Shigella, Enterobacter, Escherichia* LAB: *Streptococcus, Leuconostoc*	1	7	Ice cream plant	C	(Gunduz and Tuncel 2006)
37		16			20				*Stenotrophomonas* (15%) EB: *Serratia*	1	4	Milk processing plant	C	(Cleto and others 2012)
Other food production														
20	3	21		B: 6 P: 6	7				*Ralstonia* 12%, EB: *Rahnella* 15%, *Enterobacter* 7%	2	11	Fresh-cut produce processing plants	C	(Liu and others 2013)
									LAB: *Lactobacillus*	-	6	Green table olive processing	C	(Grounta and others 2015)
									LAB: *Leuconostoc*	1	-	Pastry processing	C	(Mettler and Carpentier 1998)
									EB: *Erwinia, Pantoea* LAB: *Lactobacillus, Leuconostoc*	4	4	Bakeries (sourdough)	NC	(Minervini and others 2015)
2							95		LAB: *Streptococcaceae* 58% *(dominant)*, *Lactobacillus* 38%	1	2/4	RTE food processing	NC	(Pothakos and others 2015)

(*Continued*)

Table 2–Continued.

Pseudomonas	*Acinetobacter*	*Enterobacteriaceae*	*Aeromonas (A)* /*Shewanella (S)*	*Bacillus/Paenibacillus (P)*	*Staphylococcus*	Lactic acid bacteria (LAB)	Yeast	Other genera >10% *Enterobacteriaceae* (EB) genera LAB genera	Plants	Samples[a]	Environment	Approach[b]	Reference
			A	P				*Psychrobacter* >10%, LAB: *Streptococcus* EB: *Serratia, Klebsiella*	8	72	RTE (meat, cheese, vegetables), slicers	NC	(Mertz and others 2014)
									1	13	Winery	NC	(Bokulich and others 2013)

Color codes for prevalence:

Dominant, most frequently isolated genus/group
Not dominant but >20% of microorganisms identified
11% to 19%
5% to 10%
<5%
Present; quantitative level not reported or could not be estimated
No color; not present (below detection limit)

[a]Number of samples taken. When some samples were below the detection limit, the data presented are the no. of samples with identified bacteria/no. samples total.
[b]Identification approach. C, based on cultivation; NC, Non-cultivation sequence-based approach. The data presented for NC are based on operational taxonomic units (OTUs).
[c]The relative prevalence in percent (rounded to whole percent) is presented for studies providing quantitative data.

very different from the sampling site conditions may fail to support growth of the residential bacteria. A number of investigations on bacteria from a low-temperature environment have used incubation temperatures of 30 °C or more, selecting for mesophiles and suppressing psychrotrophs, which may be the most important species (Gounadaki and others 2008; Gutierrez and others 2012; Malek and others 2012). Some members of the residential bacteriota may have particular growth requirements, such as casein for dairy isolates (Bore and Langsrud 2005), and may not be detected on general laboratory media lacking these nutrients. The general medium tryptic soy broth is used in many investigations, but some studies have used media and incubation temperatures that are more targeted to the conditions in the environment the bacteria are selected from (Mettler and Carpentier 1998; Guδbjornsdottir and others 2005; Tang and others 2009; Møretrø and others 2016). To ensure the detection of specific bacterial groups, selective media covering several types of bacteria that are expected to occur in the environment are sometimes used (Gounadaki and others 2008; Schlegelova and others 2010; Calasso and others 2016; Stellato and others 2016). However, the bacterial levels on selective media for the genera that most likely dominate in the environment may be less than 10% of that obtained on a plate for total counts (Gounadaki and others 2008).

Ideally, to obtain a nonbiased quantitative overview of the dominant bacteriota, bacterial colonies should be picked randomly from plates that support growth of the most important clones. However, in most studies, the colonies are picked to cover the different morphologies present in the sample, and only 4 out of the 20 studies referred to in Table 2 that identified colonies (Bagge-Ravn and others 2003; Teixeira and others 2005; Schirmer and others 2013; Møretrø and others 2016) randomly selected the colonies. Thus, for the majority of studies using cultivation before identification, one can expect biased quantitative results, with overreporting of bacteria with a colony morphology that is distinct from the dominant bacteria and with under-reporting of bacteria with a morphology that is more common among the most dominant genera.

Identification

Identification of colonies. Conventional bacterial identification is based on microscopy and on phenotypic and biochemical tests. It is usually not possible to identify bacterial colonies to the genus level based on morphology on nonselective agar-based medium only. Microscopy, Gram-staining, and simple biochemical tests, such as catalase and oxidase tests, also have limited resolution. Thus, extensive phenotypic and biochemical tests are usually needed to identify bacteria to the genus level. There are commercial kits for identification based on the ability to grow on different substrates and assessment of enzymatic activities, such as API systems (Biomerieux) or the Biolog system (Biolog, Hayward, Calif., U.S.A.), but most systems have the disadvantage that the databases provided by the manufacturers are dominated by clinical isolates and may provide inaccurate results for food-associated bacteria. For example, only approximately 50% and 30% of bacterial isolates from raw milk were identified to the species level by the API and Biolog systems, respectively. A further 5% to 10% were identified at the genus level, although the remaining isolates either were not identified or had profiles that, according to the identification systems, were doubtful, under-discriminated, or unacceptable (Munsch-Alatossava and Alatossava 2006). In most studies, colonies are identified by molecular methods, such as genus- or species-specific PCR or 16S rDNA sequencing. In general, the 16S rDNA sequence databases are large and contain sequences from bacteria that are relatively closely related to the dominant bacteria in food processing, and this method will normally identify bacteria to the genus level and in some cases to the species level.

Typing of isolates. The best analyses for confirming that the bacteriota is residential is tracking clones or the bacteriota over time by fingerprinting (as by pulsed-field gel electrophoresis

[PFGE], multiple-locus variable number tandem repeat analysis [MLVA], multilocus sequence typing [MLST]) or by whole-genome sequencing. These resource-consuming approaches are, however, almost exclusively used to investigate the persistence of pathogens such as *L. monocytogenes*, where genome sequencing or other fingerprinting methods may also provide information about virulence or a link to human clinical strains (Larsen and others 2014). One exception is the investigation by Padilla-Frausto and others (2015), who used PFGE to profile lactic acid bacteria (LAB) from the environment and food products in a sausage production facility. Over a period of 2 y, residential clones of *Lactobacillus* and *Leuconostoc* were detected in the equipment used for sausage production, some of them surviving the heating process. *Staphylococcus* spp. are frequently found on food processing equipment, but typing techniques are rarely used to look for persistent clones. However, a persistent, enterotoxigenic clone of *Staphylococcus aureus* was reported to be found on defeathering equipment in turkey production for a 6-mo period by Adams and Mead (1983), who used phage typing and biochemical tests for the typing analysis.

Bacteriota identification without precultivation. Recently, the introduction of cultivation-independent sequence-based bacteriota analyses have provided new insights into the identity of bacteria on surfaces in the food industry (Cocolin and Ercolini 2015; Bokulich and others 2016). This Next generation sequencing methodology provides high-throughput and in-depth identification compared to most cultivation-based techniques. Another advantage is that some of the factors discussed above, such as neutralization of disinfectant, growth conditions, and selection of colonies, will not affect the final results. The sampling plan, swabbing procedure, and transport conditions will, however, still be relevant for bacteriota identification. These methods can also identify viable but nonculturable bacteria (Peneau and others 2007; Carpentier 2009). However, a serious drawback of sequence-based identification without prior cultivation is that DNA from both viable and dead bacteria is sequenced. The dead population represents bacteria unable to survive in the environment; if this population is large (as it may be after a disinfection step), the analysis may give a false impression of the composition of the residential bacteriota. There are methods available that may lead to identification of majorly viable bacteria, such as the treatment with propidium monoazide before PCR and sequencing (Zeng and others 2016). However, such methods may not function for all types of bacteria and lethal stress conditions, and we are not aware that such methods have been used to study the residential bacteriota on surfaces in the food industry. The results from sequenced based identification may also be biased, since the number of copies of the 16S rRNA gene may vary between different types of bacteria. An additional challenge of sequence-based approaches without prior cultivation is that the number of residential bacteria on surfaces after cleaning and disinfection may in many cases be too low to obtain a sufficient amount of DNA for identification (Pothakos and others 2015). The data analyses are rather complex, but established bioinformatics pipelines are available (Meyer and others 2008; Schloss and others 2009; Caporaso and others 2010).

