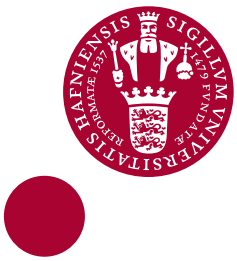

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SPECIAL ISSUE-CURRENT EVIDENCE

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

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Scientific Significance Statement

Due to their small particle size and wide distribution, microplastics can be incorporated 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 on microbe-plastic interactions and consider the biogeochemical relevance. Particular focus is on new methods and analytical approaches to understand the two-way interactions between microorganisms and microplastics and the implications for the environmental fate of marine plastic litter.

Abstract

Microorganisms drive the biogeochemical cycles that link abiotic and biotic processes in the aqueous environment and are intricately associated with plastic debris. The presence of microplastics in water and sediment introduces new concerns as small particle size allows for increased pathways of microplastics in the food web and element cycles. In this review, we present the current state of knowledge on 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 microplastics and plastic degradation products. Key methods used to elucidate biofilm development, microbial biodegradation, and microplastic 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.

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Though plastic debris have been reported in the marine environment as early as the 1970s, in the past decade, microplastic particles have come into focus as a major environmental pollutant (Carpenter and Smith 1972). The discovery of widespread microplastic pollution generates further questions related to the potential sources, impact, transport, and environmental fate of this contaminant. Microorganisms play an integral part in aquatic biogeochemical cycles, and are found associated with plastic debris in both water and sediment (Zettler et al. 2013). The interplay between microorganisms, biogeochemical cycles, and microplastics may drive the environmental fate of marine plastic, but through which pathways and to what extent, remains an active area of research.

Interactions between microorganisms and microplastics change the pollutant characteristics over time and define how and why cells attach to plastic particles. 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 microplastic particles (Rummel et al. 2017; Roager and Sonnenschein 2019; Oberbeckmann and Labrenz 2020). 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 studies done in freshwater settings to elucidate how plastics influence and are influenced by biogeochemical pathways at the water surface, water column, and sediment of aquatic environments. In this review, we emphasize mainly on microplastics, but we note that some of the processes and interactions between microbes and the plastic we describe can apply to larger plastic pieces as well. In addition, we address the degradation processes of plastic as a polymer and do not constrain our discussion here by particle size.

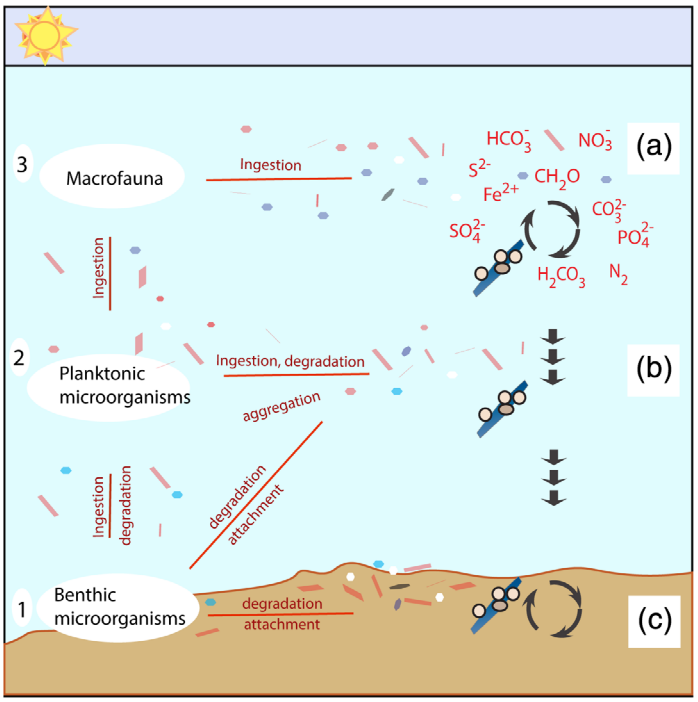

Fig. 1. Microplastics potentially interact with microorganisms in the food web, as well as in biogeochemical cycles in marine water and sediment. In the water column, aggregates or flocs are formed, usually being microbe-plastic-mineral composites (a). These aggregates quickly incorporate into biogeochemical 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 settled 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).

