



The Aquatic Plastisphere: Methodology, Biofilm Formation Mechanism, and Microbial Diversity

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Abstract

From 2019 to 2060, the amount of plastic accumulated in the aquatic environment is expected to increase from 140 million tons to 493 million tons. The continuous release of microplastics (MPs) into the environment has negatively impacted aquatic ecosystems. MPs tend to develop biofilms on their surface in natural waters, and this new micro-ecosystem created by man-made plastic pollution is called plastisphere. The biofilm modifies the migration, transformation and fate, biological effects, and degradation processes of MPs. Although there have been numerous studies on MP biofilm, most focus on microbial diversity and structure. In addition, there are relatively few comprehensive descriptions of biofilm formation and research methods. In this paper, we review the recent works on microbes in the plastisphere, describe microbial interactions in the plastisphere, and examine the research methods, their benefits, and drawbacks concerning MP biofilms, and the four primary environmental factors (nutrient conditions, water temperature, the flow state of water, salinity) that influence microbial colonization. Next, we illustrate the whole process of how microorganisms colonize the MP surface. Finally, we study the microbial community of plastisphere in freshwater, marine, and wetland environments, and provide an outlook for future biofilm research on MPs.

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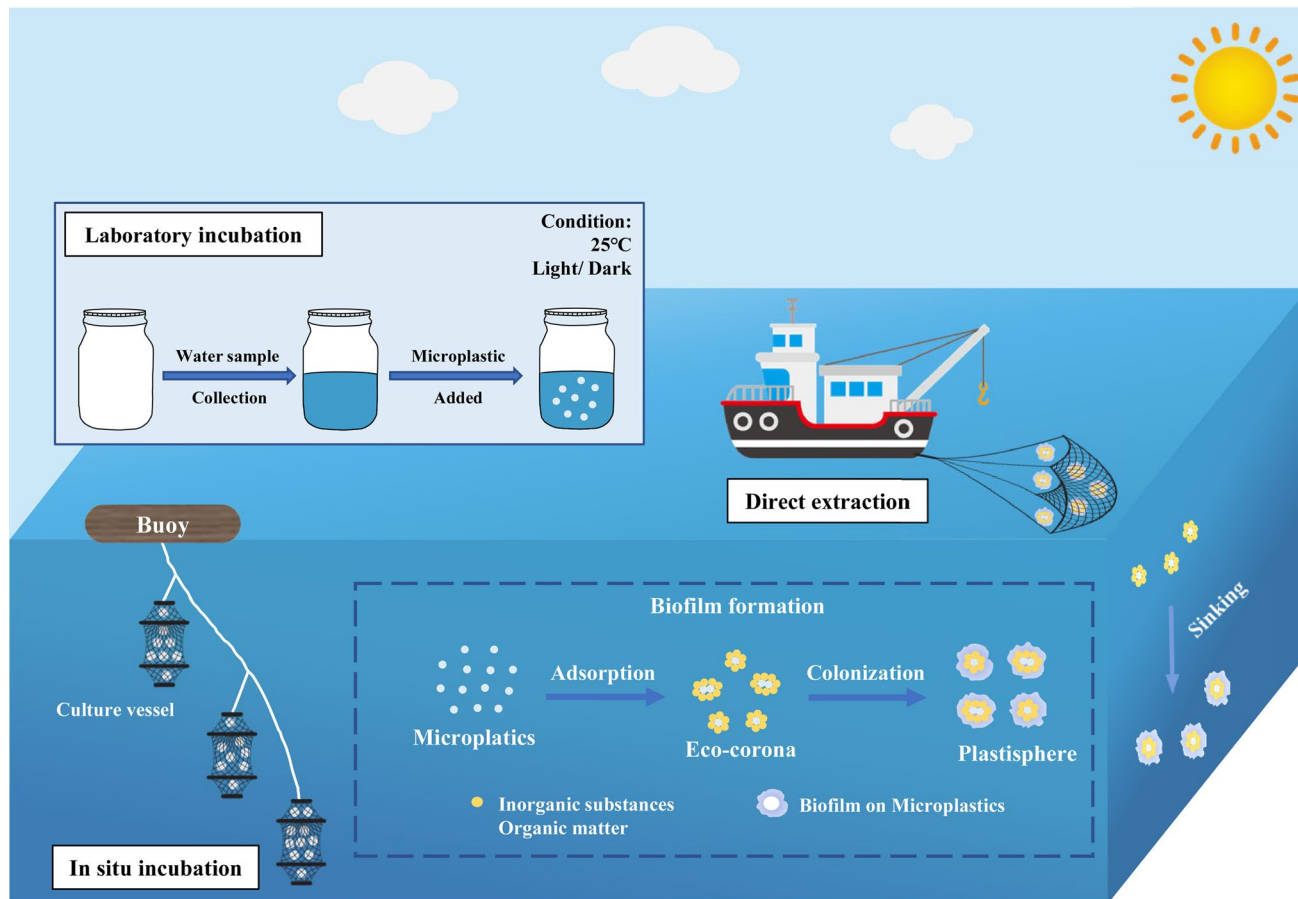
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Graphical Abstract



Introduction

Plastic use is expected to increase from 460 million tons in 2019 to 1231 million tons in 2060. Plastic waste is expected to nearly triple, from 353 million tons in 2019 to 1014 million tons in 2060 (OECD 2022). Less than 10% of plastic is recycled, 12% is incinerated in solid waste treatment, and most of the remainder leaks directly into the environment (Lebreton et al. 2017). The amount of plastic introducing into the environment is expected to double to 44 million tons per year, thus exacerbating environmental and health impacts (Chelsea et al. 2013). The accumulation in rivers and oceans is expected to increase more than threefold (Law and Thompson 2014), from 140 million tons in 2019 to 493 million tons in 2060. In 2004, Richard Thompson et al. (2004b) first proposed defining microplastics (MPs) as plastic fragments with a particle size of less than 5 mm. Since then, research on MPs has garnered increasing interest, particularly in aquatic environments.

MPs have generally been detected in lakes, rivers, and oceans. The middle and lower reaches of the Yangtze River in China (Su et al. 2016), the Hudson River in the United States of America (Miller et al. 2017), the Saigon River in Vietnam (Lahens et al. 2018), and the Auckland City River in New Zealand (Dikareva and Simon 2019) contained 500–3100 particles/m³ (p/m³), 625–2450 p/m³, 1.72 × 10⁵–5.19 × 10⁵ p/m³, and 625–2450 p/m³, respectively. The suspended MPs can enter inland lakes and reservoirs, resulting in an enrichment of MPs. The levels of MP abundance in Taihu Lake, China (Su et al. 2016), Kusugul Lake, Mongolia (Free et al. 2014), and Winnipeg Lake, Canada (Anderson et al. 2017), were 3.4 × 10⁶–25.8 × 10⁶ p/m³, 20.26 p/m³, and 53–748 p/m³, respectively. Currently, ocean is the largest source and sink for pollutant circulation. There are approximately 5.25 trillion plastic fragments in the surface seawater of the world, with at least 3540 tons being MPs (Eriksen et al. 2014). The relative abundances of MPs in the Pacific Ocean (Desforges et al. 2014), the Atlantic Ocean (Lusher et al. 2014), the Indian Ocean (Koongolla et al. 2018), and the Northern Ice Oceans

(Morgana et al. 2018) were 8–9200 p/m³, 1.5 p/m³, 0–29 p/m³, and (2.4 ± 0.8) p/m³, respectively.

The aquatic ecosystem is one of the most microbially diverse ecosystems on the planet. Microorganisms play crucial roles in plant growth and nutrient cycling, carbon cycling and biomass maintenance, as well as biodiversity conservation (Calbet and Landry 2004; Moore et al. 2013). In the aquatic environment, most microorganisms exist as complex communities attached to surfaces, named as biofilms (Qian et al. 2022). There are different types of microbes in biofilm such as bacteria, fungi, algae, archaea (Battin et al. 2016). The colonization of microorganisms happens not just on natural substrates but also on artificial ones like MPs (Miao et al. 2019), creating ‘plastisphere’ communities comprising heterotrophic and autotrophic microbes (Zettler et al. 2013). Researchers are becoming increasingly interested in the formation process. According to Fig. 1A, research topics in biofilm formation included bacteria (Qinghui Sun et al. 2022c), resistance genes (Lu et al. 2022), and pathogens (Li et al. 2022). The attention shifted from MPs and bacteria to plastisphere and biodegradation as time passed (Fig. 1B). The shift in research hotspots is primarily driven by the recognition of the importance of utilizing microorganisms for plastic degradation. The MP biofilms have been studied for more than 10 years. There are various methods to study the formation of biofilms. The main experimental methods include direct extraction, in situ incubation, and laboratory incubation, while the main testing tools are confocal laser scanning microscope, Fourier transform infrared spectrometer, high-throughput sequencing techniques, among others as depicted in Fig. 2. However, biofilm research conducted in the past lacks a unified standard. Therefore, it is necessary to summarize the aquatic plastisphere based on published work to provide direction for future studies.

In this review, we first summarize the commonly used methods for studying MP biofilm in aquatic ecosystems and highlight the advantages and disadvantages of each method. Then, we discuss the five stages of microbial colonization on the surface of MPs, the interactions between different microorganisms during the colonization process, and the factors that influence the biofilm on the surface of MPs. The major components of the surface microbial communities of MPs in freshwater, marine, and wetland environments are subsequently described. Lastly, perspectives on MP biofilm research are provided.

Research Methods for Microbial Colonization of MP Surface

There are numerous methods for studying microbial colonization of the MP surface in aquatic environments. Currently, three primary methods are recognized and adopted by most

scholars: (1) direct extraction, (2) in situ incubation, (3) laboratory incubation. This chapter primarily reviewed the advantages and disadvantages of three experimental designs (Fig. 2).

