Review

A critical review of interactions between microplastics, microalgae and aquatic ecosystem function

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A B S T R A C T

With the widespread occurrence of microplastics in aquatic ecosystems having been firmly established, the focus of research has shifted towards the assessments of their influence on ecosystem functions and food webs. This includes interactions between microplastics and microalgae, as fundamental components at the base of aquatic food webs and pivotal organisms in a wide range of ecosystem functions. In this review, we present the current state of knowledge on microalgae–microplastic interactions and summarize the potential effect on their respective fate. Microplastics can and do interact with microalgae and the available literature has suggested that the epiplastic community of microalgae differs consistently from the surrounding aquatic communities; however, it is still not clear whether this different colonization is linked to the composition of the surface or more to the availability of a "hard" substrate on which organisms can attach and grow. Further studies are needed to understand to what extent the properties of different plastic materials and different environmental factors may affect the growth of microalgae on plastic debris. Biofouling may alter microplastic properties, especially increasing their density, consequently affecting the vertical fluxes of plastics. Moreover, microplastics may have toxic effects on microalgae, which could be physical or related to chemical interactions with plasticizers or other chemicals associated with plastics, with consequences for algal growth, photosynthetic activity, and morphology. Microplastics seems to have the potential to affect not only the quality (e.g., fatty acids and lipids composition, food dilution effect) but also the quantity of algal production, both positively and negatively. This may have consequences for energy fluxes, which may propagate throughout the whole food web and alter aquatic productivity. Even though experimental results have indicated reciprocal impacts between plastics and microalgae, it is currently difficult to predict how these impacts may manifest themselves at the ecosystem level. Therefore, further studies are needed to address this important topic.

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1. Introduction

Plastic has become an inherent part of daily life and millions of tons of plastic material are manufactured globally every year. Due to the broad application of plastic in many different sectors and its long-lasting characteristics, the amount of plastic litter has increased dramatically over the last few decades in both aquatic and terrestrial environments (Galafassi et al., 2019). The slow breakdown of plastic items produces successively smaller pieces, called microplastics (MPs)– a term that is now commonly used to define particles whose larger dimension is lower than 5 mm (Van Cauwenberghe et al., 2015). Agreement on this higher limit of the microplastic range (5 mm) is quite consistent throughout the literature; however, some researchers have recently suggested different thresholds (e.g., 1 mm) (Hartmann et al., 2019). Besides the microplastics derived from the degradation of larger plastic items (i.e., secondary MPs), MPs can also be specifically manufactured in the micrometer size range (i.e., primary MPs), for instance, those used in industrial abrasives for sandblasting, plastic pre-production pellets ('nurdles'), or 'microbeads' in personal care products (Horton et al., 2017).

The term 'plastic' includes many different polymers, but the most abundant classes of polymers detected in aquatic environments are polyethylene (PE), polypropylene (PP), polystyrene (PS), polyester (PEST), polyamide (PA), and acrylic. This is not surprising, given the fact that these materials constitute a major proportion of global plastic production and are widely used in short life-cycle products (Erni-Cassola et al., 2019).

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Different plastic polymers have different chemical and physical properties and, depending on their composition, density, and shape, can be buoyant, neutrally-buoyant, or sink in aquatic systems (Cole et al., 2011). In particular, the density of most common plastic polymers ranges from 0.85 to 1.41 g/cm³ and, as this range includes materials of lower, equal, or higher density than sea and freshwater, microplastics can be easily distributed throughout the water column. The density can determine whether a particle occupies a pelagic versus benthic transport route: microplastics with a density greater than that of water sink into sediments where they accumulate, while those with low density float on surfaces (Cole et al., 2011; Woodall et al., 2014). Moreover an increase in density, through biofouling by organisms, can eventually result in sinking of microplastics (Auta et al., 2017).

Microplastic occurrence in the marine environment has been documented in almost every open and enclosed sea habitat, extending from surface water to deep-sea sediments, and from the equator to the polar regions (Peng et al., 2017). Recent estimates suggest that 4.85 trillion microplastic particles are floating in the global ocean (Eriksen et al., 2014). The majority of the research about microplastics has focused on seawater environments, while less than 4% of microplastic-related studies concern freshwater environments (Li et al., 2018). This limited information, however, has revealed that the abundance of microplastics in freshwater is comparable to that in marine environments (Li et al., 2018; Peng et al., 2017).

With the widespread occurrence of microplastics in aquatic ecosystems now firmly established, focus has been shifting towards the assessment of their influences on ecosystem functions and food webs. Despite growing research efforts, understanding of the ecological implications that the presence of microplastics may have on aquatic ecosystems, particularly regarding lower trophic levels (e.g., phytoplankton), are still largely unknown (Bryant et al., 2016). Different studies have already reported that microplastics can and do interact with aquatic microalgae and this has impacts on their respective fates (Long et al., 2015; Yokota et al., 2017). Microplastic surfaces constitute suitable substrates for the formation of biofilms (Amaral-Zettler et al., 2020; McCormick et al., 2014), and microalgae are an important constituent of colonizing biotic communities (Yokota et al., 2017). The growth of microalgae on plastic surfaces is important for the plastic degradation process, either having potential for biodegradation or, on the contrary, protecting plastics from ultraviolet radiation and photo-catalysis (Carson et al., 2013). Moreover, microplastics could potentially be incorporated along with microalgae into hetero aggregates with associated changes in buoyance, thus resulting in settling and influencing the fate and bioavailability of MPs (Carson et al., 2013; Long et al., 2015). At the same time, microalgae may suffer toxic effects as inhabitants of pelagic areas contaminated with microplastics, with consequences for their growth, photosynthetic activity, and changes in morphology (Fu et al., 2019; Mao et al., 2018; Zhao et al., 2019). In addition, transport via rafting of the microalgae themselves is also of concern, as this community is distinct from that of the surrounding water, with potential impacts such as the introduction of harmful or non-native algae into new environments (Carson et al., 2013; Masó et al., 2016). Thus, the interactions between microplastics and microalgae may also be relevant at the ecosystem level, with possible implications for the productivity of aquatic ecosystems, which have already been affected by other anthropogenic impacts such as climate change, eutrophication, and food web alterations (Troost et al., 2018; Yokota et al., 2017).

