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# Marine Microbial Assemblages on Microplastics: Diversity, Adaptation, and Role in Degradation

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## Keywords

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## Abstract

We have known for more than 45 years that microplastics in the ocean are carriers of microbially dominated assemblages. However, only recently has the role of microbial interactions with microplastics in marine ecosystems been investigated in detail. Research in this field has focused on three main areas: (a) the establishment of plastic-specific biofilms (the so-called plastisphere); (b) enrichment of pathogenic bacteria, particularly members of the genus *Vibrio*, coupled to a vector function of microplastics; and (c) the microbial degradation of microplastics in the marine environment. Nevertheless, the relationships between marine microorganisms and microplastics remain unclear. In this review, we deduce from the current literature, new comparative analyses, and considerations of microbial adaptation concerning plastic degradation that interactions between microorganisms and microplastic particles should have rather limited effects on the ocean ecosystems. The majority of microorganisms growing on microplastics seem to belong to opportunistic colonists that do not distinguish between natural and artificial surfaces. Thus, microplastics do not pose a higher risk than natural particles to higher life forms by potentially harboring pathogenic bacteria. On the other hand, microplastics in the ocean represent recalcitrant substances for microorganisms that are insufficient to support prokaryotic metabolism and will probably not be microbially degraded in any period of time relevant to human society. Because we cannot remove microplastics from the ocean, proactive action regarding research on plastic alternatives and strategies to prevent plastic entering the environment should be taken promptly.

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## 1. THE GENESIS OF A NONDEGRADABLE MULTIPURPOSE PRODUCT AND ITS ENTRY INTO THE MARINE ENVIRONMENT

Since the Paleolithic era, a hallmark of the human experience has been the development of tools essential for survival. Biopolymers of high molecular mass, such as wood, wool, flax, hemp, bones, resin, and latex, have served to make tools, clothes, and residences, but their benefit is limited by their restricted formability, modifiability, consistency, and vulnerability to degradation. As a consequence, humans tried very early on to modify biopolymers and create materials of better quality for their daily needs. Dating back to the Middle Pleistocene, the distillation of birch bark and modification of polymers led to the generation of birch-bark tar that has been used as an adhesive (Kozowyk et al. 2017). Ancient Mesoamericans harvested latex [high-molecular-weight poly(*cis*-1,4-isoprene)] from *Castilla elastica*, processed it using *Ipomoea alba* juice, and fashioned rubber tools (Tarkanian & Hosler 2011), a process that dates back to at least 1600 BC. Around 3,000 years later, in 1839, Charles Goodyear developed vulcanization, a major breakthrough in the development of new and synthetic polymers. Originally, vulcanization involved the cross-linking of linear poly(*cis*-1,4-isoprene) chains by sulfur bridges, leading to superior physical properties (Akiba & Hashim 1997). The first synthetic polymer with industrial relevance was Bakelite; in the early years of the twentieth century, Leo Hendrik Baekeland discovered and published a technique to produce this phenol- and formaldehyde-based polymer (Baekeland 1909), which could be pressed and hardened into shape, resisting mechanical damage, heat, and acids. Since then, and especially after the 1950s, the development of new synthetic polymers with various societal benefits increased significantly, making plastics an easily producible and almost indispensable product (Andrady & Neal 2009, Thompson et al. 2009). Plastic is now crucial in such diverse areas as medicine, building and construction, packaging, electronics, and aeronautics.

More than 348 million tons of plastic was produced worldwide in 2017 (PlasticsEurope 2018). The European demand for polymers was highest for low- and high-density polyethylene (17.5% and 12.3%, respectively), polypropylene (19.3%), polyvinyl chloride (10.2%), polyurethane (7.7%), polystyrene (7.4%), and polyethylene terephthalate (7.4%). Of the remaining ~20%, polyamide, acrylonitrile butadiene styrene, and polycarbonate represent the industrially important polymers (PlasticsEurope 2018). A certain portion of this plastic ends up in the global oceans (Barnes et al. 2009, Galgani et al. 2013, Law 2017), and studies have estimated that floating marine plastic totals somewhere between 70,000 and 270,000 tons (Cozar et al. 2014, Eriksen et al. 2014, van Sebille et al. 2015). On the other hand, estimates suggest that 4.8–12.7 million tons of plastic litter was introduced into marine systems in 2010 alone (Jambeck et al. 2015). This means that only 1% of plastic introduced in marine systems is recovered as floating debris, indicating that the particles only remain on the ocean surface for a limited period of time (Cozar et al. 2014, Eriksen et al. 2014). Thus, because the fate and behavior of plastic in the marine system are still largely unclear, there is a large gap between knowledge of plastic entry into the ocean and knowledge of its retention.

Human-generated litter enters the oceans from land and offshore (Law 2017, Sheavly & Register 2007). Approximately 80% of the marine plastic debris originates from land-based sources (Andrady 2011), whether discarded directly into the environment by beach-related tourism, improperly managed farther inland and blown into the sea, or introduced by rivers, municipal drainage systems, or sewage effluents (Andrady 2011, Auta et al. 2017a, Barnes et al. 2009, Browne et al. 2011, Derraik 2002, Pruter 1987). The most substantial offshore source is the world's fishing fleet (Andrady 2011), followed by marine aquaculture (Hinojosa & Thiel 2009); illegally discarded litter from vessels or offshore platforms (Sheavly & Register 2007) and the content of lost cargo containers also contribute (Derraik 2002). The relative prevalence of macro- and microplastics in the ocean is still unknown and is the subject of current research.

Microplastics (particles less than 5 mm in size) are divided into two groups according to their origin. So-called primary microplastics are directly synthesized for consumer products, such as hand and facial cleansers, shower gels, or toothpaste (Fendall & Sewell 2009, Gregory 2009). Along with clothing fibers rinsed out by washing machines, these microplastics can reach the sea via sewage effluents (Browne et al. 2011). Primary microplastics also include abrasive materials from the air-blasting industry and virgin preproduction resin pellets lost during transport (Ogata et al. 2009). Hence, primary microplastics are already on a millimeter size scale when they reach aquatic environments. Secondary microplastics, on the other hand, are formed from larger floating plastic fragments as a result of fragmentation in the environment (Arias-Villamizar & Vazquez-Morillas 2018, Cooper & Corcoran 2010); fragmentation is a main topic in the second part of this review and is discussed in more detail in Section 4.

The ubiquitous presence of microplastics in the marine environment has been demonstrated. These plastics not only concentrate in the large ocean gyres but are also found everywhere from the polar regions (e.g., Peeken et al. 2018) to the equator, from densely populated areas to remote islands (Ivar do Sul et al. 2009), and from beaches (Claessens et al. 2011) down to the deep sea (Van Cauwenberghe et al. 2013). Plastic particles are found floating at the sea surface, suspended in the water column, and contained in sediments, depending on their density relative to seawater. Most consumer polymers are less dense than seawater, but the density of a virgin polymer particle is altered when the end product is manufactured (e.g., increased due to fillers or decreased by foaming), as well as through aging and biofouling (Harrison et al. 2011, Kaiser et al. 2017). Consequently, the polymer composition found in environmental samples depends on the sampling depth. Most of the microplastic particles found in neustonic samples are low- and high-density polyethylene, polypropylene, and expanded polystyrene (Moret-Ferguson et al. 2010, Reisser et al. 2014). Sediment studies have also reported the accumulation of polymers such as polyamide, solid polystyrene, polyvinyl chloride, polyurethane, polyester, polyethylene terephthalate, acrylic polyoxymethylene, polyvinyl alcohol, polymethyl methacrylate, and alkyd (Browne et al. 2010, Hidalgo-Ruz et al. 2012, Moret-Ferguson et al. 2010). Beaches serve as intermediate environments, connecting land-based debris with aquatic ecosystems, and their sediments can accumulate all polymer densities. The highest concentration of microplastic particles, at  $1.2 \times 10^7$  particles per cubic meter, was recently detected in a core taken from the pack ice of Fram Strait (Peeken et al. 2018).

