



Foodborne pathogens in the plastisphere: Can microplastics in the food chain threaten microbial food safety?

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ABSTRACT

Background: Microplastics (MPs) contaminate the global marine and terrestrial ecosystems. This environmental contamination can enter the food chain, with MPs found in drinking water, fishery products and other food categories. Consequently, ingestion is considered the main route of human exposure to MPs. Concerns exist on the potential of MPs to act as vectors for pathogenic bacteria, possibly threatening microbial food safety.

Scope and approach: Starting from the current evidence on foodborne pathogens associated with MPs, we review the state of knowledge on the putative role of MPs in enhancing harmful bacterial traits and transporting them to humans. Finally, we focus on the simultaneous uptake of MPs and pathogens in the human gut.

Key findings and conclusions: Overall, we identify major knowledge gaps, both on the mechanisms and the possible health outcomes. The scarce and inconclusive results regarding the effect of MPs on microbial virulence and evolution, together with the insufficient knowledge about the attachment of microbial toxins to MPs, highlight the need for further studies. We conclude that biofilm-coated MPs in foodstuffs may pose several risks to food safety, but further research will be essential to determine the extent of their effect on human health.

1. Introduction

Since the beginning of this century, there is an increased awareness that millimeter-sized or smaller plastic particles, often referred to as microplastics (MPs), are ubiquitous in the environment (Thompson et al., 2004). Improper waste disposal and limited recycling cause tremendous masses of plastic litter to enter seas, lakes, rivers, coastal areas, and landfill sites worldwide (Carson et al., 2013). Subsequently, multiple degradation pathways (e.g. biodegradation, photooxidation, mechanical abrasion) break them down (Galloway et al., 2017) into MPs and nanoplastics (NPs). While the upper limit for MPs is conventionally fixed at 5000 μm , the MP-NP boundary is still object of debate: sometimes the threshold is set at 1 μm (Gigault et al., 2018), while others set it at 0.1 μm (Chain (CONTAM), 2016). In this review, we adopt the former scale for NPs (1–1000 nm) and MPs (1–5000 μm), bearing in mind that the MPs above 10 μm of size are not likely to be transported through an intact intestinal barrier.

As MPs are ubiquitous in aquatic, terrestrial, and atmospheric environments, humans are frequently exposed to them (Gasperi et al.,

2018). An average intake ranging between 39000 and 52000 MP particles/person/year was estimated from food alone (Cox et al., 2019). Direct evidence for human ingestion of MPs has been provided by their detection in human feces (Zhang et al., 2020). Indeed, MP contamination can occur at potentially any stage of the food chain. For example, fish and other seafood often take up MPs both directly, mistaking them for food (Cole et al., 2013), and indirectly via trophic exchange (X. Sun et al., 2019). In particular, some filter feeders including edible shellfish and crustaceans are often eaten without the removal of the digestive tract, where MPs mostly accumulate (Browne et al., 2008). In their scientific advice on contaminants in the food chain and undesirable substances, the CONTAM Panel Members of the European Food Safety Authority reported that consumption of a 225g portion of Chinese mussels would expose the consumers to nearly 900 MP particles (Chain (CONTAM), 2016). Recurrent detection of MPs into feedstuff such as fish meal expands the issue to aquaculture animals (Q. Wang et al., 2022) and even, beyond the ocean borders, to intensive animal farms raising poultry and pigs (Bouwmeester et al., 2015). Regarding NPs, promising analytical methods for detection in the food chain are being developed,

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but are still not sufficient to confirm and quantify their presence (Chain (CONTAM), 2016; Correia & Loeschner, 2018). Based on this information, it becomes crucial to set maximum permissible levels for MPs in seafood and assess the effect of their ingestion on human health to protect the public.

Besides seafood, other food categories, such as honey, sugar and beer, are also found to contain MPs (Liebezeit & Liebezeit, 2014). Moreover, external sources such as food packages can offer an additional route for MP pollution. Estimates indicate that eating regularly from take away plastic containers can result in the ingestion of up to 203 MPs/person/week (Du et al., 2020), while drinking only bottled water is equivalent to ingesting an extra 90000 MPs/person/year (Cox et al., 2019). In fact, previous studies had already proven human exposure to MPs through plastic packages directly in contact with food, for example plastic tea bags and water bottles (Hernandez et al., 2019; Winkler et al., 2019). Additionally, with sea salt sometimes being heavily contaminated with MPs, a much wider array of canned and salt-conserved foods is jeopardized (Iñiguez et al., 2017). Finally, given the voluntary addition of MPs into cosmetics as scrubbing agents or facilitating the delivery of active ingredients (Boucher & Friot, 2017), several personal care products such as toothpastes, make up products and creams, can serve as an additional source of MP ingestion and exposure.

The consequences of MP ingestion on human health are still largely unknown (Catarino et al., 2021). Laboratory studies have observed direct toxic effects upon exposure to MPs at often unrealistically high doses. Additionally, co-exposure to other biotic and abiotic substances attached to MPs may result in indirect toxicity (Sheng et al., 2021). For example, multiple bacterial species including potential human pathogens are attached on the surface of MPs (Nosyk et al., 2008). Hence, recent literature suggests that MP vectors could enhance the movement of food pathogens towards the food chain and possibly result in human exposure to foodborne contaminants (Crawford & Quinn, 2017). The hazards posed by this indirect route of MP toxicity are currently uncertain.