The microbial Plastisphere: A new ecological niche

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 diverse and distinct from the surrounding planktonic communities (Zettler et al. 2013; Harrison et al. 2014; Oberbeckmann et al. 2014; De Tender et al. 2015). Organisms such as diatoms, coccolithophores, bryozoans, barnacles, dinoflagellates, isopods, as well as cyanobacteria, heterotrophic bacteria, and fungi have been catalogued on plastic debris (i.e., Carpenter and Smith 1972; Reisser et al. 2014; Tables 1, 2). The composition and development of biofilm on microplastics is influenced by a number of factors, including environmental conditions, sample location, substrate type, particle size, and surface properties (Fig. 2b,c) (Zettler et al. 2013; Oberbeckmann et al. 2014; Eich et al. 2015). The microorganisms of the *Plastisphere* are also phenotypically diverse, represent a broad range of preferred environmental conditions including aerobes, anaerobes, motile and nonmotile organisms, as well as extremophiles. Environmental sampling and in situ incubation studies (Fig. 3) on microbial communities associated with plastic particles in water and sediment show diversity among and similarities between distinct *Plastisphere* communities (Tables 1, 2). In the marine environment, *Prochlorococcus* sp. and *Synechococcus* sp. are prevalent on plastics, along with oil degraders (e.g., *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*, *Comamonadaceae*, and *Chitinophagaceae* have been found in both environments (Table 1) (McCormick et al. 2014). The diverse microbial composition of marine biofilms leads to interspecies interactions that can affect