Dominant Residential Bacteria

The considerable progress that has recently been made in understanding residential bacteriotas in food production can be partially explained by the introduction of novel bacterial identification methods, such as high-throughput sequencing. Still, some of the pioneering investigations, such as the description of the bacteriota in the fish industry by Gram's research group in 2003 and in various food processes by Mettler and Carpentier in 1998 (Mettler and Carpentier 1998; Bagge-Ravn and others 2003), are important contributions to the field.

In this section, we will discuss the most dominant residential types of bacteria in different food production environments. An overview is presented in Table 2. The following literature selection criteria were used to define a minimum methodological requirement for identifying a dominant residential bacteriota: (1) Samples were taken from clean surfaces. Thus, studies were excluded if sampling was done during processing, sampling time was not specified, or soiled surfaces were sampled. (2) Nonselective approach used for identification. When a cultivation approach was used, nonselective nutrient agar was used for microbial collection and identification. Investigations solely based on plating on selective growth media were excluded. Based on these selection criteria, 27 studies covering the processing of meat (7), seafood (4), dairy products (9), fresh produce (2), wine (1), bakery products (1), and mixed foods (4) were reviewed (Table 2). Studies based on both the identification of cultivated bacterial isolates and microbiota analysis of samples without prior cultivation (cultivation-independent approaches) were included. The introduction of powerful high-throughput sequence-based identification techniques has shown that the bacterial diversity on surfaces in the food industry is high. There are reports of up to hundreds of different operational taxonomic units (OTUs) in individual processing plants (Bokulich and Mills 2013; Stellato and others 2016). In this review, we refer only to the most dominant members of the bacteriotas; for further details, we refer to the original papers. An overview of the characteristics of the dominant residential bacteria important for growth and survival in food processing environments is presented in Table 3, and the effect of the residential bacteria on food quality is summarized in Table 4. In addition to the studies reviewed here, there are several studies on bacteria in environments where surfaces are not routinely cleaned. An example is production environments for traditional cheeses, where the microbial flora involved have been previously reviewed by Montel and others (2014).

Dominant Bacteriota in Food Processing

As mentioned above, many factors influence the distribution of bacteria isolated and identified from food processing environments (such as type of food industry, conditions in processing plants, methodology used for sampling and identification). Many of the reported studies have weaknesses that may have caused biased results, but some general trends can still be observed. Studies based on high-throughput sequencing have shown that hundreds of different bacteria can be present in a single processing plant, but there are still only a few types/genera of residential bacteria that dominate in food processing environments (Table 2 and Figure 1). Only 6 groups/genera were found to have the highest prevalence in at least one study: *Pseudomonas*, *Acinetobacter*, *Enterobacteriaceae*, spore-forming bacteria, *Staphylococcus* spp., and LAB. In addition, the following bacterial genera/groups were comprised of >10% of the bacteria identified in at least one processing plant: *Aeromonas* spp., *Brochothrix* spp., *Microbacterium* spp., *Micrococcus* spp., *Neisseriaceae*, *Psychrobacter* spp., *Ralstonia* spp., *Rhodococcus* spp., *Shewanella* spp., *Sphingomonas* spp., *Stenotrophomonas* spp., and *Vibrio* spp. When data for all types of food industry are seen together, Gram-negative bacteria dominate over Gram-positive bacteria (Table 2 and Figure 1). Exceptions where Gram-positive bacteria are isolated more frequently include processes with dry conditions or where starter cultures are used (meat and dairy industries).

Table 3–Stress conditions encountered by bacteria in the food processing environment.

Stress condition	Examples of areas/situations	Bacteria with high tolerance
Dry conditions	Pastry production, areas subjected to dry cleaning only	Gram-positive and spore-forming bacteria (*Staphylococcus* spp., *Bacillus* spp., *Paenibacillus* spp.)
High salt	Brine, salting areas	Gram-positives (*Staphylococcus* spp., *Micrococcus* spp., Coryneform bacteria), *Psychrobacter* spp.
High temperatures (>50 °C)	Pasteurization lines, CIP systems, dairy, heat exchangers	Spore formers (*Bacillus* spp., *Paenibacillus* spp.), thermophilic bacteria (*Streptococcus thermophilus)*
Low temperatures (<5 °C)	Storage rooms, chilled processing rooms	*Pseudomonas* spp., *Acinetobacter* spp., *Enterobacteriaceae*, *Aeromonas* spp., *Shewanella* spp., lactic acid bacteria (LAB), *Brochothrix* sp., *Psychrobacter* spp.
Low pH	Processing of acidified and fermented foods	LAB
Low nutrients	Areas often cleaned, easy to clean, processes using a lot of water	*Pseudomonas* spp., *Acinetobacter* spp., *Enterobacteriaceae*
Cleaners/disinfectants	During sanitation and afterwards if rinsing is insufficient	*Pseudomonas* spp., *Acinetobacter* spp., *Enterobacteriaceae* (for example, *Serratia marcescens*), *Sphingomonas* spp., spore-forming bacteria (*Bacillus* spp., *Paenibacillus* spp.)
Shear forces	During sanitation, moving parts in production, inside tubes with flowing liquids	Biofilm formers (*Pseudomonas* spp., *Acinetobacter* spp., *Staphylococcus* spp.), adhesive spores (*Bacillus* spp., *Paenibacillus* spp.)

Sources: Fratamico and others (2009), McDonnell (2007), Wong (2011), and references included throughout the text

Table 4–Spoilage potential of bacteria dominant in food processing environments.

Genus/group	Importance as spoiler[a]	Type of food spoiled	Storage and packaging conditions for spoilage
Pseudomonas	+++	Fresh vegetables, meat, poultry and fish, eggs, dairy products, low-salt foods	Chilled, aerobic
Acinetobacter	+	Fresh vegetables, meat, poultry, and fish	Chilled, aerobic
Enterobacteriaceae	++	Fresh vegetables, meat, poultry, and fish, eggs, dairy products, processed meats, bread	Aerobic, modified atmosphere, vacuum, insufficiently chilled foods
Aeromonas	+	Fresh meat, poultry and fish, eggs	Chilled, vacuum
Shewanella	+++	Seafood, especially fish products, high-pH meat and poultry	Chilled, aerobic, vacuum
Psychrobacter	+	Salted fish, fresh meat and poultry	
Sphingomonas	–		
Lactic acid bacteria	+++	Fresh meat, poultry, vegetables, fish, dairy products, deli meats, lightly processed meat and fish products, fermented foods, acidified foods, bakery products	Chilled/insufficiently chilled, vacuum, modified atmosphere
Bacillus, spore formers	++	Pasteurized/heat-treated foods, dairy products, fresh vegetables, bakery products	Aerobic
Staphylococcus spp., *Micrococcus* spp.	(+)	Fresh produce, meat, poultry, fish and seafood, refrigerated milk, high-salt products (cured meat)	Aerobic
Brochothrix thermosphacta	++	Meat and poultry, high-pH meat, cured meat	Aerobic, modified atmosphere
Coryneform	(+)	Cheese	

[a]+++, Recognized as the most important spoilage organism in several foods; ++, frequently reported as an important spoiler of food; +, reported as a spoilage organism; –, not reported to spoil food.
Sources: Casaburi and others (2015), Gram (2009), Iulietto and others (2015), Lund and others (2000), Ragaert and others (2007), and Sperber and Doyle (2009).