The consumption of food products contaminated with microbial foodborne pathogens can result in a foodborne disease (Adley & Ryan, 2016). Depending on the specific cause of the illness, which can be identified either in the pathogens themselves or in their toxins, foodborne diseases are respectively classified into food infections and food poisonings. Hence, foodborne pathogens can also be divided accordingly into food infectants and food intoxicants (Bari & Yeasmin, 2018). While both categories encompass a broad spectrum of viruses, eukaryotic parasites, and a variety of bacteria (Tauxe, 2002), we keep our focus on bacterial species in the plastsphere.

While most of the information available on the behavior of microbiome-loaded MPs can be found in the field of environmental sciences, the association of foodborne pathogens and secreted toxins with MPs is still scarcely documented. Yet, the biofilm-forming behavior of foodborne pathogens is well reported in the fields of health sciences and food processing and safety (Galié et al., 2018).

In this review, we explore the risks posed by MP contamination for microbial food safety. To this end, we present an overview of the biofilm-forming properties of hazardous bacteria on MPs, with a particular focus on human foodborne pathogens. Next, we briefly analyze the impact of MPs (and to some extent NPs) on bacterial growth, toxin production, virulence, antibiotic resistance and evolution. Finally, we highlight the potential transport routes of these MPs-associated foodborne pathogens and hazardous toxins through the gastrointestinal tract and their potential health outcomes. Overall, we pinpoint the current knowledge gaps and critically assess in which situations the ingestion of food-related MPs might have negative health impacts.

2. Attachment of microbial food pathogens to MPs

2.1. Biofilm formation on the surface of MPs

MPs generally tend to be quickly covered with an organic layer of proteins and other biomolecules, which is known as protein corona in biological fluids, or ecocorona in freshwater and seawater (Galloway et al., 2017). More specifically, it is possible to make a further distinction between the inner tightly adhered, irreversibly fixed “hard corona” and the outer loosely attached, exchangeable “soft corona” (Milani et al., 2012). This highly dense nutritious layer, in turn, determines the further interaction of MPs with living cells and even whole tissues, for instance attracting bacteria in aquatic environments. Consequently, bacteria also attach on the MP surface, leading to the formation of a biofilm (Nosyk et al., 2008) (Fig. 1). Biofilms are stratified multicomponent structures consisting mainly of water (95%), followed by the extracellular polymeric matter, and the actual microorganisms. This biofilm ecosystem forming on plastic debris is often referred to as the “plastsphere” (Zettler et al., 2013). Bacteria in a biofilm are embedded into a self-secreted exopolymeric substance (EPS), which can have various functions and compositions. For instance, in the EPS of the food pathogen *Salmonella enterica*, cellulose and O-antigens have been found to be crucial components for respectively facilitating attachment/biofilm initiation and ensuring biofilm persistence, specifically on plastic surfaces (Maruzani et al., 2019). The specific microbial composition of the plastsphere depends on many factors, such as geographical location, season, and polymer type (Oberbeckmann et al., 2014). However, recent literature suggests that a core microbiome may be shared by different plastsphere communities. According to (Di Pippo et al., 2020), MPs from distinct freshwater samples are all characterized by the presence of typical biofilm forming taxa, e.g. *Sphingorhabdus*, *Sphingomonas*, *Rhodobacter*, *Aquabacterium* and *Acidovorax* genera. The genus *Vibrio*, which comprises of several fish and human pathogens, was also found to be an early MP colonizer by (Kesy et al., 2021). These species act as pioneers by initiating the MP colonization and facilitating the subsequent attachment of other microbial species.

2.2. Pathogenic bacteria in the MP plastsphere: overt and potential foodborne pathogens

The presence of potentially harmful microbes such as the dinoflagellates *Ostreopsis* sp., *Coolia* sp., and *Alexandrium taylori* on Mediterranean plastic debris was first observed by (Masó et al., 2003). Since then, more and more studies report of various pathogenic species present on both larger marine litter and MP particles. Since MPs are widely found in the food chain, they might act as vectors for contamination from human pathogens. For a more detailed explanation of the MP plastsphere, and argumentation of this vector hypothesis, the reader may also refer to (Bowley et al., 2021), clarifying the link between oceanic MP pollution and marine pathogens. Moreover, the vector hypothesis is supported by the recent finding of increased amounts of *Vibrio* spp. in the intestines of fish fed with MPs (Jang et al., 2022). Foodborne diseases result from the consumption of food products contaminated with microbial pathogens (Adley & Ryan, 2016). As such, the plastsphere could promote foodborne diseases outbreaks, and hence represent a threat to microbial food safety. While a broad spectrum of viruses, parasites, and a variety of bacteria can cause foodborne illnesses (Adley & Ryan, 2016), we focus on bacterial species in the plastsphere.

3. Reports of bacterial food infectants on MPs

A food infection is a type of foodborne disease directly resulting from the ingestion of pathogenic microorganisms (food infectants) with food. The *Campylobacter* genus is the first cause of foodborne infections in Europe, with undercooked poultry being its main reservoir (Gölz et al., 2018). Upon ingestion, they colonize the human intestine and disrupt