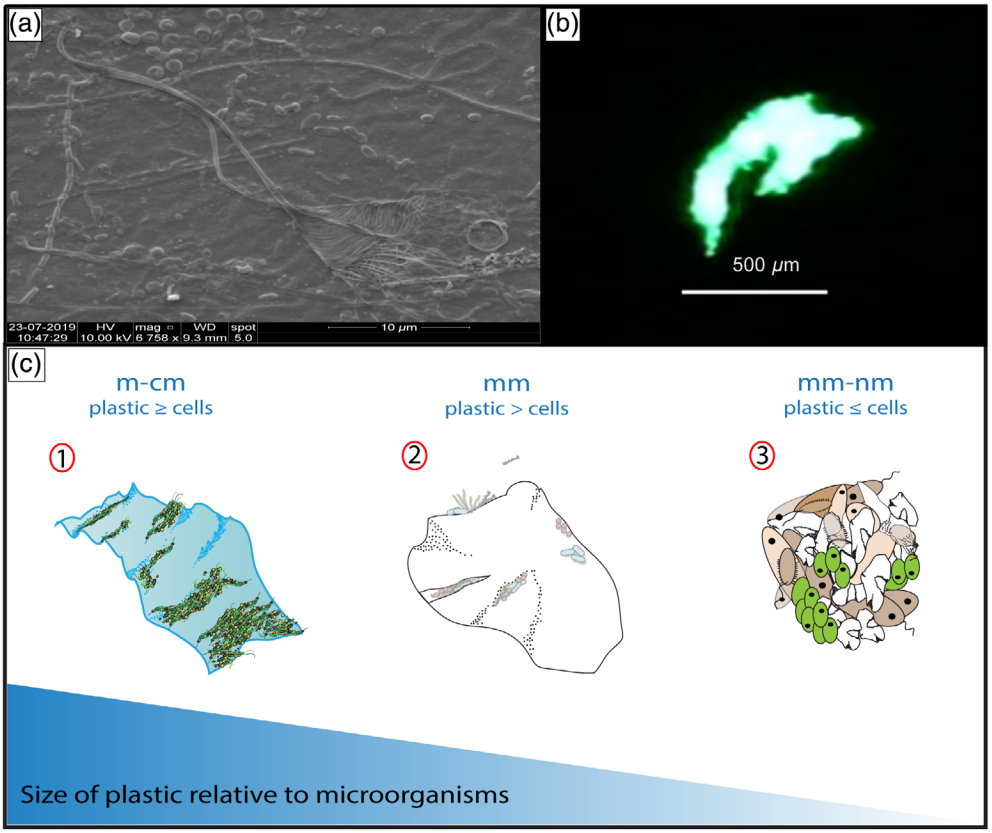

Fig. 2. (**a**) SEM image showing the microbial diversity found on a PE sheet placed in the surface water column of Svanemøllehavnen, Copenhagen, Denmark. The plastic was exposed to the environment for 6 months (January–June 2019). (**b**) Polyvinyl chloride (PVC) floc of 500 μm made of 10–20 μm particles size in unfiltered seawater as determined by PCam camera-system (courtesy of Thorbjørn J. 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 (microplastics, < 5 mm), 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.

microplastics fate in the water column and sediment. Interspecies interactions, such as competition, viral infections, and horizontal gene transfer, influence the structure, stability, and behavior of the biofilms and can influence plastic colonization and biodegradation (Arias-Andres et al. 2018*a*; Pollet et al. 2018; Oberbeckmann and Labrenz 2020). In a recent study, Pollet et al. (2018) explored these interactions and argue that symbiotic rather than competitive interspecies interactions might evolve due to a strong connection between bacterial species, revealing that microbial assemblages in marine biofilms are remarkably cohesive.

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) (Harrison et al. 2014; Bryant et al. 2016). With smaller particles on the nanometer-centimeter scale, biofilm builds on the plastic particles, embeds in the surface (i.e., accessing holes and crevices), and captures other floating organic or plastic particles in extracellular polymeric substances (EPS). In this manner, cell-plastic aggregates form that function as hotspots for biogeochemical cycling during their residence in the water column and as settled material (Fig. 2c) (Arias-Andres et al. 2018*b*; 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 (Fig. 2c; Table 2). In a recent study, Roager and Sonnenschein (2019) proposed that marine microorganisms have adapted to plastics as a surface for colonization and potentially degradation. For example, a common marine plastic-colonizing family of Erythrobacteraceae has been identified on different types of plastic and was found on both macro- and microplastics.

Communities on plastic debris in surface water differ from those of the surrounding seawater. One example is the photosynthetic filamentous cyanobacteria, that is, *Phormidium* and *Rivularia*, that dominate plastic debris but are not abundant in the seawater (Zettler et al. 2013). These differences between biofouling and ambient communities may be explained by the

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- freshwater[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- freshwater[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,r]	*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], mouth of Warnow river in Baltic Sea[r]	PE[a,b,e,f,i,l], PS[e,f,l], PP[a,b,f,l], PA[l], PET[l], Paint[r]
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- freshwater[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]	*Photobacterium*[r]	North Atlantic[a], North Sea-water/sediment[d], mouth of Warnow river in Baltic Sea[r]	PE[a,d], PP[a,d], Paint[r]

(Continues)

Table 1. Continued

Family	Genus	Environment	Plastic type
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- freshwater[q]	PE[a,f], PS[f], PP[a,f,], PET[h], LDPE[h]
Pseudomonadaceae[q]	*Pseudomonas*[q]	Downstream waste water treatment plant- freshwater[q]	
Chitinophagaceae[a,f,b,q]	*Sediminibacterium*[q]	Downstream waste water treatment plant- freshwater[q]	
Verrucomicrobiaceae[a]	*Prosthecobacter*[q]	North Atlantic[a], downstream waste water treatment plant-freshwater[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- freshwater[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,r], 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], Desulfobulbaceae[r], Burkholderiaceae[r], Christensenellaceae[r], Spirochaetaceae[r]	*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], *Maritimimonas*[r], *Maribacter*[r], *Planktomarina*[r], *Desulfatitalea*[r], *Phaselicystis*[r], *Anderseniella*[r], *Aegiribacteria*[r], *Leptospiraceae*[r], *Thermodesulfovibrionia*[r]	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-freshwater[q], mouth of Warnow river in Baltic Sea[r]	PE[a,b,c,f,i,l], PS[c,f,l], PP[a,b,c,f,l], PET[h,l], PA[l], LDPE[h], Paint[r]

(Continues)

