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Micro-by-micro interactions: how microorganisms influence the fate of marine microplastics

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Current evidence

Micro-by-micro interactions: how microorganisms influence the fate of marine microplastics

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Author contribution statement

JAC-C, KLR, EG and NRP conceived of the manuscript structure and JAC-C and KLR led the writing effort. All authors contributed to the manuscript writing. There are no conflicts of interest.

SCIENTIFIC SIGNIFICANCE STATEMENT:

Due to its small particle size and wide distribution, microplastics can incorporate into the biogeochemical pathways and food webs of the marine water column and sediment. Our understanding of microplastics in these pathways is still nascent, but of fundamental importance to estimate plastic´s environmental fate and potential remediation. A massive research effort across fields in the last years has brought our understanding further, but there is a strong need to streamline and converge findings. Here, we discuss evidence from controlled laboratory experiments and field studies. Particularly focus is on new methods and analytical approaches to understand the two-way interactions between microorgansims and plastics. We review the stat-of-the art on microplastic-microorganisms interactions to determine the fate of plastic litter in marine environments.

ABSTRACT:

Microorganisms drive the biogeochemical cycles that link abiotic and biotic processes in the aqueous environment and are intricately associated with plastic debris. The detection of microplastics in water and sediment introduces new concerns as small particle size allows for yet unconsidered pathways for plastics in the food web and element cycles. In this review, we present current knowledge of microbe-plastic interactions and summarize the potential impact of biogeochemical processes on plastic distribution, cycling, transport, and sedimentation. We explore how microbe-plastic interactions influence the exposure of consumers to plastics and plastic degradation products. Key methods used to elucidate biofilm development, microbial biodegradation, and plastic detection in the aqueous environment are discussed. Finally, we comment on potential future questions and research directions needed to further define the role of microorganisms in the environmental fate of microplastics.

Keywords: microorganisms, microplastics, biogeochemical cycles, plastic degradation, food webs

1. The microbial *plastisphere*: a new ecological niche

Though plastic debris has been reported in the marine environment as early as the 1970s, in the past decade, microplastic has come into focus as a major environmental pollutant (Carpenter and Smith 1972; Thompson et al. 2004). The discovery of widespread microplastic pollution generates further questions related to the potential sources, impact, transport, and fate of this contaminant. Furthermore, the environmental fate of plastic litter and how microorganisms interact with it, remains undefined. Microorganisms play an integral part in aquatic biogeochemical cycles, and are found associated with plastic debris both in water and in sediment (Jørgensen 1995; Zettler et al. 2013).

The interaction between plastic and microorganisms changes the plastic characteristics over time and defines how and why cells attach to the surface. Previous reviews succinctly describe the complex relationship between plastic particles and microorganism attachment, discussing the factors that influence community development of biofilm and changes in the physical characteristics of plastic particles (Kale et al. 2015; Oberbeckmann et al. 2015; Rummel et al. 2017). In the current review, we therefore expand our discussion to how microbe-plastic interactions are woven into the aquatic biogeochemical tapestry (Fig.1). We focus primarily on the marine environment here, but introduce some comparisons to recent work carried out in freshwater settings to elucidate how plastic influences and is influenced by biogeochemical pathways at the water surface, in the water column, and in the sediment.

The term *plastisphere*, coined by Linda Amaral-Zettler, Tracy Mincer and Erik Zettler, describes the new ecological niche created by the introduction of plastic litter to the marine environment (Zettler et al. 2013) (Fig. 2a). The community composition of epiplastic microorganisms is found to be diverse and distinct from the surrounding planktonic communities (Zettler et al. 2013; Harrison et al. 2014). Organisms such as diatoms, coccolithophores, bryozoans, barnacles, dinoflagellates, isopods, as well as cyanobacteria, heterotrophic bacteria, and fungi have been catalogued (Carpenter and Smith, 1972; Reisser et al. 2014; Table 1, 2). The composition and development of biofilm on plastics is influenced by a number of factors, including environmental conditions, sample location, microplastic size, plastic surface properties, and substrate type (Fig. 2b,c) (Cardinale et al. 2002; Zettler et al. 2013; Oberbeckmann et al. 2014; Eich et al. 2015; Ogonowski et al. 2018). The microorganisms of the *plastisphere* are phenotypically diverse, represent a broad range of preferred environmental conditions, and include aerobes, anaerobes, motile and non-motile organisms, as well as extremophiles. Recent field and *in situ* studies (Fig. 3) on microbial communities associated with plastic in water and sediment show both diversity among and similarities between distinct *plastisphere* communities (Tables 1, 2). In the marine environment, *Prochlorococcus* sp. and *Synechococcus* sp. are prevalent, along with oil degraders (i.e., *Colwellia* sp.), and potential pathogenic species, like *Mycobacterium* (Table 1). A freshwater study of an urban river likewise revealed high diversity within the community, but similarities to the marine epiplastic community in that species of *Saprospiraceae*, *Comamondaceae* and *Chitinophagaceae* have been found in both environments (Table 1) (McCormick et al. 2014). The diverse microbial composition of marine biofilms leads to inter-species interactions that can affect plastic fate in the water column and sediment. Inter-species interactions such as competition, viral infections, and horizontal gene transfer, influence structure, stability and behavior of the biofilms and can influence plastic colonization and biodegradation (Pollet et al. 2018). Ecological pressures such as predation, may also impact the epiplastic community composition. Indeed, a recent study suggests that symbiotic rather than competitive interspecies interactions might evolve (Pollet et al. 2018).

Both micro-and macro-organisms colonize plastic debris in classical ecological succession from biofilms composed of microorganisms, to complex biofouling communities consisting also of aquatic plants and macrofauna (Fig. 2) (Salta et al. 2013; Harrison et al. 2014; Bryant et al. 2016). With smaller particles on the nm-cm scale, biofilm builds on the plastic particles, embeds in the surface (i.e., accessing holes and crevices) and captures other floating plastic or organic particles in extracellular polymeric substances (EPS). In this manner, cell-plastic aggregates form that can function as hot spots for biogeochemical cycling during their residence in the water column and as settled material (Fig. 2c) (Decho and Gutierrez 2017; Arias-Andres et al. 2018; Porter et al. 2018). Many *in situ* and field studies of biofilm growth on plastic focus on larger plastic pieces, usually on the cm scale. These larger plastic particles allow for the colonization of communities formed of microorganisms and larger organisms, like barnacles and mussels (Fig. 2c, Table 2).

Communities on plastic debris in surface water differ from that of the surrounding seawater, one example being the photosynthetic filamentous cyanobacteria, i.e., *Phormidium* and *Rivularia,* that dominate plastics, but are not abundant in the seawater (Zettler et al. 2013). These differences between biofouling and ambient communities may be explained by the longevity and relative mobility of plastics in the water column. Once in the sediment, these long-lived plastic particles become immobile, yet an investigation of biofilm structure and composition on plastics buried in estuary marine sediments also reported differences between the communities on the plastic versus those found in the surrounding sediment (Harrison et al. 2014). These observations open new questions as to whether epiplastic communities specifically build on plastics or whether they simply select a surface-attached lifestyle. Whereas the communities differ between biofilms and the ambient environment, the biofilms between different substrates do not differ. Oberbeckmann et al. 2016 analyzed the composition of microbial and eukaryotic colonizers on Polyethylene terephthalate (PET) plastic bottles and control glass slides placed in buoys in the North Sea. Between communities, they found significant seasonal and locational differences, but no differences within PET and glass communities, suggesting that the microbes forming biofilms on plastic are not substrate selective. A biogeography study comparing plastic-associated communities from the North Atlantic and North Pacific subtropical gyres also supports this, showing that microbial communities clustered more strongly by geography than by plastic type (Amaral-Zettler et al. 2015). A key issue in understanding the plastisphere, therefore, is whether and how the natural theory postulated by Baas-Becking (1934) “everything is everywhere, but the environment selects” applies to the *plastisphere*. Surrounding environment, i.e., whether a plastic particle is residing in the water column, sediment, coastal or oceanic environment, may select for community composition. As redox environment and microbial community composition are intricately intertwined, it follows that biogeochemical setting, particularly in sediment communities (Thamdrup et al. 1994; Nauendorf et al. 2016), may play a strong role in the structure and dominant metabolic processes in epiplastic communities. Much still needs to be done to understand modes of colonization on plastic, but further investigation focusing on the biogeochemical setting of epiplastic communities would help to address the mechanisms of microbial attachment to polymer surfaces.