Gram-negative bacteria

Pseudomonas. As shown in Figure 1, the Gram-negative genus *Pseudomonas* is the most frequently reported genus of the bacteriota found after sanitation of food processing surfaces across all types of food production. As part of the residential bacteriota, *Pseudomonas* was reported in 23 of the 27 studies and represented more than 20% of the bacteriota in 12 of the 27 investigations. *Pseudomonas* spp. are commonly isolated from plant surfaces, soil, water, and raw materials and may be frequently introduced into the processing environment through many routes. Because *Pseudomonas* is a very heterogeneous genus, the nomenclature has changed considerably over time, and different methodologies provide different species identities (Baltrus 2016), it is difficult to determine the most frequent species across different studies. However, it appears from single studies that the diversity among isolated *Pseudomonas* is high and that the human pathogen *P. aeruginosa* is uncommon (Guðbjornsdottir and others 2005; Liu and others 2013; Møretrø and others 2016). *Pseudomonas* spp. occur ubiquitously, as they are associated with a wide range of niches in the production environment with respect to nutrients, temperatures, surface materials, and stress factors (biocides; Table 3). *Pseudomonas* is found in machines (conveyor belts and slicing and milking machines), disinfecting footbaths, floors, and drains, and has also established itself on stainless steel coupons placed in the processing environments (Table 2).

The highest prevalence is found in the fish industry, where 19% to 69% of microorganisms in the reported studies are *Pseudomonas*. In their study of 4 seafood factories (2 producing smoked salmon, 1 semipreserved herring, and 1 caviar), Bagge-Ravn and others (2003) noted that the microbiota obtained during processing reflected the microorganisms introduced from raw materials and specific processing parameters (such as high salt concentrations in caviar production). However, independently of process, *Pseudomonas* and yeasts survived cleaning and oxidative disinfectants, although many of the other bacteria were eliminated. Biofilm formation is a survival mechanism that can allow bacteria to withstand both the mechanical and chemical stresses encountered during cleaning and disinfection. Liu and others (2013) characterized *Pseudomonas* surviving cleaning and disinfection in a fresh produce plant and suggested that biofilm production at low temperatures could partly explain their establishment as a part of the residential bacterial community. Another study showed that biofilm formation is relatively extensive in *Pseudomonas* at temperatures relevant for food production; interestingly, the maximal amount of biofilm formation of *P. lundensis* was higher at low (4 and 10 °C) than at high (30 °C) temperatures (Liu and others 2015). Tolerance to

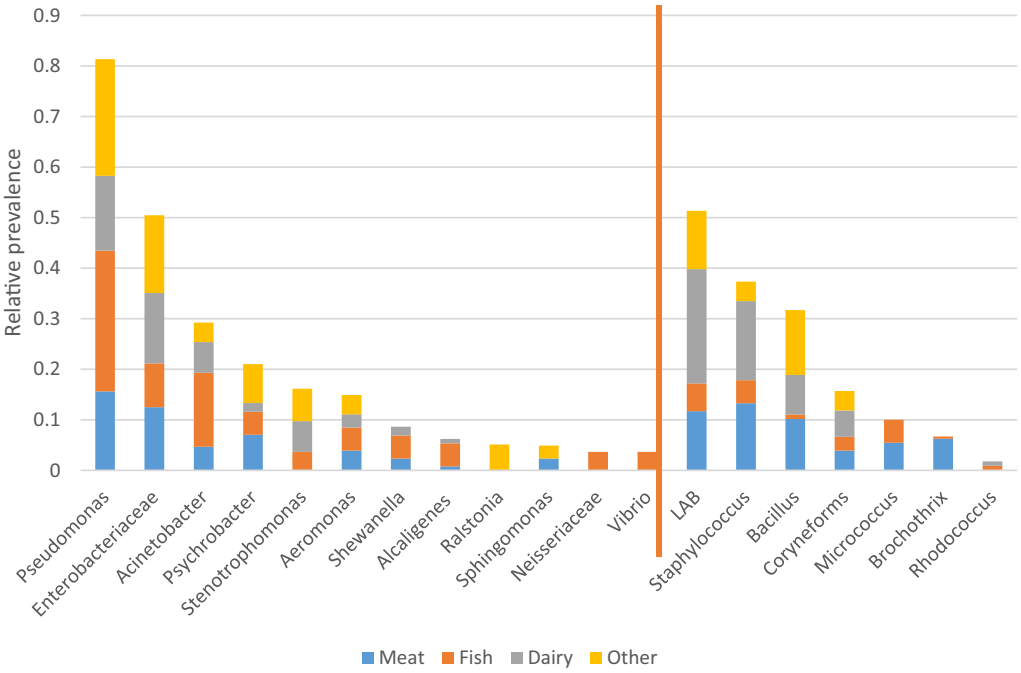

Figure 1–Relative prevalence of residential bacteria based on a metaanalysis of 27 studies. The studies (defined in Table 2) were selected based on the criteria that samples were taken from cleaned surfaces and that bacteria were identified by a nonselective approach. For each processing plant or group of processing plants (defined as the rows in Table 2), bacterial genera/groups were given points equaling the product of prevalence (present; 1p, 11% to 20%; 2p, >20%, 3p) and number of samples (≤10; 1p, 11 to 20; 2p, and >20; 3p). For each food processing category (fish, meat, dairy, others) the numbers for the various studies were added and divided by the total points rewarded for each category. Only genera/groups comprising >10% of the bacteria identified in at least one processing plant were included. Results shown for *Bacillus* is based on combined data for *Bacillus* and *Paenibacillus,* and data for *Microbacterium* are included under coryneforms. LAB, lactic acid bacteria. The vertical orange line separates gram negative (left) and gram positive (right) bacteria.

disinfectants may also partly explain survival after cleaning and disinfection. *Pseudomonas* isolated after practical disinfection may grow at recommended user concentrations of the disinfectant, and some strains even grow in disinfectant solution without any other available nutrients (Sundheim and Langsrud 1995; Langsrud and others 2003b). Examples of *Pseudomonas* able to use quaternary ammonium compounds (QACs) as the sole carbon, nitrogen, and energy source have also been reported from sewage sludge (Takenaka and others 2007). *Pseudomonas* spp. are also highly capable of competing with other bacteria from food environments (Chorianopoulos and others 2008; Langsrud and others 2016). Psychrotrophic *Pseudomonas* spp. grow rapidly at 2 to 5 °C compared to most other food-associated bacteria (Herbert and Sutherland 2000; Munsch-Alatossava and Alatossava 2006). *Pseudomonas* spp. are relatively sensitive to drying (Kramer and others 2006; Møretrø and others 2013) and can be killed by pasteurization, and their growth is limited in acid and high-salt environments. Thus, in some environments, genera other than *Pseudomonas* will dominate, as discussed more below (as under *Bacillus*). Apparently, several characteristics of *Pseudomonas* spp. can explain the dominance and persistence of this genus in a large range of environments, such as frequent introduction into the food production environment and its ability to survive cleaning and disinfection and to grow even with low levels of nutrients and at low temperatures (Moore and others 2006; Table 3).

Enterobacteriaceae. *Enterobacteriaceae* cells are commonly isolated from processing surfaces in several types of food industries (Table 2 and Figure 1). Some food processing plants sample for *Enterobacteriaceae* in their hygienic monitoring program as an indicator of fecal contamination (Vanschothorst and Oosterom 1984), but this may lead to misleading conclusions. Although many genera of *Enterobacteriaceae* are present in the mammalian intestine, others are commonly present in the natural environment. A wide range of *Enterobacteriaceae* genera were reported to be part of the bacteriota in food processing environments in only a single study or in a couple of studies (*Enterobacter, Morganella, Citrobacter, Klebsiella, Pantoea, Hafnia, Kluyvera, Rahnella, Providencia, Escherichia, Yersinia, and Shigella*), and the only genus that occurs in several investigations across different food production environments is *Serratia*. *Serratia* spp. are commonly present in water, soil, plants, insects, and vertebrates (Grimont and Grimont 2006). In an investigation of bacteriota in a milk processing plant, *Serratia* was the second most occurring genus after *Pseudomonas*. Interestingly, *Serratia* stood out as superior to *Pseudomonas* and other members of the bacteriota in adherence capacity and production of a biofilm matrix (Cleto and others 2012). In addition, other survival mechanisms were suggested in the investigation. Approximately half of the isolates produced compounds that inhibited growth of other bacteria, and one-third produced siderophores to collect iron from the environment. *Serratia* also shows extraordinarily high resistance to tenside-based disinfectants, and some strains even grow in user concentrations of amphoteric disinfectants (Langsrud and others 2003a). These properties together with its ability to grow at low temperatures make *Serratia* fit to survive in a range of environments, able to withstand shear forces and chemicals, and to compete with other psychrotrophs. *Yersinia* spp. were reported to dominate in a meat processing plant (Hultman and others 2015) and were also found in low numbers in 2 salmon processing plants

(Møretrø and others 2016). *Yersinia* spp. are common in the environment, especially in water. *Yersinia enterocolitica,* which causes yersiniosis, has been reported in both the environment and abattoirs, but the strains are usually nonpathogenic (Samarco and others 1997).