Table 1. Continued

Family	Genus	Environment	Plastic type
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], *Thalassiosira*[k], *Chaetoceros*[a], *Cyclotella*[m], *Navicula*[a], *Pleurosigma*[m], *Sellaphora*[a], *Stauroneis*[a]	North Atlantic[a], Coastal Australia[k], Sargasso Sea[m]	PE[a,k], PS[k], PP[a,k]
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. (2018)[#], [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)[#], [r]Tagg et al. (2019).

longevity and relative mobility of microplastics in the water column. Fazey and Ryan (2016) tested the relationship between plastic buoyancy and time finding that after 17–66 d most of the microplastics had buoyancy changes that would cause sinking. Once in the sediment, these long-lived plastic particles likely become immobile. An investigation of biofilm structure and composition on microplastics buried in estuarine marine sediments also reports differences between the communities on microplastics and those found in the surrounding sediment (Harrison et al. 2014). These observations open new questions as to whether epiplastic communities specifically choose plastic particles over other surfaces to colonize.

Whereas it has been shown that the communities differ between biofilms and the ambient environment, there is no consensus on whether biofilms differ between substrates. Oberbeckmann et al. (2016) analyzed the composition of microbial and eukaryotic colonizers on polyethylene terephthalate (PET) bottles and glass slides placed in buoys in the North Sea. They found significant seasonal and locational differences, but no differences between the PET and glass associated 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 finding, showing that microbial communities clustered more strongly by geography than by polymer type (Amaral-Zettler et al. 2015). Therefore, a key issue to understand the *Plastisphere* is whether and how the natural theory postulated by Baas-Becking (1934) "everything is everywhere, but the environment selects" applies to this new niche. The surrounding environment, that is, whether microplastics are residing in the water column, sediment, coastal or oceanic environment, may select for community composition. As redox environment and microbial community composition

Table 2. Organisms identified on plastics placed in situ for experimental incubation.

Family	Genus	Location	Plastic type
Bacteria			
Flavobacteriaceae[b]	*Eudoraea*[a], *Maritimimonas*[a,], *Psychroserpens*[a,g], *Mesonia*[g], *Tenacibaculum*[a,g], *Pibocella*[g], *Polaribacter*[a,g], *Lacinutrix*[a], *Maribacter*[g], *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,]	*Profundibacterium*[a], *Ahrensia*[g], *Leisingera*[g], *Loktanella*[g], *Nereida*[g], *Octadecabacter*[g], *Paracoccus*[g], *Roseobacter*[g,h], *Roseovarius*[g], *Sulfitobacter*[a,g]	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]	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], Planctomycetaceae[b], Phycisphaeraceae[b], Rubritaleaceae[d], Simkaniaceae[b], Cryomorphaceae[b], Saprospiraceae[b], Flammeovirgaceae[b], Rhodospirillaceae[b]	*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]	North Sea[a,b] Mediterranean[d], Yellow Sea[g]	PE[a], dolly rope[a], PET[b], PVC[d,g], Plexiglas[g]
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]

[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).