2. The biogeochemistry of microbe-plastic interactions

In all aquatic ecosystems, biogeochemical cycling forms the foundation for synthesis and degradation of organic matter (i.e., Thamdrup et al. 1994; Jørgensen 1995). The redox environment influences the dominant microbial communities and key microbial respiratory pathways. The prevalence of plastic debris in all areas of the ocean suggests that some microorganisms may use plastic and its degradation intermediates as a carbon source, substrate or co-substrate, to drive these biogeochemical cycles (Fig 1). Microorganisms may passively attach to plastic, using it primarily for surface colonization. Alternatively, plastic may be utilized by the microorganisms as a substrate. The interaction of microbes and plastic, however, has further impact in water and sediment, where microorganisms associated with plastic debris play an integral role in aquatic biogeochemical cycles and in food webs (Jørgensen 1995; Zettler et al. 2013). Biofilm growth influences the residence time of plastic particles in the photic zone, particle aggregation in the water column, uptake by organisms, vertical and horizontal transport of microorganisms, pollutants, plastic particles and intermediate degradation products in freshwater and marine environments and possibly sedimentation and diagenetic processes effecting plastic fate (Kale et al. 2015; Rummel et al. 2017; Harrison et al. 2018; Michels et al. 2018; Porter et al. 2018). Redox setting therefore becomes a key consideration of which electron acceptors and donors are available for abiotic and biotic reactions with plastic in the water and sediment. Such redox driven constraints may even be one explanation for observations that geographic location influences the microbial community colonizing plastic particles (Amaral-Zettler et al. 2015).

The biodegradation of natural and synthetic polymers transpires via the breakdown of polymers to monomers and, depending on oxygen availability, ultimately leads to the production of water, hydrogen, methane, and carbon dioxide. However, how these processes translate to degradation of plastic in the marine environment is less clear. Compounding this problem, synthetic polymers are notoriously hard to biodegrade (Debroas et al. 2017). Due to this difficulty, individual microbes may not be able to access plastics as a carbon source because they lack a suitable enzymatic pathway, or lack necessary co-substrates, and nutrients. Microbial interactions with natural polymers, like cellulose and chitin (Shah et al. 2008; Zettler et al. 2013) and our understanding of interactions between bacteria, fungal communities and plastic in the terrestrial environment may also help to foresee the pathways of fossil-based polymers in the oceans (Kale et al. 2015). Furthermore, symbiotic relationships between microorganism(s) in biofilms enhance the step-wise breakdown and degradation of synthetic polymers, as seen in laboratory studies and co-cultures (Shah et al. 2008; Yang et al., 2015; Kawai, 2010). In addition to this symbiosis, interactions between abiotic secondary products and microorganisms (i.e., Royer et al. 2018), could further incorporate plastics into biogeochemical cycling over time.

3. Microbe-mediated transport of plastic

When released to aquatic environments, plastic particles lighter than the surrounding media float and are transported by the water. A combination of physio-chemical and biological mechanisms drive the transport of microplastics from surface waters to sediments (Wakeham and McNichol 2014; Taylor et al. 2016; Kaiser et al. 2017; Porter et al. 2018). In coastal regions, plastic particles are prone to high-energy processes, such as waves, tides, and wind, which cause vertical mixing or surface drifting until final deposition in beach sediments (Zhang 2017). Bulk transport of plastics offshore to convergence zones in central gyres, which include wind mixing and density differences in thermohaline gradients affect the concentrations of microplastics in the surface of the water column (Kukulka et al. 2012). Particle settling and velocity are also regulated by plastic debris properties, i.e., density, shape, and dimension (Zhang 2017) and biofilm growth. Environmental factors (e.g., salinity, temperature, oxygen and high nutrient concentrations) will influence microbial growth and may alter plastic density and transport (Oberbeckmann et al. 2018).

Biogeochemical processes related to microbial aggregate transport, degradation, and final burial in the sediment have long been studied in sedimentology, microbial ecology and marine biogeochemistry, but in the context of plastic aggregation, it remains poorly understood (i.e., Summers and Silver 1978;

Ploug et al. 2010; Posth et al. 2014; Kamp et al. 2016; Stief et al. 2016). Like organic or mineral particles, microplastic particles are found in the marine ecosystem as free particles, as homoaggregates consisting purely of plastic (flocs) (Fig. 2b), or as microbe-plastic aggregates (e.g. marine snow and fecal pellets) (Posth et al. 2014; Katija et al. 2017; Jiang et al. 2018; Porter et al. 2018). A variety of factors influence the aggregation of microplastics. Differences in surface charge, as well as collision due to high particle concentration can stimulate particle aggregation (Alimi et al. 2018). Biofilms facilitate aggregate formation by providing a sticky matrix as has been reported for microplastics (Michels et al. 2018). This stickiness, due to exopolymeric substances, and cell-to-cell interactions may explain the increased aggregation and downward transport of plastics (Petrova and Sauer 2012; Michels et al. 2018). Other factors affecting plastic aggregation, such as the influence of particle size, however, remain to be determined. Once formed, aggregates play a strong role in the vertical transport of plastics otherwise anticipated to float at the surface or sink only very slowly (Wakeham and McNichol 2014; Kaiser et al. 2017).

Plastic-associated biofilm, however, is dynamic and will grow, degrade and be fed upon by predators (Harrison et al. 2014; De Tender et al. 2015; Rummel et al. 2017), with further effects on sedimentation rates (Kaiser et al. 2017). Marine microbe-plastic aggregation may influence organic carbon preservation. More than 90% of organic matter in marine sediment is closely associated with mineral surfaces and typically, labile molecules, such as amino acids and simple sugars are shielded from degradation via sorptive protection (Mayer 1993; Keil et al. 1994). These same sorption processes may play a role in the preservation of organic matter associated with plastic. This could have implications not just for the longevity of plastics in the marine environment, but also for carbon transport and burial. In marine sediments, turnover is faster in the oxic layer that extends from millimeters to centimeters below the surface in coastal areas and can reach to at least one meter depth in pelagic sediments (Glud 2008; Fischer et al. 2009). Where pelagic aggregates are buried, organic matter will enter anoxic zones and be decomposed via fermentation, denitrification, sulfate-reduction and methanotropy, yet little is known about how plastic particles are preserved or degraded under anoxic conditions.

4. Plastic degradation by microbial processes

The longevity of plastic is due to its durability, which is one of its celebrated characteristics, but also makes plastic difficult to biodegrade. Chitin and high molecular weight petroleum compounds are naturally occurring durable polymers that are also biodegradable. The rate of biodegradation of these polymers is not finite but exists along a continuum. The processes of their degradation may serve as models for the biodegradation of plastic (Liao et al. 2009; Souza et al. 2011). Chitin is the most abundant natural polymer in the ocean, making up the shells of crustaceans and fungal cell walls (Souza et al. 2011). However, very little chitin is found in marine sediments because of the efficient biodegradation occurring at roughly the same rate as production (Poulicek and Jeuniaux 1991). Chitinases, the enzymes produced by various bacteria, including *Achromobacter*, *Flavobacterium*, *Micrococcus*, *Pseudomonas*, and *Vibrio* spp., hydrolyze chitin, breaking the polymer down (Souza et al. 2011). *Pseudomonas* sp. have been found to degrade plastics (Table 3); however, the precise pathway has not yet been identified.

Petroleum is composed of a suite of compounds with various molecular weights and biodegradation rates. Compounds in petroleum most similar to plastics include resins, asphaltenes, and other higher molecular weight compounds, which have incredibly slow biodegradation rates (Liao et al. 2009; Atlas et al. 2011). Many bacteria are able to degrade different petroleum compounds with several species of *Bacillus* and *Pseudomonas* known to degrade asphaltenes (Tavassoli et al. 2012). Other petroleum-degrading species include *Pseudoalteromonas*, *Vibrio*, *Acinetobacter*, *Alteromonas*, *Oceanospirillales*, *Colwelli*a, and *Cycloclasticus*, but their activity depends on different environmental factors, such as nutrient availability, temperature, oxygen, and sunlight (Hazen et al. 2016). Photooxidation, evaporation and dissolution are the key abiotic petroleum degradation processes (Overton et al. 2016).

Whereas the biodegradation of chitin does not require abiotic predegradation via light or heat, the degradation rates of both oil and plastic are enhanced by the presence of ultraviolet (UV) light and oxygen. Indeed, light and oxygen are the main limiting factors to the abiotic degradation of plastic in seawater, which primarily occurs through photodegradation, thermooxidative degradation and hydrolysis (Gewert et al. 2015). The photo-oxidation of plastics through exposure to UV radiation leads to chemical and physical changes in the surface of the plastic. Oxidation products form on the surface such as carbonyl groups that create a more hydrophilic surface on the plastic and are more easily biodegraded (Hakkarainen et al. 2004). Plastic develops micro cracks and becomes brittle under extended exposure to UV, which facilitates the physical breakdown of plastic pieces (Andrady 2011). Low nutrient concentrations and low temperatures limit oil degradation (Atlas et al. 2011). The impact of these abiotic environmental factors on plastic degradation has not been determined, but Arias-Andres et al. (2018) found a relationship between nutrient concentration and biomass quantity, with biofilm growth being higher on plastics in oligo-mesotrophic and dystrophic lakes than in nutrient-rich lakes.