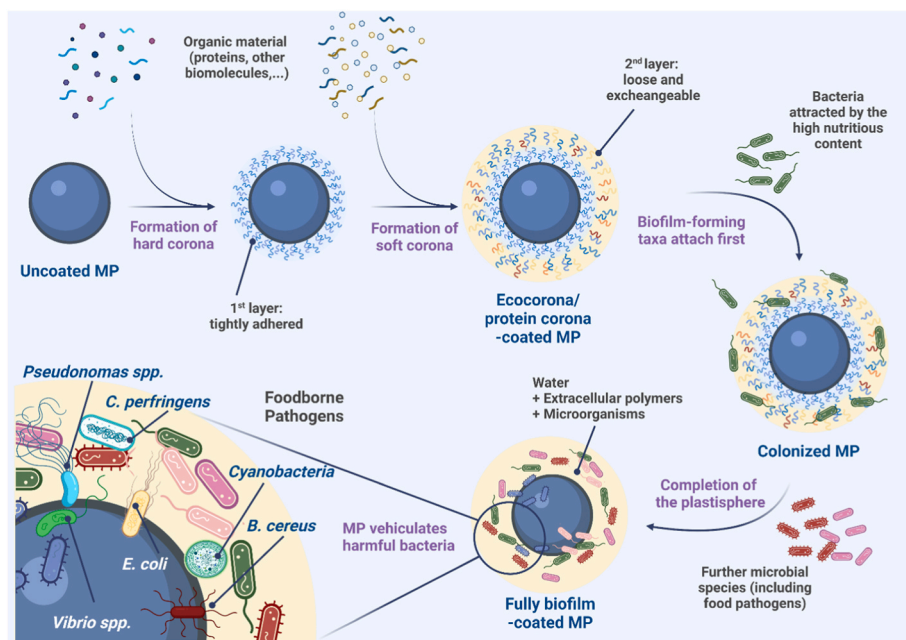


Fig. 1. Step-by-step formation of the plastisphere on the surface of microplastics (MPs) in aquatic environment. First, MPs are coated by a protein-layer, known as ecocorona or protein corona. Later, bacteria gradually colonize the MP-surface. Eventually, the plastisphere encompasses many diverse microbial species, including bacterial foodborne pathogens such as *Pseudomonas*, *Vibrio*, *Cyanobacteria*, *E. coli*, *C. perfringens*, *B. cereus*. Created with BioRender.com. (Color required in print). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the commensal microbiota, causing a range of symptoms (Bari & Yeasmin, 2018). For example, some *Vibrio* spp. and *Shewanella* spp. species cause septicemia or diarrhea in humans after ingestion of contaminated seafood/water (Bowley et al., 2021; Janda, 2014). Pathogenic strains of *E. coli* carry multiple virulence genes that can cause intestinal and extraintestinal disorders, in the most severe cases escalating to deadly hemolytic uremic syndrome (Kaper et al., 2004).

Various studies report the presence of bacterial food infectants on a range of MP particles. Besides being a key player in early MP colonization, *Vibrio* spp. is frequently found to be a major component of the plastisphere community (Bowley et al., 2021). In particular, *V. parahaemolyticus*, *V. cholerae*, and *V. vulnificus*, have been found to reside on the surface of predominantly Polypropylene (PP) and Polyethylene (PE) particles by (Kirstein et al., 2016). Specimens of *Aeromonas salmonicida*, a fish pathogen which can occasionally harm humans upon consumption of infected fish, were also found on predominantly PE particles (Viršek et al., 2017). *Pseudomonas* spp. and *Campylobacter* spp. were found to prevail on predominantly PE MPs by (Jiang et al., 2018) and (Kelly et al., 2020) respectively. Besides the widely known pathogenicity of *Campylobacter* spp. (Gözl et al., 2018), *P. aeruginosa* may also play an underrecognized role in food quality and safety (Xu et al., 2019).

4. Reports of bacterial food intoxicants on MPs

Food intoxication is another type of foodborne disease, caused by poisoning from biological toxins or chemical agents (Bari & Yeasmin, 2018). Because of the requirement for outgrowth (10^5 CFU/g and higher) and the necessity of compliance to the environmental conditions for toxin production, only highly contaminated foods are likely to cause disease. *Clostridium perfringens* is able to produce enterotoxin during sporulation in the human gastrointestinal tract (Murphy et al., 2020; Rajkovic, 2007). Alongside, *Staphylococcus aureus* enterotoxins (SE) can induce nausea, vomiting and diarrhea (Rajkovic, 2012). *Bacillus cereus* is another major food intoxicant, due to its ability to produce both diarrheal toxins and an emetic one, cereulide (CER) (Jovanovic et al., 2021). Less common examples include photosynthetic microorganisms such as cyanobacteria and dinoflagellates, producing paralytic shellfish toxins (PSTs), which can accumulate in edible shellfish and threaten the food safety for the consumers (Ogata et al., 2009). Compared to food infectants, fewer food intoxicants have also been detected on the surface of

MPs. However, evidence for the possible presence of pathogenic *C. perfringens* on MPs has been recently provided (Murphy et al., 2020). Moreover, two common *Synechococcus elongatus* strains, often used as model cyanobacterial species, have been shown to form aggregates with 0.1 μm and 10 μm PS beads (de Oliveira et al., 2020). The question of whether attachment to MPs can alter the toxin production of certain microorganisms will be addressed in the next section.

5. Reports of other common food pathogens on larger plastic debris

Multiple hazards associated with the presence of particular pathogens in the MP plastisphere are briefly summarized in Table 1. Additionally, the finding of some of the most common food pathogens on larger plastic debris may also be of concern. For example, *B. cereus* was isolated from plastic litter deriving from the food packaging sector (Schmid et al., 2021). Moreover, biofilm formation on plastic litter suggests for the possibility to also attach to MPs, which offer them an additional route of contamination. For example, pathogenic *Listeria*

Table 1

A summary of the relevant foodborne pathogens identified on MP biofilms. PE = polyethylene, PP = polypropylene, PS = polystyrene/ = non specified, + = other polymers also present in minor fractions.