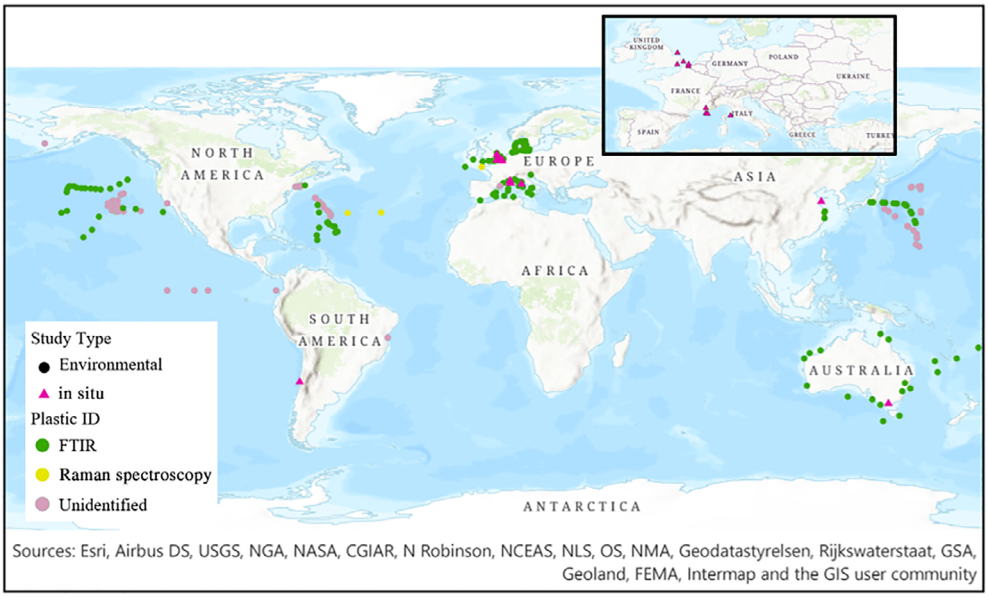

Fig. 3. Global map of studies exploring the microbial communities associated with plastic. Circles show locations of samples taken from the water or sediment. Pink triangles are the locations of in situ experiments with known plastic placed into water or sediment for colonization. In environmental samples, the green, yellow, and light pink circles depict whether plastic was identified with FTIR, Raman spectroscopy, or left unidentified, respectively. Environmental studies: Carpenter et al. (1972), Carpenter and Smith (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. (2018), and 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), and Pollet et al. (2018).

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 particles, but further investigation focusing on the biogeochemical setting of epiplastic communities would help to address the mechanisms of microbial attachment to polymer surfaces.

The biogeochemistry of microbe-plastic interactions

In all aquatic ecosystems, biogeochemical cycling forms the foundation for synthesis and degradation of organic matter (Thamdrup et al. 1994; Jørgensen 1995). The widespread introduction of microplastics to the marine environment has promoted interactions between microorganisms and microplastics (Roager and Sonnenschein 2019) which may include microbial utilization of microplastics or its degradation intermediates as a carbon source, substrate, or cosubstrate. In water or sediment, microbial carbon utilization is linked to available electron acceptors, that is, oxygen, sulfate, nitrate, and ferric iron (Fig. 1). In this regard, redox environment influences the microbial community composition and key microbial respiratory pathways. Therefore, microorganisms may actively interact with microplastics linking available electron acceptors to the utilization of these polymers.

Alternatively, microorganisms may passively attach to microplastics using them primarily for surface colonization. Through active or passive interactions, microorganisms, microplastics and their degradation, and metabolic products are transported within the aquatic environment, passed through food webs and made available for biotic or abiotic reactions within aquatic biogeochemical cycles (Jørgensen 1995; Zettler et al. 2013). Redox setting therefore becomes a key consideration for microplastic fate in the water and sediment, which requires further study. Constraints imposed by redox driven processes in water and sediment may even be one explanation for observations that geographic location influences the microbial community colonizing plastic particles (Amaral-Zettler et al. 2015).

The incorporation of microplastics and their intermediate degradation products into the carbon cycle may begin at the water surface through a combination of abiotic and biotic processes. Plastic interaction with sunlight releases methane and other hydrocarbon gases into surrounding water (Royer et al. 2018). In addition to gases, plastic particles also release dissolved organic carbon (DOC) in water when breaking down under abiotic processes (Romera-Castillo et al. 2018). These intermediate degradation products are potential electron donors to be utilized by microorganisms. Beyond the leaching of intermediates and degradation products from microplastics, which affect marine carbon cycling, the formation of microbe-plastic aggregates also acts as a biogeochemical pathway. As microplastics floats in the water, biofilm forms, in

some cases producing aggregates that trap microplastics (Long et al. 2015; Porter et al. 2018). These aggregates are hotspots of heterotrophic microbial activity that can vary by nutrient load in aquatic environments (Arias-Andres et al. 2018*b*). The aerobic respiration of the biofilm, and potentially the plastic particles increases oxygen utilization in the water column and within the aggregates (Arias-Andres et al. 2018*b*). Aggregates like marine snow and fecal pellets can develop anoxic inner cores, which may cause the incorporated microplastics to degrade more slowly (Arias-Andres et al. 2018*b*). The presence of oxygen enhances abiotic degradation of microplastics (Andrady 2011), so with little to no oxygen present in aggregate cores, two potential scenarios can occur: (1) anaerobic microbes are not able to utilize the plastic as an electron donor, or (2) plastic can be degraded under low to no oxygen through biotic or abiotic processes. In any case, further research is needed to constrain the impacts of both oxic and anoxic environments on biotic and abiotic microplastic degradation.