Direct Extraction from the Environment

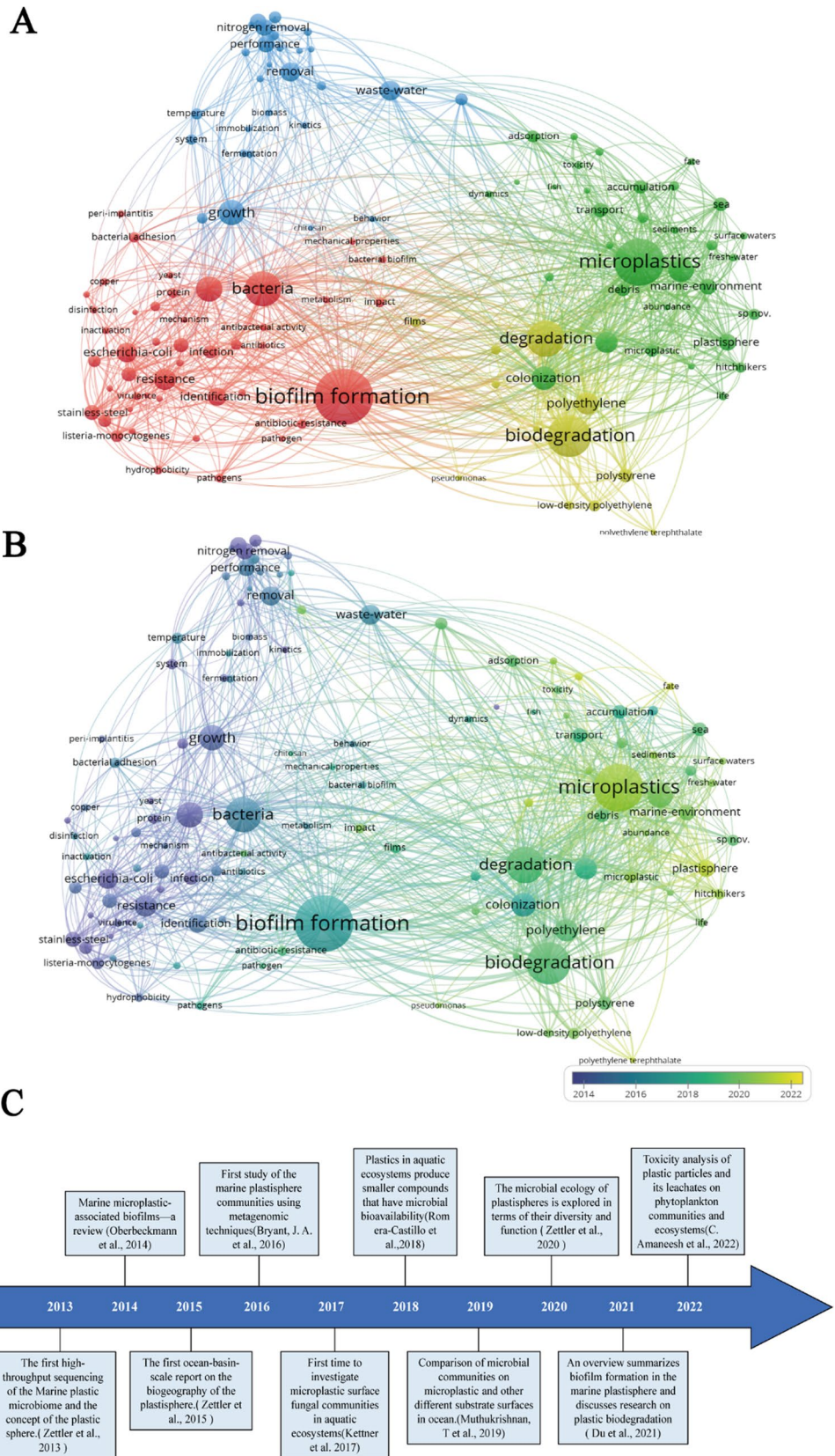
In the early studies on MPs in aquatic environments, emphasis was placed on the relative abundance, type, color, shape, and spatial distribution characteristics of MPs. Few studies focused on biofilms attached to MP surfaces. In addition to the study of MPs itself, subsequent experimental studies began to investigate the biofilm on the surface of MPs. Direct extraction, a practical and straightforward method for studying biofilms, involves the utilization of trawl, in situ pump, and manual direct collection techniques to collect microplastics (MPs) from water, extract biofilms, and analyze the microbial community.

Most studies on the bacterial and fungal community composition of biofilms employed direct extraction. Di Pippo et al. (2020) evaluated MPs and surface biofilms in seven Italian lentic lakes and found that the polymer types were mainly polyethylene (PE), Expanded polystyrene (Expanded PS), polypropylene (PP), and a small amount of polyamide. The core groups of biofilms on their surfaces mainly belong to Sphingomonadaceae, Rhodobacteraceae, Burkholderiaceae, and Ilumatobacteraceae. PP and PE were detected in two urban rivers in Jiaxing, Zhejiang, China. Proteobacteria, Cyanobacteria, and Bacteroidetes were the main microorganisms on the surface of MPs (Wang et al. 2020a). Li et al. (2021) found that Ascomycota, Chytridiomycota, Basidiomycota, Rozellomycota, Mortierellomycota, and Cercozoa dominated the fungal communities on MPs in three urban rivers and one bay in Qingdao and Yantai.

Since MPs collected by the direct extraction method are mainly found in surface water, the types of polymers are PP (0.89–0.91 g/cm³), PE (0.926–0.940 g/cm³), and high-density polyethylene (HDPE, 0.941–0.960 g/cm³), all of which are slightly less dense than water (Zhang et al. 2022b). Martínez-Campos et al. (2022) collected the MPs for biofilm analysis at a depth of 2 m below the sea’s surface. The microbial community composition varied among different types of MPs (Peng et al. 2022). Most experiments have utilized direct extraction to investigate biofilms only in the surface layer of the water column, resulting in a limited understanding of biofilms at varying depths in aquatic environments (e.g., middle and bottom layers).

In conclusion, compared to the other two methods, the direct extraction method potentially offers a more accurate reflection of the actual situation of microorganism colonization on MPs in aquatic ecosystems. Furthermore, it can streamline biofilm cultivation and reduce experiment duration. While biofilm formation typically spans a considerable

Fig. 1 Visualization of bibliometrics based on MP biofilms. **A** High-frequency keywords co-occurrence map by VOS viewer of plastic and biofilm in last decade, **B** temporal changes in research hotspots for keywords, and **C** a timeline of research development in the MP biofilms



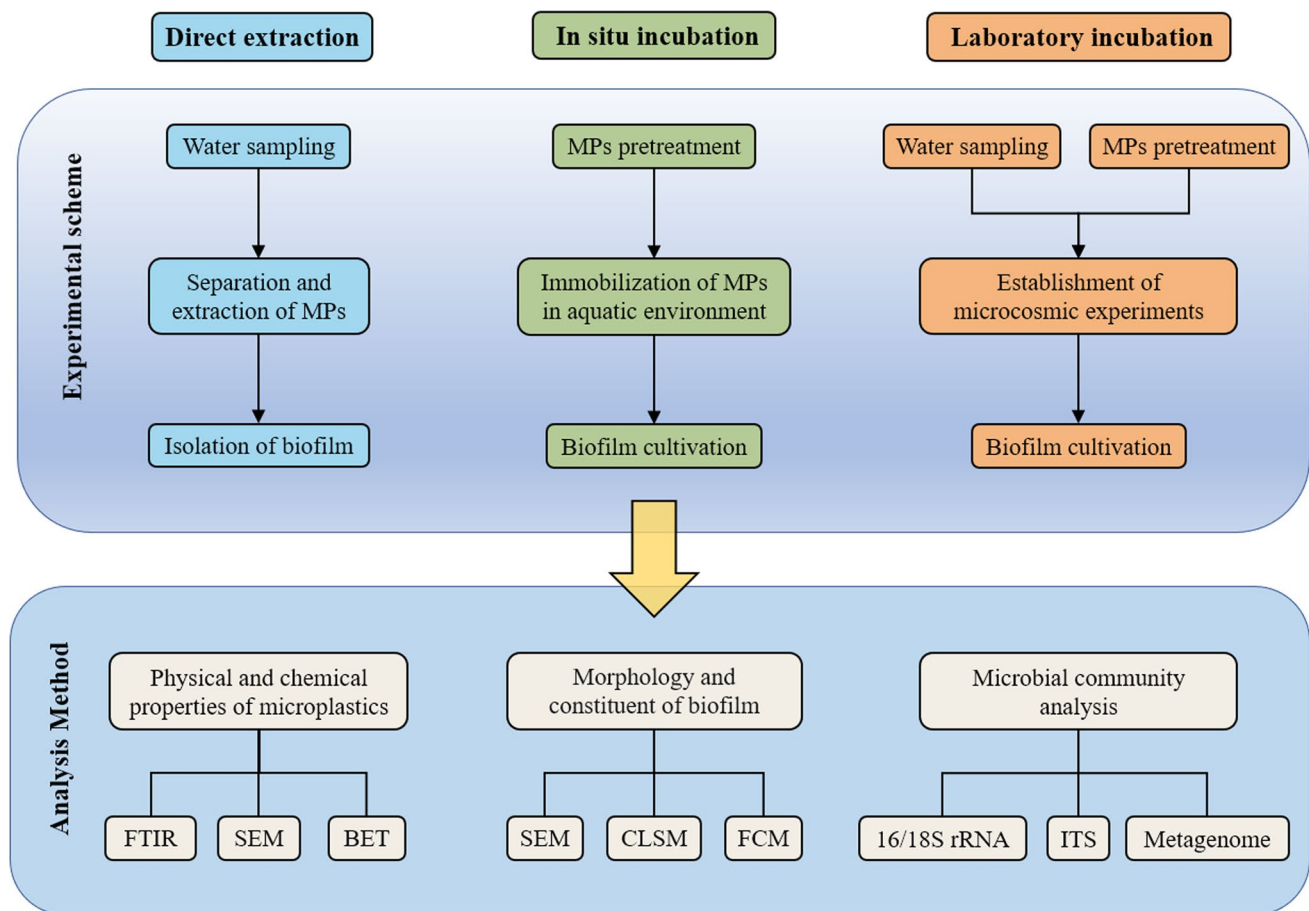


Fig. 2 Roadmap for the research of plastisphere. Experimental methods and the analysis method of plastisphere were summarized. *FTIR* Fourier transform infrared reflection, *SEM* scanning electron microscope, *BET* Brunauer–Emmett–Teller specific surface area

test method, *CLSM* confocal laser scanning microscope, *FCM* flow cytometry, *16/18S rRNA*, *ITS*, and *metagenome* microbial sequencing method

timeframe, the direct extraction method allows for the sampling and investigation of MP surface biofilms within a single day. This method lacks observation on the time scale and therefore, cannot provide a comprehensive understanding of the details of the biofilm formation process. In addition, most of the MP biofilm investigations were conducted at one specific depth in a particular aquatic ecosystem, and no differential analysis of MP biofilms at different depths in a particular aquatic ecosystem was done. Subsequent studies may compare MP biofilms from different vertical depths of the water column.

Microbiological Cultivation of MP Biofilm

Apart from collecting MPs directly from aquatic environments and extracting biofilms, laboratory incubation and in situ incubation are two of the most common methods to investigate MP surface biofilms. They both have a common feature that requires MPs to be immobilized in aquatic

environments for biofilm culture. The difference between laboratory culture and in situ incubation is that laboratory culture can control the experimental conditions, while in situ incubation relies mainly on natural environmental effects with many uncertainties. The advantages and disadvantages of the two experimental procedures will be examined.

Laboratory Incubation

Natural water samples from oceans, lakes, or rivers are collected and transported back to the laboratory, and the water samples and pre-treated sterile MPs are added to experimental vessels to construct an aquatic microcosm system for biofilm cultivation. This process is known as laboratory incubation. Compared to direct extraction methods and in situ incubation, laboratory incubation can provide a better understanding of the factors that shape MP biofilms in water.

The factors affecting biofilm have been investigated by a number of scholars over recent years. Liu et al. (2022)

discovered that microbial adhesion on the surface of aged MPs was found to be more difficult than that of pure MPs. Through microcosm experiments, the researcher demonstrated that along the river gradient, biofilms are primarily influenced by geographical location and salinity (Qiang et al. 2021). Song et al. (2022) added 500 ml of lake water, tap water, and two types of plastics, PE and polyethylene terephthalate (PET), to a 1 l carbon-free glass bottle for biofilm incubation, and found that the biofilm structure of the lake water samples was more stable than that of the tap water; Usually, for the laboratory incubations, water samples (ranging from a few tens of milliliters to a few liters) and pretreated MPs (PP, PET, PE, PS, etc.) are directly added to a container (beakers, conical flasks, glass bottles, self-designed containers, etc.), to incubate the biofilm from 48 h (Parrish and Fahrenfeld 2019) to 27 months (Vannini et al. 2021). Although laboratory incubation can be used to investigate the factors affecting the biofilm, certain limitations have been spotted. First, it is essential to regularly add nutrients to water samples. Miao et al. (2019) used Woods Hole culture solution periodically to promote biofilm formation. Second, the lake and ocean are moving bodies of water. However, many experiments are conducted in a completely static state. This approach defeats the original purpose of simulating the aquatic environment. Instead, it results in lower dissolved oxygen levels and anaerobic conditions at the bottom of the vessel. These conditions hardly reflect the actual environment found in natural aquatic systems. We need to make water flow in the laboratory incubation, Wang et al. (2021b) used a self-made experimental device to maintain the water flow at 3 m/s. They regularly replenished the water source to compensate for evaporation loss and recreate the real environmental conditions.