Type of pathogen	Bacterial species	Plastic type	Size range	Reference
Food infectants	<i>Vibrio parahaemolyticus</i>	PE, PP +	0.5–5 mm	Kirstein et al. (2016)
	<i>Vibrio cholerae</i>	PE, PP +	0.5–5 mm	Kirstein et al. (2016)
	<i>Vibrio vulnificus</i>	PE, PP +	0.5–5 mm	Kirstein et al. (2016)
	<i>Aeromonas salmonicida</i>	PE +	<5 mm	Viršek et al., 2017
	<i>Campylobacter</i> spp.	PE +	0.330–2 mm 0.3–4.75 mm	Kelly et al. (2020)
Food intoxicants	<i>Pseudomonas (aeruginosa)</i>	PE, PP, PS	/	Jiang et al. (2018)
	<i>Clostridium perfringens</i>	PE	1 mm	Murphy et al. (2020)

monocytogenes occasionally causes listeriosis outbreaks mostly due to biofilm formation in food-processing plants (Nowak et al., 2021), and has already been identified within the plastisphere bacterial community on PE debris (Yang et al., 2020). Pathogenic *E. coli* was also found on PP, PE and PET debris (Silva et al., 2019). This confirmed previous pathogenicity suspects raised from the finding of unspecified *E. coli* strains, together with *B. cereus*, on larger marine litter from Oostende, Zeebrugge and Nieuwpoort (Belgium) (Van Der Meulen et al., 2014). Moreover, *Shewanella* spp. was found to be able to colonize polyvinyl chloride (PVC) (W. Li et al., 2019). Similarly, *Aeromonas hydrophyla*, together with *Citrobacter freundii*, can readily attach and form biofilms on PE and PP surfaces (Thomas et al., 2020). Cyanobacteria have also been identified as one of the most abundant phyla on PE biofilms regardless of age (Schlundt et al., 2020). A range of dinoflagellates, including potentially pathogenic *Alexandrium* spp., have been detected in the plastisphere by DNA sequencing (Zettler et al., 2013). For most of these species, the possibility to be dispersed into food products via MP-colonization deserves further clarification.

5.1. Antibiotic resistant foodborne pathogens in the plastisphere

Antibiotic resistance in bacteria, including foodborne pathogens, poses a major global health threat by rendering antibiotics ineffective for treating infections. The food industry further contributes to the problem by applying antimicrobial compounds in animal farming and aquaculture (Capita & Alonso-Calleja, 2013). Since many common food pathogens such as *Campylobacter*, *Salmonella*, *Yersinia*, *E. coli* and *Listeria* are zoonotic agents, meaning they spread from food-producing animals to humans (Foodborne zoonotic diseases, 2022), the large scale overuse of antibiotics on farmed fish and livestock accelerates the development of antibiotic-resistant strains of bacterial food pathogens (Robinson et al., 2017).

At the same time, the selective enrichment of antibiotic resistance genes in the plastisphere compared to the planktonic community has been reported on various MP types, as comprehensively reviewed by (Y. Liu, Qiu, et al., 2021). Multiple antibiotic resistant pathogenic bacteria were found to be more abundant in the plastisphere, and holding more antibiotic resistance genes compared to planktonic bacteria in the aquatic environment (Zhang et al., 2020). In comparison to biofilms on natural particles such as fine sands, establishment and proliferation of bacteria carrying antibiotic resistance genes and pathogens was found to be specifically promoted in the plastisphere (Pham et al., 2021). Although other studies suggest that an enriched resistome can emerge in any biofilm (e.g. rock or leaf particles), MPs still register a distinct and broader spectrum of antibiotic resistance genes (X. Wu et al., 2019). While the exact development process of the antibiotic resistome in the plastisphere is largely unknown (Yang et al., 2020), provided some useful insights into the temporal dynamics of the phenomenon. For example, they highlighted the key role of the class 1 integron-integrase genes (*intI1*), persistently detected in the plastisphere, in favouring the transmission of antibiotic resistance genes among Gram-negative bacteria.

The perfect combination between the selective pressure provided by antibiotic usage in aquaculture and mariculture, together with the enrichment of antibiotic resistance genes in the plastisphere, makes MPs in aquatic environments the ideal hotspots for the emergence and spread of pathogenic antibiotic resistant bacteria. Marine MPs were found to harbour opportunistic human pathogens, including the already mentioned *A. salmonicida*, carrying new antibiotic resistance genes variants (Radisic et al., 2020). Similarly, antibiotic resistance was reported on MP-colonizing communities of the pathogenic *V. vulnificus*, *V. parahaemolyticus*, and *V. cholerae* (Laverty et al., 2020). Future analyses should focus on non-culturable bacteria and determination of antibiotic resistance genes expression levels to enable a more comprehensive view of the phenomenon.

5.2. Influence of the plastisphere on heavy metal cargo of MPs

While attachment to MPs has the potential to impact on microbial food pathogens' circulation, physiology and evolution (see section 3), vice versa bacteria may also play an active role. In fact, presence of a microbial biofilm is unlikely to leave MPs undisturbed. Recent literature accounts biofilm formation as one of the most relevant biological factors in changing the chemical properties of the MP surface (S. Liu, Qiu, et al., 2021). This alteration, in turn, can be responsible for an increased absorption of heavy metals and other pollutants onto the MP surface. For example, some studies report increased heavy metals concentrations in mature biofilms compared to early biofilms on MPs (Qi et al., 2021). Given the documented individual presence of heavy metals and biofilms on the surface of MPs, the possibility of a synergistic interaction between these two carries should not be understated.