Dissolved organic pollutants in the ocean interact with microplastics, and this interaction is dependent on the physicochemical properties of the organic compounds. Microplastics have a large surface-to-volume ratio when compared with relatively larger plastics and thus are more likely to accumulate hydrophobic organic substances (Engler 2012, Mato et al. 2001), including persistent organic pollutants such as polychlorinated biphenyls, polycyclic aromatic hydrocarbons, and organic chlorine compounds such as DDT. In addition to the polymer, plastics usually contain potentially toxic plasticizers or additives, which leach into the environment. Therefore, research is being carried out to determine whether microplastics cause a significant accumulation of toxic substances in the marine food web. Currently, however, the ecological consequences cannot be assessed.

## **2. EXISTING KNOWLEDGE AND RESEARCH GAPS FOR MARINE MICROPLASTIC BIOFILMS**

Besides accumulating organic pollutants, microplastic surfaces serve as colonization grounds for diverse microbial communities in aquatic habitats (De Tender et al. 2015, Dussud et al. 2018, Hoellein et al. 2017, McCormick et al. 2014, Oberbeckmann et al. 2014, Zettler et al. 2013).

The collection of microbial communities inhabiting plastic debris is commonly termed the plastisphere.

Marine microplastic biofilms are shaped primarily by biogeographical and environmental factors, such as salinity and nutrient concentration (Amaral-Zettler et al. 2015, Oberbeckmann et al. 2018). Although not as strong a contributor, the microplastic surfaces themselves also influence the colonization processes, and there has been discussion of whether specific overrepresented and potentially hydrocarbonoclastic members of marine microplastic biofilms could use plastics as an energy source because of their ability to degrade highly complex biopolymers such as lignin and petroleum derivatives (Oberbeckmann et al. 2016, 2018; Ogonowski et al. 2018; Zettler et al. 2013).

In recent years, increasing concern has been raised about the hazard potential of microplastic-associated microbial communities. Potential pathogens might be distributed into formerly unaffected ecosystems while hitchhiking on microplastics that originated, for instance, from sewage treatment plants or animal guts (Oberbeckmann et al. 2015). Studies have suggested that members of the genus *Vibrio* are particularly enriched on microplastics (Frere et al. 2018, Zettler et al. 2013), but others have disputed the preferential colonization of microplastics by *Vibrio* spp. (Bryant et al. 2016, Oberbeckmann et al. 2018, Schmidt et al. 2014). Besides colonization with pathogens, the role of microplastics as carriers for antibiotic resistance genes has been discussed. In this context, two freshwater studies compared microplastic assemblages with their corresponding water communities and demonstrated that the microplastic-associated assemblages had an increased transfer frequency of a plasmid coding for trimethoprim resistance (Arias-Andres et al. 2018) and higher abundance of the gene *int1*, a proxy for anthropogenic pollution (Eckert et al. 2018).

Knowledge of the microbial composition of biofilms associated with microplastics has increased in the last five years (Ivar do Sul et al. 2018). The first groundbreaking studies on marine biofilms on microplastics showed that these communities can differ significantly from those of the surrounding water (Amaral-Zettler et al. 2015, Bryant et al. 2016, Debroas et al. 2017, Frere et al. 2018, Oberbeckmann et al. 2014, Zettler et al. 2013). This can be expected, however, since microbial community compositions on natural particles usually differ from free-living microorganisms (Crespo et al. 2013, Rieck et al. 2015) due to their dissimilar lifestyles as sessile organisms. Thus, until it is established whether there is a true microplastic-indicative plastisphere, as compared with natural-particle-associated assemblages (e.g., those on wood, cellulose, or glass), the role of biofilms on microplastics will remain obscure.

The aim of this review is to critically evaluate the potential role of marine microorganisms in relation to ocean-polluting microplastics. We present the current state of knowledge of marine microbial assemblages on microplastics, with a focus on pathogenic bacteria, and attempt to deduce their impact on marine ecosystems and potential risk for humans. We evaluate whether plastic-specific microbial communities may indicate microplastic degradation, or at least the possibility of adaptation of microorganisms to its degradation. Based on this evaluation, we critically assess whether marine bacteria have the potential to remediate the ocean from plastic pollution in the future and conclude with recommendations for further action in scientific and societal contexts.

### 3. AN EVALUATION OF THE PLASTISPHERE

#### 3.1. Data Selection for Meta-Analysis

Our approach to evaluating the plastisphere was to merge the relevant worldwide data and re-analyze the microbial communities in a comparative way. We focused on bacterial 16S rRNA gene databases because of the large number of comparable (harmonized) data sets available. When selecting sequences for the meta-analysis, we focused on polyethylene samples as a model

polymer surface because it represents the most common plastic pollutant in the ocean. Additional sequences came from polystyrene, unknown polymers, natural (i.e., control) surfaces (wood, cellulose, and glass), sediment, and, if available, the particle-attached water fraction ( $>3\ \mu\text{m}$ ) or otherwise the whole surrounding water. In November 2018 we performed independent searches in Web of Science using the following keywords: microplastic(s) and biofilm(s), microplastic(s) and microbial/bacterial assemblages, microplastic(s) and colonization/colonisation, and microplastic(s) and plastisphere. This led to a list of 61 peer-reviewed publications, of which 16 represented community analyses regarding microplastics. We selected studies for the meta-analysis that met the following criteria: (a) The study had been carried out in marine or brackish waters, (b) the study used Illumina technology for sequencing, (c) the targeted 16S rRNA fragment contained the V4 region, (d) the data were deposited at the National Center for Biotechnology Information's Sequence Read Archive, and (e) the description of the sampling source in the database was sufficient (e.g., clear differentiation between seawater and plastic samples). Five studies met all of these criteria: one from the North Sea (De Tender et al. 2015), three from the Baltic Sea (Kesy et al. 2019, Oberbeckmann et al. 2018, Ogonowski et al. 2018), and one from the Yangtze Estuary (Jiang et al. 2018). **Supplemental Table 1** lists all of the data used in the meta-analysis, and the **Supplemental Appendix** describes the methods applied for data processing and statistical analyses.

### 3.2. Geographical Factors Play a Larger Role than the Particle Surface in Shaping Biofilms

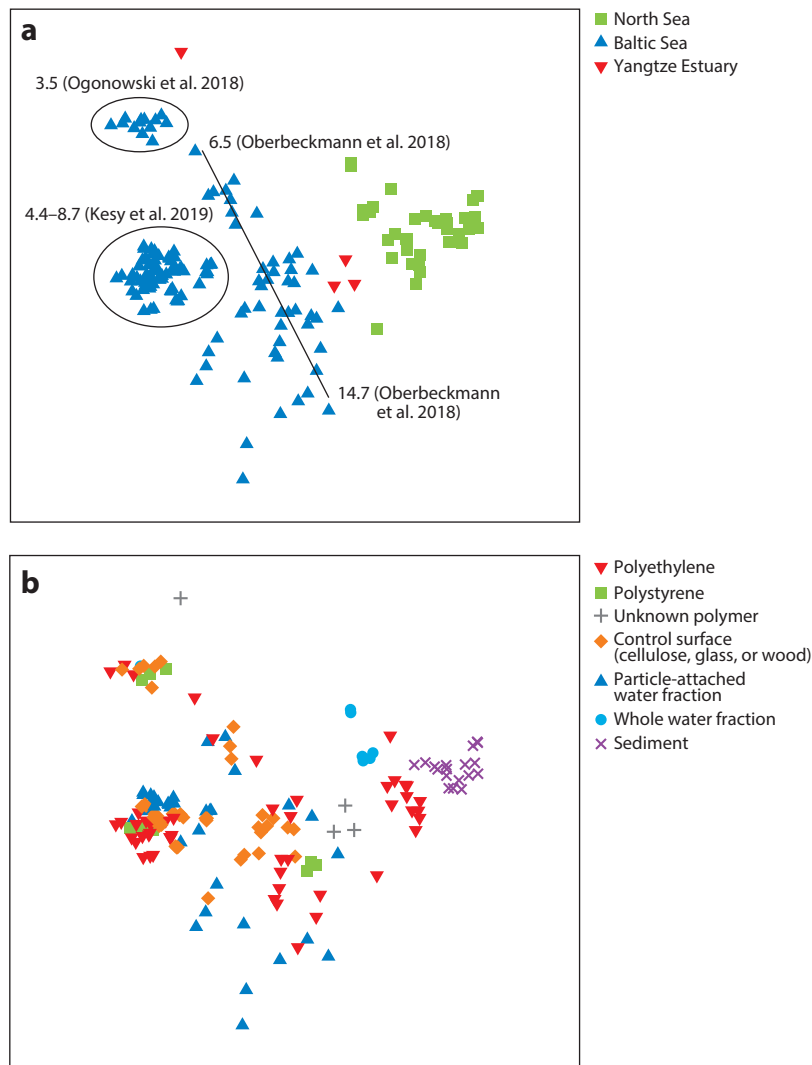
Our comparative analyses revealed that the plastic itself was a minor factor in determining microplastic-associated biofilms. Instead, the first-order determinant shaping the bacterial assemblages was the sampling area (i.e., geographical region), which discriminated the communities into distinct clusters, as supported by pairwise PERMANOVA ( $p = 0.001$ , North Sea versus Baltic Sea versus Yangtze Estuary) (**Figure 1**).