The minimum temperature for growth varies between genera within *Enterobacteriaceae,* and this may partly explain why some genera, despite frequently being introduced to the environment, do not remain over time. For example, *Hafnia* spp. and *Serratia* spp. from meat grow in temperatures as low as at +0.2 °C, although the minimum growth temperature for *Escherichia coli* is 8 °C (Ridell and Korkeala 1997), explaining why the latter is rarely found as a dominant part of the residential biota in cold production environments. *E. coli* persistence has, however, been reported. In a comprehensive study of 4 factories producing cooked, chilled, or mixed foods, 2 ribotypes of *E. coli* persisted in one factory for nearly a year, indicating that they were part of the residential bacteriota (Holah and others 2004). In the study, selective enrichment was used for detection, and a low prevalence (0.08%) was found, indicating that *E. coli* was not a dominant species in the factory environment. The temperature conditions in the niches for *E. coli* were unfortunately not provided, but the authors claimed that persistence appeared to be more linked to products than to environmental niches.

Acinetobacter. *Acinetobacter* is another Gram-negative genus frequently found in the food industry, especially the fish industry, similar to *Pseudomonas* (Figure 1). In one salmon processing plant, *Acinetobacter* spp. were more prevalent than *Pseudomonas* spp. (Langsrud and others 2016), but in other studies from fish/seafood processing, *Pseudomonas* spp. were more prevalent than *Acinetobacter* spp. In the meat and dairy industries, the prevalence of *Acinetobacter* spp. is lower. In dairies, *Acinetobacter* was not found or was found only in low numbers (<5% of total bacteria; Table 2). An exception was the surface of disinfecting footbaths with chlorine, where the prevalence was higher (25%; Langsrud and others 2006). This may indicate a selective pressure in this niche favorable for *Acinetobacter*, but it should also be taken into account that the data were based on only 12 identified isolates and that *Acinetobacter* spp. were only found in 1 out of 4 dairies. Like *Pseudomonas* spp. and other Gram-negative bacteria, *Acinetobacter* spp. are relatively sensitive to drying (Kramer and others 2006; Møretrø and others 2013) and may thrive better in the humid fish processing plants than in more dry production lines. *Acinetobacter* spp. are found in many outer environments (soil, water, and sewage), exhibit metabolic versatility, grow at low temperatures, and can form biofilms (Towner 2006; Habimana and others 2010a; Table 3). For example, 2 *Acinetobacter* spp. isolates from a meat abattoir formed thick biofilms on polystyrene, in amounts comparable to those of *Pseudomonas* spp., at both 12 and 20 °C (Møretrø and others 2013). Overall, *Acinetobacter* shares many of the same survival and growth characteristics as *Pseudomonas*, and this can explain why they are relatively common in the same niches.

Other Gram-negative bacteria. *Shewanella* spp. and *Aeromonas* spp. are more commonly isolated from fish and seafood processing plants than other food industries (Table 2 and Figure 1; Guðbjornsdottir and others 2005; Langsrud and others 2016; Møretrø and others 2016). *Shewanella* spp. are commonly present in marine environments and live fish, and most genera are psychrotrophic (Gram 2009). *Aeromonas* spp. are ubiquitous in different types of water environments, and most genera grow at low temperatures and are commonly found in fresh foods (Krovacek and others 1994; Hanninen and others 1997).

Psychrobacter spp. can be found in different types of processing environments (Figure 1; Rodriguez and McLandsborough 2007; Stellato and others 2015, 2016; Møretrø and others 2016). *Psychrobacter* spp. are psychrotolerant and halotolerant bacteria and are common in marine environments (Juni and Heym 1986; Bowman 2006), but they are also present in land-based animals, such as in cows and their milk (Kuehn and others 2013).

Sphingomonas spp. were not detected on conveyor belts in a meat plant using a cultivation-based approach, but 83% of the bacteria were found to be *Sphingomonas* spp. using a sequence-based cultivation-independent approach (Brightwell and others 2006). *Sphingomonas* spp. were also reported in a dairy after fogging disinfection (Bore and Langsrud 2005). These bacteria are known to be resistant to various antimicrobial compounds and are widely distributed in nature, such as in soil and aquatic environments, and are associated with plants (White and others 1996; Stolz 2009; Sun and others 2013).

The presence of some types of Gram-negative bacteria on food industry surfaces seems to be specific to the raw materials. In a produce processing plant, *Rahnella* spp. (family *Enterobacteriaceae*) and *Ralstonia* spp. were frequently isolated. Both genera are soil- or plant-associated and are probably introduced with the raw materials (Liu and others 2013). Similarly, marine *Vibrio* spp. were found in a plant processing salmon farmed in seawater (Langsrud and others 2016).

Many other types of gram-negative bacteria are present in food industries, and many of the less common genera may be underestimated in some studies, as the isolation and identification methods used do not cover all genera. In some cases, bacteria may be wrongly identified, assigned to a genus that does not reflect the current standard nomenclature of bacterial taxonomy or, due to low resolution of the method, not identified at the genus level. Bagge-Ravn and others (2003) reported a relative prevalence of *Neisseriaceae* of 7% to 10% in 3 out of 4 seafood producing plants (Table 2); however, because the bacteria were not identified to the genus level, this result is difficult to compare with other studies.

Gram-positive bacteria

As stated above, Gram-positive bacteria are outnumbered by Gram-negatives in many food processing plants. The prevalence of Gram-positives seems to be higher in dairies and in the meat industry than in fish processing plants (Table 2 and Figure 1).

Lactic acid bacteria. LAB are isolated from many types of food processing plants, with the highest prevalence in dairies (Table 2 and Figure 1). Many different genera have been reported from surfaces, such as *Streptococcus, Leuconostoc, Lactobacillus, Lactococcus, Enterococcus,* and *Aerococcus*. *Leuconostoc* spp. have been shown to persist in a sausage producing plant (Padilla-Frausto and others 2015). LAB are used as starter cultures in food fermentation, such as in the production of cheeses and fermented sausages, and they are in such cases introduced to the processing environment in high numbers. Otherwise, LAB may originate from a large variety of sources, as they are abundant in environments with a rich nutrient supply, including decomposing plant material, vegetables, sourdough, beverages, water, juices, sewage, and cavities (such as the mouth, genitals, and the intestinal and respiratory tracts) of humans and animals (König and Fröhlich 2009). Many LAB have the ability to grow at low temperatures (Axelsson 2004; Table 3), which may be advantageous in many processing plants. LAB are, in general, relatively tolerant to drying and salt. Many genera grow at 6% NaCl, although the halophilic *Tetragenococcus* grows at 20% NaCl (Von Wright and Axelsson 2012). *Aerococcus* spp.

dominated on surfaces in a meat abattoir and had higher tolerance to air-drying on stainless steel (70% RH, 12 °C) than isolates from other types of bacteria isolated from the same abattoir (Møretrø and others 2013).