Briefly, the advantage of laboratory culture over in situ culture and direct extraction methods is that variables can be controlled, and experiment reproducibility is higher than that of in situ culture. The drawback is that many current laboratory cultivations require improved environmental conditions, such as maintaining water flow and supplementing nutrients when conducting laboratory culture to investigate the factors that influence biofilm, as much of the natural water environment must be simulated as possible to obtain more convincing experimental results.

In Situ Environmental Incubation

The laboratory-prepared MPs were fixed in the water body with containers (e.g., nylon bags, stainless steel mesh) so that microorganisms in the aquatic environment gradually attached to the surface of the MPs and formed biofilms—in situ incubation. In situ cultivation experiment is a popular plastisphere incubation method.

The duration of in situ incubation ranges from 48 h to 719 days, and it is now widely accepted. Parrish and Fahrenfeld (2019) conducted a biofilm incubation for 48 h to assess the effects of water quality and MP types on the biofilm community. To investigate biofilm composition in a deep-sea environment, Agostini et al. (2021) selected four types of MPs for 719 days of biofilm incubation: HDPE, PP, HDPE with the oxo-biodegradable additive (HDPE-OXO). They discovered that bacteria could degrade hydrocarbons on the surface of MPs. In addition to the total incubation period, it is essential to have appropriate intervals for biofilm detection and observation throughout the cultivation process. Bacteroidetes are the pioneers of microbial attachment to the plastic surface in the early stages of MP microbial colonization (from minutes to hours), which are replaced over time by other microorganisms such as Proteobacteria (Latva et al. 2022). Biofilm culture experiments still need to be set with appropriate detection time according to the average time of each stage of biofilm formation to ensure the accuracy of the experiment. In situ incubation requires containers to hold the MPs in the natural water column, and the choice of containers varies from stainless steel mesh cages, nylon mesh boxes (Wen et al. 2020), incubation tubes (Steinman et al. 2020), etc. Nylon as a plastic can be attached by microorganisms in water, and it is commonly used as the container to fix MPs in biofilm culture experiments, although it may inhibit microbial growth on the MP surface. Therefore, when conducting an in situ incubation experiment, it is more rigorous to choose container made from a non-plastic material. The recent in situ incubation experiments covered diverse aquatic environments, including rivers, lakes, and oceans at different depths (Kelly et al. 2022; Miao et al. 2021).

To sum up, in situ incubation is the most prevalent experimental method for MP biofilm research. In comparison to laboratory incubation, it is possible to reproduce the entire MP biofilm formation process to the greatest extent, and the data are more convincing when the biofilm is formed under the influence of the natural water environment. In recent years, there has been an increase in the types of MPs that leak into the aquatic environment, including not only PE, PP, and PS, which are difficult to degrade, but also many biodegradable plastics, such as PLA, poly (butylene succinate) (PBS), poly (butylene adipate-*co*-terephthalate) (PBAT), polycaprolactone (PCL), and polyhydroxyalkanoates (PHA). In contrast to the direct extraction method, in situ incubation provides the selection of different types of MPs and a thorough understanding of the MP biofilms. Although in situ experiments are more selective in terms of location and depth, they are susceptible to hydrological conditions and weather disturbances (e.g., river floods and typhoon weather), potentially leading to the loss of experimental samples and impacting results. For in situ incubation, the experimental vulnerability must be minimized by

focusing on the selection of MPs fixation containers and the time of regular biofilm extraction and testing, as mentioned previously.

Microbial Colonization of MP Surface

When MPs enter the aqueous environment, they rapidly form a coating of multiple substances mixed on the surface of the plastic. Then, aquatic microorganisms quickly gather on the plastic surface to form biofilms, and the microcosm composed of MPs and biofilms is called the plastisphere (Zettler et al. 2013). Microorganisms in biofilms have an advantage over planktonic microorganisms regarding survival strategies and competition. Within biofilms, microorganisms form stable alliances that enhance gene exchange, nutrient accumulation, and defense against toxins and harsh conditions, illustrating the complex interactions that support microbial resilience. However, there is also a strong competition for nutrients among microorganisms in biofilms, whereas a single microbe is free to uptake nutrients from the water. Microorganisms attach to the surface of MPs and proliferate, forming biofilms that completely alter the water–MPs interface properties. Furthermore, understanding the biofilm formation process on the surface of MPs, its microbial composition, and intramembrane microbial interaction mechanisms is essential for predicting MPs' environmental behavior and fate in diverse aquatic environments.

Formation of MP Biofilms

MP is a new habitable substrate for microbial colonization. Within seconds after MPs entering the water, they quickly develop a conditioning layer/eco-corona (Junaid and Wang 2022; Rummel et al. 2021) at the plastic/water interface by attracting numerous organic and inorganic matters, and the organic matters reduce the hydrophobicity of the MPs and promote microbial colonization (Wright et al. 2020). The strong hydrophobicity, allows the MP particles to readily adsorb hydrophobic organic substances such as humic acid, protein, and bisphenol compounds in the aquatic environment (Abdurahman et al. 2020; Galloway et al. 2017; Wu et al. 2019). In the aquatic environment, MPs are always negatively charged (Li et al. 2018) and easily combined with positively charged cations such as Na^+ and Ca^{2+} (Yu et al. 2019). Biofilms slowly begin to develop, after a conditioning layer/eco-corona is formed on the surface of the MPs. Initial microbial adhesion, secretion of extracellular polymeric substances (EPS), microbial community formation, biofilm maturation, and biofilm detachment are the five phases of biofilm formation (Fig. 3).

Initial microbial adhesion is the first step (Fig. 3A). Algae, including diatoms, golden algae and green algae,

have been identified as the pioneer microorganisms that colonized plastic debris (Hitchcock 2022; Nava and Leoni 2021). Recent research has demonstrated that there is an electrostatic interaction between PS and Cyanobacteria, in which charge neutralization reduces the photosynthetic efficiency of Cyanobacteria (de Oliveira et al. 2020). Although the organic matter in the surface conditioning layer of MPs serves as a carbon source, it can only sustain microorganisms for a few days; for long-term survival, microorganisms need photosensitizing substances produced by phototrophs (Du et al. 2022). Most studies have shown that phototrophs are the sole source of nutrients and energy for microbial communities on the surface of MPs. In contrast, if MPs are incubated in the dark, the community must rely on available organic matter from the surrounding waters. The initial colonizers of MPs, such as Proteobacteria and Bacteroidetes, are also bacteria. Bacteroidetes have been shown to be the first bacteria to colonize the surface of MPs. This result contradicts previous research, which considered Proteobacteria as the first colonizing organisms (Wright et al. 2021). The main reasons may be the few data on the earliest time points (such as 15 min/4 h) and the inappropriate microbial extraction and detection methods. Schlundt et al. (2020) found that during the pre-microbial adhesion period, the bacterial community was initially dominated by Bacteroidetes, followed by the emergence of Proteobacteria, which became the core group. In addition, obligate hydrocarbon-degrading bacteria are present during the early stage of microbial attachment, but their relative abundance decreased over time as the biofilm matured (Erni-Cassola et al. 2020).

EPS is closely associated with the ability of microorganisms to successfully colonize the surface of MPs and the formation of stable biofilms (Fig. 3B). Typically, microorganisms in biofilms produce EPS. Most biofilms consist of less than 10% microbial mass and more than 90% EPS (Flemming and Wingender 2010). EPS is secreted by bacteria, fungi, and phytoplankton (Galloway et al. 2017), and it consists mainly of polysaccharides and proteins (Naveed et al. 2019). In the initial adhesion phase, microorganisms secrete EPS to immobilize themselves, facilitating attachment to the MP surface. Tu et al. (2021) detected blanket-like EPS on the top of the bacteria incubated for 10 days on a PE surface, speculating that bacteria used PE as carbon source and energy to promote biofilm formation. A study of the North Atlantic plastisphere indicated that by the third week, EPS began to appear and immobilize microorganisms on the plastic surface (Schlundt et al. 2020). EPS anchors cells within the biofilm, maintaining close contact essential for cell-to-cell communication. Paula et al. (2020) found that EPS maintained biofilm stability by wrapping cells together to form structured clusters or micro-colonies. Furthermore, EPS also prevents the shedding of clusters and micro-colonies that grow under water flow. During the early stage