These studies on plastics in freshwater and marine environments give us insight to the different factors that influence microbe-plastic interactions and degradation. Freshwater habitats and coastal areas collect large amounts of nutrients (and contaminants), in comparison with the often nutrient-poor conditions found in the open sea. Plastic residence time in river and streams commonly is shorter (excluding, for example, lakes, where the debris may persist longer and consequently be exposed to UV radiation longer than in marine environments). However, in deep marine waters, the absence of light, high pressure and low temperatures are prone to inflict selective forces on microbe-plastic aggregation that differ from those found in shallow and fresh environments (Courtene-Jones et al. 2017;Wagner and Lambert 2018). Further research in microplastic incorporation into biogeochemical cycles and plastic degradation in either the marine or the freshwater environment will help to connect these two systems.

Abiotic degradation processes cause the plastic to break down into smaller molecular weight fragments, which become available for microbial attack (Andrady 2011). Leachate from PE, PET, polystyrene (PS), and polypropylene (PP) plastic exposed to UV light in water will not just fragment, but will also leach smaller, lower molecular weight compounds (Gewert et al. 2018). Plastics also leach dissolved organic carbon (DOC) into the water, which are not typically a part of the crystal lattice of the plastic (Lithner et al. 2009), but have smaller molecular weights and are therefore more bioavailable. This initial leaching may slow down overall plastic weathering, by increasing the crystallinity of the remaining plastic, and thereby reducing the leaching over time (Ter Halle et al. 2016). Leached compounds, such as DOC, have implication for the surrounding microbial communities. Romera-Castillo et al. (2018) observed an increase in the bacterial abundance in response to plastic-derived DOC leached from LDPE, high density polyethylene (HDPE), PE, and polypropylene (PP) plastics incubated in autoclaved artificial seawater. This plastic-sourced DOC was found to stimulate heterotrophic microbial growth in batch experiments and contributes to the oceanic DOC pool and microbial contribution to the marine food web. In the presence of DOC leached from PS, diatoms responded by releasing more high molecular weight chromophoric dissolved organic matter (CDOM), which is a more recalcitrant than other forms of CDOM (Galgani et al. 2018). While less accessible to microbial cycling, high concentrations of this recalcitrant CDOM can reduce primary production by decreasing light penetration in the ocean. These studies illustrate the wide range of effects microplastic can have on microbes in the marine environment.

A hindrance to quick biodegradation of chitin, oil, and plastic is the high molecular weight and hydrophobicity of these polymers. Bacteria cannot readily take up high molecular weight substances, and the crystalline structure of chitin and plastic makes it difficult to fragment (Souza et al. 2011; Debroas et al. 2017). In addition, the hydrophobic nature of chitin, oil, and plastic, selects which microorganisms can interact with the substances (Dutta et al. 2004; Krasowska and Sigler 2014). Some microorganisms have developed mechanisms to overcome this challenge. Indications of microorganisms embedding on PE surfaces have been shown by SEM imagining (Zettler et al. 2013). Gram negative bacteria, for example, (e.g., *Acinetobacter* and *Pseudomonas;* Table 1) are able to adjust the hydrophobicity in their cell walls, by changing the composition of the lipopolysaccharides in their outer membrane, to better interact with other hydrophobic substances (Krasowska and Sigler 2014; Heipieper et al. 2017). *Vibrio* species have pili shown to ease attachment to hydrophobic surfaces made of chitin (Pruzzo et al. 2008). The anchoring ability of pathogenic bacteria, like *Vibrio* spp., help them attach to the plastic, but may also help spread these pathogens by transportation on plastic in marine environment (Keswani et al. 2016). Similar to spreading pathogenic bacteria, plastic debris can absorb hydrophobic persistent organic pollutants (POPs), concentrating these pollutants, for example in ocean gyres, and transporting them through the environment and into the food web, where they are released and bioaccumulated into larger organisms (Rios et al. 2007; Andrady 2011; Debroas et al. 2017).

The sediment is where much of the plastic debris accumulates (Woodall et al. 2014; Peng et al. 2018). Studies of oil degradation in sediments show that lower oxygen concentrations slow the degradation process (Bagby et al. 2016). As light and oxygen are the keys to the initial abiotic degradation of plastic in which lower molecular weight compounds are produced via depolymerization, low oxygen concentrations in sediment could also limit plastic degradation. The depolymerization of the polymers was the rate limiting step for the degradation of a biodegradable poly(butylene adipate-co-terephthalate) (PBAT) incubated in soil in a recent study. Over the course of a 2-day incubation, Zumstein et al. (2018) found that 1% of PBAT was remineralized to CO_2, compared to 30% of the monomers that synthesize PBAT. During plastic degradation, it remains unclear whether preliminary degradation will be followed by a secondary stage, where residues of mono- and oligomers outside the crystal lattice are quickly lost, producing a highly crystalline plastic that is very slow to degrade. However, while oxygen and light dependent pathways drive plastic degradation, plastics buried in marine sediment will be exposed to euxinic conditions (Andrady 2011; Gewert et al. 2015). The extent of potential abiotic and biotic degradation (i.e., via sulfide, iron, methane metabolism) has just begun to be explored. Tagg et al. (2019) found Desulfobacteraceae (sulfate reducing bacteria) have a high abundance in microplastic-paint associated biofilms. As plastics continue to accumulate, we need to investigate the effects of sedimentary biogeochemical cycling on plastic degradation and the effects of plastic on the sedimentary microbial community. The addition of another carbon source to the sediments through either the leached DOC or released methane may have meaningful impact on how sediment communities access and react to the plastic.

5. Evidence of Plastic Biodegradation

As plastic is degraded, measurable physical and chemical characteristics of the plastic change, including crystallinity, functional groups on the plastic’s surface, hydrophobicity, surface topography, and mass (Supporting information Table S1) (Fotopoulou and Karapanagioti 2015). Fourier-transform infrared spectroscopy (FTIR) and Raman spectroscopy identify functional groups in plastic, allowing marine plastic debris to be identified by plastic type (Araujo et al. 2018; Hendrickson et al. 2018). These analyses can also determine whether degradation has occurred by measuring changes in the relative absorbance intensities of certain functional groups (Sudhakar et al. 2008). The functional groups that form on the surface of plastic during abiotic degradation (keto carbonyls, esters, vinyls and double bonds) (Restrepo-Flórez et al. 2014) also change the hydrophobicity of the plastic surface (Fotopoulou and Karapanagioti 2015). The balance between the production and microbial consumption of these functional groups also affects the hydrophobicity of the plastic as degradation continues (Dussud et al. 2018a). Another process that changes the hydrophobicity of plastic is the formation of eco-corona, whereby biomolecules sorb onto the surface of the plastic, with or without the assistance of microorganisms (Nasser and Lynch 2016; Galloway et al. 2017). When plastics enter the marine environment, the abiotic degradation that occurs primarily via UV and oxygen exposure acts a primer for microbial attack, creating functional groups that are more labile to microbes and changing plastic surface hydrophobicity (Restrepo-Flórez et al. 2014). One of the final degradation products is CO_2 as has been detected via ^{13}C-labelled plastic incubations and analysis by $^{13}CO_2$ cavity ring-down spectroscopy in soil incubations (Zumstein et al. 2018). Another method to track plastic degradation is through mass loss (Nauendorf et al. 2016). As plastic degrades there is also loss of plastic mass, however, this can be difficult to measure in the plastic alone, due to low mass changes. Moreover, in certain plastics with added starches, the mass loss is due to degradation of the starches rather than the polymer (Andrady 2011).

Direct assessment using microbial cultivation methods is another approach to study plastic degradation. To date, several bacterial and fungal species have been found to degrade plastics in the marine environment, as well, but no specific enzymatic pathway has been discovered, as has been on land with *I. sakaiensis* (Table 3). These microorganisms cover a broad range of characteristics with some being thermophilic, aerobic, and motile, while others are anaerobic and potentially pathogenic. The variety of organisms found growing on marine plastic debris and even to be able to degrade plastic is astounding. It follows that these microorganisms would have different optimal growth conditions, changing based on the biogeochemical setting. Understanding of marine microbe-plastic interactions stems from studies of microbes and plastics in terrestrial environments (Table 3) (Cosgrove et al. 2007; Yoshida and Hiraga 2016; Auta et al. 2017). Of particular interest is *Ideonella sakaiensis*, a novel bacterium isolated from a polyethylene terephthalate (PET) bottling plant landfill (Yoshida et al. 2016). Yoshida and colleagues reported that *I. sakaiensis* catabolized 75% of the PET film to CO_2, and are currently investigating the enzyme pathway this organism employs to utilize the polymer (Han et al. 2017; Joo et al. 2018).

To date, most studies on microbial degradation of plastics have used controlled laboratory setting focusing on single strain isolates from terrestrial and marine environments. Many of these organisms were isolated from biofilms growing on plastic debris, including a marine fungi from a coastal dump site (Sangeetha et al. 2015), and a bacterium, *Ideonella sakaiensis*, from a PET recycling facility, which showed degradation through SEM imagery and weight loss (Yoshida et al. 2016). Syranidou et al. (2017) collected PS from beach sediment and studied the biofilm and degradation of plastic using FTIR, from the natural and augmented consortia. Another approach screens different bacteria and fungi found in the environment for their ability to degrade plastics. In this way, Russell et al. (2011) screened endophytes from the rainforest for the ability to degrade Polyurethane (PUR), finding that two *Pestalotiopsis* strains could utilize PUR as its only carbon source. In the marine environment, Sudhakar et al. (2008) and Paço et al. (2017) measured degradation of PE and PS caused by the bacteria, *Bacillus*, and fungus, *Zalerion*. Suzuki et al. (2018)also isolated a marine species related to *Pseudomonas pachastrellae*, which was found to degrade poly(ε-caprolactone) (Table 3).