The average similarity between communities from the Baltic Sea and Yangtze Estuary—both ecosystems strongly influenced by rivers—was 12%, slightly higher than the similarity between communities from the Baltic and North Seas (7%). Within the area of the Baltic Sea, salinity (and potentially other factors, which were not available for all studies) seemed to play an important role in the community composition, as indicated by nonmetric multidimensional scaling ordination (**Figure 1**). Overall, the results of this reanalysis are in accordance with previous studies that showed major differences among microplastic communities from distinct geographical regions (e.g., Amaral-Zettler et al. 2015). Here, we can expand this statement and show that the influence of a geographical region is greater than the influence of surface characteristics when comparing plastic polymers with natural particle surfaces.

Experimental setups, laboratory handling, and extraction methods probably led to distinct bacterial sequencing results in different studies, indicating that the study procedures themselves likely contributed to the differences between samples. This, however, cannot be proven here and is beyond the scope of this review.

### 3.3. Microbial Life on Microplastics and Natural Particles

No agreement has been reached on whether microplastic-associated communities display an increased or decreased diversity compared with their counterparts on natural particles and in the water. While some studies from aquatic ecosystems have reported similar or even higher  $\alpha$ -diversities on microplastics (De Tender et al. 2015, Debroas et al. 2017, Dussud et al. 2018, Frere et al. 2018), other studies have postulated the opposite (Hoellein et al. 2017, McCormick et al. 2014,



**Figure 1**

Nonmetric multidimensional scaling based on a Bray–Curtis similarity matrix of square-root-transformed relative abundances for the five studies analyzed, with stress = 0.13. (a) Ordination based on the sampling areas in the North Sea (De Tender et al. 2015), the Baltic Sea (Kesy et al. 2019, Oberbeckmann et al. 2018, Ogonowski et al. 2018), and the Yangtze Estuary (Jiang et al. 2018). The salinities of the three studies from the Baltic Sea are also given. (b) Ordination based on the different sample types.

Zettler et al. 2013). Ogonowski et al. (2018) detected similar  $\alpha$ -diversities among all tested biofilm communities but higher values for water communities and explained this result with an overall substrate-driven selection. Kettner et al. (2017) found that the fungal  $\alpha$ -diversity of microplastic assemblages was lower than or analogous to those of wood and water assemblages, depending on spatial factors.

When investigating the  $\beta$ -diversity in our meta-analysis, bacterial communities associated with different polymer types did not show significant differences (pairwise PERMANOVA,  $p > 0.01$ ,

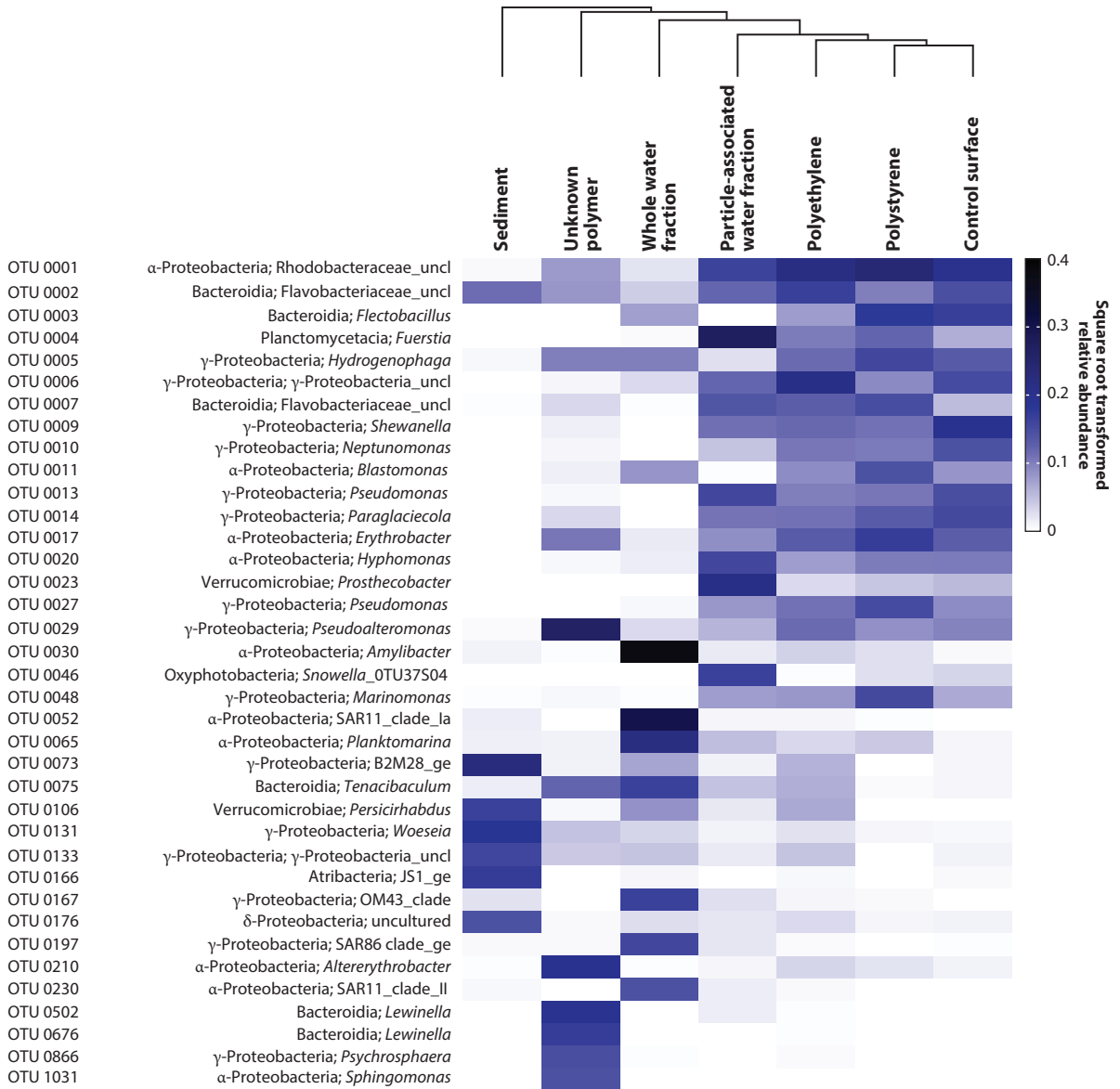
polyethylene versus polystyrene versus unknown; see **Supplemental Table 2**). Furthermore, polystyrene-colonizing communities did not significantly differ from communities on natural control surfaces ( $p = 0.127$ ). Communities from all other sample types were significantly different. Some of these differences, however, were also identified as significant by PERMDISP comparisons (e.g., polyethylene versus control surface; **Supplemental Table 2**), hinting at dispersion effects. This means that differences in variability within the sample data sets, rather than the actual sample characteristics, may have led to the significant result. The influence of the particle surface on its colonization can be shaped by characteristics such as degradability, hydrophobicity, electric charge, or roughness, or indirectly via the formation of a conditioning film over the particle. This probably explains why some studies have reported differences between communities associated with microplastics and natural particles such as cellulose (Ogonowski et al. 2018), the particle-attached water fraction (Dussud et al. 2018), or sediment (De Tender et al. 2015). Also, an incubation experiment in the Baltic Sea demonstrated a differentiation between assemblages on polyethylene and polystyrene from assemblages on wood (as a model of a natural particle), but only under certain environmental conditions (Kettner et al. 2017, Oberbeckmann et al. 2018), highlighting the importance of the sampling area in the development of the microbial biofilm.