Staphylococcus. *Staphylococcus (S.)* is one of the most common Gram-positive genera found in food production environments. The presence of both *Staphylococcus aureus* and coagulase-negative staphylococci (CNS) has been reported, with CNS dominating in most studies (Sundheim and others 1992; Schlegelova and others 2010). Staphylococci may be introduced from raw materials or from personnel, as the bacteria are common on the skin and mucus of humans and animals (Götz and others 2006). Staphylococci are resistant to desiccation and can survive for long periods on dry surfaces and at high salt concentrations (Baird-Parker 2000; Kramer and others 2006; Møretrø and others 2011; Table 3). For example, among 16 isolates from different genera from a meat abattoir, 2 isolates of a *Staphylococcus* sp. were among the most tolerant to air-drying, with a reduction of only 1 to 2 log after 14 d at 12 °C and 70% RH on stainless steel (Møretrø and others 2013). In 2 feed processing plants, with very dry processing environments, *Staphylococcus* was the dominant bacterial genus (Habimana and others 2010b). The biofilm-producing ability of staphylococci may contribute to persistence in the food processing environment as it does in clinical environments (Møretrø and others 2003; Rode and others 2007). We found that food isolates representing several species of *Staphylococcus* were able to form similar amounts of biofilm as the strong biofilm formers of clinical origin *Staphylococcus aureus* and *S. epidermidis*, both of which are known to cause severe human infections due to their biofilm formation (Møretrø and others 2003). Although staphylococci in the planktonic state are generally sensitive to user concentrations of disinfectants, biofilm growth can protect them against sanitation. For example, food-associated staphylococci in a biofilm may survive user concentrations of QACs (Fagerlund and others 2016). Furthermore, comparisons of the resistance of biofilm-associated and suspended bacteria have indicated that the staphylococcal biofilm matrix provides a more effective protective barrier against chlorine than a matrix produced by *Pseudomonas* (Langsrud and others 2006). As staphylococci cannot grow at low temperatures, they may be outcompeted by psychrotrophic Gram-negative bacteria in humid, cold conditions. Their main competitive advantage is most likely their survival on dry or salt surfaces.

Bacillus. *Bacillus* spp. are present in raw milk and in natural environments, such as in soil (Granum and Baird-Parker 2000; Ledenbach and Marshall 2009), and can therefore be introduced into the food processing environment relatively frequently. *Bacillus* spp., including the food pathogen *B. cereus,* are often present in dairies and in the meat industry where heat treatment and disinfection normally will reduce other types of bacteria to low numbers in many areas (Svensson and others 1999; Granum and Baird-Parker 2000). *Bacillus* spp. in their spore form are resistant to environmental stresses, such as heat treatment, drying, and disinfection (Table 3). *Bacillus* spores have a decimal reduction (*D*) value at 100 °C of 0.4 to 3.5 min in various foodstuffs and can survive pasteurization and most heating regimes used in food processing (Soni and others 2016). *Bacillus cereus* has been reported to persist in a dairy plant (Svensson and others 1999) and can adhere to surfaces as spores or vegetative cells. Over time, they develop biofilms, thus avoiding removal by mechanical forces such as fluid flow inside tubes, and brushing, and water pressure during cleaning (Marchand and others 2012). In addition, *Bacillus* spp. are frequently found within multispecies biofilms (Faille and others 2014). The spore coat protects *Bacillus* cells against the lethal activity of several biocides, including those commonly used in the food industry (McDonnell and Russell 1999). *Paenibacillus* and *Geobacillus* are other spore-forming genera reported on surfaces in some studies (Liu and others 2013; Schirmer and others 2013; Mertz and others 2014). Although less studied, one can assume that they, like *Bacillus*, are also highly resistant in their spore form.

Other Gram-positive bacteria. Other types of gram-positive bacteria have been isolated from food production environments, but fewer data are available regarding the characteristics relevant for growth and survival in food production environments, likely because such bacteria are recognized as less important for food safety and quality than *Staphylococcus*, *Bacillus,* and LAB. Among other Gram-positive bacteria, coryneform bacteria, as defined by Funke and others (1997), including genera such as *Corynebacterium*, *Brevibacterium*, *Microbacterium,* and *Rothia*, have been reported in several processing plants in high numbers. Their sources of contamination are usually soil, animals, or humans (Mettler and Carpentier 1998; Guδbjornsdottir and others 2005; Marouani-Gadri and others 2009; Schirmer and others 2013). There are only very few studies on the characteristics of coryneform bacteria related to growth and survival in food processing environments; however, coryneform bacteria are usually halotolerant (Mounier and others 2007). *Micrococcus* spp. dominated in a fish processing plant (Guδbjornsdottir and others 2005) and were among the dominant bacteria in a meat processing plant (Marouani-Gadri and others 2009). *Micrococcus* spp. are, similar to their *Staphylococcus* spp. relatives, tolerant to low-water conditions and grow at high salt concentrations, but they may grow at lower temperatures than *Staphylococcus* spp. (Robinson and Gibbons 1952; Vivier and others 1994). The closely related *Kocuria* spp. were frequently isolated in small scale cheese producing plants (Schirmer and others 2013) and have been reported in other studies (Mettler and Carpentier 1998; Stellato and others 2015; Møretrø and others 2016). *Kocuria* spp. have been shown to be tolerant to chlorine in biofilms (Leriche and others 2003) and to air-drying on stainless steel (Møretrø and others 2013). *Brochothrix* spp. have been reported in both meat and fish processing environments (Langsrud and others 2016; Stellato and others 2016). Limited information is available on characteristics relevant to food processing environments; however, *Brochothrix* spp. grow at temperatures as low as 1 °C and have relatively complex growth requirements (Sneath and Jones 1976; Casaburi and others 2015).

Yeasts and molds

In most studies, bacteria are reported as the dominant microorganisms. Some studies have focused entirely on bacteria and do not mention eukaryotic microorganisms. The novel identification approaches based on 16S rDNA sequencing are specific for the domain *Bacteria*. However, when the cultivation-based methodology is able to identify microorganisms from both *Eukarya* and *Bacteria,* bacteria seem to dominate in most production environments. An exception is very dry production environments, as in pastry and dry herring production, where yeasts were the dominating microorganisms (Mettler and Carpentier 1998; Bagge-Ravn and others 2003; Minervini and others 2015; Table 2). In production environments where eukaryotic microorganisms play an active role in the production process (such as breweries, wine production, and production of certain cheeses), yeast and molds may be present in high numbers (Bokulich and others 2012, 2013; Bokulich and Mills 2013; Stellato and others 2015; Calasso and others 2016).

Implications of Residential Bacteria

Residential bacteria are normally present in the food processing environment. However, as the vast majority of them are nonpathogenic, does their presence matter? Do the residential bacteria have any negative or positive effects on food quality or food safety?

Food Quality

The sensory quality and shelf-life of many food products are restricted by bacterial growth and spoilage. To cause food spoilage, a microorganism must be able to grow and form spoilage products and compete with other microorganisms under the food-specific conditions within the shelf-life of the product. Here, pH, water activity, the presence of preservatives, and storage conditions (temperature, packaging atmosphere) are important factors (Sperber and Doyle 2009). The great composition and storage variation among foods results in different spoilage bacteriota for different types of food products.

Bacteria that spoil food products may originate as unavoidable contaminants of raw materials in the primary production that are not eliminated or removed during processing. The microbial quality and shelf-life will then mostly be dependent on whether the food composition and storage conditions allow growth. This situation can be the case for food with little processing, such as raw meats, milk, fish, and fresh produce. The microbial quality and shelf-life may also be dependent on microorganisms contaminating food later in the chain (Cousin 1982). This is most obvious for thermally processed foods (pasteurized milk, cold cuts, and so on), where most bacteria from the raw materials are eliminated, and the spoilage bacteriota consists of bacteria transferred from the environment (equipment and machines, air, people) after heat treatment. In these cases, both contamination from the environment and the food composition and storage conditions will determine the shelf-life. Table 4 provides an overview of important food spoilage bacteria that may restrict the sensory quality of food and that are commonly found in food processing environments. Below we discuss the influence of the major types of residential bacteria in the food industry on food quality.

Gram-negative bacteria

Pseudomonas. In addition to being the dominant bacterial genus in food processing environments, *Pseudomonas* is also the most important genus for spoilage of food stored aerobically at low temperatures (Ternstrøm and others 1993; Shah 1994; Gram and Huss 2000; Ledenbach and Marshall 2009; Iulietto and others 2015; Table 4). The spoilage potential of *Pseudomonas* spp. varies, but in general, the members of the genus produce extracellular enzymes in large amounts and degrade foods, resulting in off-flavors and off-tasting foods (Dogan and Boor 2003; Iulietto and others 2015).