Finally, the use of carbon isotopes as a tracer for the movement of plastic-derived carbon in the microbial ecosystem may be a useful tool to elucidate the pathways of biodegradation and help identify the microorganisms able to degrade plastic. Analytical methods, such as nanoscale secondary ion mass spectrometry (nanoSIMS), stable isotope pairing (SIP), and pyrolysis-GC-MS paired with an isotope ratio mass spectrometer (CSIA), used with success in the exploration of microbial respiration pathways and remediation of pollutants have potential applications to further exploring the microbe-plastic realm.

Zumstein et al. (2018) analyzed ^{13}C labelled biodegradable polyester with nanoSIMS to illustrate the use of plastic derived C used to build biofilm. The nanoSIMS results showed both changes in the surface topography, degradation and incorporation of the carbon from the plastic into the biofilm (Zumstein et al. 2018). Pairing isotope and DNA analysis through SIP could also allow us to demonstrate how specific microbes are consuming and incorporating the labelled plastic into their biomass. Furthermore, pyrolysis-compound specific stable isotope analysis (CSIA) may allow us to identify the dissolved leachates in the marine waters and potentially detect the differences between plastic derived DOM and other natural sources of DOM through their isotopic signatures. Pyrolysis-CSIA has thus far been used to detect differences between types of PE (González-Pérez et al. 2015), and to identify microplastics in marine sediment (Fries et al. 2013). Overall, techniques employing carbon isotopes and ^{13}C labelling show promise in their ability to track the fate of plastics in biofilm growth and the environment.

6. Microorganisms mediate microplastic exposure and impacts in the food webs

Pelagic and benthic microbial communities associated with microplastic can affect their ingestion and transfer in the food webs (Fig. 1), and thus the internal exposure of consumers to these environmental contaminants (Rummel et al. 2017). In theory, epiplastic biofilms may increase polymer uptake by consumers via: (1) relocation of microplastics in the water column and its accumulation in some habitats, such as sediment; (2) microplastic aggregation with concomitant change in size distribution (Zhao et al. 2018), increasing availability for a broader range of consumers, and concentration of plastics in the food source (Botterell et al. 2019); (3) improvement of olfactory (Procter et al. 2019) and nutritional appearance and quality of these otherwise indigestible fragments; and (4) physicochemical surface modifications that increase probability of microplastic uptake via ingestion, adherence to soft tissues of animals or plants (Gutow et al. 2016; Goss et al. 2018) that grazers feed upon. All these pathways would result in the increased exposure levels to the polymers and their leachates for biota. However, mechanistic studies on the importance of these processes are very limited. In sediments and suprabenthic layers, ingestion of marine aggregates by suspension-feeders can scavenge and concentrate microplastic (Zhao et al. 2018). However, we know very little about the distribution of these aggregates along the water column and, how much of microplastics are in the aggregated vs. free-floating state. The estimates on nutritional quality of the aggregates carrying different polymer materials and their physical overlap with feeding areas of aquatic consumers (de Haan et al. 2019) are also lacking, which hampers assessment of exposure.

Only a few studies have compared microplastic ingestion between the solitary and aggregated particles of the same type exposed to the same consumers under controlled conditions. When studying pathogen transmission to snails via ingestion, Shapiro and co-workers used 10µm PS beads as a surrogate for a protozoan parasite and found that beads embedded in aggregates <0.5 mm were much more likely to be ingested (Shapiro et al. 2014). Similarly, biofilm-mediated aggregation was found to facilitate the trophic transfer of nanoparticles (Ward and Kach 2009) and micrometer-sized spheres (PS and PE) and fibers (PP) in suspension-feeding bivalves (Porter et al. 2018). In the field, Zhao et al. (2018) used kernel density estimation to demonstrate that the size and shape of plastic particles ingested by mussels were representative of microplastics found in marine aggregates and mussels were able to selectively reject different particle sizes and shapes.

Deeper in the water column, fish and zooplankton (e.g., krill, copepods) that feed on aggregates generate fast-sinking fecal pellets with high settling rates (Saba and Steinberg 2012), which may contribute to the downward export of microplastic (Long et al. 2015). Moreover, after passing through the animal, the plastic-associated biofilm will become enriched with gut microbiota. Of note is that such gut microbiota often show capacity for biodegradation of persistent organic pollutants and potentially plastics (Yang et al. 2015; Bombelli et al. 2017). These new biofilm-plastic associations would modify the microbial component of the sinking aggregates and concomitantly affect polymer degradation. Microbial communities ingested together with microplastics may also impact intestinal homeostasis, the functioning of host gut microflora, and the production of key biogeochemical compounds, such as methane. However, the hypotheses that ingestion of microplastics can alter the gut microbiota of aquatic animals, whereas egested microplastics experience enhanced degradation, remains to be investigated (Lu et al. 2018; Jin et al. 2019).

To date, most experimental studies addressing plastic ingestion by specific consumers or microplastic transfer in artificial food chains have used virgin particles without monitoring their size spectra, particle aggregation and biofilm quantity during the experiment. As a result, the trophic transfer might be underestimated, because plastic particles embedded in nutrient-rich biofilms could be preferentially ingested by many common olfactory foragers (Egbeocha et al. 2018). These foragers are stimulated by chemical signaling molecules and the biofilm may disguise the inert nature of the plastic particles making them similar to food items. Selective feeders, such as copepods and shrimps, which constitute an important trophic link from particulate material to higher consumers would be particularly discriminative (Egbeocha et al. 2018). Indeed, some copepods, showed a preference for aged microbeads. The primary reason for this preference was related to the presence of biofilm resulting from exposure to natural seawater during the aging process (Vroom et al. 2017). By contrast, in the scleractinian corals known to use chemosensory cues for feeding (Allen et al. 2017) and sea urchin larvae (Kaposi et al. 2014), the opposite was observed, with significantly higher ingestion rate for pristine than fouled microplastic. How feeding mechanisms determine plastic selection is still an active area of research. In neither of these studies, has the biofilm been characterized, thus hindering the interpretation of ingestion and comparative analysis between treatments and across studies. Molecular attractants (e.g., algae-derived dimethyl sulfide, DMS) adsorbed to plastics in marine environments would also stimulate active ingestion by marine animals as a result of prey confusion and association with chemical signaling molecules from phytoplankton. Other studies have demonstrated that biofilm formation is not essential to increase the attractiveness of microplastic to marine grazers, such as copepods; microbeads spiked with DMS were sufficient to induce selective feeding in copepods (Procter et al. 2019). In addition, olfactory mechanisms were also implicated to activate the ingestion of plastic debris by fish (Savoca et al. 2017).

Adsorbed organic matter and bacterial biofilm on the particle surface can be assimilated by zooplankton and contribute to growth (Arruda et al. 1983; Rellstab and Spaak 2009). Therefore, if the microorganisms growing on polymer surfaces have not only different community structure but, also different nutritional qualities compared to those growing on natural substrates and free-living prey, the intake of microplastic and associated biofilms would impact animal nutrition and growth. In line with this, snails feeding on biofilms grown on polymer surfaces had lower ingestion and growth compared to controls (Vosshage et al. 2018). The biofilms growing on the polymers in the latter study had lower nutritional value because of the lower contribution of algae, indicating lower primary production, and higher contribution of lectin-specific glycoconjugates that are crucial for biofilm structure and stability (Flemming and Wingender 2001).

To understand the mechanisms by which microplastics affect aquatic organisms and thus credibly address the environmental impacts of these contaminants, the three-way interactions between microplastics, microorganisms and consumers need to be considered from an ecological perspective. Systematic comparative studies should be undertaken on microbial and chemical components of microplastic aggregates to discern the uptake, degradation in the gut, effects in the consumers, and food-web consequences in environmentally relevant settings. This, in turn, requires explicit information on the realistic concentrations of free-floating and aggregate-embedded microplastics in different matrices through appropriate instrumental analysis.

7. Future directions:

As the study of marine microplastics evolves, a number of immediate and long-term challenges must be met to understand microbe-microplastic interactions. First, the relative size of microorganisms to the microplastic they interact with fundamentally controls biogeochemical interactions in the water and sediment; the dominant modes of microbial attachment, potential processes of electron exchange and biodegradation, aggregate shape, composition and size, and the resulting transport and deposition processes (Fig. 2). Future studies must address these differences in size between plastics and microorganisms and weigh the implications of their findings to this reality.