Like other bacteria that prefer an attached over a free-living lifestyle (e.g., Nesse & Simm 2018), we can assume that overall most microplastic-biofilm members are opportunistic general colonizers. Even early colonizers might be attracted not by the polymer surface itself but rather by the conditioning film, which increases (for instance) their access to nutrients. This is the case for all particles in suspension in the oceans and does not represent a microplastic-specific phenomenon (e.g., Witt et al. 2011). The family Rhodobacteraceae, for example, is well known for its early and abundant colonization of a broad range of particle surfaces (Dang & Lovell 2016, Elifantz et al. 2013, Mata et al. 2017, Moura et al. 2018) and also colonizes polyethylene microplastics, as revealed by our reanalysis (see Section 3.4).

Other opportunistic colonizers seem to be particularly successful in occupying microplastics as their niche. Several studies have reported that members of the family Hyphomonadaceae thrive on microplastics (Bryant et al. 2016, Oberbeckmann et al. 2018, Zettler et al. 2013), probably because they are able to adhere firmly to the smooth plastic surface by forming the polysaccharide holdfast and because their prosthecae enable more efficient nutrient uptake compared with other biofilm members.

When analyzing all operational taxonomic units (OTUs) from our meta-analysis that reached a mean relative abundance of more than 2% in at least one sample type, we found a high similarity among bacterial communities associated with polyethylene, polystyrene, and natural particles (**Figure 2**). However, some bacteria appeared to prefer polyethylene (OTU 0002, unclassified Flavobacteriaceae; OTU 0006, unclassified  $\gamma$ -proteobacteria), polystyrene (OTU 0005, *Hydrogenophaga*; OTU 0011, *Blastomonas*; OTU 0027, *Pseudomonas*; and OTU 0048, *Marinomonas*), or unknown polymer types (OTU 0017, *Erythrobacter*). Abundant OTUs associated with unknown polymers were in several cases classified as members of the Sphingomonadaceae family, which the core analysis showed play an important role in polyethylene-associated communities (see Section 3.4). We can deduce that, first, those unknown polymers are in fact polyethylene microplastics or that, second, members of these family are particularly associated with microplastics, such as polyethylene and polystyrene.

After the genera of the formerly independent family Erythrobacteraceae had been assigned to the family Sphingomonadaceae, according to release 132 of the SILVA database, this family became an important one—if not the most important one—associated with microplastic-associated biofilms. Two characteristics of this bacterial family might lead to its dominance in microplastic biofilms: its ability to degrade hydrocarbons and its formation of carotenoids. Due to their



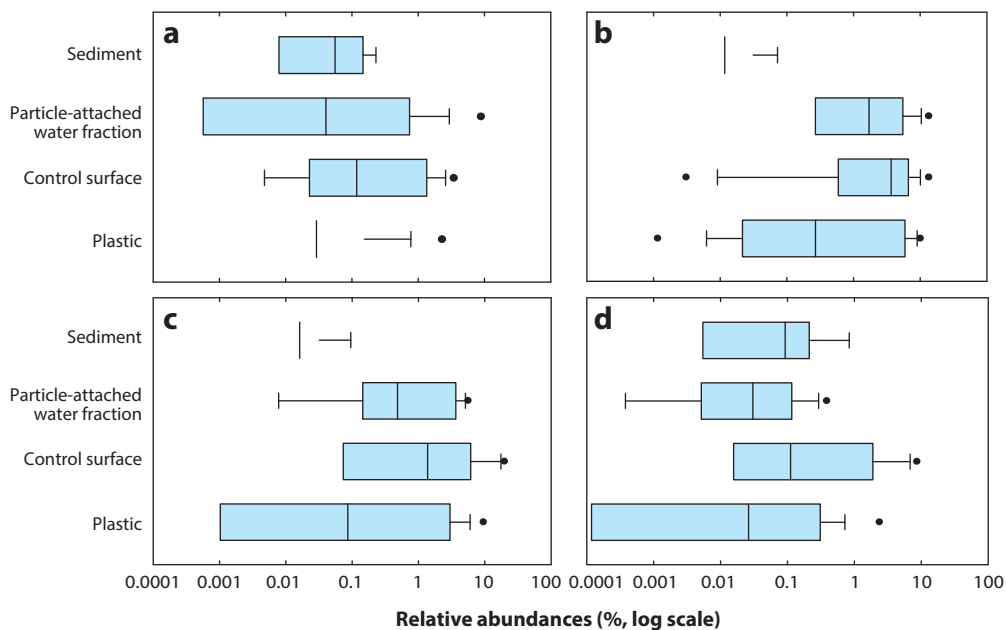
**Figure 2**

Shade plot illustrating the relative abundances (square root transformed) of operational taxonomic units (OTUs) with a mean relative abundance of more than 2% in at least one sample type. The displayed sample types are polyethylene ( $n = 52$ ), polystyrene ( $n = 12$ ), unknown polymer ( $n = 4$ ), control surface (cellulose, glass, or wood;  $n = 42$ ), particle-associated water fraction ( $n = 34$ ), whole water fraction ( $n = 7$ ), and sediment ( $n = 18$ ). The hierarchical cluster of sample types on top is based on a Bray–Curtis similarity matrix using square-root-transformed mean relative abundances of all OTUs from the meta-analysis (including the ones with an abundance of less than 2%). The class and genus of the OTUs are given according to classification with release 132 of the nonredundant SILVA database.



ability to degrade aromatic or halogenated hydrocarbons, including petroleum and pesticides, several members of the Sphingomonadaceae are already being used for remediation purposes (Kertesz et al. 2017, Rosenberg et al. 2014). This ability also makes them prime candidates to potentially degrade pollutants associated with microplastics, which either leach out of the plastics or accumulate on them because of their hydrophobic surfaces (as is the case, e.g., for polycyclic aromatic hydrocarbons). The formation of carotenoid pigments, on the other hand, protects bacterial cells from oxidative stress caused by UV light in the ocean surface, giving the members of Sphingomonadaceae an advantage over nonpigmented bacteria. Therefore, this family could either use the plastic or associated pollutants as an energy source (see Section 4.2) or take advantage of the carotenoid pigments to more efficiently resist the UV light, as has been reported for bacteria from the genus *Erythrobacter* (Matallana-Surget et al. 2012).