As microplastics settle to the seafloor, they become buried and incorporated in the aerobic sediment–water interface and bioturbation zones, as well as in anoxic sediment (Brandon et al. 2019). Microplastics buried in sediment encounters different biogeochemical zones and associated microbial communities that could affect the degradation processes of microplastics. In marine sediment, sulfate reduction is the dominant microbial respiration pathway (Jørgensen and Kasten 2006), and therefore is a key pathway of interest for microplastic fate. In support of this, a study of marine paint particles taken from surface sediments in Germany, Tagg et al. (2019) found higher abundances of the sulfate reducer, *Desulfatitalea tepidiphilia*, on the plastic surface than in the surrounding sediment. While yet undemonstrated, this selective attachment of sulfate reducing bacteria to plastic in sediment indicates potential affinity for and utilization of the carbon-derived from plastic as an electron donor. Other important anaerobic respiratory pathways in environments like mangrove forests, fish farms, or estuaries include nitrogen, iron, or manganese. Studies such as Auta et al. (2017) have found plastic degrading bacteria in mangrove sediments; the connection between the *Plastisphere* and these anaerobic pathways has not been explored yet.

The impact of biogeochemical cycles on plastics is not limited to the microbial processes of carbon utilization, but they can also include abiotic processes. For example, sulfate reduction in the presence of iron can cause the abiotic precipitation of iron sulfide minerals, which could theoretically trap the microplastic particles in the mineral structure (Li et al. 2019). Beyond the major element cycles, microplastics may have a notable interaction with trace elements. A recent study measured selenium concentrations in biofilms collected from larger marine plastic debris and found elevated levels compared to background seawater (Mitchell et al. 2019). Similarly, Holmes et al. (2014) found that trace metals (Cd, Co, Cr, Cu, Ni, Pb) adsorbed onto polyethylene (PE) pellets, with more adsorbing onto degraded pellets than virgin pellets, due to differences in surface properties. Selenium, and many other trace elements, acts as bio essential nutrients, but as of yet studies are lacking which test the adsorption by plastic or the natural concentrations present in plastics (Mitchell et al. 2019). The extent of potential abiotic and biotic degradation (i.e., via sulfide, iron, or methane metabolism) is just beginning to be explored. Where pelagic aggregates are buried, organic matter will enter anoxic zones and be decomposed via fermentation, denitrification, sulfate-reduction, and methanotrophy, yet little is known about how plastic particles are preserved or degraded under anoxic conditions.

Microbe-mediated transport of microplastics

When released to aquatic environments, plastic particles lighter than the surrounding media float and are transported by the water. A combination of physiochemical and biological mechanisms drives the transport of microplastics from surface waters to sediments (Kaiser et al. 2017; Porter et al. 2018). In coastal regions, microplastics 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 microplastics offshore to convergence zones in central gyres, which include wind mixing and density differences in thermohaline gradients, affects the concentrations of microplastics in the surface of the water column (Zhang 2017). Particle settling and velocity are also regulated by microplastics properties, that is, density, shape, and dimension (Zhang 2017) and biofilm growth. Biofilm growth influences the residence time of microplastics 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 microplastic fate (Rummel et al. 2017; Michels et al. 2018; Porter et al. 2018). Environmental factors (e.g., salinity, temperature, oxygen, and high nutrient concentrations) will influence microbial growth and may alter microplastics density and transport.

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 microplastics aggregation, it remains poorly understood. Like organic or mineral particles, microplastics are found in the marine ecosystem as free particles, as homoaggregates consisting purely of plastic particles (flocs) (Fig. 2b), or as microbe-plastic aggregates (e.g., marine snow and fecal pellets) (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 plastic particles (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 (Kaiser et al. 2017).