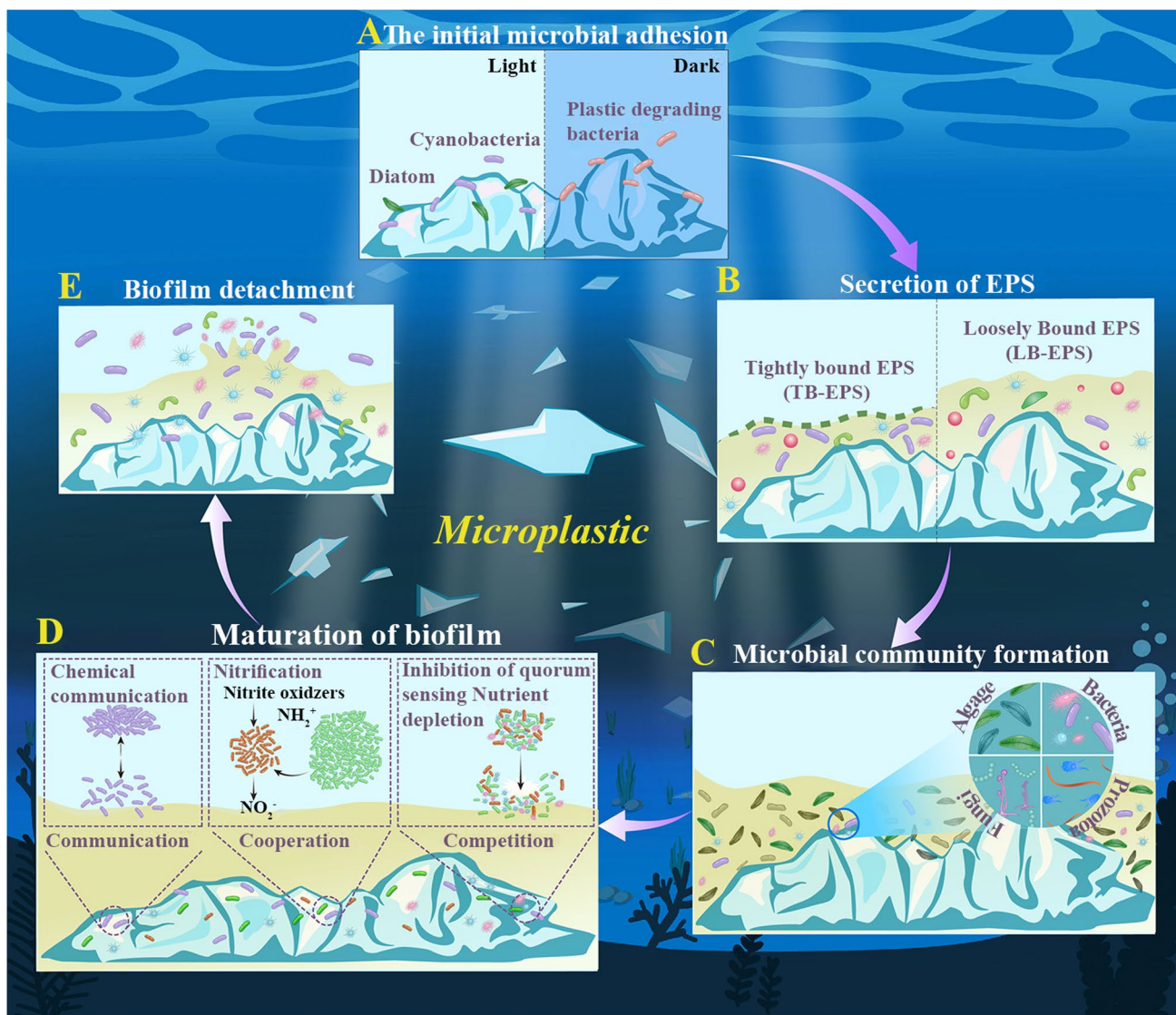


Fig. 3 The whole process of MP surface biofilm formation in aquatic environment. MP biofilms are divided into five phases: **A** The initial microbial colonization under light and dark conditions. **B** The microbes secrete different types of EPS. **C** The main microbes con-

tained in the initially formed biofilm. **D** The three interactions of microbes in the mature biofilm, diagram of the bacterial biofilm mechanism used as a source of reference (Flemming et al. 2016). **E** The partial microbial detachment from the biofilm

of biofilm formation, EPS secreted by algae is essential for subsequent attachment of bacteria, fungi, and other microorganisms in the water. Ye et al. (2021) showed that MPs restrained the growth of *Microcystis aeruginosa*, but the content of EPS gradually increased. Algae EPS flocs mainly consisted of loosely bound EPS (LB-EPS) and tightly bound EPS (TB-EPS), where the organic fractions in LB-EPS and TB-EPS had different variation responses, with the polysaccharide-to-protein ratio in TB-EPS increasing otherwise the polysaccharide-to-protein ratio in LB-EPS decreasing. A recent study demonstrated that Ca^{2+} bridged with EPS to promote bacterial growth and thickened biofilms on the MP surface (Xiong et al. 2023). Interestingly, bacteria allocated

a portion of their early colonization resources to the production of EPS, resulting in a lower bacterial colonization rate (Oliveira et al. 2021). Moreover, EPS-producing bacteria are superior to non-EPS-producing bacteria, because their offspring are embedded in the top layer of the nutrient and oxygen-rich biofilm (Schludt et al. 2020).

The number of cells and their species will increase after the initial colonization (Fig. 3C). The microbes on the surface of MPs are bacteria, fungi, algae, and some Metazoa. These fungi include Ascomycota, Basidiomycota, Chytridiomycota, and Rozellomycota. There are Cyanophyta, Chlorophyta, and Bacillariophyta in the algae. Rhizaria, Opisthokonta, Stramenopiles are several common

metazoans. The bacterial community primarily comprises Proteobacteria, Bacteroidetes, Cyanobacteria, and Actinobacteria (Li et al. 2021). On the third day of the in situ culture experiment at Baltimore's Inner Harbor, Proteobacteria, Bacteroidetes, Planctomycetes, and Firmicutes were present on the polylactic acid (PLA) surface. At the same time, the relative abundance of Firmicutes was higher on the PP surface than on the PLA surface (Sosa and Chen 2022). The microorganisms on the biofilm were mainly Proteobacteria, Bacteroidetes, Actinobacteria, Firmicutes, and Cyanobacteria in 2 weeks of incubation (Feng et al. 2020). Coons et al. (2021) demonstrated that regardless of MP type or in situ culture location, Proteobacteria and Bacteroidetes are always the most central members of the bacterial community. Burkholderiales, Sphingomonadales, Rhizobiales, and plant chloroplasts dominate the surface of MPs incubated in situ in German rivers (Weig et al. 2021). Ascomycota, Basidiomycota, and Chytridiomycota were the most dominant fungal organisms on the surface of MPs in the aquatic environment (Kettner et al. 2017). Lacerda et al. (2020) discovered no significant geographic differences in plastic epizootic fungi at the community level, in contrast to bacterial community patterns. After the microbial community had substantially formed, algae (diatoms, Cyanobacteria) and some zooplankton began to decline, and Schlundt et al. (2020) speculated the cause of diatom mortality was caused by bacteria. With the formation of microbial communities, the density of the biofilm grew as the incubation time increased (Tu et al. 2021). Tu et al. (2020) revealed that during growth, surface biofilms of MPs predominantly exhibited planar bulking and 3D thickening. Until biofilm maturation, community stability increased over time (Wang et al. 2021b). Interestingly, there was a correlation between the plastic particle size and the stability of the surface biofilm. The larger the MPs, the higher the complexity of the microbial community, and the biofilm can better resist environmental perturbations and maintain the stability of the microbial community (Schlundt et al. 2020).

After irreversible adhesion and the formation of a microbial community of bacteria, algae, fungi, and other microorganisms, the biofilms gradually mature (Fig. 3D). A circulatory system is formed within the mature biofilm, which has a highly organized structure and various channels between communities of bacteria, algae, and fungi that can transport nutrients, enzymes, and metabolites (Flemming et al. 2016). At the maturity stage of biofilms, the relative abundance of phototrophs such as diatoms and Cyanobacteria, is low in the maturity stage of biofilms. Miao et al. (2023) found that the complexity of microbial community diversity decreased during the maturation stage due to increased interspecies competition and ecological niche differentiation of microorganisms. Moreover, the biofilms on the surface of biodegradable plastics were more complex (Miao et al. 2023). The

maturation of biofilms on natural or artificial substrates in the ocean will fluctuate with the seasons (Miao et al. 2023; Qian et al. 2022).

Due to the paucity of literature on the biofilm separation process of the surface of MPs, we hypothesize that MPs in aquatic ecosystems, like biofilms on other natural substrates. Microbes will detach from biofilms actively or passively (Kaplan 2010). Passive detachment is generally due to the erosion of the biofilm by external disturbances, resulting in the detachment of microorganisms, while active detachment involves the gradual transition of cells from the biofilm form to the free. Nutrient limitation, oxygen depletion, and temperature variation can drive microbes out of their current environment to find a new one (Flemming and Wingender 2010; Rumbaugh and Sauer 2020) (Fig. 3E).

Microbial Interactions in Biofilm

Few studies have focused on the interactions between microorganisms within MP biofilms at present. The purpose of this section was to provide a theoretical foundation for future research on MP biofilms by reviewing the progress of microbial interactions in stream/marine biofilms and the scarce literature on microbial interactions within the plastisphere (Battin et al. 2016; Qian et al. 2022; Wyatt et al. 2019). In biofilms, microbial interactions influence the formation of the spatial structure within the biofilm. According to the classification of the interaction relationship, the primary interactions within biofilms are cooperation, competition, and signaling (quorum sensing) (Kaur et al. 2022; Qian et al. 2022); in terms of classification between different microbes, algae–bacteria, and bacteria–bacteria are the two types of systems that have been investigated within MP biofilms to date.

The interactions between algae and bacteria are parasitic, competitive, and synergistic (Li et al. 2023c). Algal photosynthesis provided oxygen to aerobic bacteria and promoted bacteria to reduce organic pollutants, while bacterial respiration released CO₂ and enhanced algal photosynthesis (Kube et al. 2020). Algae provide nutrients by liberating organic compounds or breaking down algal cells, promoting bacterial growth. During the initial stages of microbial colonization (Wright et al. 2020), algae serve as a secondary habitat for bacteria, protecting them from adverse environmental conditions. Bacteria can produce iron carriers that bind iron and vitamin B, thus promoting algal growth. Schlundt et al. (2020) demonstrated that numerous bacterial communities congregated around diatoms on the surface of biofilms incubated for 2 weeks, indicating that algae are an important habitat for bacteria in the pre-biofilm formation phase. The bacteria directly in contact with diatoms were primarily Bacteroidetes, Rhodobacteraceae, and γ -Proteobacteria. As for the bacteria–bacteria interactions, bacteria in a

community compete with each other for nutrients, space, and oxygen. Schlundt et al. (2020) demonstrated different associations between bacteria within MP biofilms, such as α -Proteobacteria and Bacteroidetes, Rhodobacteraceae, and Cyanobacteria.

Habitat heterogeneity, habitat fragmentation, environmental adversity, and resource scarcity reduce species interactions, reduce network complexity, strengthen competitive links, and promote ecological niche differentiation (Mo et al. 2021). Compared to aquatic environments, the microbial network complexity of the plastisphere is lower and competition links are more frequent in freshwater ecosystems, while the opposite is true for marine ecosystems (Li et al. 2021). Due to the plastisphere's filtration, the ecological niches of plastisphere surfaces overlapped in freshwater ecosystems, intensifying competition among species, while in marine ecosystems, the biomass and activity of microbes on plastisphere surfaces were lower and mainly affected by high salinity and low nutrient concentration (Li et al. 2021). Further research can combine CLASI-FISH and metagenomics to investigate the mechanism of microbial interaction, which may provide a comprehensive understanding of microbial activities within the plastisphere micro-ecosystem.

Effect of Environmental Factors on Microbial Colonization

Biofilm formation on the surface of MPs is known to be a complex multifactor process. It is primarily modified by the MP properties and hydro-biochemical characteristics. The polymer type (Feng et al. 2020; Miao et al. 2019), size (Hou et al. 2021), and degradation (Roager and Sonnenschein 2019), all influenced the initial attachment of the pioneer microbes. And the hydro-biochemical characteristics, such as water temperature, pH, nutrients, and planktonic microorganisms determined the biofilm growth trends (Li et al. 2020; Oberbeckmann et al. 2018; Wang et al. 2020b). Since many review articles (Wang et al. 2021a; Wright et al. 2021) have summarized the factors that affect biofilm formation (substrate properties, exposure time, geographical location), the most dominant impact factors: nutrient conditions, salinity, temperature, and water flow rate are analyzed and discussed in this chapter.

Nutrient status is one of the critical factors affecting biofilm development, and the growth rate of the biofilm is typically positively correlated with the concentration of nutrients. The concentration of total nitrogen (TN) and total phosphorus (TP) are conducive to biofilm formation and promote the formation of microbial-specific communities (Frère et al. 2018). An investigation revealed that nutrients influenced the average growth rate of biofilm communities in the Haihe River watershed, and TP and TN concentrations were positively correlated with the average biofilm

growth rate (Li et al. 2019). Miao et al. (2021) discovered that the carbon metabolism function was influenced by TN and TP. When more nutrients were available, primary biofilm formation accelerated, allowing the biofilm to mature more quickly (Oberbeckmann et al. 2018). It indicated (Stanley and Lazazzera 2004) that oligotrophic condition would trigger bacterial attachment to the MP surface, and it was hypothesized that some bacteria that can degrade polymers, such as Mycobacteriaceae (Sun et al. 2022a) would use MPs as a carbon source for decomposition and digestion. Because the MPs themselves would leach DOM into the aquatic environment, making it accessible to microorganisms (Sun et al. 2022b). While a hypertrophic environment can limit microbial attachment to MPs, large amounts of organic matter are more easily accessible to planktonic microbes, thereby decreasing the likelihood of microbial colonization of the MP surface. Remarkably, diatoms and green algae are the main autotrophs on the biofilm surface in lakes with low to medium trophic levels, and MPs are transferred to higher trophic levels when the autotrophs are fed on by water predators (heterotrophic ciliates) (Arias-Andres et al. 2018).