Studies have suggested that members of the genus *Vibrio* use plastic as a favorable transport platform (Frere et al. 2018, Kirstein et al. 2016, Zettler et al. 2013), but *Arcobacter* spp., *Cokwellia* spp., *Escherichia* spp., *Pseudomonas* spp., and other taxa have also been discussed as potentially pathogenic plastic colonizers (Curren & Leong 2019, Harrison et al. 2014, Keswani et al. 2016). In our reanalysis, no OTUs classified as *Enterococcus* sp. were found in the data set. In all sample types (microplastics or natural particles), the mean relative abundances were very low for members of *Aeromonas* (<0.23%), *Cokwellia* (<0.08%), the taxonomic unit *Escherichia–Shigella* (<0.01%), and the family Enterobacteriaceae (<0.03%). Members of the genera *Arcobacter*, *Pseudomonas*, *Shewanella*, and *Vibrio*, which contain potentially pathogenic species, were indeed associated with microplastics (**Figure 3**), but their median relative abundances remained below those from communities associated with natural control surfaces (wood, cellulose, or glass) and/or



**Figure 3**

Box plots displaying the distribution of relative abundances (log scale) within the 5th–95th percentile of (a) *Arcobacter*, (b) *Pseudomonas*, (c) *Shewanella*, and (d) *Vibrio* associated with different surfaces in marine and brackish waters. The different sample types comprise plastic particles (polyethylene, polystyrene, and unknown polymers;  $n = 68$ ), control surfaces (cellulose, glass, and wood;  $n = 42$ ), particle-attached water fractions ( $n = 34$ ), and sediment ( $n = 18$ ).

the particle-attached water fraction. The reanalysis reveals that microplastics do not per se represent a higher risk to transport or enrich marine pathogenic microorganisms when compared with natural particles. Nonetheless, the high durability of plastics, potentially enabling associated microorganisms to travel longer distances horizontally as well as vertically in the oceans, can be significant when compared with many natural particles, which biodegrade in shorter time periods. Considering the sampling area as a major determinant on the community composition (Amaral-Zettler et al. 2015, Oberbeckmann et al. 2018; see Section 3.2), we can assume that microplastic-associated bacterial communities will rapidly adapt their composition to changing environments rather than remaining stable over long distances. Once again, the nature of the particle will have a small role in the spread of pathogens over large areas.

Another concern related to potential pathogens transported by plastics (including microplastics) is the introduction of invasive species, especially microbial eukaryotes (Barnes & Fraser 2003, Goldstein et al. 2014, Tutman et al. 2017). In particular, the 2011 tsunami in Japan raised concerns about the distribution of living organisms via plastic debris (Miller et al. 2018). For example, Maso et al. (2003) reported the colonization of floating plastic by harmful dinoflagellates (*Ostreopsis* sp., *Coolia* sp., and *Alexandrium taylori*) when sampling during a bloom of *A. taylori*. Likewise, potentially harmful diatom species were found to raft on plastic fragments in Mediterranean coastal waters (Maso et al. 2016). The specific processes regarding the potential spread of invasive microorganisms, including harmful microalgae, need to be further investigated.

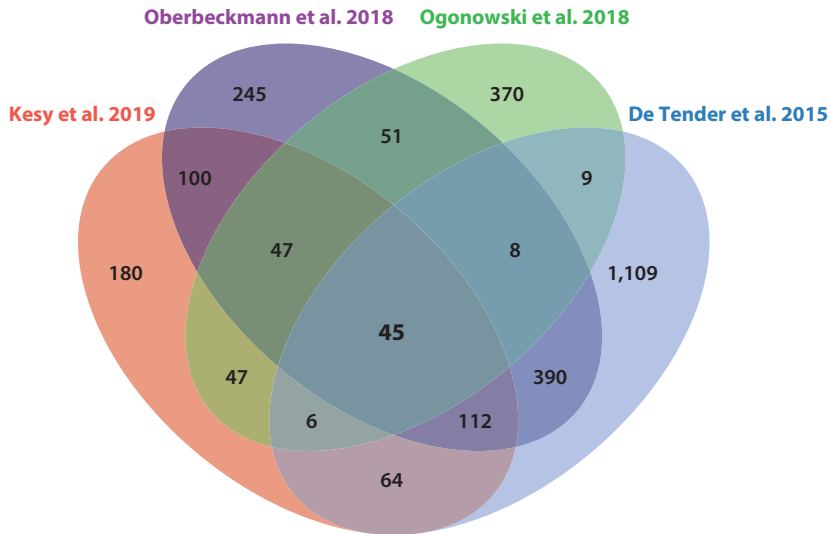
### 3.4. The Core Bacterial Community Associated with Polyethylene Microplastics Remains to Be Established

Four of the data sets in our meta-analysis contained sequences clearly attributed to polyethylene, our model plastic chosen to screen for a core of associated bacteria across different sampling areas. While most OTUs occurred in just one of the data sets, 45 OTUs were detected in all of them (Figure 4, Supplemental Table 3). Of these, 27 were classified as  $\alpha$ -proteobacteria, in particular within the families Rhodobacteraceae (11 OTUs) and Sphingomonadaceae (8 OTUs). The relatively higher abundances of these families within microplastic biofilms have been reported by several additional studies (Bryant et al. 2016, Curren & Leong 2019, Debros et al. 2017, Dussud et al. 2018) that did not meet all of the criteria for inclusion in our reanalysis (see Section 3.1) and were discussed above (see Section 3.3). A mean relative abundance of greater than 1% across all polyethylene samples was reached by five of the core OTUs, which were classified as members of the families Rhodobacteraceae and Flavobacteriaceae (unclassified at the genus level) and the genera *Albirhodobacter*, *Methylotenera*, and *Hydrogenophaga*.

By excluding bacterial communities that were also associated with polystyrene, unknown polymers, and natural particles, we were able to identify 13 of the core 45 OTUs specifically associated with polyethylene, including members of the Microbacteriaceae (3 OTUs) and Sphingomonadaceae (3 OTUs). Most of these polyethylene-specific OTUs, however, had low abundances (<0.1%) within the polyethylene data set, with only OTU 0040 (classified as *Erythrobacter*) exceeding this threshold, with a mean relative abundance of 0.47%. These first results indicate that very few bacterial communities are associated exclusively with polyethylene microplastics.

### 3.5. Microplastics Potentially Impact Ecological Processes in the Oceans

Microplastics are relatively recently introduced particles in the ocean and are increasing in amount over time; consequently, the ratio of attached to free-living communities and the microbial biomass colonizing those microplastics are also increasing. Therefore, regardless of the properties



**Figure 4**

Venn diagram displaying both study-specific and overlapping core operational taxonomic units (OTUs) in polyethylene-associated microbial communities sampled in studies in the North Sea (De Tender et al. 2015) and Baltic Sea (Kesy et al. 2019, Oberbeckmann et al. 2018, Ogonowski et al. 2018). Most OTUs occurred in just one data set, but 45 were common to all of them (for taxonomy and mean relative abundances, see **Supplemental Table 3**).

**Supplemental Material** >

of the new material (i.e., the plastic), the large quantities of the newly introduced plastic particles and their biofilms can influence the ecosystem processes in their surroundings, along with other natural particles. Studies have already demonstrated the immense regulatory potential of biofilms, particularly in streams, rivers, and intertidal systems (e.g., Battin et al. 2016, Decho 2000, Sabater et al. 2002). On the other hand, the plastic leachate can significantly increase the dissolved organic carbon in the oceans (Romera-Castillo et al. 2018), which, in turn, has the potential to increase the marine microbial activity and its biomass in the oceans. Studies on the functional impact of microplastic biofilms on ecosystems are scarce and are mostly lacking natural controls to account for general particle effects. Michels et al. (2018), however, showed that microplastic biofilms promote the aggregation of plastic and biogenic particles.

One may also speculate that the introduction of microplastics as new surfaces into the ocean will selectively enrich previously resting or less active members of the marine rare biosphere, which are most likely subjected to ecological processes such as selection (Galand et al. 2009). If so, microplastics would increase the number of metabolically active microbial species in the ocean and potentially affect fluxes of dissolved organic matter.