Second, analytical and methodical challenges remain fundamentally limiting for our understanding of microbe-plastic interactions, transport, and plastic biodegradation pathways in the environment. The study of microplastics is still nascent and highly interdisciplinary, and this need for development of standard sampling and analysis methods across these various fields is acknowledge in the community and ongoing (i.e., Gago et al. 2018). One of the specific challenges is to resolve and identify microplastics on the scale of mm to nm in environmental matrices. To be applicable in field studies, we need standardized analytical approaches designed to separate microplastics from large volumes of seawater or sediment in a realistic and efficient timeframe. These approaches must also take into account knowledge reaped from other fields, i.e., that the taxonomic composition of microorganisms of a filtered seawater sample may change depending on the amount of water filtered (Padilla et al. 2015). To study microbe-microplastic interactions as discussed herein, culture methods and analyses must be developed and shared in order to draw comprehensive and environmentally-relevant conclusions as to how microorganisms function in the *plastisphere*. One specific target area is the further development of reliable methods to assess plastic surface modifications in the presence of epiplastic communities. Another area is the need for laboratory and field experiments that monitor community changes in biofilms to capture the molecular mechanisms of microbial biodegradation and functional relationships in the biodegrading consortia. Laboratory experiments focused on these questions must take into account potential microbial adaptation to laboratory conditions with concomitant functional alterations. Across the field, we must develop consistent and efficient methods in how we collect, treat, and analyze microbe-plastic interactions. The difficulty starts in analyzing the plastic itself, from identifying environmental samples of originally different polymer types, particle sizes, and even different stages of degradation. Almost all of the techniques currently used to identify and separate microplastics from their surrounding matrix are incredibly time consuming, i.e., density separation, but are a necessary processing step for later analyses. Currently, FTIR and Raman spectroscopy are used to identify environmental plastic samples, down to about 20µm and 500nm, respectively (Käppler et al 2015; Araujo et al 2018). Some success has been made automating the Raman analysis, which shortens the analysis time. FTIR analysis is more time consuming, but it can also measure changes in functional groups, which is an indication of degradation (Sangeetha et al. 2015). One method that could speed up the separation process stains synthetic polymers with the fluorescent Nile Red dye (Araujo et al. 2018; Wiggin and Holland 2019). Using UV light, the particles can then be separated visually and then analyzed using FTIR or Raman. However, there is no consensus on whether this dye interferes with the identification of the plastic type using FTIR or Raman (Araujo et al 2018). The treatment of plastics for experiments, including pre-UV degradation and sterilization should be uniform. Along the same lines as the plastic pretreatment, methods for microbe isolation and culture work must homogenized. Standardizing the methods used to make these analyses is an active field of research and will allow for better interpretation of data collected in all fields.

A third challenge is to develop our fundamental understanding of microplastic aggregate behavior, as these aggregates are the primary vector for microplastic transport in the water column and food webs (Michels et al. 2018; Zhao et al. 2018). Once incorporated into aggregates, various microplastic transformations can occur, including an increase in the effective particle size and change in surface topography and density as a result of the physical and biological processes in the aggregate microcosm. Future studies should: (1) detail the characteristics of microplastics in marine aggregates on a global scale and estimate the contribution of aggregates to the downward flux of plastic, (2) elucidate the interaction between microplastics and microbes harbored in organic aggregates and the resulting changes of both plastic and microorganisms (Arias-Andrés 2018), and (3) track the role of the aggregates in the microplastic uptake and food web transfer.

Lastly, in microbe-microplastic interaction research is defining the drivers behind *plastisphere* community composition. On the one hand, the habitat in which the plastic is located may drive which microorganisms gain access to the plastic. The environment can influence the structure of attached organisms and biofilm development due to physiological requirements, grazing by predators, redox setting, or abiotic or biotic diagenesis of the microbe-plastic aggregate (i.e., Zettler et al. 2013; Harrison et al. 2014; Amaral-Zettler et al. 2015; Ogonowski et al. 2018). On the other hand, microbe-microplastic interaction might be driven by microbial selection for substrate surface. This selection might be passive in that the microbe seeks a surface and can attach. Alternatively, this selection might be active in that the microbe specifically colonizing plastic surfaces in order to utilize them as a carbon substrate. Evidence suggests *plastisphere* community composition is distinct from ambient communities and those found on other substrates (wood, glass, metal) (Zettler et al. 2013; Harrison et al. 2014; Amaral-Zettler et al. 2015).

Next steps must explore how these factors influence microbe-plastic interactions in the water and sediment, to continue assessing community composition of the *plastisphere*, but also how the key metabolic processes they carry out differ from the ambient communities. Extension of molecular approaches, such as metagenomics, proteomics and metabolomics, may yield new perspectives here.

Such research would improve mechanistic understanding of the fate and environmental impacts of plastic litter, while also delivering much needed information to environmental managers on the microplastic exposure routes and levels in the environment. This information is necessary for exposure assessment and risk characterization as well as suggestions of adequate regulatory measures for plastic litter.

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Tables:

Table 1. Organisms identified on plastic particles in the marine and freshwater environments

Family	Genus	Environment	Plastic Type
Bacteria[a,k,m,c,n,q]		North Atlantic[a,n], Coastal Australia[k], North Pacific Gyre[c], Sargasso Sea[m], downstream waste water treatment plant- fresh water[q]	PE[a,c,k],PS[c,k,n], PP[a,c,k]
Mycobacteriacea[d]	*Mycobacterium*[d,q]	North Sea-water/sediment[d], downstream waste water treatment plant- fresh water[q]	PE[d], PP[d]
Cytophagaceae[f]	*Cytophaga*[e], *Marinoscillum*[a]	North Atlantic[a], North Sea[e], Yangtze estuary[f]	PE[a,e,f], PS[e,f], PP[a,f]
Flammeovirgaceae[b,f]	*Reichenbachiella*[b]	, North Pacific Gyre[b], Yangtze estuary[f]	PE[b,f], PP[b,f], PS[f]
Flavobacteriaceae[b,f]	*Tenacibaculum*[a,i], *Muricauda*[a,b], *Marinitalea*[e], *Nonlabens*[e,l], *Algibacter*[e], *Polaribacter*[e], *Lutibacter*[e], *Flavobacterium*[e], *Krokinobacter*[e], *Olleya*[e], *Aquimarina*[b,e], *Gaetbulibacter*[e], *Croceitalea*[l,i], *Amoebophilus*[a], *Leeuwenhoekiella*[i],	North Atlantic[a,i], North Pacific Gyre[b], North Sea[e], Yangtze estuary[f], Adriatic Sea[l]	PE[a,b,e,f,i,l],PS[e,f,l] ,PP[a,b,f,l], PA[l], PET[l]
Rhodothermaceae[f]	*Rubrimonas*[a], *Thalassobius*[a], *Albidovulum*[a,e], *Rhodovulum*[a], *Roseovarius*[a,l,i], *Pseudoruegeria*[l], *Loktanella*[e]	North Atlantic[a], North Sea[e], Yangtze estuary[f], Adriatic Sea[l]	PE[a,e,f,l],PS[e,f,l], PP[a,f,l], PA[l], PET[l]
Hyphomonadaceae[b,f]	*Hyphomonas*[a,e]	North Atlantic[a], North Pacific Gyre[b], North Sea[e], Yangtze estuary[f]	PE[a,b,e,f],PS[e,f], PP[a,b,f]
Erythrobacteraceae[f,i]	*Erythrobacter*[a,e,l,h,i]	North Atlantic[a,i], North Sea[e], Yangtze estuary[f], Adriatic Sea[l], Mediterranean[h]	PE[a,e,f,i,l],PS[e,f,l], PP[a,f,l], PA[l], PET[l], LDPE[h]
Sphingomonadaceae[f]	*Parasphingopyxis*[l], *Sphingomonas*[i]	Yangtze estuary[f], Adriatic Sea[l], North Atlantic[i]	PE[f,i,l],PS[f,l],PP[f,l], PA[l], PET[l]
Sneathiellaceae[b]	*Sneathiella*[b]	North Pacific Gyre[b],	PE[b], PP[b]
Enterobacteriaceae[a,f]	*Proteus*[l], *Klebsiella*[j]	North Atlantic[a], Yangtze estuary[f], Southern India[j], Adriatic Sea[l]	PE[a,e,f,j,l],PS[e,f,l], PP[a,f,l], PA[l], PET[l]
Moraxellaceae[f]	*Acinetobacter*[a,l], *Psychrobacter*[e]	North Atlantic[a], North Sea[e], Yangtze estuary[f], Adriatic Sea[l]	PE[a,e,f,l],PS[e,f,l],PP[a,f,l], PA[l], PET[l]
Alteromonadaceae[a,f]	*Alteromonas*[a,l,h], *Aestuariibacter*[l]	North Atlantic[a], Yangtze estuary[f], Adriatic Sea[l]	PE[a,f,l],PS[,f,l], PP[a,f,l], PA[l], PET[l]