5.3. Attachment of microbial toxins to MPs

5.3.1. MPs and biotoxins

Besides pathogenic microorganisms and inorganic pollutants, the association between MPs and common persistent organic pollutants such as polycyclic aromatic hydrocarbons and polychlorinated biphenyls as well as various heavy metals have been well documented in the literature (Verla et al., 2019). The ability of MPs to carry these toxic chemicals is due to their hydrophobic nature and high surface to volume ratio and may result in potentiated toxicity upon co-exposure or sequential exposure. In comparison to the above-mentioned contaminants (polycyclic aromatic hydrocarbons, polychlorinated biphenyls, and heavy metals), less attention was paid to biotoxins, hazardous substances of a biological origin. The possible association of bacterial toxins and cyanotoxins to MPs that contaminate the food chain may also represent an unravelled food safety hazard. Not only bacterial contact with MP and resulting risk of attachment of bacterial toxins, but also co-existence of fungi and their mycotoxins, and MP in soils warrants co-contamination of plant based foods both in pre-harvest and post-harvest phases (Accinelli et al., 2020; J. Zhang et al., 2021). While discussing the links between fungal toxins and MPs goes beyond the scope of this paper, no information is available in literature on attachment of toxins produced by typical bacterial food intoxicants (*Clostridium*, *Bacillus*, *S. aureus*) to MPs.

5.3.2. MPs and cyanotoxins

With the increasing phenomenon of water eutrophication, cyanotoxins are becoming more and more frequent in aquatic environments, with microcystin-LR (MC-LR) being the most notable one both in terms of toxicity and reported occurrence (Buratti et al., 2017). Produced as secondary metabolites by several cyanobacterial species, they can also be found in association with MPs (Huisman et al., 2018). Polystyrene (PS) MPs (>125 µm) are capable of adsorbing microcystin-LR dissolved in water (Pestana et al., 2021). This physical binding between MPs and microcystin-LR can partially explain their co-occurrence at high concentrations in drinking water (Buratti et al., 2017) and in seafood (EFSA Panel on Contaminants in the Food Chain & EFSA, 2016), besides their independent contamination routes. While literature shows the hepatic toxicity of individual exposure to MPs and microcystin-LR (Svirčev et al., 2017), the combined effect of MPs and microcystin-LR co-exposure needs to be investigated. Microcystin-LF, analogue of microcystin-LR with similar toxicity but higher hydrophobicity, also showed clear adsorption on the surface of PS, PVC and PE MPs of various sizes (Pestana et al., 2021). No data on MP absorption is available for other food and environmentally relevant cyanotoxins, e.g. anatoxin-a, saxitoxin (paralytic shellfish toxin), cylindrospermopsin (Miglione et al., 2021).

6. Micro- and nanoplastics can affect bacterial growth, toxin production, virulence and evolution

In addition to selectively enriching pathogenic and antimicrobial resistant microorganisms in the environment, micro- and nanoplastics pollution has also been found to impact on bacterial growth, gene expression (e.g. virulence and toxin production), and morphology (Yokota et al., 2017). Additionally, micro- and nanoplastics pollution may be able to influence evolutionary dynamics in bacteria, potentially promoting the emergence of novel antibiotic resistant bacteria and virulent strains.

6.1. Impact of micro- and nanoplastics on bacterial growth

With the aim of filling the gap of knowledge around the direct effects of MPs on marine bacterial growth (Fernández-Juárez et al., 2021), exposed multiple species to different sizes of MPs ranging between 1 and 120 μm . While cyanobacterial growth was generally enhanced regardless of the particles' size, heterotrophs displayed opposite trends depending on MP dimensions. Although further investigation is needed, disruption of bacterial cell division by the aggregation of small PS particles and the cells could possibly explain these results. Similarly (Yi et al., 2021), found both 0.1 μm and 0.55 μm NPs and 5 μm polystyrene (PS) MPs to inhibit the growth of *E. coli* but promote *B. cereus*. Such Gram-specific or even species-specific responses could be hypothetically linked to varying degrees of adsorption of bacteria to MP surface (Fernández-Juárez et al., 2021), but also vice versa of MPs and NPs to microbial cell wall. In fact, given that the size of most bacteria is between 0.5 and 5 μm , small MPs and NPs can also adhere on bacterial surface. Finally, presence of MPs seems to have a negligible impact on microalgal growth, at least at environmentally relevant concentrations (Sjollema et al., 2016). These results suggest the need to determine the threshold levels of MPs starting from which significant effects can be observed for key microbial populations such as foodborne pathogens.

6.2. Impact of micro- and nanoplastics on bacterial toxin production and virulence

A few studies have shown that micro- and nanoplastics can have a direct impact on the production of some food-contaminating toxins produced by several species of cyanobacteria and dinoflagellates. For instance, the marine dinoflagellate *Alexandrium tamarense* has higher intracellular concentrations of paralytic shellfish toxins when exposed to 0.1 μm polystyrene (PS) nanoplastic particles (NPs) (Q. Liu et al., 2022). Similarly, paralytic shellfish toxin production was increased when the congeneric species *A. pacificum* was exposed to both PS 0.1 μm NPs and 1 μm MP (C. Liu, Qiu, et al., 2021). However, these two studies also reported decreased concentrations of paralytic shellfish toxins respectively upon variation of particle size (exposure to 1 μm MP) and prolonged exposure time. Furthermore, micro- and nanoplastics can directly alter the cyanobacterial production of microcystins, a class of environmental toxins which also play an emerging role as food contaminants due to the increased anthropogenic activities and climate change (Abdallah et al., 2021). Independent studies (X. Wu et al., 2019; Zheng et al., 2021) already found a consistent increase in the intracellular concentration of microcystin-LR in *Microcystis aeruginosa* when exposed to micro- and nanoplastics of various materials, ranging from 50 nm to 3 μm . However, they found contrasting results about the impact of micro- and nanoplastics on extracellular microcystin-LR concentrations. While Wu et al. observed no or negative effects on extracellular microcystin-LR concentrations upon exposure of *M. aeruginosa* to PS micro- and nanoplastics, Zheng et al. reported higher concentrations, which they attributed to micro- and nanoplastics-induced damage to cell membranes and transporter protein upregulation. Overall, while the interaction with micro- and nanoplastics may alter toxin production, the predominant direction of this phenomenon is still unclear. Although