Salinity is a crucial factor for biofilm formation on the MP surface in aquatic environments. Salinity influenced the phytoplankton diversity in MP biofilms more than any other environmental factor (pH, temperature, DO) (Xu et al. 2019). Salinity was negatively correlated with the growth rate of MP biofilms, positively correlated with the diversity of the bacterial community, and altered the distribution of specific bacteria within biofilms (Oberbeckmann et al. 2018). Carson et al. (2013) demonstrated a negative correlation between salinity and the density of bacteria and algae on the surface of MPs. Li et al. (2019) discovered that the abundance of *Vibrio* spp. on the surface of MPs in estuaries with salinity above 26‰ was 2–10 times higher than that in seawater and sediments. De Tender et al. (2017) observed that as seawater salinity decreased, the bacterial community's structure on the MP surface shifted from Proteobacteria to Bacteroidetes. Jiang et al. (2018) discovered higher bacterial abundance and diversity on the surface of MPs at Chongming Island (located at the Estuary of the Yangtze River), presumably due to the higher particle settling rates and sediment resuspension resulted in a stronger exchange between water and sediment bacterial communities, leading to higher microbial diversity on microplastic surfaces at this site.

Temperature is a common factor that affects microorganisms' metabolic and intracellular enzymatic reaction processes. Long-term exposure to MP biofilms in aquatic ecosystems made them susceptible to temperature changes (Oberbeckmann et al. 2018). Variation in water temperature is caused primarily by seasonal turnover and secondly by the vertical depth at which the plastisphere is located in the aquatic environment. In general, microbial diversity on the surface of MPs is positively correlated with temperature,

whereas microbial density decreases as temperature increases. During summer, when seawater temperature is 29.08 °C, the microbial community diversity is most abundant on the surface of MPs (Xu et al. 2019). The biofilm thickness was thicker in summer in comparison to winter (Oberbeckmann et al. 2014). Carson et al. (2013) revealed a weak negative correlation between the effect of temperature on algal and bacterial densities. Tu et al. (2020) showed that total biofilm decreased with increasing vertical depth (2–12 m) of the MPs, probably affected by the temperature difference caused by the depth change. Thompson et al. (2004a) also found a positive correlation between *Vibrio* and temperature. Boyd et al. (2013) found that diatoms grew with twice the normal growth rate due to increased ocean temperature. Algae are early colonists of the plastisphere, and algal proliferation provided a large amount of nutrients that would accelerate bacterial attachment to the MP surface and shorter biofilm formation. Dong et al. examined that pathogenic bacteria on the surface of MPs were positively correlated with the temperature of the surrounding water column when they studied the plastisphere in winter and summer. The low seawater temperature in winter may inhibit bacterial growth on MPs and thus slow down biofilm formation (Dong et al. 2021).

The flow state also affects biofilm formation, and microorganisms thrive in environment with a low Reynolds number (a dimensionless number used to characterize the flow of a fluid) ($Re < 10^{-5}$). With rapid water flow, a high Reynolds number, and obvious inertia, it is difficult for microorganisms to remain on the surface of MPs, resulting in the smaller size of the biofilm clusters on the MP surfaces. And the large-scale biofilm communities were hard to develop (Chen et al. 2023). In comparison to lakes, the plastisphere has more abundant biomass, but lower algal levels in riverine ecosystems, which may be affected by hydrodynamic conditions. Additional evidence that hydrodynamics may alter the structure and dynamics of biofilms (Miao et al. 2021). However, there are a few works on hydrodynamic conditions as physical factors affecting the early colonization of initial microorganisms (Chen et al. 2023), and it is desirable to devote more attention to this aspect in future. Researchers may consider simulating changes in hydrodynamic conditions in the laboratory to explore the extent to which microbial colonization is affected.

In summary, the nutrient conditions of the aquatic environment affect the rate of MP biofilm formation. Biofilm diversity and formation time are controlled by environmental salinity. Among these indicators, salinity and hydrodynamic conditions act as the dominant factors, and other factors also influence biofilm communities. Due to the complexity of water chemistry parameters in natural water bodies, further works may consider the combined effects of these indices (Li et al. 2023a). Currently, relatively few experiments

specifically explore the above environmental factors, and further work can be conducted to understand the mechanism of environmental conditions in the biofilm by controlling environmental variables using the laboratory incubation method.

Microbial Community Characteristics of MP Surface in Aquatic Ecology Systems

In order to clarify the mechanism of interaction between film-forming microorganisms and MPs, it is necessary to understand the distribution and community composition of microorganisms on MPs. In general, aquatic ecosystems are categorized into freshwater ecosystems and marine ecosystems. Wetland is the transitional area between terrestrial and aquatic environments and forms a unique type of ecosystem due to land–water interaction. There are some differences between it and freshwater and marine ecosystems. Therefore, we divide aquatic ecosystems into freshwater ecosystems, marine ecosystems, and wetland ecosystems. Aquatic environments vary in freshwater, seawater, and wetland environmental conditions, resulting in different biofilms on the surface of MPs. Currently, there are numerous studies on the plastisphere in the ocean, fewer studies on the composition of the plastisphere in freshwater, and almost no investigations on biofilms in wetland environments. The composition of MP biofilms in three aquatic ecosystems was summarized.

Microbial Community in the Marine Ecosystem

MPs are widely distributed on the world's ocean coasts, marginal seas, open oceans, and even in the deep sea, polar seas, and marine ecosystems have become the largest sink for MPs worldwide. At present, the research on MP biofilms in the ocean is mainly focused on offshore, estuary, and deep ocean (Table 1). It has been demonstrated that the core members of the bacterial community on MPs in seawater are Proteobacteria, Bacteroidetes, Cyanobacteria, and Firmicutes, with the dominant group consisting of Proteobacteria and Bacteroidetes. Bacteria on the surface of MPs are mainly from the surrounding environment (De Tender et al. 2017; Sun et al. 2020), suggesting that this difference may be caused by the microbial diversity of the surrounding environment (Sooriyakumar et al. 2022). Proteobacteria are the most frequently observed phylum on the surface of MPs in the ocean, among which α -Proteobacteria and β -Proteobacteria are the two relatively higher abundance (Bryant et al. 2016; Debros et al. 2017). Plastisphere is more diverse and uniform than seawater, and microbial colonization is influenced by environmental factors, polymer type, and exposure time (Zhang et al. 2022a). Erythrobacteraceae are also prevalent alpha morphogens in marine biofilms and have been

Table 1 Overview of the literature reporting the plastisphere in marine

Microbial type	Phylum	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	Reference
Bacteria	Proteobacteria Bacteroidetes Cyanobacteria Actinobacteria Planctomycetes	HDPE	The surface water of Xinglin Bay, Xiamen, China	Incubation	30 days	Bay	Surface water	The V4–V5 hypervariable region of the 16S rRNA gene	Lab	Yang et al. (2020)
Bacteria	Proteobacteria Bacteroidetes Actinobacteria Firmicutes	–	Northeast of Jiaozhou Bay, Southwest of Jiaozhou Bay, and Dingzi Bay, China	Collection	–	Bay	Surface water	The V4 regions of 16S rRNA gene	Field	Li et al. (2021)
fungi	Ascomycota Basidiomycota Chytridiomycota Rozellomycota							The ITS1 region of the ITS gene		
Bacteria	Proteobacteria Bacteroidetes Cyanobacteria Planctomycetes	HDPE	The Larnaka District, Cyprus	Collection	–	Sea	2 m Depth	The V3–V4 region of the 16S rRNA-gene	Field	Martínez-Campos et al. (2022)
Bacteria	Planctomycetes Bacteroidetes Proteobacteria Actinobacteria	PE PHBV	Banyuls Bay, France	Incubation	45 days	Bay	4 m Depth	The V3–V5 region of the 16S rRNA-gene	Lab	Dussud et al. (2018)
Bacteria	Bacteroidetes Proteobacteria Actinobacteria	PP PE PS EVA	Western Mediterranean Sea	Collection	–	Sea	Surface water	The V3–V5 region of the 16S rRNA-gene	Field	Dussud et al. (2018)
Bacteria	Proteobacteria Planctomycetes Bacteroidetes	PP PE PS	The Bay of Brest, France	Collection	–	Bay	Surface water	The V4–V5 region of the 16S rRNA-gene	Field	Frère et al. (2018)

Table 1 (continued)

Microbial type	Phylum	–	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	Reference
Bacteria	Cyanobacteria Bacteroidetes Proteobacteria Firmicutes	<i>Rhodothermaceae</i> <i>Comamonadaceae</i> <i>Blastocatellaceae</i> <i>Acetobacteraceae</i> <i>raceae</i>	PE PP PS	Xiangshan Bay, China Lyxi Port, China Chongming Island, China	Collection	–	Estuary	Surface water	The V3–V4 variable region of the 16S rRNA genes	Field	Jiang et al. (2018)
Prokaryota	Proteobacteria Planctomycetes Chloroflexi Lentisphaerae	<i>Granulosicoccus</i> <i>Rhodopirellula</i> <i>Caldilineae</i> Latescibacteria*	HDPE LDPE PP PS PLA PVC PET SAN	North Sea, Germany	Incubation	15 months	Sea	Surface water	The V3–V4 region of the 16S rRNA-gene	Lab	Kirstein et al. (2018)
Eukaryota	Vertebrata Basidiomycota Alveolata Rhizaria	Mammalia Agaricomycetes Pseudovorticella Pseudopirsonia	Unknown	Lazarus Island Sembawang Beach Changi Beach	Incubation	1 week	Sediment	The top most 5 cm of sand sediment	The V4 region of the 18S rRNA gene	Lab	Curren and Leong (2019)
Bacteria	Proteobacteria Cyanobacteria Bacteroidetes Firmicutes	Rhodobacteraceae Unidentified chloroplast Dracomibacterium Novosphingobium	Unknown	Lazarus Island Sembawang Beach Changi Beach	Incubation	1 week	Sediment	The top most 5 cm of sand sediment	The V3–V4 region of the 16S rRNA gene	Lab	Curren and Leong (2019)
Bacteria	Bacteroidetes Archaea Proteobacteria Firmicutes	<i>Prevotella</i> Thaumarchaeota <i>Shewanella</i> <i>Faecalibacterium</i>	PE PP PS PVC PU	Haihe Estuary of Bohai Bay	Incubation	6 weeks	Bay	The interface between seawater and sediment	The V4 region of the 16S rRNA gene	Field	Li et al. (2019)
Bacteria	Proteobacteria Bacteroidetes Verrucomicrobia Actinobacteria	Alphaproteobacteria Flavobacteriia Verrucomicrobiae	PP PVC	Qingdao (Shandong Province), China Bai'an (Guangdong Province), China	Incubation	1 year	Sea	PP surface seawater PVC submerged at a depth of 2 m by ropes	The V3–V4 region of the 16S rRNA gene	Field	Xu et al. (2019)