Shewanellaceae[f]	*Shewanella*[e,q]	North Sea[e], Yangtze estuary[f], downstream waste water treatment plant- fresh water[q]	PE[e,f],PS[e,f],PP[f]
Cowelliaceae[f]	*Colwellia*[e]	North Sea[e], Yangtze estuary[f]	PE[e,f],PS[e,f],PP[f]
Pseudoalteromonadaceae[d,f]	*Pseudoalteromonas*[e]	North Sea[e], North Sea-water/sediment[d], Yangtze estuary[f]	PE[d,e,f],PS[e,f], PP[d,f]
Vibrionaceae[a,d]		North Atlantic[a], North Sea-water/sediment[d]	PE[a,d], PP[a,d]
Anaerolinaceae[a]	*Anaerolinea*[l]	North Atlantic[a], Adriatic Sea[l]	PE[a,l], PP[a,l], PP[a,l], PA[l], PET[l]
Leptolyngbyaceae[b]	*Leptolyngbya*[h]	North Pacific Gyre[b], Mediterranean[h]	PE[b], PET[h], LDPE[h]
Comamonadaceae[a,f,q]	*Comamonas*[i], *Pelomonas*[i], *Hydrogenophaga*[q], *Aquabacterium* [q]	North Atlantic[a], Yangtze estuary[f], Mediterranean[h], downstream waste water treatment plant- fresh water[q]	PE[a,f], PS[f], PP[a,f,], PET[h], LDPE[h]
Pseudomonadaceae [q]	*Pseudomonas*[q]	downstream waste water treatment plant- fresh water[q]	
Chitinophagaceae[a,f,b,q]	*Sediminibacterium*[q]	downstream waste water treatment plant- fresh water[q]	
Verrucomicrobiaceae[a]	*Prosthecobacter* [q]	North Atlantic[a], downstream waste water treatment plant- fresh water[q]	PE[a]
Saprospiraceae[a,f,b,q]	*Lewinella*[a,b], *Haliscomenobacter*[q]	North Atlantic[a], North Pacific Gyre[b], Yangtze estuary[f], downstream waste water treatment plant- fresh water[q]	PE[a,b,f],PS[f], PP[a,b,f]
Planococcaceae[f], Streptococcaceae[f], Clostridiaceae[f], Lachnospiraceae[f], Nocardiaceae[f], Acidimicrobiaceae[f], Cryomorphaceae[f], Rhodobacteraceae[a,b,f,i,q], Acetobacteraceae[f], Aurantimonadaceae[f], Oxalobacteraceae[f,q], Nannocystaceae[a], Sinobacteraceae[a], Halieaceae[f], Cellvibrionaceae[f], Gemmatimonadaceae[f], Xanthomonadaceae[f], Roseiflexineae[f], Deinococcaceae[f], Blastocatellaceae[f], Phyllobacteriaceae[i], Veillonellaceae[q], Ruminococcaceae [q], Porphyromonadaceae [q]	*Bacillus*[c], *Haliscomenobacter*[a], *Microscilla*[a], *Algoriphagus*[e], *Tunicatimonas*[b], *Rivularia*[a,b], *Pleurocapsa*[a,h], *Prochlorococcus*[l], *Synechococcus*[a,e,h], *Prochlorothrix*[b], *Limnothrix*[b], *Stanieria*[e], *Pseudophormidium*[e], *Phormidium*[a,b,e], *Oceanibaculum*[l], *Thalassospira*[h,i], *Hellea*[a,l], *Parvularcula*[a,l], *Devosia*[a,i], *Calothrix*[h], *Scytonema*[h], *Pelagibacter*[h], *Pelagibaca*[h], *Roseobacter*[h], *Tateyamaria*[i], *Azospirillum*[i], *Microvirga*[i], *Caenispirillum*[i], *Oceanicaulis*[i], *Parvularcula*[i], *Ralstonia*[i], *Streptomyces*[i], *Thiothrix*[q], *Arcobacter*[q], *Aeromonas*[q], *Zymophilus*[q], *Desulfovibrio* [q], *Albidiferax* [q], *Sulfurospirillum* [q], *Nitrospira* [q], *Bacteroides* [q], *Prevotella* [q], *Anaerosinus* [q], *Desulfobulbus* [q], *Turneriella* [q], *Zoogloea*[q], *Thauera* [q]	North Atlantic[a,i], North Pacific Gyre[c,b], North Sea[e], Yangtze estuary[f], Adriatic Sea[l], Mediterranean[h], downstream waste water treatment plant- fresh water[q]	PE[a,b,c,f,i,l],PS[c,f,l] ,PP[a,b,c,f,l], PET[h,l], PA[l], LDPE[h]
Fungi[i]		North Atlantic[i]	PE[i]
Diatoms	*Amphora*[k], *Achananthes*[k], *Cocconeis*[k], *Cymbella*[k], *Grammatophora*[k], *Haslea*[k], *Licmophora*[k], *Mastogloia*[k,m], *Microtabella*[k], *Minidiscus*[k], *Nitzschia*[a,k], *Thalassionema*[k],	North Atlantic[a], Coastal Australia[k], Sargasso Sea[m]	PE[a,k],PS[k],PP[a,k]

	Thalassiosira[k], *Chaetoceros*[a], *Cyclotella*[m], *Navicula*[a], *Pleurosigma*[m], *Sellaphora*[a], *Stauroneis*[a]		
Dinoflagellates	*Ceratium*[k], *Ostreopsis*[j], *Coolia*[j], *Alexandrium*[j]	Coastal Australia[k], Mediterranean[j]	PE[k],PS[k],PP[k]
Coccolithophores	*Calcidiscus*[k], *Emiliania*[k], *Gephyrocapsa*[k], *Umbellosphaera*[k], *Umbilicosphaera*[k], *Coccolithus*[k], *Calcioslenia*[k]	Coastal Australia[k]	PE[k],PS[k],PP[k]
Ochraphyta	*Synedra*[e], *Amphora*[e], *Psammodictyon*[e], *Saccharina*[e], *Fucus*[e], *Asterionella*[e]	North Sea[e],	PE[a,e],PS[e],PP[a]
Other Eukaryotes	Barnacles[k], Bryozoa[k,a,b,o,r],Anthrozoa[b], Hydrozoa[b], Maxillopoda[b], insect eggs[k,p,g], Dinophyceae[b], Aphragmophora[b], Eukaryota[b], Cnidaria[b], Nematoda[b], Intramacronucleata[b], Gastropoda[b], Malacostraca[b]	North Pacific Gyre[b,p], Coastal Australia[k], Brazil sediment[o], East/West Pacific[g]	PE[k,b],PS[k],PP[k,b]

[*]classification only to family; [-]classification above family; [#]mix classifications

[a]Zettler et al. 2013[#], [b]Bryant et al. 2016[#],[c]Carson et al. 2013, [d]De Tender et al. 2015[#], [e]Oberbeckmann et al. 2014, [f]Jiang et al. 2018[*], [g]Goldstein et al. 2014, [h]Dussud et al. 2018b[#], [i]Debroas et al. 2017[#], [j] Masó et al. 2003, [k]Reisser et al. 2014[#], [l]Viršek et al. 2017, [m]Carpenter and Smith, 1972, [n] Carpenter et al. 1972, [o] Majer et al. 2012, [p] Goldstein et al. 2012, [q]McCormick et al. 2014[#]