it can be concluded that size and concentration are likely to play a role, the scarcity of available data currently makes it difficult to precisely assess the relevance of micro- and nanoplastics-induced microbial toxin production under environmental conditions for food safety. In addition to this direct impact of micro- and nanoplastics on toxin production, an indirect impact on the virulence of foodborne pathogens can also be expected. Several studies have already indicated that biofilm-associated microorganisms are often physiologically differentiated from their planktonic counterparts, potentially exhibiting an increased virulence. For both *A. hydrophyla* and *C. freundii*, Shiga-like toxin virulence factor (*slt-II*) expression increased more than two-fold when adhered to MPs compared to planktonic cells, with a peak of six-fold upregulation for *C. freundii* on PP (Thomas et al., 2020). When growing in a biofilm, *V. cholera* becomes hyperinfective (Gallego-Hernandez et al., 2020) due to the overexpression of virulence factors such as the toxin-coregulated pilus (required for intestinal colonization) and cholera toxin (responsible for inducing watery diarrhea). Interestingly, removing particles >20 μm from surface waters can drastically reduce cholera incidence, suggesting that particle-associated *V. cholera* encompass an important route for disease transmission (Colwell et al., 2003). These studies indicate that MP contamination in food might indirectly increase the infectivity and virulence of a variety of foodborne pathogens by increasing opportunities for biofilm formation. Furthermore, biofilm formation is also known to enhance environmental survival of food contaminating pathogens when exposed to sanitizing agents (Pan et al., 2006). MP-associated biofilms of food contaminating pathogens might thus also enhance their persistence in food production environments and subsequent transmission into the food chain. Although the dimensions of small MPs and NPs do not allow for microbial cargo, their co-presence in the food via independent routes of contamination is a realistic possibility. From the above-mentioned studies, we cannot exclude that MPs and NPs have the potential to alter virulence and toxin production profiles of foodborne pathogens.

6.3. Impact of MPs on bacterial evolution

The propensity of bacteria to form biofilms on MPs might also promote the emergence of novel virulent and antibiotic-resistant strains. Firstly, the closer physical proximity between bacteria on MPs is likely to facilitate the mobilization of genetic elements (Eckert et al., 2018). Increased horizontal gene transfer of a broad-host range conjugative plasmid carrying antibiotic resistance in the presence of MPs was experimentally confirmed by (Arias-Andres et al., 2018), who found virtually no horizontal gene transfer between *E. coli* and *Pseudomonas* spp. in a planktonic state, opposed to a large number of transconjugants when PS particles were added to the microcosms. Often encoded by mobile genetic elements, antibiotic resistance genes can spread via various horizontal gene transfer mechanisms taking place on MPs (Abe et al., 2020). Therefore, the increase in horizontal gene transfer on MPs, combined with the selective enrichment of antibiotic resistance genes (Y. Sun et al., 2021), is expected to facilitate the evolution of antibiotic resistance on MPs. For example (Santos-Lopez et al., 2019), showed that bacterial lifestyle (biofilm versus planktonic) results in specific resistance mechanisms and fitness level in ciprofloxacin-exposed *Acinetobacter baumannii*. At the same time, virulence evolution of *V. cholera* was also found to be enhanced in MP biofilms, where a ~1000-fold increase in transduction efficiency by the virulence-conferring lysogenic bacteriophage CTXF was observed (Gallego-Hernandez et al., 2020). Although information on the effect of MPs on the emergence of novel virulent and antibiotic-resistant strains is currently limited, the studies mentioned above indicate that these subjects warrant further investigation. This is especially relevant for food contaminating pathogens, where both accessory virulence factors and antibiotic resistance profiles can influence the severity of a foodborne infection.

6.4. Uptake of biofilm-loaded MPs in the human intestinal tract and associated health effects

The documented presence of MPs in human tissues indicates that they can pass the epithelial barriers including the intestinal one (Ibrahim et al., 2021). Although both *in vitro* and animal studies have confirmed the MPs uptake by gut epithelium, evidence in humans is still scarce. In contrast, the interactions of foodborne pathogens with the human intestinal tract are well documented. Gate keeper for unwanted substances, the intestinal barrier is mainly composed of a thick mucus layer loaded with antimicrobial compounds, microvilli-containing enterocytes for improved absorption, dynamic junction proteins between cells to regulate paracellular transport, and immune cells. Many pathogens have developed highly specialized tools to evade this host-protective environment. Therefore, although the transport routes of MPs are well characterized and considered to be limited to paracellular transport and transcytosis (Bredeck et al., 2022), the combination with live and even dead biofilms may increase their bioavailability and worsen their overall health impact. As recapitulated in Fig. 2, in this section we focus on the interactions of foodborne pathogenic species and toxins found in the plastsphere with the intestinal barrier and their potential effect on MP transport.

6.4.1. MPs and foodborne pathogens influence mucin secretion

Mucin secretion by the intestinal epithelium is one of the driving forces to eliminate undesired microbes, both chemically and mechanically. Animal studies showed that the permeability for MPs through mucus decreases with MP size and is impaired in double-layered intestinal sections (B. Paul et al., 2020). Yet, studies on mice also show that mucus thickness and mucin-producing gene expression is decreased upon MP intake (Choi et al., 2021), which may potentially lead to higher permeability for both particles and pathogens. In parallel, some pathogenic *E. coli* strains and *V. cholerae* secrete mucin-degrading compounds (Kaper et al., 2004). Moreover, presence of advanced cellular structures such as flagella in food pathogens like *Campylobacter* sp. and *V. vulnificus*, and pili in *Aeromonas* sp. and *E. coli*, also help to penetrate the mucin layers. Taken together all these aspects, we may hypothesize that the protective function of mucins may be impaired by MPs loaded with live pathogenic biofilms.