Ralyea and others (1998) showed that *Pseudomonas* spp. could recontaminate milk post-pasteurization and that the likely source was *Pseudomonas* spp. persisting in filling nozzles. Spoilage of milk is related to protein degradation, which results in bitterness, or lipid degradation, which causes a soapy or rancid flavor. Cleto and others (2012) characterized the bacteriota after sanitation of milk processing equipment and reported that *Pseudomonas* spp. were dominant in number and were also the most abundant protease producers among the residential bacteria. The degradation of nutrients by bacteria is not unexpected, but the finding still underlines the importance of the residential bacteriota as a source of spoilage organisms.

The role of contact surfaces in spoilage may be obvious for unpacked heat-treated products, but in the production of raw products, it can be difficult to determine whether spoilage organisms growing on the final product primarily originate directly from the raw materials or from the production environment. There is a general opinion that the hygienic level in the production of raw food is less important for the contamination of food, as a relatively high number of potential spoilage organisms are already present on the raw materials. There is also a lack of studies documenting any quantitative relationship between the contributions from raw materials and the environment. Recently, we found similar types of *Pseudomonas* in salmon-processing plants and in prepared raw salmon fillets, indicating that the fillets are cross-contaminated during processing. This was supported by the findings that industrially processed fillets contained higher levels of *Pseudomonas* spp. than fillets processed hygienically outside processing plants (Møretrø and others 2016).

Enterobacteriaceae. *Enterobacteriaceae* are commonly found in processing environments and are recognized as spoilage organisms in many types of food (Sperber and Doyle 2009). *Enterobacteriaceae* can spoil dairy products by reducing the diacetyl content of buttermilk and sour cream and by gas formation in cheeses (Ledenbach and Marshall 2009). *Serratia* spp. are commonly found in food production environments, (Table 2; Cleto and others 2012), and 60% of the residential *Serratia* from a milk-processing plant produced high levels of proteinase, which could contribute to milk spoilage. *Enterobacteriaceae* have occasionally been reported to spoil modified-atmosphere-packed (MAP) and vacuum-packed meats (Cerveny and others 2009). *Serratia marcescens* produces the red pigment prodigiosin and may produce red spots on products such as meat and bread (Cook and Johnson 2009). *Enterobacteriaceae* may also spoil fish, for example, cold smoked salmon (Gram 2009), and vegetables, with the genus *Erwinia* being especially responsible for spoilage of the latter (Barth and others 2009). Storage at elevated temperatures will often lead to spoilage by *Enterobacteriaceae* instead of *Pseudomonas* spp. (Gram 2009).

Acinetobacter. *Acinetobacter* spp., commonly isolated from food production environments, are also frequently found on cold-stored foods and are involved in spoilage, especially of aerobically stored foods (Cerveny and others 2009; Gram 2009; Table 4). Cross-contamination of *Acinetobacter* spp. from mechanical pickers to poultry carcasses has been shown (Hinton and others 2004). Compared to *Pseudomonas* spp., *Acinetobacter* spp. are generally less common in production environments and have less importance as food spoilers.

Other Gram-negative bacteria. *Shewanella* spp. are important spoilage bacteria of fish. *Shewanella* spp. can reduce trimethylamine oxide to the fishy smelling compound trimethylamine (TMA), and most strains also produce H_2S (Gram 2009). Recently, we found indications of the transfer of *Shewanella* spp. from the processing environment to salmon fillets (Møretrø and others 2016). *Shewanella* spp. are sensitive to low pH, which often limits its spoilage potential in many types of meat products. However, an off-odor due to *Shewanella* spp. in high-pH meats has been reported (Edwards and Dainty 1987; Nealson and Scott 2006).

Aeromonas spp. are important spoilage bacteria of fish and produce TMA and H_2S (Gram 2009). *Aeromonas spp.* may also spoil MAP meat (Cerveny and others 2009) and eggs (Shebuski and Freier 2009). Hinton and others (2004) showed transfer of *Aeromonas* spp. by mechanical pickers onto poultry due to cross contamination.

Psychrobacter spp. may spoil fish and they have been shown to produce a rancid odor in salted cod (Bjørkevoll and others 2003); they may also spoil poultry stored aerobically in the refrigerator (Cerveny and others 2009).

Gram-positive bacteria

Lactic acid bacteria. LAB are important spoilers of foods, especially food stored cold and packed under a vacuum or modified atmosphere (Doulgeraki and others 2012; Iulietto and others 2015). Thermally processed meats often contain high numbers of LAB, and the processing environment is an important source of these bacteria in the finished product. LAB may spoil food by souring, H_2S production, slime formation, and gas formation, causing blown packages (Ledenbach and Marshall 2009; Iulietto and others 2015). However, certain LAB may have a positive effect on food and are used in fermentations, often deliberately added to food as a starter culture, as in the production of cheeses and fermented sausages (Beresford and others 2001). Some types of food production depend on spontaneous fermentation, which may involve microorganisms from the production environment. In such cases, the microorganisms from the processing environment are seen as beneficial for the product. An example is the production of some cheeses using wooden vats, where LAB are the dominant bacteria (Licitra and others 2007; Didienne and others 2012). In cases dependent on the production environment as the source of microorganisms to carry out spontaneous fermentation, the sanitation is often less strict compared to other types of food production, as elimination of the beneficial bacteria is unwanted.

Staphylococcus. *Staphylococcus* spp., although abundant in many food processing plants, are not recognized as important food spoilage bacteria; however, they are often prevalent in fresh foods and in salted/cured foods. *Staphylococcus* spp. are used as starter cultures in the production of fermented sausages (*S. xylosus*; Cerveny and others 2009) and certain cheeses (*S. carnosus, S. equorum, S. xylosus*; Bockelmann 2010).

Bacillus. *Bacillus* spp. are important spoilers of pasteurized milk and may also spoil other types of food, such as bread, due to production of extracellular enzymes (Pepe and others 2003; Ledenbach and Marshall 2009). The major sources of *Bacillus* spp. in pasteurized milk are raw milk, but *Bacillus* spp. from post-pasteurization equipment may also contaminate milk (Svensson and others 1999; Ledenbach and Marshall 2009). *Bacillus* spp. grow slower than psychrotrophic Gram-negative bacteria at temperatures below 10 °C; thus, raw milk is normally dominated by Gram-negatives at such temperatures, but *Bacillus* spp. may dominate when the milk is stored above 10 °C (Samarzija and others 2012). Svensson and others (1999) reported persistence of *B. cereus* in a dairy; however, because these strains were mesophilic, they had no influence on the quality of refrigerated milk.

Other Gram-positive bacteria. *Brochothrix* spp. may spoil meat and fish products as well as cheeses and are especially known for spoilage of vacuum-packed and MAP foods (Cerveny and others 2009). *Brochothrix* spp. are facultative anaerobes that may grow at low temperatures and form spoilage products, such as esters and volatile fatty acids (Casaburi and others 2015). Coryneform bacteria are of relatively minor importance for food spoilage; however, they may have a role in the spoilage of cheeses (Beresford and others 2001; Sperber and Doyle 2009). *Microbacterium* spp. and *Arthrobacter* spp. are used as starter cultures in the production of some surface-ripened cheeses, where they contribute to texture and the aroma, by producing aromatic sulfur compounds and through their enzymatic activity, and to color development due to their yellow/beige pigmentation (Bockelmann 2010). Psychrotrophic *Micrococcus* spp. are abundant in refrigerated milk and may have a role in spoilage (Ledenbach and Marshall 2009). *Micrococcus* spp. and *Kocuria* spp. are used as starter cultures for improving the color and flavor of fermented sausages (Tremonte and others 2007).

Common spoilage bacteria that are not residential

Some bacteria that are important food spoilers are not commonly isolated from the food processing environment. One example is *Photobacterium* spp., which is a major spoilage organism, especially in MAP products (Gram 2009). In a study of salmon processing, *Photobacterium* spp. were not detected in 97 samples from a processing environment, contrary to the other spoilage bacteria, *Pseudomonas* spp. and *Shewanella* spp., which were frequently isolated from the processing environment (Møretrø and others 2016).