Table 1 (continued)

Microbial type	Phylum	–	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	Reference
Bacteria	Proteobacteria Actinobacteria Verrucomicrobia Firmicutes	Alphaproteobacteria Flavobacteriia Verrucomicrobiae <i>Clostridia</i>	OXO-PE PET	Marina Shangri La, Muscat Oman	Incubation	80 days	Sea	The depths of 2 m and 6 m	The V4 region of the 16S rRNA gene	Field	Abed et al. (2020)
Bacteria	Proteobacteria Actinobacteria Bacteroidetes Cyanobacteria	–	PE PP PS	Western and Eastern coast of Italy, Italy	Collection	–	Sea	On the shore in the inter-tidal area	The V3–V4 regions of the 16S rRNA gene	Field	Basili et al. (2020)
Prokaryota	Planctomyces Bacteroidetes Proteobacteria	<i>Pirellulaceae</i> <i>Flavobacteriaceae</i> <i>Rhodobacteraceae</i>	PET HDPE LDPE PVC PS PP	Almirante Bay, Panama	Incubation	6 weeks	Bay	1 m Below the surface water	The V4–V5 region of bacterial 16S rRNA genes	Field	Dudek et al. (2020)
Eukaryota	Rhizaria Alveolata Stramenopiles	<i>Vampyrellida</i> <i>Dinophyceae</i> Araphid-pennate	–	–	–	–	–	–	The V4 region of eukaryotic 18S rRNA genes	–	–
Bacteria	Bacteroidetes Proteobacteria Cyanobacteria	–	Weathered and non-weathered PE	Mallorca, Spain	Incubation	9 days	Sea	1.5 m depth	The V4–V5 region of bacterial 16S rRNA genes	Field	Ermi-Cassola et al. (2020)
Bacteria	Bacteroidetes Proteobacteria Actinobacteria Patescibacteria	<i>Vibrionaceae</i> <i>Rhodobacteraceae</i> <i>Microtrichaceae</i> <i>Flavobacteriaceae</i>	PP PC PA ABS LDPE PS PET EPS PVC	Three artificial coral culture areas and one wild coral areas	Incubation	2 weeks	Sea	–	The V3–V4 regions of the 16S rRNA gene	Field	Feng et al. (2020)
Bacteria	Bacteroidetes Proteobacteria Firmicutes Cyanobacteria	Rhodobacterales Rhodovibrionales Caenarcanaiphilales Erysipelotrichales	PET bottle	Near a volcanic seep off Shikine Island, Japan	Incubation	3 weeks	Sea	20 cm above the seabed	The V4–V5 region of bacterial 16S rRNA genes	Field	Harvey et al. (2020)

Table 1 (continued)

Microbial type	Phylum	–	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	Reference
Bacteria	Bacteroidetes Proteobacteria Firmicutes Cyanobacteria	Flavobacteriales Sphingomonadales Bacillales Subsectional	HDPE fiber	Interior area of Xiangshan Bay, China	Incubation	8 weeks	Bay	0.5–3.5 m below the surface water	The V3–V4 regions of the 16S rRNA gene	Field	Jin et al. (2020)
Fungus	Ascomycota Basidiomycota Mucoromycota Chytridiomycota	Eurotiales Agaricales Diversisporales Spizellomycesales	PE PP PA PS PU CA	The subtropical western South Atlantic The Antarctic Peninsula	Collection	–	Sea	Surface water	The V4/V9 region of the 18S rRNA gene/The ITS2	Field	Lacerda et al. (2020)
Bacteria	Proteobacteria Actinobacteria Bacteroidetes Firmicutes	<i>Rhodobacteraceae</i> <i>Corynebacteriaceae</i> <i>Flavobacteriaceae</i> <i>Staphylococcaceae</i>	HDPE HDPE- OXO PP	ES/RJ/SP, along the southeastern Brazilian continental margin, Brazil	Incubation	23.6 months (719 days)	Sea	On the sea floor (–3300 m)	The V4 variable region of 16S rRNA gene	Field	Agostini et al. (2021)
Bacteria	Proteobacteria Actinobacteria Cyanobacteria Bacteroidetes	<i>Hyphomicrobiaceae</i> <i>Sporichthyaceae</i> <i>Phormidismiaceae</i> <i>Saprospiraceae</i>	PP PE PS PET PA	Adriatic Sea, Italy Ionian Sea, Italy Ligurian Sea, Italy Tyrrhenian Sea, Italy	Collection	–	Sea	–	The V6 variable region of 16S rRNA gene	Field	Amaral-Zettler et al. (2021)
Eukaryota	Alveolata Rhizaria Opisthokonta Stramenopiles	<i>Dinophyceae</i> <i>Chlorarachniophyceae</i> <i>Cnidaria</i> <i>Thraustochytriales</i>							The V4 eukaryotic hypervariable regions of SSU rRNA genes		

Table 1 (continued)

Microbial type	Phylum	–	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	Reference
Bacteria	Proteobacteria Bacteroidetes Cyanobacteria Firmicutes Planctomy- cetes	<i>Methy- lotrophic_ Group_3 Myroides Cyanobium_ PCC-6307 Fusibacter Propionigenium</i>	PE PP PS PVC ABS	In the Daya Bay of the South China Sea	Incubation	8 weeks	Bay	0.5–1.0 m below the seawater surface	The V4–V5 variable region of the 16S rRNA genes	Field	Zhang et al. (2022a)
Bacteria	Proteobacteria Actinobacteria Bacteroidetes Firmicutes	<i>Acidiphilium Brevibacterium Sunxiuqinia Bacillus</i>	PET (powder/ amorphous/ weathered powder)	Porthcawl Beach (Wales, UK)	Incubation	42 days	Sea	–	The V4–V5 region of the 16S rRNA gene	Lab	Wright et al. (2021)
Bacteria	Proteobacteria Cyanobacteria Bacteroidetes Planctomy- cetes	<i>Halioglobus Synecococcus Muricauda Blastopirellula</i>	PVC micro- beads	Yantai, Shandong Province, China	Incubation	7 days	Sea	The depth of 0–0.5 m	The V4–V5 region of the 16S rRNA gene	Field	Wang et al. (2021a)
Bacteria	Proteobacteria Bacteroidetes Verrucomi- crobia	<i>Roseobacter Fluviicola Rubritalea</i>	LDPE PA	Whakaraupō- Lyttelton Harbour, New Zea- land	Incubation	12 weeks	Estuary	0.2–0.6 m below the seawater surface	The V3–V4 region of the 16S rRNA gene	Field	Wallbank et al. (2022)
Fungi	Ascomycota Basidiomy- cota Chytridiomy- cota	<i>Exophiala Malassezia Thoreauomyces</i>							ITS2 region of the nuclear ribosomal gene		
Eukaryota	Opisthokonta Alveolata Ochrophyta	Arthropoda Ciliophora Bacillariophyta Perkinsozoa	Facemask (PP)	Dapeng Bay, China	Incubation	21 days	Bay	A depth of 1 m in seawater	The V4 region of the 18S rRNA gene	Field	Ma et al. (2023)
Bacteria	Proteobacteria Bacteroidetes Cyanobacteria Planctomy- cetes	<i>Rhodobacte- raceae Flavobacte- riaceae Phormidemi- aceae Pirellulaceae</i>	PP PE	The Bay of Brest, France	Incubation	About 5 months (147 days)	Sediment	(i) Fixed on cultivation racks, (ii) laying on the sediment, (iii) fixed to a floating buoy or (iv) laying on sediment	The V4–V5 region of the 16S rRNA gene	Field	Lemonnier et al. (2022)

Table 1 (continued)

Microbial type	Phylum	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	Reference
Bacteria	Proteobacteria Planctomy- cetes Bacteroidetes Cyanobacteria	PE PLA	In Banyuls Bay, France	Incubation	66 days	Sea	14 m depth	Universal small subunit ribosomal RNA	Lab	Cheng et al. (2021)
Bacteria	Proteobacteria Bacteroidetes Actinobacteria	PLA PET PS LDPE PVC PBAT	Calvi, Corsica, France	Incubation	82 days	Surface sea- water and sediment	In the water column at 4.5 m of depth/on the sediment at 8 m depth	The V3-V4 region of the 16S rRNA gene	Field	Delacuvellerie et al. (2021)

PP polypropylene, PS polystyrene, PE polyethylene, OXO-PE PE with pro-oxidant, PA polyamide, PU polyurethane, CA cellulose acetate, PET polyethylene terephthalate, PLA polylactic acid, PVC polyvinyl chloride, ABS acrylonitrile-butadiene-styrene, SAN styrene-acrylonitrile, EVA ethylene-vinyl acetate, EPS expanded polystyrene, HDPE high density polyethylene, HDPE-OXO HDPE with pro-oxidant, LDPE low density polyethylene, PHBV polyhydroxy-butyrate-co-valerate, PBAT poly (butyleneadipate-co-terephthalate)

identified on PP, PE, PS, and PET surfaces (Dussud et al. 2018; Oberbeckmann et al. 2018, 2014; Zettler et al. 2013). In Bacteroidetes, *Tenacibaculum* was repeatedly detected on the surface of plastic, indicating its potential role as a plastic-degrading bacterium (Frère et al. 2018). In PS samples, *Syranidou* was identified as a relatively high abundance of the genus Bacillaceae among Firmicutes (Syranidou et al. 2017). Cyanobacteria spotted on the surface of a wide species of MPs in the ocean, and its enrichment on the surface of suspended MPs may result from greater access to light. Planctomycetes are one of the most common bacteria in the ocean, and they prefer low-oxygen environments (Sosa and Chen 2022). Ascomycota, Basidiomycota, Chytridiomycota, Rozellomycota, and Aphelidiomycota comprised most of the fungal community. The relative abundance of archaea on MPs was low, and some researchers showed that the abundance of Crenarchaeota in the Mediterranean Sea (2–5%) was higher than that of the MP samples (0–2%), speculating that the low availability of sulfur in the plastisphere is not conducive to archaea growth (Sosa and Chen 2022). Bacteria and phytoplankton are not homogeneously distributed on the MP surface at any period of time, and diatoms, Cyanobacteria, and microfauna such as bryozoans are ocean's pioneers of MP colonization (Schlundt et al. 2020). Microbial communities on MPs in the ocean changed over time, and Schlundt found that Rhodobacteraceae and filamentous Bacteroidetes were dominant in the first week, followed by an increase in α -Proteobacteria and γ -Proteobacteria until the fifth week (Schlundt et al. 2020). Predators and pathogens were also observed in the marine-plastisphere, such as Ciliates, Choanoflagellates, *Clostridium*, and small flagellates that feed on bacteria and other microorganisms. Latva et al. (2022) detected the predators Tunicata, Protalveolata, and Cnidaria in the plastisphere incubated in a seawater environment. In the Mediterranean Sea, Delacuvellerie et al. (2022) reported the occurrence of flagellates, nematodes, cnidarians, and chordates in the surface biofilms of two MPs, PP and PE. MP surfaces are capable of harboring a large number of pathogens and can therefore serve as carriers for certain types of bacteria. Multiple human pathogenic bacteria were identified in MP samples from the North Sea and North Atlantic Ocean (Kirstein et al. 2016). Large numbers of the pathogenic *Vibrio parahaemolyticus* were discovered on MPs in the Baltic Sea (Kirstein et al. 2016). The plastisphere in the estuary provided anaerobic conditions favorable to denitrifying bacteria, and the plastisphere exhibited higher denitrification activity and N₂O production than the surrounding water column, indicating that estuarine plastisphere was a potential hotspot for N₂O production (Su et al. 2022a). Furthermore, PLA could accelerate *Burkholderia* sp. phosphorus-related metabolism and promote the breakdown of methyl phosphate into methane (Li et al. 2023b).