#### 4. MICROBIAL DEGRADATION OF PLASTICS

As discussed above, biogeography is overall the most important determinant for microbial assemblages on microplastics. However, microplastics themselves can also affect biofilm formation, especially in nutrient-poor conditions (Oberbeckmann et al. 2018), and can selectively enrich hydrocarbon-degrading bacteria, such as members of the family Sphingomonadaceae. It is unclear, however, whether this is due to microplastic surface properties or if microplastics could be

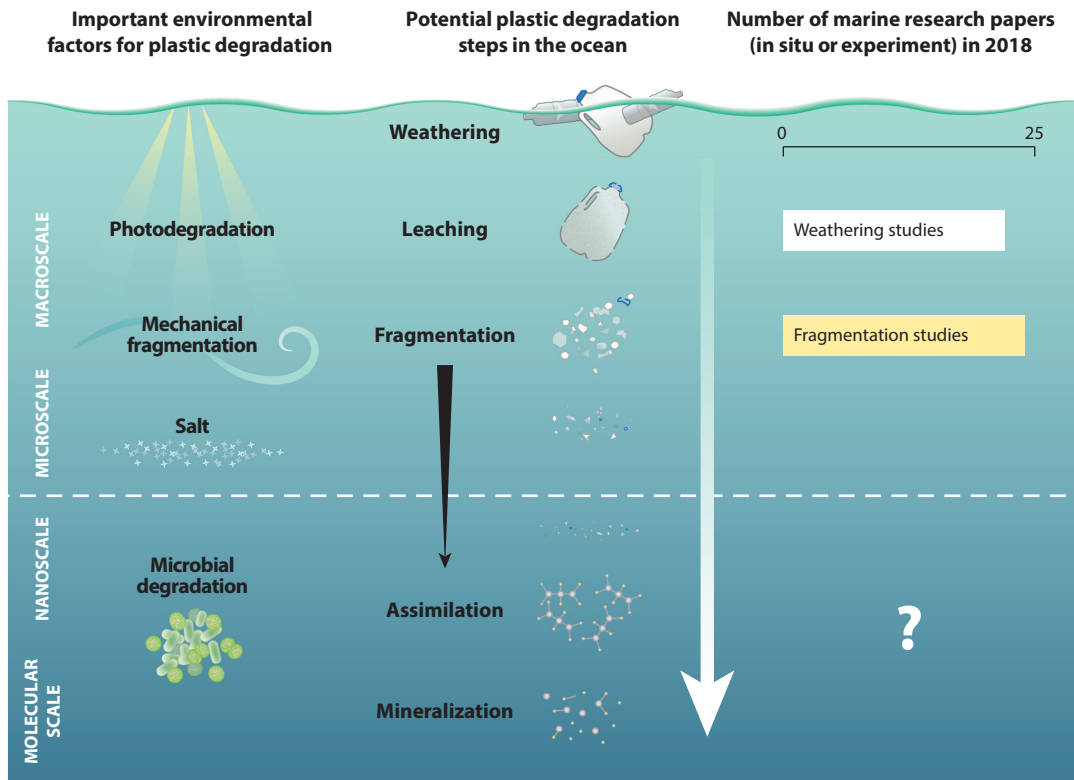
actively biodegraded. Because biodegradation is the only way of finally remediating the plastic pollution in the oceans, we discuss the potential of microbial plastic degradation in more detail.

#### 4.1. Definition of Biodegradation

The term biodegradation is one of the most misleading in the field of potential plastic degradation. Lucas et al. (2008) and Harrison et al. (2018) suggested three principal successive stages for the process of biodegradation of synthetic polymers: biodeterioration, biofragmentation, and assimilation. Andrady (2017), on the other hand, differentiates weathering from fragmentation and defines, from an ecological point of view, degradation as the complete mineralization of synthetic polymers. According to his definition, weathering describes a biotic or abiotic superficial degradation that modifies the mechanical, physical, and chemical properties of a polymer. Weathering can be verified by determining the accumulation of oxidized moieties, especially carbonyl functionalities, via Fourier transform infrared spectroscopy, changes in crystallinity, and the mechanical properties of plastics (Andrady 2017). The eventual fragmentation into smaller components is likely due to mechanical forces such as friction and shearing during wave movements or abrasion, as well as surface ablation (concerning surface ablation, see figure 8 in Andrady 2017). These processes enhance the polymer surface and reduce its molecular weight, which is a precondition for further microbial cleavage and degradation on a molecular level. The total mineralization of polymers into  $\text{CO}_2$ ,  $\text{H}_2\text{O}$ , and salts, accompanied by the generation of new biomass, is the final part of the assimilation step. We assume that, for biologists, the term biodegradation is often defined as mineralization, or is at least differentiated from degradation and assimilation (Debroas et al. 2017). But other perspectives exist, such as those of polymer scientists or the plastic industry. From their perspective, plastic fragmentation during managed degradation processes, such as composting, is sufficient to propagate biodegradability. In this case, biodegradation is being equated with the eventual formation of microplastics from larger plastic items, without significantly reducing the quantity of plastic in the environment. For society, these differentiations might not be transparent, and it might be assumed that a label of “biodegradable” or “biocompostable” is automatically associated with remediation. Several reviews have covered these discrepancies (e.g., Gewert et al. 2015, Harrison et al. 2018, Lambert & Wagner 2017), and there is no need to go into further detail here. It is important, however, to understand that the term biodegradation, when associated with plastic pollution, as it is currently used in the literature and by the public, does not necessarily include plastic remediation from polluted oceans. For this review, we define the biodegradation of synthetic polymers as its assimilation and mineralization (and, therefore, its eventual removal) in the natural environment.

#### 4.2. Biodegradation of Microplastics in the Ocean

The weathering and consequent fragmentation of larger plastics can be attributed to UV radiation, leaching of additives (and thus the loss of stabilizing properties), biofouling, and mechanical processes (Jahnke et al. 2017). Photodegradation probably plays the most important role (Andrady 2017), especially in combination with wave action in the beach zone. Other factors include the salts in saline water (Da Costa et al. 2018) and potentially microorganisms themselves, as it has been suggested that their metabolic products can indirectly influence, for instance, the discoloration of plastics in the environment (Ghosh et al. 2013), probably due to a loss in surface properties (Andrady 2015). As a result of the fragmentation of larger plastic items, secondary microplastics have a significantly increased surface-to-volume ratio, offering larger surfaces for microbial colonization and potential microbial attacks on the polymer. However, instead of degrading the



**Figure 5**

Important environmental factors that may potentially catalyze different plastic degradation steps in the ocean. The areas below the horizontal dashed line indicate steps that can be extrapolated from optimized laboratory experiments (*left of the arrow*) but still require confirmation for the ocean (*right of the arrow*).

plastics, microorganisms can also increase their stability. Biofilms formed on microplastics can protect the particles from photodegradation in the ocean surface (Weinstein et al. 2016) or increase their relative density to above seawater density, which leads to microplastic sedimentation and consequently protection from photodegradation (Jahnke et al. 2017). In combination, these changes in the plastic properties shift the factors that predominantly determine the potential plastic degradation from physicochemical forces to microbial activity. As a consequence, the highest remineralization rates of synthetic polymers are expected in the size range of smaller microplastics (Figure 5).