Plastic-polymer 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, similar to plastic polymers; however, the pathways of plastic degradation are still nascent. 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 particles (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 (Souza et al. 2011). 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 plastic particles (Table 3); however, the precise pathway has not yet been identified. Further exploring microorganisms that can degrade chitin will help us to better understand the mechanisms behind polymer degradation (Wright et al. 2019).

Petroleum is composed of a suite of compounds with various molecular weights and biodegradation rates. Compounds in petroleum most similar to plastic particles include resins, asphaltenes, and other higher molecular weight compounds, which have incredibly slow biodegradation rates (Liao et al. 2009). Many bacteria are able to degrade different petroleum compounds with several species of *Bacillus* and *Pseudomonas* known to degrade asphaltenes, but also plastic-polymers (Table 3). Other petroleum-degrading species have also been found on plastic particles (Tables 1, 2) including *Pseudoalteromonas*, *Vibrio*, *Acinetobacter*, *Alteromonas*, *Oceanospirillales*, and *Colwellia*. Similar to chitin degradation, the mechanisms for petroleum degradation could also model for plastic degradation. Petroleum degradation depends on both biotic and abiotic processes. Biotic degradation is limited by nutrient availability, temperature, oxygen, and sunlight whereas photooxidation, evaporation, and dissolution are the key abiotic petroleum degradation processes (Hazen 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-polymer are enhanced by the presence of ultraviolet (UV) light and oxygen. Indeed, light and oxygen

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. (2008), [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 Devi 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).

are the main limiting factors to the abiotic degradation of plastic particles 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 polymer surface. 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 and Albertsson 2004). Plastic particles develop microcracks and become brittle under extended exposure to UV, which facilitates its physical breakdown (Andrady 2011). The impact of these abiotic environmental factors on plastic degradation has not been determined, but Arias-Andres et al. (2018*b*) found a relationship between nutrient concentration and biomass quantity, with biofilm growth being higher on microplastics in oligo-mesotrophic and dystrophic lakes than in nutrient-rich lakes.

These studies on plastic particles 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, e.g., lakes, where the debris may persist longer and consequently be exposed to UV radiation longer than in marine environments). In deep marine waters, the absence of light, high pressure, and low temperatures is prone to inflict selective forces on microbe-plastic aggregation that differs from those found in shallow and freshwater environments (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 plastic particles 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). Plastic particles also leach 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. 2017). 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 high-density polyethylene (HDPE), PE, and 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 microplastics can have on microbes in the marine environment.

A hindrance to quick biodegradation of chitin, oil, and plastic particles 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 (Krasowska and Sigler 2014). Some microorganisms have developed mechanisms to overcome this challenge. Indications of microorganisms embedding on PE surfaces have been shown by scanning electron microscope (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). *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., helps them attach to the plastic, but may also help spread these pathogens by transportation on plastic in marine environment (Keswani et al. 2016).

The sediment has been identified as a major sink of plastic debris (Peng et al. 2018; Brandon et al. 2019). 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-d 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). 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.

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 particles, allowing marine plastic debris to be identified by plastic type (Araujo et al. 2018; Wiggin and Holland 2019). 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 forming on the polymer surface 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 (Restrepo-Flórez et al. 2014). 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 (Rummel 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-labeled 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, but no specific enzymatic pathway has been discovered (Table 3). These microorganisms cover a broad range of characteristics with some being thermophilic, aerobic, and motile, while others are anaerobic and potentially pathogenic. 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). Of particular interest is *Ideonella sakaiensis*, a novel bacterium isolated from a 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 (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 Devi et al. 2015), and a bacterium, *I. sakaiensis*, from a PET recycling facility, which showed polymer 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. In another study, Russell et al. (2011) collected different bacteria and fungi from the Amazonian rainforest. They cultured these endophytes, which are known to have broad metabolic capabilities and found that two *Pestalotiopsis* strains could utilize polyurethane (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).

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-gas chromatography-mass spectrometry (GC-MS) paired with an isotope ratio mass spectrometer (compound specific stable isotope analysis [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 labeled biodegradable PS 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 labeled plastic into their biomass. Furthermore, pyrolysis-

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 labeling show promise in their ability to track the fate of plastics in biofilm growth and the environment.