In addition to the biofilm composition on MPs in the ocean, the microbial community assembly mechanism is also the research hotspot. Sun et al. (2021) used the null model to analyze and found that the plastsphere bacterial community is mainly driven by the stochastic processes of drift (58.34%) and diffusion limitation (23.41%), which played more significant effects than the deterministic processes. The diffusion limitation affected the pattern of microbial succession. In other words, MP surfaces mainly act as rafts for microbial attachment rather than selectively attracting plastic-specific microbial colonizers (Sun et al. 2021; Zhang et al. 2022a).

Microbial Community in the Wetland Ecosystem

Wetlands are known to be a central hub for MPs accumulation, and industrial emissions and household dumping are the main routes of MP sources in wetlands (Su et al. 2022b). Few studies on MP biofilms in wetland environments have been conducted in recent years, and most studies have focused on the environmental concentration, shape, color, vertical distribution, and transformation processes of MPs (Ouyang et al. 2022). Kumar et al. (2021) identified fibers (threads), fragments, filaments, foams, and microbeads as common shapes of MPs observed in wetland ecosystems. Currently, few studies have been published about the plastsphere in wetlands.

The MP surface bacterial community in mangrove sediments mainly consisted of Proteobacteria, Actinobacteria, Bacteroidetes, Chloroflexi, and Acidobacteria (Table 2). Deng et al. (2023) incubated MPs in mangrove sediments for 70 days and discovered that mangrove degradation can reduce the network complexity and stability of MP-associated bacteria by shaping the composition of bacterial communities on MPs. The microorganisms on the surface of PLA were primarily associated with sulfur metabolism, and those colonizing PE and PP surfaces were mainly involved in carbon cycle processes. There is no literature on the fungal community on the surface of MPs in wetlands. Fungi play a primary role in the decomposition of organic matter in natural water in wetland ecosystems. They can degrade some unavailable carbon sources (non-degradable plastic) and contribute to the wetland carbon cycle.

The accumulation of MPs in artificial wetlands reshaped the co-occurrence patterns of wetland microbial communities, enhanced the “small-world” properties of wetland microbes, and substantially altered the ecological niche of wetland microorganisms. Yang et al. (2022) found that the accumulation of MPs in artificial wetlands reduced the removal of ammonia from wastewater and microbial diversity that MPs exposure caused changes in nonrandom species assemblages, and that MPs accumulation produced alternative ecological niches for typical nitrifying and denitrifying bacteria. Among MP surface microorganisms in

Table 2 Overview of the literature reporting the plastsphere in wetland

Microbial type	Phylum		Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	References
Bacteria	Proteobacteria	<i>Pseudoecoecol</i>	LDPE PS PET	Zhanjiang	Incubation	1 month and 3 months	The mangrove rhizosphere soil	Top 2–3 cm	The V3-V4 region of bacterial 16S rRNA genes for Illumina deep sequencing	Field	Xie et al. (2021)
	Bacteroidetes	<i>Ilumatobacter</i>	PP PA ABS PVC	Mangrove National Nature Reserve							
	Actinobacteria	<i>Denitromonas</i>									
	Nitrospirae	<i>Nitrospira</i>									
Bacteria	Proteobacteria	<i>Uliginosibacterium</i>	Non-additive PS	Constructed Wetland	Incubation	300 days	Wetland water	20 cm beneath the surface water	The V4–V5 hypervariable region of the 16S rRNA gene	Lab	Yang et al. (2022)
	Chloroflexi	<i>Longilinea</i>									
	Actinobacteria	<i>Paenarthrobacter</i>									
	Firmicutes	<i>Lachnospira</i>									

LDPE low density polyethylene, PS polystyrene, PET polyethylene terephthalate, PP polypropylene, PA polyamide, ABS acrylonitrile-butadiene-styrene, PVC polyvinyl chloride

mangrove sediments, some bacteria such as Actinomycetes and $\alpha/\beta/\delta$ -Proteobacteria accumulate on PLA, *desulfovibrio*, the dominant sulfate-reducing bacteria is associated with δ -Proteobacteria, and PLA promoted the sulfate reduction process. However, PET and polyvinyl chloride (PVC) derived from petroleum were less impact on the sulfate reduction process than PLA (Wang et al. 2023).

In general, there are insufficient microbial studies on the surface of wetland MPs, and the direction of research tends to focus on the effects of MPs on wetland microorganisms in carbon, nitrogen, and phosphorus cycling while neglecting the microbial colonization process. More attention should be paid to the fungi community composition of the plastisphere in wetland environments in future research.

Microbial Community in the Freshwater Ecosystem

Freshwater is the main route for land-based plastic pollutants to enter the ocean and is one of the most significant MP enrichment regions. At present, studies on biofilm composition on MPs in freshwater mainly focus on urban water environments (creeks, rivers, and lakes), and there are similarities with microbial communities on the surface of MPs in the ocean (Table 3). The bacterial community in freshwater is more commonly reported. Furthermore, Proteobacteria, Bacteroides, Actinomycetes, and Cyanobacteria are found to be the dominant groups (Zhang et al. 2022c). Wang et al. (2021b) demonstrated that the key taxa on the PE were Enterobacteriales of γ -Proteobacteria and Caulobacteriales of α -Proteobacteria. In contrast, the key taxa on the PP were the Gaiellales of Actinobacteria and Acidithiobacillales of γ -Proteobacteria. Several potential PE-degrading bacteria belonging to *Flavobacterium*, *Rhodococcus*, and *Pseudomonas* were identified in the freshwater plastisphere (Di Pippo et al. 2020). Freshwater biofilms also contained pathogens like *Pseudomonas* and *Acinetobacter* (Xue et al. 2020). There are fewer studies of fungi on MPs than bacteria. Cyanobacteria, green algae, and diatoms are typical algae on the surface of MPs. Chytridiomycota, Cryptomycota, and Peronosperales with saprophytic or parasitic lifestyles were detected in MP surface biofilms in several lakes in northern and central Italy (Di Pippo et al. 2022). In the Arctic freshwater lake, *Betamyces*, *Cryptococcus*, *Arrhenia*, and *Paranamyces* are the most abundant fungi on the surface of MPs (González-Pleiter et al. 2021). Many planktonic microbes in freshwater can be enriched by MPs. Wen et al. (2020) found that the relative abundance of Proteobacteria on the surface of the MPs was higher compared to the aquatic environment. Bacteroidetes, Verrucomicrobia, and Proteobacteria are more abundant on the MP surface than on natural substrates (Miao et al. 2019). Fungal community composition on MPs in freshwater included Ascomycota, Basidiomycota, Chytridiomycota, Rozellomycota, Blastocladiomycota, and

Mucoromycota (Lacerda et al. 2020; Wang et al. 2021b). Xue et al. (2021) discovered that Ascomycota and Basidiomycota were much more abundant on the plastic surface than in the surrounding environment and that Blastocladiomycota and Mucoromycota were plastic-specific fungi that were not found in the surrounding water. Algae play an important role in the freshwater plastisphere, where oxygen-rich phototrophic microbes such as Cyanobacteria, diatoms, and green algae can release photosynthetically produced organic carbon metabolites and support heterotrophic metabolism with extracellular polymeric substances (Di Pippo et al. 2020). In Arctic freshwater lakes, diatoms were found to be attached to the surface of MPs and cyanobacteria were also present in MP biofilms (González-Pleiter et al. 2021). In addition to bacteria, fungi, and algae, there are some protozoa on the biofilm, mainly Spirotrichea, Chaetonotida, and Craspedida (Weig et al. 2021). It has been shown that the total biofilm biomass is higher in oligotrophic and undernourished lakes than in eutrophic lakes, and the functional abundance of biofilm is higher in oligotrophic lakes than in surrounding water (Arias-Andres et al. 2018). Interestingly, MP surface microbes were an additional source of zooplankton in turbid rivers (Balkić et al. 2022).

Although the biofilm composition in freshwater and marine is relatively similar, there are still significant differences. MPs cultivated in seawater showed a gradual increase in the number of salt crystals as the incubation time increased, while this phenomenon was not observed in freshwater, presumably due to the difference in salinity between the two incubation mediums (Ramsperger et al. 2020). The network complexity of the plastisphere in freshwater ecosystems is lower, modularity is higher, and there is more competition among microorganisms, while the contrary in marine ecosystems. The main reason might be that the biomass and activity of microorganisms on the surface of MPs was generally low due to the high salinity and low nutrient concentration of the ocean, and microbes were more cooperative than competitive with each other (Li et al. 2021). Significant alterations in MP biofilm accumulation and heterotrophic activity can be caused by varying environmental conditions (Arias-Andres et al. 2018).

Knowledge Gap and Outlook

The plastisphere consists of biofilms, and MPs can promote the diffusion of microbes and the transmission of pathogenic bacteria, posing a potential threat to ecosystems and human environmental health (Xia et al. 2023). Here, we examine the formation of MP surface biofilms formation process, the incubation methods for MP biofilms, and the composition of MP biofilms in various aquatic environments. In order to elucidate the MP biofilm formation process and how

Table 3 Overview of the literature reporting the plastisphere in freshwater

Microbial type	Phylum	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	References
Algae	Cyanophyta Chlorophyta Bacillariophyta	PP PE	Wuhan East Lake, China	Incubation	30 days	Lake	–	Microscope/UV-Vis spectrophotometer	Field	Chen et al. (2019)
Bacteria	Proteobacteria Bacteroidetes Planctomycetes	LDPE PP	Nanjing Xuanwu lake, China	Incubation	21 days	Lake	–	The V4 regions of 16S rRNA gene	Lab	Miao et al. (2019)
Bacteria	Proteobacteria Bacteroidetes Actinobacteria	PS PE	Raritan River, China	Incubation	48 h	River	At the surface 0.5 m	The V3–V4 hypervariable region of the 16S rRNA gene	Lab	Parrish and Fahrenfeld (2019)
Bacteria	Proteobacteria Bacteroidetes Firmicutes Fibrobacteres Chlamydiae	PVC	Haihe River, China	Incubation	2 weeks	River	–	The V3–V4 variable region of the 16S rRNA genes	Lab	Wu et al. (2019)
Bacteria	Proteobacteria Bacteroidetes Actinobacteria	PE PP EPS PA	Iseo Lake/ Como Lake/ Maggiore Lake/Garda Lake/Trasimeno Lake/ Bracciano Lake/Paola Lake, Italian	Collection	–	Lake	0.2 m below the surface	The V1–V3 region of bacterial 16S rRNA gene	Field	Di Pippo et al. (2020)
Bacteria	Proteobacteria Bacteroidetes Actinobacteria Chloroflexi	PET	The Laguna Madre, a bar-built coastal lagoon, America	Incubation	424 days	River	At the sediment–water interface	The V3–V4 variable region of the 16S rRNA genes	Field	Pinnell and Turner (2020)