6.4.2. MPs may facilitate intestinal adhesion of foodborne pathogens

Various human cell types can sense the presence of microbes by using multiple pattern recognition receptors (PRR), which are proteins, typically expressed in epithelial and immune cells, that sense and respond to a diverse set of molecules from pathogenic microbes and host cell damaging signals. Amongst the PRRs, Toll-like receptors (TLR) and nucleotide oligomerization domain-like receptors (NLR) specifically bind to lipopolysaccharides (LPS), also called endotoxins. These bind to PRRs thereby generating immune responses, and are typically present in the cell wall of Gram-negative bacteria including *E. coli*, *V. cholerae* and *C. jejuni* (Baker-Austin et al., 2018; Callahan et al., 2021; Kaper et al., 2004). Hence, PRRs play a key role in pathogen recognition and the induction of innate effectors and inflammation (Wells et al., 2011). Ingestion of MPs has been shown to upregulate the expression of TLR4 and other pro-inflammatory genes in the gut of mice (B. Li et al., 2020). Whether this upregulation is the result of a direct interaction of the MPs with the intestinal cells, or indirectly caused by shifts in microbial composition (e.g. increased prevalence of *Staphylococcus* sp.), is still to be clarified. Besides (LPS mediated) binding to PRRs, pathogens also use a diverse set of adhesins to colonize the intestinal epithelial cells. Morphological structures such as pili or fimbriae, expressed in for instance *V. cholerae* and *E. coli* (Baker-Austin et al., 2018; Kaper et al., 2004), help in the adhesion process and increase toxin production. Some pathogenic *E. coli* strains produce intimin, which binds to a specific receptor and hence causes inflammatory responses (Kaper et al., 2004). Given the possible upregulation of PRRs upon MP consumption, and the possible enhanced recognition of MPs loaded with live or even dead pathogens by these receptors, we may suggest a more hazardous effect on intestinal colonization by (foodborne) pathogens.

6.4.3. Foodborne pathogens possibly facilitate paracellular transport of MPs

In contrast to nanoplastics (NPs), which may be taken up inside the cell by transcellular transport, the predominant route for MPs is paracellular transport through tight and adherent junctions between epithelial cells (Fournier et al., 2021). Some pathogens such as *V. cholerae* and *C. jejuni* are able to increase paracellular transport by secreting proteases and altering the expression levels of junction proteins (Baker-Austin et al., 2018; Callahan et al., 2021). Similarly, pathogenic *E. coli* injects different effectors in the cell cytoplasm, which also

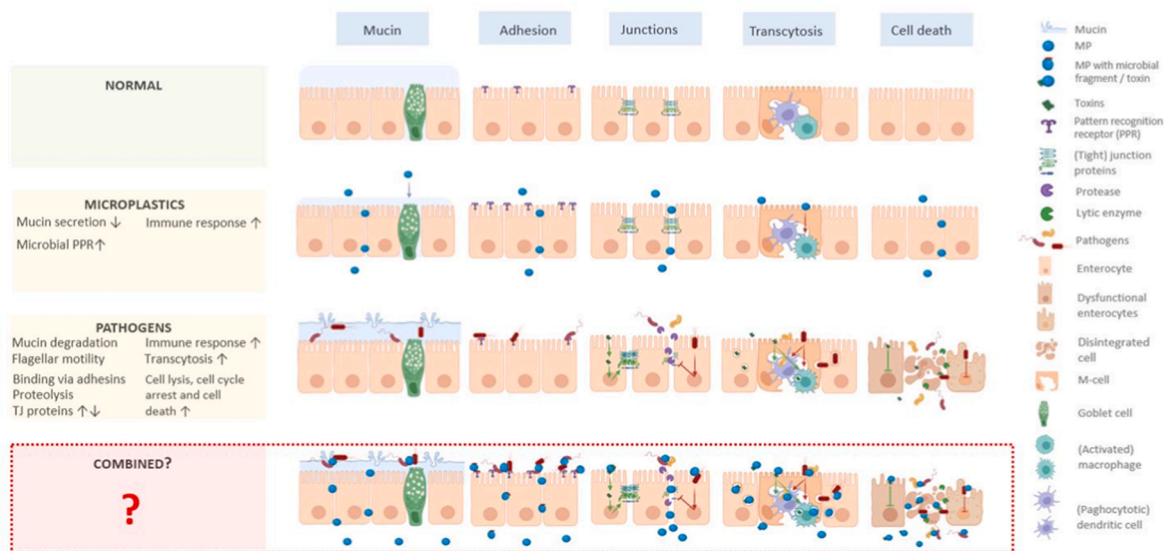


Fig. 2. Presence of pathogens or microplastics (MPs) affects the physiology of the human intestinal barrier on many levels (mucin secretion, adhesion, paracellular transport, transcytosis, cell death). The impact of biofilm-loaded MPs, combining pathogens and MPs, is still uncertain. Created with BioRender.com. (Color required in print). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

impairs tight junction stability. Besides live pathogens, some secreted bacterial toxins such as cereulide (CER) from *B. cereus* can influence tight junction protein expression, although the final direction of their impact is not yet completely understood, as contrasting results of both increased and decreased expressions have been collected hitherto (X. Wang et al., 2019). Finally, microcystins from cyanobacteria can affect the barrier integrity of intestinal epithelium by decreasing trans-epithelial electrical resistance, which is the measurement of the resistance of an epithelial monolayer, and expressing occludin enzyme and zonula occludens (ZO)-1 protein (J.-X. Wu et al., 2018). Overall, we may suggest that a live pathogenic biofilm on MPs may possibly facilitate paracellular transport of MPs, but the effect of a toxin-loaded MP particle is still more difficult to predict.