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 et al. (2014) used 10 μm 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. 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 (POPs) and potentially plastics (i.e., Lu et al. 2019). Similar to spreading pathogenic bacteria, plastic debris can absorb hydrophobic 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 (Andrady 2011; Debroas 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 (i.e., Lu 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 due to biofilm presence that resulted 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), 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 (Rellstab and Spaak 2008). 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 control biofilms grown on glass surfaces (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.

Future directions

As the study of marine microplastics evolves, a number of key directions in microbe-plastic interactions warrant further study. First, we must continue to define epiplastic community composition. A collective global database on microorganisms associated with plastic is needed to capture the full breadth of organisms in the *Plastisphere*. This collection will help clarify the *Plastisphere*'s core microbiome and functionalities (full review in Roager and Sonnenschein 2019), as well as define the drivers behind *Plastisphere* community composition. One driver of community composition may be microbial selection for substrate surface. Selection might be passive in that the microbes seek a surface to attach or selection may be active in that the microbes colonize plastic surfaces and utilize them as a carbon substrate. Evidence suggests *Plastisphere* composition is distinct from ambient communities; however, investigations must include other substrates like wood, glass, metal to clarify whether community is unique to plastic (Zettler et al. 2013; Harrison et al. 2014; Amaral-Zettler et al. 2015).

Herein, we discuss how biogeochemical processes impact microbe-plastic interactions. It is now apparent that plastics moved through various redox environments from their introduction to the aqueous environment, through their transport in food webs and as aggregates in the water column and to their eventual place of deposition. In the water column, the biogeochemical environment may influence biofilm development, mineralization, grazing by predators, transport, and abiotic or biotic diagenesis of microbe-plastic aggregates (i.e., Zettler et al. 2013; Harrison et al. 2014; Amaral-Zettler et al. 2015). Studies show microplastics accumulate in sediment (Brandon et al. 2019) and therefore likely experience a variety of abiotic and biotic processes controlled by aerobic and anaerobic respiratory pathways. Therefore, the dominant abiotic and biotic biogeochemical processes impacting plastic in the environment are another new and important area of research to determine plastic fate. Accordingly, we recommend biogeochemical parameters and redox setting be characterized and considered in future studies of plastic degradation and fate. Extension of molecular approaches, such as metagenomics, proteomics, and metabolomics, may yield new perspectives here as well. Several studies have shown the interactions of microorganisms and microplastics in the water column, further research regarding the processes and interactions happening in both freshwater and marine sediments will elucidate the fate of buried microplastics.

Last, analytical and methodical challenges remain a fundamental frontier for the study of microbe-plastic interactions, transport, and plastic biodegradation pathways in the environment. The need for standard sampling and analytical method development across fields is both acknowledged in the community and ongoing. 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. 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, that is, 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 20 μm and 500 nm, respectively (Araujo et al. 2018; Wiggin and Holland 2019). 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 Devi 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 spectroscopy. However, there is no consensus on whether this dye interferes with the identification of the plastic type using FTIR or Raman spectroscopy (Araujo et al. 2018). The treatment of microplastics for experiments, including pre-UV degradation, and sterilization, should be uniform. Along the same lines, methods for microbe isolation and culture work must be homogenized. To study the interactions between microorganisms and microplastics 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* (also argued in Roager and Sonnenschein 2019). We must develop consistent and efficient methods in how we collect, treat, and analyze epiplastic communities. These approaches must integrate knowledge reaped from other fields, that is, that the taxonomic composition of microorganisms of a filtered seawater sample may change depending on the amount of water filtered (Padilla et al. 2015). 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 (i.e., Wiggin and Holland 2019).

As we continue to define the environmental fate of plastic in aquatic environments, our key challenges remain the synthesis of interdisciplinary approaches and understanding, analytical limitations and development, and the placement of our observations into the environmental context. Biogeochemical cycling lies at the heart of the two-way interactions between microplastics and microorganisms. Future research must 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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Conflict of Interest

None declared.

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