Food Safety

The food pathogen *Listeria monocytogenes* is a residential bacterium in many types of food industries. However, *L. monocytogenes* is generally outnumbered by residential nonpathogenic bacteria and is therefore not the focus of this review. However, interactions with other residential bacteria *and L. monocytogenes* are described below. For further information about the persistence of *L. monocytogenes* in the food industry, readers are referred to other review articles (Møretrø and Langsrud 2004; Carpentier and Cerf 2011; Ferreira and others 2014).

Bacillus cereus may produce different types of toxins and cause disease due to preformed toxins in food (emetic type) or intestinal infection (diarrheal type), and it is frequently found in food and in food processing environments, especially dairies (Granum and Baird-Parker 2000). *B. cereus* from the processing environment can contaminate food, but the most likely source of *B. cereus* in food is raw materials. *B. cereus* survives heat treatment and other stress factors in the processing environment due to its formation of spores and its adherence to surfaces. In the United States, most outbreaks are caused by rice, meat or poultry dishes, and time and temperature abuse is linked to most outbreaks. Outbreaks caused by cross-contamination are less common (Bennett and others 2013). It has been proposed that strains from the *B. cereus* group that are able to grow at low temperatures belong to the new species *B. weihenstephanensis*; this species is commonly regarded as nonpathogenic, but this is disputed, as psychrotolerant toxin-producing strains have been described (Stenfors and others 2002).

S. aureus can form toxins in foods and cause foodborne intoxications. *S. aureus* may be isolated from equipment, especially in dairies (Schlegelova and others 2010) and may be transferred to food by cross-contamination. In a study of foodborne outbreaks caused by *S. aureus* in the United States, contamination from raw materials and food handlers was listed as the most common source of *S. aureus*, although cross-contamination due to insufficient cleaning of processing equipment and storage in a contaminated environment have also been reported (Bennett and others 2013). Recently, there has been an increased awareness of the presence of livestock-associated (LA) MRSA. Although LA-MRSA may be transferred from animals to farmers or others in close contact with the animals (Kadariya and others 2014), the direct transfer of MRSA to humans via food has not been proven.

Although some of the frequently isolated residential bacteria of food processing plants may be regarded as opportunistic

pathogens, such as *Klebsiella* (Struve and Krogfelt 2004) and *Acinetobacter* (Towner 2009), food is not regarded as a common route for infection in humans by such opportunistic pathogens.

The majority of bacteria in the food production environment are nonpathogenic. That means that if pathogens occasionally are present, they will face an environment dominated by other bacteria. These bacteria may affect the fate of pathogens in the processing environment and subsequently the risk of pathogen transfer to foods. However, in most instances, the bacterial level after sanitation is very low. The bacteria will then be situated as single cells or in clusters of small numbers of cells. Interactions between bacteria are probably not very important for the fate of the pathogens in such cases. Nevertheless, in some niches where the sanitation is less intensive (as non-food contact surfaces) and/or less effective (as worn equipment, inside machines), biofilms with large clusters of cells may develop in which interactions between cells may be important for growth, development, and survival. Bacteria in biofilms are protected against stress factors, such as cleaning and disinfection, drying, and low-nutrient environments. Interactions between the most common residential bacteria in the food industry and the most important food pathogenic bacteria in laboratory studies have been reported, with both positive and negative effects of the background bacteriota on the fate of pathogens. The effects seem to be species/strain specific, but variations among the cultivation/biofilm methods used may also influence the results. Here, we provide some examples of the effect of the residential bacteria on *Listeria monocytogenes*, which may persist on surfaces in food processing plants and contaminate food during production (Møretrø and Langsrud 2004). *Pseudomonas putida* (Hassan and others 2004), *Pseudomonas* spp. (Guδbjornsdottir and others 2005), and *Flavobacterium* (Bremer and others 2001) have been reported to enhance adhesion/biofilm formation of *L. monocytogenes*, although *P. fluorescens* (Daneshvar Alavi and Truelstrup Hansen 2013), *P. fragi* (Norwood and Gilmour 2001), *Serratia* spp. (Daneshvar Alavi and Truelstrup Hansen 2013), *Aeromonas* spp. (Daneshvar Alavi and Truelstrup Hansen 2013), and staphylococci (Leriche and Carpentier 2000) are described to have a negative effect on *L. monocytogenes* in biofilms. Carpentier and Chassaing (2004) showed that out of 29 bacteria from processing plants, 15, 10, and 4 strains had no effect, negative effects, and positive effects, respectively, on counts of *L. monocytogene*s in the biofilm. *Ralstonia* spp., frequently isolated from fresh-cut produce processing plants (Liu and others 2013), were shown to coaggregate with *L. monocytogenes* (Guo and others 2016) and to increase the incorporation of *L. monocytogenes* and other foodborne pathogens into biofilms (Liu and others 2016a). Together, these studies show that other bacteria may affect *L. monocytogenes* in laboratory studies. In addition, studies from the food industry have shown that *L. monocytogenes* is commonly isolated together with residential bacterial genera/groups, such as *Pseudomonas* spp., *Enterobacteriaceae*, *Aeromonas* spp., LAB, *Bacillus* spp., and *Psychrobacter* spp. (Fox and others 2014; Langsrud and others 2016; Liu and others 2016b). Thus, *L. monocytogenes* is present in the same niches as these bacteria in the food industry, and interactions may be possible. There are also indications that *Listeria*-positive and *Listeria*-negative floor drains contain different bacteriota, which may indicate that other bacteria promote/inhibit *Listeria* (Fox and others 2014). The addition of *Lactococcus lactis* and *Enterococcus durans*, both strains shown to inhibit *L. monocytogenes* in laboratory studies, to floor drains in a poultry processing plant eliminated *L. monocytogenes* in 5 out of 6 drains (Zhao and others 2013). For information regarding interactions of other pathogenic bacteria with bacteria from genera commonly present among the residential bacteriota, readers are referred to the review by Giaouris and others (2015).

Spread of Antibiotic Resistance

Resistance to antibiotics is increasing globally and is regarded as one of the largest threats to human health in the future. The role of the food chain in the transmission of antibiotic resistance from animals and environments to humans is gaining increasing interest, and the topic has been thoroughly discussed in a number of reviews and reports (Safe Food 2010; Capita and Alonso-Calleja 2013; Verraes and others 2013; Friedman 2015; Allen and others 2016). Bacteria with high intrinsic or acquired resistance (such as mutations, conjugative plasmids, or transposons with antibiotic resistance genes) may be introduced to food processing environments through raw materials and people. It has been speculated that resistant strains may have selective advantages in the food processing environment and that the transmission of antibiotic determinants between bacteria is enhanced in these environments. A residential bacteriota could therefore act as a source of either resistant bacteria or genes encoding antibiotic resistance. There are, however, very few studies on residential bacteria that support these speculations. In an evaluation of the antimicrobial resistance of enterococci isolated from raw milk, cleaned production equipment and fresh and aged cheeses, a higher frequency of resistance was observed in isolates from raw milk and the equipment than products (Didienne and others 2012; Gaglio and others 2016). The authors proposed that antibiotic resistance may provide some bacteria a competitive advantage in the production environment, although sensitive bacteria have a selective advantage during further processing, but they did not suggest the advantages that could be relevant. The study was too limited to draw conclusions about the occurrence of resistance on the equipment or raw materials. Therefore, there is no reason to believe that the environmental contamination reflected anything other than the antibiotic resistance profile of the bacteria introduced through raw materials. However, the study showed that antibiotic-resistant enterococci may be a part of the residential bacteriota in cheese production environments, though they may not necessarily be selected for.