Table 2. Organisms identified on *in situ* experimental plastics

Family	**Genus**	**Location**	**Plastic Type**
	Bacteria		
Flavobacteriaceae[b,i]	*Eudoraea*[a], *Maritimimonas*[a,i], *Psychroserpens*[a,g], *Mesonia*[g], *Tenacibaculum*[a,g], *Pibocella*[g], *Polaribacter*[a,g], *Lacinutrix*[a], *Maribacter*[g,i], *Formosa*[g], *Dokdonia*[g], *Ulvibacter*[g]	North Sea[a,b], Yellow Sea[g], mouth of Warnow river in Baltic Sea[i]	PE[a], dolly rope[a], PET[b], PCV[g], Plexiglas[g], Paint[i]
Rhodobacteraceae[a,i]	*Profundibacterium*[a], *Ahrensia*[g], *Leisingera*[g], *Loktanella*[g], *Nereida*[g], *Octadecabacter*[g], *Paracoccus*[g], *Roseobacter*[g,h], *Roseovarius*[g], *Sulfitobacter*[a,g], *Planktomarina*[i]	North Sea[a], Yellow Sea[g], Coastal Atlantic[h], mouth of Warnow river in Baltic Sea[i]	PE[a], dolly rope[a], PCV[g], Plexiglas[g], PU[h], Paint[i]
Erythrobacteraceae[a,b]	*Erythrobacter*[g]	North Sea[a,b], Yellow Sea[g]	PE[a], dolly rope[a], PCV[g], Plexiglas[g]
Verrucomicrobiaceae[b,d]	*Persiccirhabdus*[a]	North Sea[a,b], Mediterranean[d]	PE[a], dolly rope[a], PET[b], PVC[d]
Alteromonadaceae[b]	*Alteromonas*[g,h], *Glaciecola*[g]	North Sea[b], Yellow Sea[g], Coastal Atlantic[h]	PET[b], PCV[g], Plexiglas[g], PU[h]
Sphingomonadaceae[b]	*Sphingopyxis*[g]	North Sea[b], Yellow Sea[g]	PET[b], PCV[g], Plexiglas[g]
Oceanospirillaceae[b]	*Oceanospirillum*[g], *Oleispira*[g]	North Sea[b], Yellow Sea[g]	PET[b], PCV[g], Plexiglas[g]
Moraxellaceae[b]	*Psychrobacter*[g]	North Sea[b], Yellow Sea[g]	PET[b], PCV[g], Plexiglas[g]
Vibrionaceae[b]	*Vibrio*[g], *Photobacterium*[i]	North Sea[b], Yellow Sea[g], mouth of Warnow river in Baltic Sea[i]	PET[b], PCV[g], Plexiglas[g], Paint[i]
Rickettsiaceae[b], Piscirickettsiacea[b], Alcanivoracaceae[b], Colwelliaceae[b], Desulfobulbaceae[b,i], Planctomycetaceae[b], Phycisphaeraceae[b], Rubritaleaceae[d], Simkaniaceae[b], Cryomorphaceae[b], Saprospiraceae[b], Flammeovirgaceae[b], Rhodospirillaceae[b], Burkholderiaceae[i], Christensenellaceae[i], Spirochaetaceae[i]	*Robiginitomaculum*[a], *Hellea*[a], *Anderseniella*[a], *Halomonas*[g], *Methylotenera*[a], *Kangiella*[a], *Acidiferrobacter*[a], *Arencella*[a], *Sulfurovum*[a], *Methylococcus*[g], *Ochrobactrum*[g], *Pelagibacter*[g], *Fluviicola*[g], *Pseudoalteromonas*[g], *Desulfatitalea*[i], *Phaselicystis*[i], *Anderseniella*[i], *Aegiribacteria*[i], *Leptospiraceae*[i], *Thermodesulfovibrionia*[i]	North Sea[a,b] Mediterranean[d], Yellow Sea[g], mouth of Warnow river in Baltic Sea[i]	PE[a], dolly rope[a], PET[b], PVC[d,g], Plexiglas[g], Paint[i]
	Diatoms[c]		
	Cylindrotheca[e,f], *Nitzschia*[e,f], *Navicula*[e,f], *Amphora*[e,f], *Diploneis*[e], *Striatella*[e,f], *Amphora*[e,f], *Licmorphora*[e,f], *Pleurosigma*[e], *Gyrosigma*[e,f], *Asterionellopsis*[e], *Thalassionema*[f], *Rhoicospheenia*[f], *Actinoptichus*[f]	Mediterranean[e,f], Chile[c]	PE[e], Mater-bi[e], PS[f,c]
	Other Eukaryotes		
	Hydrozoa[c], Barnacles[c], Bryozoa[c], Tunicata[c], Nudibranchia eggs[c], Rhodophytas[c], Ectocarpales[c], Brown Seaweed[c], Ulvales[c]	Chile[c]	PS[c]

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[a] De Tender et al. 2017, [b] Oberbeckmann et al. 2016, [c] Bravo et al. 2011, [d] Pollet et al. 2018, [e] Eich et al. 2015, [f] Briand et al. 2012, [g] Dang et al. 2008, [h] Dang and Lovell 2000, [i] Tagg et al. 2019

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Table 3. Known Plastic Degraders in Marine and Terrestrial Habitats

Marine			**Habitat**
LDPE	Bacteria	*Kocuria palustris*[a], *Bacillus pumilus*[a], *Bacillus subtilis*[a], *Bacillus sphericus*[b], *Bacillus cereus*[b]	Pelagic water India[a,b]
HDPE	Bacteria	*Bacillus sphericus*[b], *Bacillus cereus*[b], *Brevibacillus borstelensis*[l]	Pelagic water India[b], sea water[l]
HDPE	Fungi	*Aspergillys tubingensis*[h], *Aspergillus flavus*[h]	Coastal sediment India[h]
PE	Fungi	*Zalerion maritimum*[c]	Marine water Portugal[c]
PET	Bacteria	*Bacillus cereus*[e], *Bacillus gottheilii*[e]	Mangrove sediment[e]
PP	Bacteria	*Rhodococcus* sp. [f], *Bacillus* sp. [f]	Mangrove sediment[f]
PS	Bacteria	*Bacillus cereus*[e], *Bacillus gottheilii*[e]	Mangrove sediment[e]
PCL	Bacteria	*Pseudomonas* sp.[i]	Plastic in coastal Japan[i]
Land			**Habitat**
PET	Bacteria	*Ideonella sakaiensis*[d],	PET recycling facility[d]
PE	Bacteria	*Brevibacillus* [n], *Pseudomonas* [n], *Rhodococcus sp.*[n]	Amazon[j], Waste disposal site sediment[n]
PU	Bacteria	*Geomyces pannorum*[g], *Phoma* sp.[g]	UK soil[g]
PUR	Bacteria	*Pestalotiopsis microspora*[j]	Amazon[j]
LDPE	Fungi	*Aspergillus japonicas*[m], *Aspergillus flavus*[m], *Penicillium* sp.[m], *Aspergillus niger*[k]	Polluted soil India[m], landfill soil Iran[k]
LDPE	Bacteria	*Lysinibacillus xylanilyticus*[k]	landfill soil Iran[k]

[a]Harshvardhan and Jha 2013, [b]Sudhakar et al. 2018, [c]Paço et al. 2017, [d]Yoshida et al. 2016, [e]Auta et al. 2017, [f]Auta et al. 2018, [g]Cosgrove et al. 2007, [h]Sangeetha et al. 2015, [i]Suzuki et al. 2018, [j]Russell et al. 2011, [k]Esmaeili et al. 2013, [l]Mohanrasu et al. 2018, [m]Singh and Gupta, 2014, [n]Nanda and Sahu, 2010

Figures:

Fig. 1: Microplastics potentially interact with microorganisms in the food web, as well as in biogeochemical cycles in marine water and sediment. In the water column, aggregates or flocs are formed, usually being microbe-plastic-mineral composites (A). These aggregates quickly incorporate into biogeochemical cycles in the water column, acting as a surface for element cycling or as a carbon source. The particles and aggregates are suspended, transported and settle in the water column (B), where they interact with marine organisms (2, 3). Settling particles and aggregates undergo abiotic or biotic diagenetic processes at the sediment-water interface or when buried in the sediment (C). Here, physical and chemical degradative processes can occur. Benthic microorganisms may attach to these particles, interacting with the associated biofilm or directly using plastic as a carbon source (1). Plastic may travel in the food web, from microorganisms to apex feeders. Planktonic microorganisms can attach to, form aggregates with, or may actively engulf or degrade plastics (2). Macrofauna comes into contact with microplastics via ingestion (3). Humans may unwillingly ingest microplastics (4).