Table 3 (continued)

Microbial type	Phylum	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	References
Bacteria	Proteobacteria	Burkholderiales	Muskegon River, America	Incubation	3 months	River	2 m below the surface/on the sediment bottom	The V4 regions of 16S rRNA gene	Field	Steinman et al. (2020)
	Bacteroidetes	<i>Chitinophagaceae</i>								
	Planctomycetes	<i>Planctomycetaceae</i>								
	Nitrospirae	<i>Nitrospiraceae</i>								
Bacteria	Proteobacteria	<i>Sphingomonadaceae</i>	Zhejiang Pinghu/Huanggu Creek, China	Collection	–	River	30 cm beneath the surface water	The V3–V4 hypervariable regions of 16S rRNA gene	Field	Wang et al. (2020a, b)
	Bacteroidetes	<i>NS11</i>								
	Actinobacteria	<i>12_marine_group</i>								
	Nitrospirae	<i>Sporichthyaceae</i> <i>Norank Nitrospira</i>								
Bacteria	Proteobacteria	<i>Chthoniobacteriaceae</i>	A freshwater pond in Yangtze Estuary, China	Incubation	30 days	Pond	30 cm below the surface	The V3–V4 hypervariable regions of 16S rRNA gene	Field	Wen et al. (2020)
	Cyanobacteria	<i>Rhizobiaceae</i>								
	Bacteroidetes	<i>Burkholderiaceae</i>								
	Chloroflexi	<i>Sphingomonadaceae</i>								

Table 3 (continued)

Microbial type	Phylum	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	References
Bacteria	Proteobacteria	PHB HDPE	An ephemeral shallow freshwater lake, the international Arctic research base	Incubation	11 days	Lake	A depth of 20 cm into the lake	The V3—V4 hypervariable regions of 16S rRNA gene	Field	González-Pleiter et al. (2021)
	Bacteroidetes	<i>Mycoplana erythromicrobium</i>								
	Cyanobacteria	<i>Rhodobacter</i>								
	Actinobacteria									
Algae	Ciliophora							18S rRNA (563f/1132R)		
	Ochrophyta									
	Cryptophyta									
	Chlorophyta									
Fungus	Chytridiomycota							ITS regions (4/86F)		
	Ascomycota									
	Rozellomycota									
	Basidiomycota									
Bacteria	Proteobacteria	—	The Dagu River, the Moshui River, and the Wulong River, China	Collection	—	River	The surface water	The V4 regions of 16S rRNA gene	Field	Li et al. (2021)
	Bacteroidetes									
	Actinobacteria									
	Verrucomicrobia									
Fungus	Ascomycota	—						The ITS1 region of the ITS gene		
	Basidiomycota									
	Chytridiomycota									
	Rozellomycota									
Bacteria	Proteobacteria	PPR HDPE	Maludam River, Malaysia	Incubation	6 months	River	Depth of 50 cm from the surface	The V3 hypervariable region of the 16S rRNA gene	Field	Chen et al. (2021)
	Actinobacteria	PVC PE								
	Acidimicrobia	PET PP								
	Actinobacteria									
Firmicutes										

Table 3 (continued)

Microbial type	Phylum	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	References
Bacteria	Proteobacteria	PET PMMA	Xuanwu Lake, China	Incubation	40 days	Lake	Depth of 30 cm from the surface	The V4 regions of 16S rRNA gene	Field	Shen et al. (2021)
	Bacteroidetes									
	Acidobacteria									
	Cyanobacteria									
Bacteria	Proteobacteria	PP PE	Qinhuai River, China	Incubation	28 Weeks	River	At the bottom of the tank	The V3–V4 regions of the 16S rRNA gene	Lab	Wang et al. (2021b)
	Bacteroidetes									
	Actinobacteria									
	Cyanobacteria									
Fungus	Ascomycota							ITS2R(GCT GCGTTC TTCATCGAT GC)		
	Basidiomycota									
	Blastocladiomycota									
	Tremellomycota									
Bacteria	Proteobacteria	PP	A shallow reservoir, Hungary	Incubation	3 months	Reservoir	Depth of 50 cm from the surface water	The V3–V4 variable regions of the 16S rRNA gene	Field	Szabó et al. (2021)
	Planctomycetes									
	Cyanobacteria									
	Bacteroidetes									

Table 3 (continued)

Microbial type	Phylum	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	References
Prokaryota	Proteobacteria	PP PE PS PVC	The freshwater stream Truppach in northern Bavaria, Germany	Incubation	28 days	River	Depth of 20 cm from the surface water	The V3 hypervariable region of the 16S rRNA gene	Field	Weig et al. (2021)
	Bacteroidetes									
	Planctomycetes									
	Verrucomicrobia									
		Burkholderiales								
		Sphingobacteriales								
		Flavobacteriales								
		Rhizobiales								
		Cytophagales								
		Chlorophyceae								
Eukaryota	Ciliophora									
	Ochrophyta									
	Choanoflagellata									
		<i>Codostigidae</i>								
	Ascomycota	PP PE PS PBT	The Urumqi River, China	Incubation	30 days	River	Depth of 50 cm—100 cm from the surface/Floated on the surface of the water	The TAREu-k454FWD1 and modified TAREu-kREV3	Field	Xue et al. (2021)
	Basidiomycota									
		<i>Didymelaceae</i>								
		<i>Dothideales</i>								
		<i>Thelebolaceae</i>								
		<i>Kondoaecae</i>								
	<i>Cryptococcaceae</i>									
Fungus	Proteobacteria	PE PP PS	The intakes of two drinking water plants, which are located in Jialing River and Yangtze River, China	Incubation	21 days	River	Surface water at the top 0–10 cm	The V3–V4 region of the 16S rRNA-gene	Lab	Li et al. (2022)
	Actinobacteria									
	Acidobacteria									
	Bacteroidetes									
		<i>Blastocatellaceae</i>								
		<i>Saprosiraceae</i>								
		<i>Hyphomonadaceae</i>								
		<i>Acetobacteraceae</i>								
		<i>raceae</i>								
		<i>Desulfarcellaceae</i>								
Bacteria	Proteobacteria	LDPE	River Delta, Cyprus	Collection	–	River	–	The V3–V4 region of the 16S rRNA-gene	Field	Martinez-Campos et al. (2022)
	Bacteroidetes									
	Cyanobacteria									
	Planctomycetes									
		Cytophagales								

Table 3 (continued)

Microbial type	Phylum	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	References
Bacteria	Proteobacteria Planctomycetes Actinobacteria Bacteroidetes	Aquabacterium <i>Fimbricella</i> <i>Gemmata</i> <i>Pirellula</i>	In-house plumbing system Nansi Lake, China	Incubation	30 days	Lake	–	The V3–V4 region of the 16S rRNA gene	Lab	Song et al. (2022)
Bacteria	Proteobacteria Bacteroidetes Cyanobacteria Actinobacteria	–	The Lhasa River, China	Collection	–	River	–	The V4 regions of 16S rRNA gene	Field	Zhang et al. (2022c)
Bacteria	Proteobacteria Actinobacteria Bacteroidetes Firmicutes	<i>Burkholderia</i> <i>Sphingomonadaceae</i> <i>Rhodobacteraceae</i> <i>Ilumatobacteraceae</i>	The mainstream of the Yangtze River (length of 662 km) in the Three Georges Reservoir area, China	Collection	–	River	Surface water at the top 0–20 cm	The full-length 16S rRNA V1–V9 region	Field	Zhang et al. (2022b)
Bacteria	Proteobacteria Acidobacteria Actinobacteria	Alphaproteobacteria Betaproteobacteria Nitrospira Acidimicrobia	The Raritan River, America	Incubation	31 days	River	–	The full-length rRNA operons	Lab	Qiang et al. (2021)
Bacteria	Proteobacteria Cyanobacteria Actinobacteria Bacteroidetes	–	The Blue Sea Aquaculture Farm in Fengxian District, Shanghai, China	Incubation	28 days	Pond	Surface water at the top 10 cm	The V3–V4 region of the 16S rRNA gene	Field	Huang et al. (2022b)

Table 3 (continued)

Microbial type	Phylum	Type of plastic	Studied area	Incubation or collection	Incubation time	Sample type	Depth	Method	Lab or field	References
Bacteria	Proteobacteria Cyanobacteria Firmicutes Bacteroidetes	<i>Lactobacillaceae</i> <i>Cyanobiaceae</i> <i>Enterobacteriaceae</i> <i>ritaceae</i> <i>Prevotellaceae</i>	The Weihe River, China	Incubation	60 days	River	-	The V3-V4 region of the 16S rRNA-gene	Lab	Liu et al. (2022)
Bacteria	Proteobacteria Cyanobacteria Bacteroidetes Planctomycetes	- LDPE film	The Yangtze River in Nanjing, China	Incubation	28 days	River	-	The V4 regions of 16S rRNA-gene	Lab	Huang et al. (2022a)

PPR polypropylene, *PS* polystyrene, *PE* polyethylene, *PA* polyamide, *PET* polyethylene terephthalate, *PVC* polyvinyl chloride, *PBT* polybutylene terephthalate, *PHB* poly-β-hydroxybutyrate, *PPR* polypropylene random, *EPS* expanded polystyrene, *HDPE* high density polyethylene, *LDPE* low density polyethylene, *PMMA* polymethyl methacrylate

biofilms affect the environmental fate of MPs, the following knowledge gaps must be addressed, according to reviews of the literature:

- (1) Current research has discovered plastisphere in freshwater and marine environments, but the current understanding of MP biofilms in wetland ecosystems remains limited, requiring future research to investigate plastisphere in wetland environments and clarify the environmental behavior of plastisphere in wetland ecosystems.
- (2) Although in situ and microcosm incubation experiments can recreate the biofilm formation process, the lack of continuity in biofilm sampling in current studies has led to a lack of understanding of the dynamic process of biofilm attachment to MPs in the aquatic environment, as well as the role and function played by some protozoa (nematodes, ciliates, rotifers, etc.) in the plastisphere. Continuous monitoring experiments are required to gain a more complete understanding of the entire biofilm formation process. In addition, the sampling and treatment methods for MP biofilms are not yet harmonized, and further studies are hoped to have a set of harmonized methods that will make the experimental results easier to compare and more reliable.
- (3) Natural organic matter is a key component of the aquatic environment and is frequently adsorbed to the surface of MPs, where it can influence biofilm formation by altering the properties of the MPs and supplying microbes with a carbon source. Several studies have been conducted on MPs and dissolved organic matter (DOM), but the mechanism of MP–biofilm–DOM interactions in aquatic systems has not received much attention; metagenomics and environmental transcriptomics may be required to decipher the mechanism of natural organic matter interactions with the aquatic plastisphere.
- (4) There are some works of literature on the relationships among microorganisms within biofilms in the ocean/stream/wastewater. However, little is known about the interactions between different microorganisms within the plastisphere, such as the relationships between algae, bacteria, and fungi or between all of them. In subsequent research, whether these interactions alter during the various stages of biofilm development must be determined.
- (5) Currently, research on the migration and transformation of MPs by biofilms in aquatic environments is concentrated on in situ and laboratory experiments. Researchers should use a dynamic model of microbial community and other methods to model and predict the whole biofilm formation process on MPs combined under real water environment conditions to further elu-

cidate the impact of biofilms on the fate of MPs in the water environment.

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