Synthetic polymers are energy rich and theoretically represent a good source of energy and carbon for microorganisms. For instance, the maximum usable energy for the complete oxidation of polyethylene would be between  $-422$  and  $-425$  kJ per mole of  $O_2$ , similar to that of glucose ( $-479$  kJ per mole of  $O_2$ ), which is a well-known bacterial substrate. In terms of oxygen, extending the chain by more  $CH_2$  units hardly makes a difference. The complexity level of synthetic polymer depolymerization is determined instead by the polymer's hydrolyzability. Nonhydrolyzable plastics, such as polyethylene and polypropylene, consist of C-C-bond backbones where the polymer must be cleaved into smaller molecules by redox reactions before its assimilation by cells (Gewert et al. 2015, Krueger et al. 2015). By contrast, hydrolyzable plastics such as polyethylene terephthalate and polyamide, which contain well-degradable structural elements like amide or

ester bonds, could be cleaved enzymatically or via hydrolysis, analogously to natural substrates such as lignin or cellulose (Gewert et al. 2015, Krueger et al. 2015). However, the accessibility of the bonds by the crystalline structure of the plastic surface can be as complex as, for example, that of lignocellulose. Hydrolysis of lignocellulose, which is a natural substrate, depends on extracellular lignin-modifying enzymes, including manganese peroxidase, versatile peroxidase, lignin peroxidase, and multicopper oxidase laccase to initiate cometabolic biodegradation of lignin (Krueger et al. 2015). Hydrolases (lipases and cutinases) have been described for the polymer polyethylene terephthalate, a member of the polyester family that is formed by the monomers ethylene glycol and terephthalic acid. The bacterium *Ideonella sakaiensis*, which has been isolated outside a plastic bottle recycling facility, was able to cleave polyethylene terephthalate using two hydrolases and thus biodegrade their monomers completely. The result was bacterial growth based exclusively on polyethylene terephthalate energy sources (Yoshida et al. 2016).

Although polyethylene terephthalate biodegradation by *Ideonella sakaiensis* so far represents the only example of complete plastic mineralization by bacteria, it was reached under optimal laboratory conditions that do not represent natural environments. In the marine environment, where conditions are more complex, the potential degradation of synthetic polymers follows the biodegradation decalogue of Alexander (1975), a famous terrestrial soil microbiologist who studied the microbial decomposition of xenobiotic chemicals. Alexander's biodegradation decalogue specified under which conditions microorganisms should not metabolize a substrate. In the context of microplastic pollution in the marine environment, three of Alexander's (1975) commandments describe especially well why highly dense and hydrophobic polymers should have low biological degradability: A compound should not be degraded if the molecule is too large to penetrate the cell (commandment 5), the compound concentration in aqueous solution is extremely low (commandment 6), or the cleavage sites of the compound are hard to access (commandment 10). In reference to these commandments, we can deduce that, in the marine environment, it is not the energy content of synthetic polymers but factors such as the extremely low bioavailability and high chemical stability that will determine the substrate quality (i.e., propensity to biodegradation) of microplastics.

To explore the scientific literature from Alexander's decalogue in 1975 to the most recent papers, we performed a literature search in Web of Science with a set of keywords related to both (micro)plastics and degradation in marine systems (**Table 1**). The retrieved papers reflect the limited findings regarding the biodegradability of synthetic polymers in the oceans. Of the 185 retrieved papers, 69 matched with the topic under analysis. Of these, 46 were related to the occurrence or quantification of fragmented plastics in the environment, as well as to (micro)plastic degradation experiments under laboratory conditions (**Table 1**). The other 23 papers (one-third of the 69 that matched the topic) were literature review papers. There seems to be a high ratio of reviews to research papers when compared with other research topics, which indicates that (micro)plastics have been a hot topic of interest in the last few decades that has been explored by scientists of different disciplines.

The search revealed that the weathering of plastics and microplastics, according to the definition by Andrady (2017), has been experimentally proven and observed in situ. Also, although the fragmentation process is difficult to observe in the marine environment, and a global mass inventory of ocean plastics still depends on educated guesses (Koelmans et al. 2017, Thompson et al. 2004), secondary microplastics, which are the direct result of plastic fragmentation, have been detected in all marine habitats (see examples in **Table 1**) and represent the ubiquity of (micro)plastics in the world oceans.

By contrast, the potential biodegradation of (micro)plastics catalyzed by marine microorganisms in marine environments has only been assumed based on the weight loss of plastics during

**Table 1** Research papers resulting from literature searches in Web of Science (topics),<sup>a</sup> which reflect the fact that the final biodegradability of synthetic polymers in the ocean remains to be demonstrated

Study	Type <sup>b</sup>	Degradation step <sup>c</sup>	Size classification <sup>d</sup>	Plastic type <sup>e</sup>	
Ioakeimidis et al. 2016	○		W	Macro	PET
Lobelle & Cunliffe 2011		◇	W	Macro	PE
Arias-Villamizar & Vazquez-Morillas 2018		◇	W	Meso	HDPE
Artham et al. 2009		◇	W*	Meso	LDPE, HDPE, PC, PP
Balsubramanian et al. 2010		◇	W*	Not described	PE
Devi et al. 2015		◇	W*	Not described	HDPE
Karlsson et al. 2018		◇	W	Not described	PE
Khaled et al. 2018		◇	W	Not described	PS
Muthukumar et al. 2011		◇	W*	Meso	CFRP, GFRP, PET, PUR, SR, SF
Welden & Cowie 2017		◇	W*	Meso	PA, PE, PP
Sudhakar et al. 2008		◇	W*	Meso	LDPE, HDPE
Nauendorf et al. 2016		◇	W*	Meso	PE
Syranidou et al. 2017a		◇	W*	Meso	PS
Syranidou et al. 2017b		◇	W*	Meso	PE
Mohanrasu et al. 2018		◇	W*	Meso	HDPE
Dussud et al. 2018		◇	W	Meso	PE
Fotopoulou & Karapanagioti 2012	○		W	Micro	PE, PP
Paco et al. 2017		◇	W*	Micro	PE
Auta et al. 2017b		◇	W*	Micro	PE, PET, PP, PS
Auta et al. 2018		◇	W*	Micro	PP
Cai et al. 2018		◇	W	Micro	PE, PP, PS
Da Costa et al. 2018		◇	W	Micro	PE
Costa et al. 2011	○		F	All sizes	Marine debris
Alshawafi et al. 2017	○		F	All sizes	Marine debris
Cozar et al. 2014	○		F	All sizes	Marine debris
Cozar et al. 2017	○		F	All sizes	Marine debris
Eriksen et al. 2014	○		F	All sizes	Marine debris
Fok & Cheung 2015	○		F	All sizes	Marine debris
Thornton & Jackson 1998	○		F	All sizes	Marine debris
Tsiota et al. 2018		◇	F	Microplastics generation	HDPE
Weinstein et al. 2016		◇	F	Microplastics generation	HDPE, PP, PS
Hodgson et al. 2018		◇	F	Microplastics generation	HDPE
Song et al. 2017		◇	F	Microplastics generation	EPS, PE, PP
Fok et al. 2017	○		F	Micro/meso	Marine debris
Palombini et al. 2018	○		F	Micro/meso	Marine debris
Reisser et al. 2014	○		F	Micro/meso	Marine debris
Debros et al. 2017	○		F	Micro/meso	Marine debris
Jang et al. 2018	○	◇	F	Micro	PS
Jiang et al. 2018	○		F	Micro	PE, PP, PS
Jungnickel et al. 2016		◇	F	Micro	PE

(Continued)

Table 1 (Continued)

Study	Type <sup>b</sup>	Degradation step <sup>c</sup>	Size classification <sup>d</sup>	Plastic type <sup>e</sup>
Lenz et al. 2015	○	F	Micro	Marine debris
Naidu et al. 2018	○	F	Micro	Marine debris
Sagawa et al. 2018	○	F	Micro	Marine debris
Frias et al. 2016	○	F	Micro	Marine debris
Acosta-Coley & Olivero-Verbel 2015	○	F	Micro	Microplastic resin pellets
Chubarenko et al. 2018	○	F	Micro	Marine debris

<sup>a</sup>The keywords for the searches were entered as follows (with individual searches separated by semicolons): microplastic & microbial biodegradation; microplastic & fragmentation; plastic & microbial degradation & marine; synthetic polymer & microbial degradation & marine; plastic & fragmentation & marine; synthetic polymer & fragmentation & marine; plastic & biodegradation & marine; synthetic polymer & biodegradation & marine; microplastic & biodegradation; microplastic & biodegradation.

<sup>b</sup>○, environmental study; ◇, experimental study.