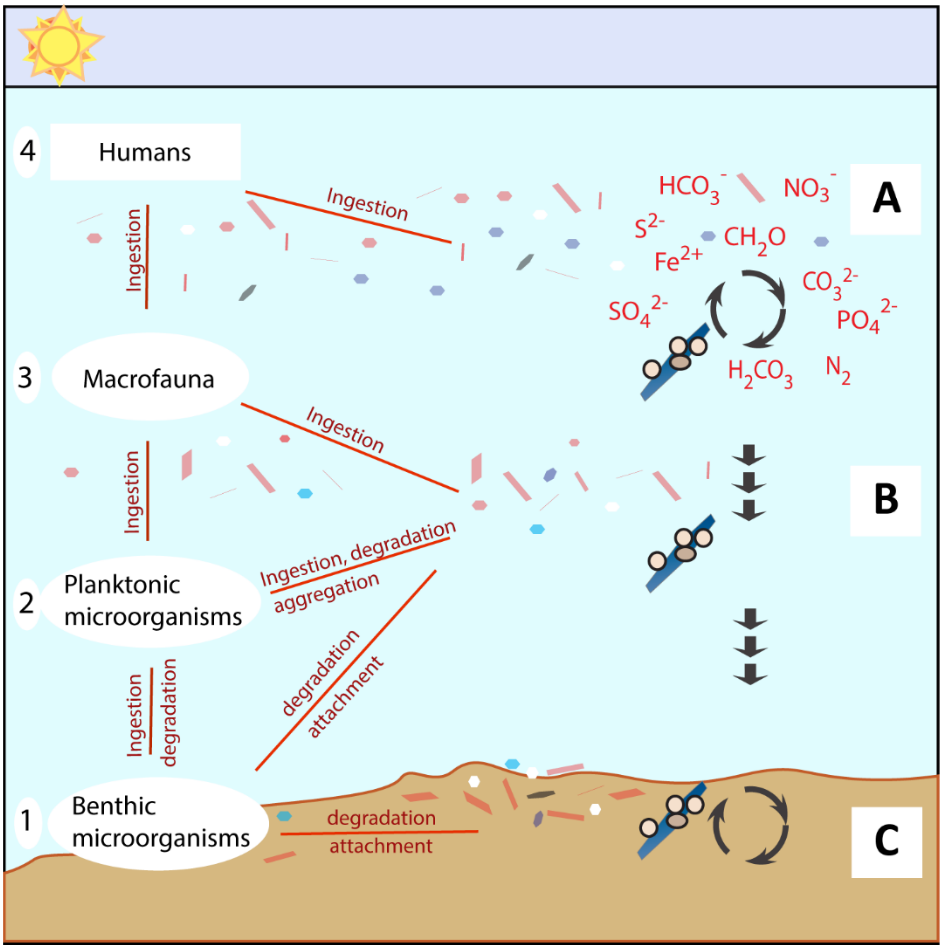


Fig. 2: A) SEM image showing the microbial diversity found on a PE sheet placed in the surface water column of Svanemøllehavnen, Copenhagen, Denmark. The plastic was exposed to the environment for 6 months (January-June 2019). **B)** Polyvinyl chloride (PVC) floc of 500µm made of 10-20µm particles size in unfiltered seawater as determined by PCam camera-system (courtesy of Thorbjørn Andersen, KU-IGN). **C)** Differences in plastic particle size defines the interaction with cells and biofilm. **1)** macroplastics become colonized by biofilms **2)** as plastic particles become smaller, cells or biofilms build on the surface, may embed themselves in the plastic or attach inside cracks, fissures or holes. **3)** when particles become as small or smaller than cells, the structure can best be described as an aggregate where cells incorporates plastic into its EPS-rich matrix. This difference in scale is important for the understanding of biogeochemical cycling, transport and fate of the plastic particles in the water and sediment.

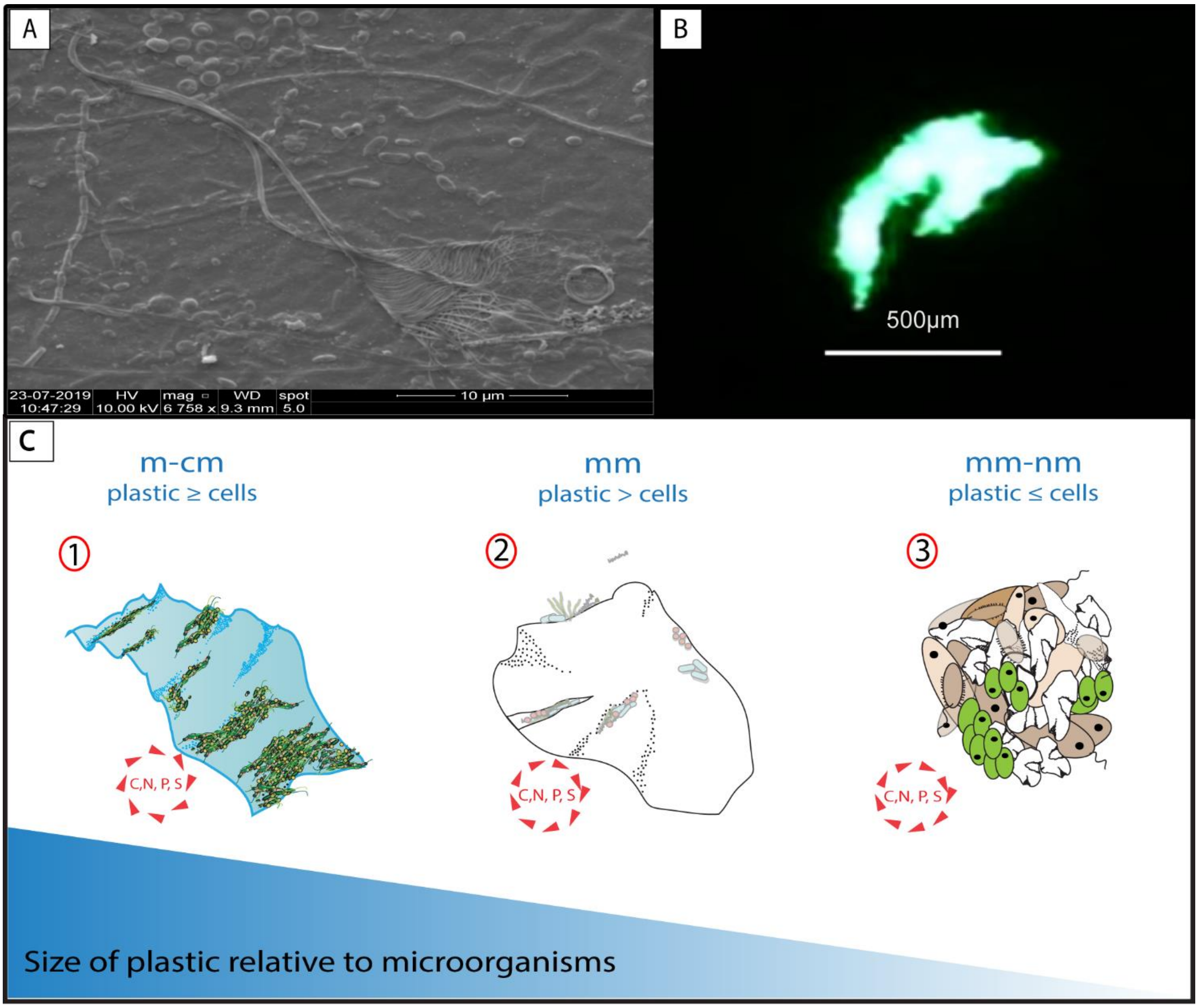
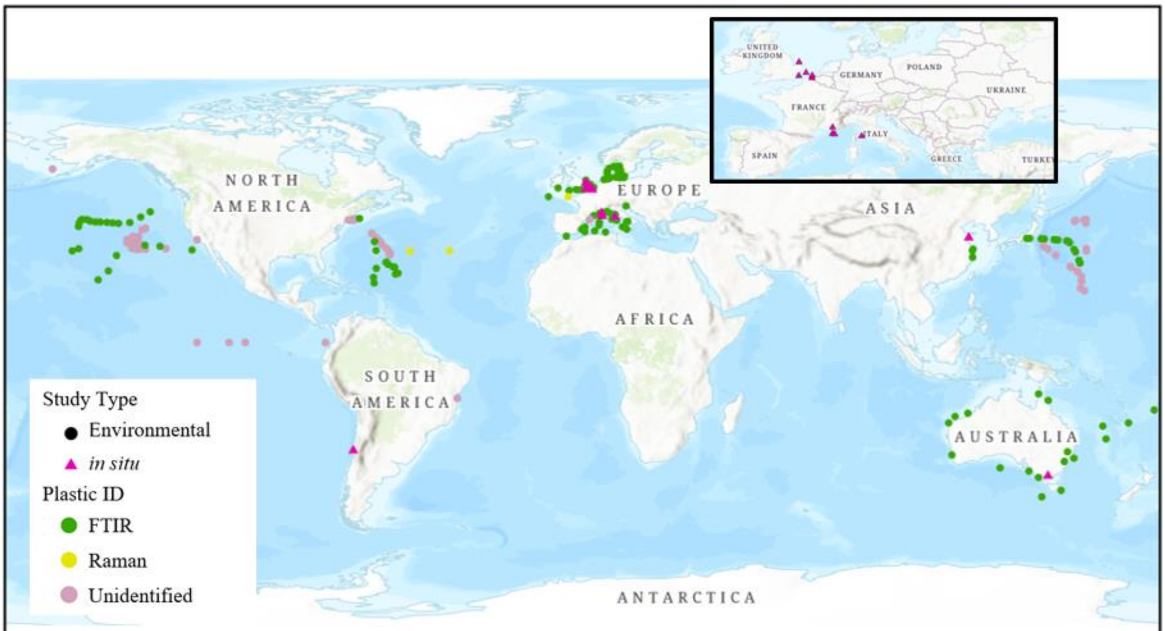


Fig. 3: Global map of studies exploring the microbial communities associated with plastic. Circles show locations of samples taken from the water or sediment. Pink triangles are the locations of *in situ* experiments with known plastic placed into water or sediment for colonization. In environmental samples, the green, yellow and light pink circles depict whether plastic was identified with FTIR, Raman, or left unidentified, respectively. Environmental studies: Carpenter et al. 1972; Carpenter, Edward J., Smith, Jr 1972; Goldstein et al. 2014; Majer et al. 2012; Goldstein et al. 2012; Zettler et al. 2013; Carson et al. 2013; Oberbeckmann et al. 2014; Reisser et al. 2014; Amaral-Zettler et al. 2015; De Tender et al. 2015; Bryant et al. 2016; Viršek et al. 2017; Debroas et al. 2017; Jiang et al. 2018; Dussud et al. 2018b; Frère et al. 2018; *in situ* studies: Dang et al. 2008; Webb et al. 2009; Bravo et al. 2011; Briand et al. 2012; Eich et al. 2015; Oberbeckmann et al. 2016; De Tender et al. 2017; Pollet et al. 2018.



Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community

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