6.4.4. Foodborne pathogens possibly trigger transcytosis of MPs

The Peyer's patches are aggregated lymphoid nodules in the small intestine, consisting of follicle-associated epithelium in which highly specialized immune cells reside in close contact with each other. Transcytosis of particles (0.1–10 µm) from small intestinal epithelium to the lymphoid tissue takes place there, but most MPs are usually too large to undergo this route of uptake (Bredeck et al., 2022). However, MPs can possibly trigger an immune response, together with the adhered microbial community and their toxins (Campanale et al., 2020). Peyer's patches are also hotspots for phagocytosis of pathogens, usually with the aim of eliminating them, as described for *C. jejuni* in dendritic cells (Ribet & Cossart, 2015). Yet, a pathogen may evade such destruction, and hence promote intracellular growth, by stimulating endocytosis in non-phagocytic cell types of the intestinal epithelium through specific mechanisms. This is followed by a cascade of immune reactions and eventually leads to cell death (Callahan et al., 2021). Endocytosis is also the main transport route of cholera toxin from *V. cholerae* (Baker-Austin et al., 2018) by GM1-ganglioside receptor binding. Overall, we may therefore suggest that, compared to uncoated MPs only transported by phagocytic cells, biofilm- and/or toxin coated MPs are more likely to be transported by endocytosis in other cell types because of the epithelial recognition of a larger diversity of adhered microbial surface factors, and hence become more bioavailable for the host.

6.4.5. Foodborne pathogens may facilitate MP intrusion in lower cell layers

Although the intestinal cell toxicity caused by MPs (in contrast to NPs) is usually limited, food pathogen ingestion frequently results in epithelial lesions. While *V. vulnificus* causes tissue damage by secretion of strong collagenases, metalloproteinases and phospholipases, *V. parahaemolyticus* secretes thermostable direct haemolysin (Tdh) and Tdh-related haemolysin (Baker-Austin et al., 2018). Additionally, *A. salmonicida* can damage cells by means of serine proteases, elastases, lipases and enolases, as well as pore-forming toxins (Martins et al., 2002). As reviewed by (Kaper et al., 2004), enteropathogenic *E. coli* have a whole wide set of strain-specific tools which interfere with basic cell functions. *C. jejuni* injects invasive antigens and produces cytolethal distending toxins to induce cell cycle effects, apoptosis and inflammatory responses (Callahan et al., 2021). Furthermore, *B. cereus* (Jovanovic et al., 2021), *S. aureus* (Rajkovic, 2012) and *C. perfringens* secrete pore-forming toxins which cause apoptosis, necrosis and necroptosis by targeting the cell membrane (Navarro et al., 2018). To conclude, we may suggest that, if microbial biofilms are formed on MPs, their cytotoxic effects may also contribute to the higher exposure of the host to these MPs and create persistent hotspots for immune responses in the inner layers of the intestine and even throughout the whole body.

7. Conclusions

The finding of human foodborne pathogens in the plastosphere, together with the ability of MPs to adsorb microbial toxins present in the environment and in food, pose major concerns for MP-contamination in the food chain. While robust and accurate analytical methods to detect

MPs in complex food matrices are indispensable to determine the exposure rate in humans, more realistic data supporting the hypothesis that MPs can mediate the entry of pathogens in food are needed. Therefore, additional studies similar to (Jang et al., 2022), for example on different types of foods, should be performed in order to provide more robust evidence for this hypothesis. Moreover, the relevancy of the putative effect of micro- and nanoplastics on various aspects of bacterial physiology (growth, toxin production, virulence) for food safety should be assessed. For example, challenge tests with MP-associated food intoxicants can be carried out to assess the effect of MPs on toxin production at the moment of contamination in a particular food matrix. Concerning the selective promotion, as well as the evolution, of virulent and antibiotic resistant strains, it should be clarified whether these phenomena are a prerogative of the plastosphere only, or else if they can equivalently take place on other types of biofilms (e.g. on natural particles found in the environment, such as sand or chitin from crustaceans' exoskeleton). Related to this aspect, a better understanding of both the temporal (Yang et al., 2020) and the evolutionary dynamics, e.g. the co-selection of antibiotic resistance with metal-resistance (Imran et al., 2019), of the antibiotic resistome is crucial.

The speculations that have been proposed for the gastrointestinal uptake of biofilm-loaded MPs and associated health effects should be tested with appropriate experiments. Besides the demonstrated direct toxicity of micro- and nanoplastics at unrealistically high doses, bioassays should be designed at host-relevant concentrations. Moreover, focusing on the numerous putative pathways proposed for indirect toxicity would enable to fill the knowledge gaps around the currently uncertain hazards for human health. Overall, the risks deriving from ingestion of MP-associated foodborne pathogens for humans should be carefully assessed by carrying out detailed investigations on each individual aspect (mucin secretion, adhesion, paracellular transport, transcytosis, cell death). In addition, inter-individual variability in host-associated microbiome and health status may strongly influence the outcome of such studies. Finally, starting from the evident differences between MPs and NPs, we acknowledge that, regardless of the investigated aspect, distinct characteristics of micro- and nanoplastics can be responsible for not only variations but even opposite trends. Therefore, different aspects related to MPs such as size, polymer type, hydrophobicity, and shape should always be considered transversally.

Declarations of competing interest

None.

Data availability

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

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