Co- and cross-resistance between antibacterial agents

Disinfection processes aim to eliminate bacteria introduced to the food production process, including those resistant to antibiotics. If disinfectant resistance is a pre-requisite for survival in the food production environment over time, an association between resistance to disinfectants and antibiotics could lead to a selective recruitment of antibiotic-resistant bacteria to the residential bacteriota. Among clinical isolates, a correlation between resistance to disinfectants and antibiotics has been reported in some studies (Sidhu and others 2002; Buffet-Bataillon and others 2011), explained by co-resistance between antibiotics and QACs (an active ingredient in many disinfectants). There is, as far as we know, only one published example of co-resistance from food production, where an *S. epidermidis* isolate from poultry processing harbored a multi-resistance plasmid (Sidhu and others 2001). In addition to co-resistance, laboratory studies have demonstrated that the same molecular mechanisms may render bacteria resistant to both antibiotics and disinfectants. For example, a number of multidrug efflux pumps mediate cross-resistance. Most of them are intrinsically present in some bacteria, but one exception is the plasmid-borne OqxAB, which confers resistance to antibiotics, disinfectants, and detergents (Hansen and others 2007). The gene *oqxAB* is chromosomally borne and has an unknown function in

Klebsiella pneumoniae, but it provides multidrug resistance when expressed in plasmids and can easily transfer between different members of *Enterobacteriaceae*. In conclusion, though a number of studies have focused on resistance mechanisms, a causal link or a correlation between resistance to disinfectants and antibiotics outside the clinical setting has not been documented (Gantzhom and others 2014; Schwaiger and others 2014; Wales and Davies 2015). It is possible that exposure to both antibiotics and disinfectants is necessary to promote co-resistance in most practical situations. Another factor to consider is that the level of resistance to biocidal agents mentioned above is often too low for survival after exposure to in-use concentrations of disinfectants. Therefore, a practical significance of co- and cross-resistance in the recruitment of antibiotic-resistant strains to the residential bacteriota is hardly plausible.

Transmission of antimicrobial resistance

The specific disinfectant resistance mechanisms discussed above are not necessarily needed to form a residential bacteriota, as it can develop in niches not reached by a daily sanitation program or in production environments without regular cleaning and disinfection. Biofilms have been termed as niches for genetic transfer between bacteria (Molin and Tolker-Nielsen 2003; Krol and others 2011), and this could indicate that a residential biofilm could act as an important reservoir, multiplier, and disseminator of antibiotic-resistance genes. The scientific evidence for this suggestion is, however, scarce. Conjugation in biofilms (including colonies on agar as a biofilm model) has been reported in a number of studies (Hausner and Wuertz 1999; Fox and others 2011; Krol and others 2011). However, in the majority of studies, conjugation processes are limited and suppressed even in model biofilms using promiscuous plasmids and optimal donor and recipients paired in relatively high concentrations, and the causes of this phenomenon have not yet been determined. Similarly, DNA transformation in biofilms requires relatively high cell numbers, matching of donor-recipient pairs, and conditions supporting competence (Molin and Tolker-Nielsen 2003). Although the scientific literature provides valuable insight into mechanisms that promote and suppress the transfer of resistance genes, the likelihood of such processes occurring in the food industry is scarce. It is most likely that the requirements for efficient conjugation (physical contact between potential donors and compatible recipients in environments allowing conjugation such as high nutrient availability, oxygen; Christensen and others 1996; Krol and others 2011; Seoane and others 2011; Reisner and others 2012; Freese and others 2014) will rarely be met in food production environments. In summary, transmission of DNA between bacteria in biofilms has been demonstrated in laboratory studies. Still, based on the present knowledge, there is little scientific support for the idea that biofilms in food production environments significantly contribute to the spread of resistance in the food chain.

Processing (Biofouling/Corrosion)

In addition to the role of residential bacteria as microbial contaminants of food, they may influence food production processes by deteriorating surface materials or by producing biofouling. Fouling and deterioration of process surfaces are costly due to increased energy consumption (compensating for reduced flow or heat transfer), the need for more heavy cleaning processes, and extended maintenance costs (Goode and others 2013).

Reduced fluid flow caused by biofilm formation inside tubing (Mittelman 1998) or membrane filters (Anand and others 2014) has been reported. In one study, *Klebsiella* spp. and *Bacillus* spp. were found to dominate on membranes used for filtration in dairies (Tang and others 2009). It is known that thermophilic bacteria may grow on heat exchangers and reduce their effect. However, we are not aware of studies describing this in the food industry, although adherence of bacteria and spores to heat exchangers has been reported (Marchand and others 2012). Apparently, food components fouling heat exchangers cause more problems than microbial fouling in dairies (de Jong 1997). Overall, the most costly fouling types in the context of food processing are not microbial but complex solid-like cohesive foulants produced during thermal processes, such as milk pasteurization or brewery wort evaporation (Goode and others 2013).

Corrosion is a challenge in many processing plants. Corroded materials may be less hygienic, as they may be difficult to clean. In addition, pores and irregularities in the material surface may act as niches for bacterial growth and survival. As an example of the latter, corrosion has been shown to enhance the adherence of the pathogen *L. monocytogenes* to stainless steel (Mai and others 2006). There is limited information about bacterial corrosion in food processing environments or from bacteria associated with such environments. Sulfide-producing *Shewanella putrefaciens* are reported to cause corrosion (Dawood and Brozel 1998), but their role in corrosion in a practical setting has yet to be demonstrated. Bacteria are likely neglected in the literature as a cause of corrosion in the food processing industry, because, in most cases, other explanatory factors are more plausible, such as corrosive compounds in sanitation agents (acids, chlorine) and food itself (acids, salts) combined with high temperatures or poor design (Jellesen and others 2006).

In summary, it is more the exception than the rule that the microbiota in the food processing environment disturbs product and water flows, reduces heat exchange processes, and causes corrosion, and most of the literature indicates that chemical and physical factors are more important.

Conclusions

Several methodological factors must be considered to isolate and identify the residential bacteriota from food processing environments. The residential bacteriota is complex; however, some bacteria are common in different types of food industries. *Pseudomonas* spp. dominate on surfaces after sanitation in many types of food industries, especially in humid conditions, such as in the fish industry. Other Gram-negative bacteria, such as *Enterobacteriaceae* and *Acinetobacter* spp., are also common in the food industry. Gram-positive bacteria are most prevalent in dairies and at dry conditions. Bacteria from surfaces in the food industry may be transferred to food and can have both positive and negative effects on food quality. Furthermore, residential bacteria in the food industry may affect the growth and survival of pathogens in processing environments.

With increased knowledge about the composition of the residential bacteriota, and also the implications of these bacteria for food safety, quality, processing, and so on, it is logical to ask whether a specific bacteriota is optimal and if resources should be used to attempt to keep or change the residential bacteriota in food processing environments. For many food processes the use of strict hygienic measures are needed to ensure control of pathogens if/when these are introduced, and such measures will also usually keep the residential bacteriota at a low level. Thus, if changes in control routines such as cleaning and disinfection are made in order to increase the level or change the composition of the

residential bacteriota, the possible increased food safety risk must be contained. Also if bacteria are introduced to exclude pathogens from the processing environment, they should not have an adverse effect on food quality. If there is a buildup of certain unwanted residential bacteria, for example, food spoilage bacteria, they may be targeted by, for example, improved cleaning and disinfection, alternating between different disinfectants, drying up the production environment, where the choice of measure used will depend on characteristics of the site and of the targeted bacteria. Although industrial actors will normally practice regular cleaning and disinfection, certain actors, like artisanal food producers, may occasionally have a less strict hygienic regime, claiming that this will keep their beneficial houseflora which will have a positive effect on the product and maybe also protecting against pathogens. The scientific support for these practices is, however, scarce. A less risky approach to change the bacteriota is to add bacteria considered beneficial to the processing environments. The bacterial species, subspecies, or strain must be carefully chosen, because even closely related bacteria may act differently. For example, some strains *of Pseudomonas* inhibit biofilm formation by *L. monocytogenes*, while other strains may have a promoting effect. Also, as mentioned above, unwanted effects, such as on final product quality must still be considered. Taken together a qualitative control or change of the residential bacteria is challenging, as both potential food safety and food quality issues must be considered.

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Conflicts of Interest

The authors declare no conflicts of interest.

Authors' Contributions

Trond Møretrø and Solveig Langsrud together planned and wrote the manuscript.

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