<sup>c</sup>W, weathering; F, fragmentation; \*, weight loss was determined, but the degradation of leachates or mineralization of plastics was unproven.

<sup>d</sup>Macro, >20 cm; meso, 0.5–20 cm; micro, <0.5 cm.

<sup>e</sup>CFRP, carbon-fiber-reinforced plastic; EPS, extracellular polymeric substance; GFRP, glass-fiber-reinforced polymer; HDPE, high-density polyethylene; LDPE, low-density polyethylene; PA, polyamide; PC, polycarbonate; PE, polyethylene; PET, polyethylene terephthalate; PP, polypropylene; PS, polystyrene; PUR, polyurethane; SF, syntactic foams; SR, silicone rubber.

in situ or laboratory experiments, and there have been fewer papers on this topic than on plastic weathering or fragmentation processes. For instance, a 12-month experiment in the Bay of Bengal, India, revealed a weight loss of 0.65–1.9% for low- and high-density polyethylene, polycarbonate, and polypropylene (Artham et al. 2009). Relatively higher weight losses have been determined in vitro when using microbial strains isolated from plastics in the marine environment. Bacteria from genera such as *Bacillus*, *Rhodococcus* (Auta et al. 2017a,b), *Arthrobacter*, and *Pseudomonas* (Balasubramanian et al. 2010) were related to weight losses of up to 7.4% for polyethylene microplastic particles (Auta et al. 2017b) and 15% for relatively larger high-density polyethylene films (Balasubramanian et al. 2010). Analogous degradation studies with fungi reported weight losses of up to 8.5% for high-density polyethylene degraded by *Aspergillus* sp. after 30 days of incubation (Devi et al. 2015) and more than 43% for polyethylene degraded by *Zalerion maritimum* after 14 days of incubation (Paco et al. 2017).

Thus, plastic weight loss can reach promisingly high values in comparatively short time frames, but the fact remains that this approach does not cover all aspects of the biodegradation process. Weight loss alone, even in combination with microbial growth, cannot discriminate between the degradation of polymers and the degradation of additives or monomers. Due to incomplete polymerization processes, the latter may also constitute a substantial proportion of the final plastic product and are often easily microbially mineralized, thus potentially leading to falsification of the polymer degradation rates even in additive-free polymers (Klaeger et al. 2019). A simple further fragmentation of microplastics into nanoplastics (particles less than 100 nm in size) has also been observed in the laboratory—for instance, through digestive fragmentation experiments in Antarctic krill (Dawson et al. 2018, Jahnke et al. 2017)—but so far remains unproven for the marine environment. Thus, in order to evaluate the retention times of microplastics in the ocean, further research on their biodegradation should focus on the final steps: assimilation and mineralization. However, because of the biodegradation decalogue (Alexander 1975), studying these steps remains challenging for microplastics. Highly sensitive approaches, such as mineralization experiments of <sup>14</sup>C-labeled synthetic polymers in marine in situ conditions [comparable to the <sup>14</sup>C-polystyrene polymer in vitro cultivation experiment using the fungus *Penicillium variable* (Tian et al. 2017)], are essential to recognize the lifetime of microplastics in the ocean.



To summarize, biodegradation of microplastics has not yet been detected in the marine environment. Due to the low bioavailability of plastics, their degradation is determined mainly by physicochemical forces, and the degradation ends (based on our current knowledge) with the enrichment of microplastics and nanoplastics in the marine system. Consequently, as has already been assumed, microplastics likely remain unmineralized in the oceans for hundreds of years (Barnes et al. 2009) or even longer (Andrady 2015). The question remains of whether marine microorganisms may adapt evolutionarily to plastic degradation in the future.

## 5. MICROBIAL ADAPTATION TO MICROPLASTIC DEGRADATION

Whether marine microorganisms will adapt, evolve, and assist in cleaning up the ocean through plastic degradation is environmentally relevant but a complex scientific question. The low bioavailability of plastics is apparently unfavorable for the evolution of productive and significant degradation pathways (Krueger et al. 2015). Furthermore, it should be considered that the large variety of plastic polymers would necessitate an equivalently large range of degradation pathways. However, in reference to Darwin's theory on the evolution of species (Darwin 1868), we asked instead whether a potential microbial adaptation to plastic degradation will increase microbial fitness, significantly enabling the growth and reproduction of cells in the ocean.

From the literature, we know that a natural dissolved organic carbon concentration below  $30.7 \mu\text{mol L}^{-1}$  would be insufficient to support prokaryotic metabolism (Arrieta et al. 2015), and this value is at the lower limit of the estimated concentration of dissolved organic carbon in the open ocean, approximately  $34\text{--}80 \mu\text{mol kg}^{-1}$  (Hansell et al. 2009). Degradation pathways should, at least in theory, evolve and result in the hydrolysis of synthetic polymers into monomers or chemical fragments, with these biodegradable substances then released at concentrations above approximately  $30 \mu\text{mol C L}^{-1}$  in the ocean. The polyethylene terephthalate degrader *Ideonella sakaiensis* isolated from outside a recycling facility (Yoshida et al. 2016) is an example of this process and indicates that relatively higher concentrations of plastics can lead to the evolution of plastic degradation in bacteria. A metagenomic study covering putative biodegradation pathways generated from marine microorganisms living on plastics indeed demonstrated that putative xenobiotic biodegradation exists in the ocean (Bryant et al. 2016). However, and not surprisingly, the global distribution of polyethylene-terephthalate-degrading bacteria and their respective genes is not significant (Danso et al. 2018).

We therefore deduce that it is unlikely that bioavailable synthetic polymers will reach sufficiently higher levels in the oceans to promote the evolution of bacteria that can effectively degrade microplastics. As research on marine microplastics is still growing, potential hot spots of marine plastics may remain unidentified, which would eventually change the scenario analyzed here. Most important, however, is to prevent these (micro)plastics thresholds from being reached in the world's oceans.

## 6. CONCLUSION AND RECOMMENDATIONS

For some decades now, the burden of microplastics has been increasing. Microplastics are an established potential microbial substrate and colonization surface in the oceans, with members of the family Sphingomonadaceae in particular selectively colonizing microplastic polymers. Potentially more relevant for society, the microplastic-microbial biofilm has been associated with (a) concerns related to the role of microplastics as a long-living vector for microorganisms, especially pathogenic species, and (b) the potential for microorganisms to degrade (micro)plastics in the long term and thus contribute to cleaning plastics from the oceans. Based on our reanalysis

and on the critical review of the available literature, we have concluded that, at present, (a) there has been no increase in the accumulation of pathogens colonizing microplastics, and (b) marine microorganisms play a negligible role in the biodegradation of microplastics. Because of the low bioavailability of microplastics in the oceans, microorganisms will not be able to adapt to significantly degrade plastics, at least on a human timescale, although this may depend on the concentration of plastics and the generation of plastics hot spots in the future.

The extremely diverse properties and benefits of plastics cannot be ignored in our everyday lives. However, due to improper treatment, microplastics are ubiquitous in the marine environment, and the available studies indicate that this contaminant is triggering an ecological disturbance. However, the extent of the potential impacts associated with marine microplastics on both spatial and temporal scales has not yet been determined. Tagg & Labrenz (2018) have discussed the need for proactive regulations for microplastics. To ensure environmental compatibility and sustainability, multiple actions are needed at the same time: (a) further research on microbial pathways potentially linked to plastic degradation, in order to improve knowledge of how to develop in situ biodegradable materials (as proposed in Quero & Luna 2017); (b) a significant reduction of all packaging materials or typical products of our twenty-first century society (from plastic foils to plastic toys); and (c) the development of an efficient recycling system that can be applied easily and cost neutrally worldwide. Such a recycling system should involve plastic-producing, plastic-recycling, and plastic-using industries alike, as the current recycling regime lags behind its potential. We further predict that research on the microbial remediation of plastics will increase in the future and lead to optimized biotechnological concepts that can be applied in vitro.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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