Given the importance of microalgae and the global occurrence of microplastic fragments in aquatic systems, a review on the topic is required, in order to identify the potential mechanisms of interaction as well as to guide further inquiries. For this reason, we conducted a broad and wide-ranging literature review, analyzing around 80 peer-reviewed papers, from 1972 to 2020, most of which (67%) were published from 2018 onwards, indicating the growing interest for this topic. We synthesize the current state of knowledge on microalgae-microplastic relationships, addressing the different aspects of these interactions. The specific objectives are:

i) to analyze whether some taxa of microalgae may preferentially colonize microplastic surfaces and to identify the features and extent of such colonization;
ii) to synthesize the environmental factors affecting microplastic colonization by microalgae;
iii) to discuss the consequences of colonization by microalgae on the fate and characteristics of microplastics;
iv) to summarize the effects that microplastics may exert on microalgae; and
v) to evaluate the effects of the interaction between microplastics and microalgae at the ecosystem level.

Moreover, we comment on potential future questions and research directions needed to further define the implications of the relationships between microalgae and these concerning pollutants.

2. Microplastic colonization

2.1. Plastic as a surface for colonization

There now exists a large body of evidence that microplastics are abundant and widespread in both marine and freshwater environments (Horton et al., 2017; Jiang, 2018; Van Cauwenberghe et al., 2015), and different studies have reported that MPs can be colonized by a wide range of organisms (biofouling) (Carson et al., 2013; Reisser et al., 2014). Microplastics harbor a distinct biota and represent a new habitat for rafting organisms to the point that the term "plastisphere" was coined by Zettler et al. (2013), to define the diverse community of heterotrophs, autotrophs, predators, and symbionts on the surface of plastic debris.

The first study on plastic colonization dated back to the beginning of the 1970, when an investigation in the Sargasso sea surface revealed the presence of microalgae (in particular diatoms) attached to the surface of plastic (Carpenter and Smith, 1972). This early study relied primarily on microscopy but, at present, the application of modern molecular methods, especially high-throughput DNA sequencing, is used to increase our understanding of the diverse micro-organisms inhabiting the plastisphere (Amaral-Zettler et al., 2020). While heterotrophic bacteria tend to be the focus of plastisphere research, the presence of both prokaryotic and eukaryotic autotrophs within the biofilm has been documented (Yokota et al., 2017). There is a growing field of research focused on the colonization process of microplastics by microalgae, but many questions are yet to be addressed (Carson et al., 2013).

It has been widely reported that the community growing on plastic debris differs consistently from the surrounding free-living organisms (Bryant et al., 2016; Dussud et al., 2018a; Kesy et al., 2019; Oberbeckmann et al., 2014; Zettler et al., 2013). In general, the dichotomy between particle-attached (PA) and free-living (FL) micro-organisms has been widely documented in several studies across different aquatic biomes and, thus, the discrepancies among organisms attached to plastic debris and planktonic communities may be not strictly linked to the composition of the surface, but more to the availability of a substrate on which organisms can attach to and grow (Oberbeckmann et al., 2016). It is likely that many taxa use plastic opportunistically as a niche but can also attach to other substrates (Oberbeckmann et al., 2016). However, experimental studies have reported differences in the communities found on plastic surfaces compared to other substrates, such as glass, which is usually used as a control substrate as it is inert (Vosshage et al.,

2018). During a short-term (two-week) experiment in which plastic particles (polyethylene, polypropylene, and polystyrene) and glass beads were exposed to brackish water from a coastal bay under controlled conditions, Ogonowski et al. (2018) found that the plastic-associated communities were distinctly different from those of the non-plastic substrates, suggesting substrate-driven selection. The same result was reported for a 6-week exposure experiment in the North Sea (UK) with polyethylene terephthalate (PET) bottles and glass slides as reference samples in which marked differences were reported in the community isolated from the two substrates with at least 57% divergence and where several biofilm members were detected solely on one of the surfaces, suggesting a preference for plastic or glass (Oberbeckmann et al., 2014). Additional studies in the same location reported no significant difference between glass and PET-attached communities (Oberbeckmann et al., 2016), thus highlighting that this topic remains controversial.

Vosshage et al. (2018) exposed different plastic materials (28 × 48 mm) for 49 days in a shallow, highly productive lake and found a significant difference in the volume of algae and biofilm height, compared to glass substrate, only for polymethyl methacrylate (PMMA) and not for polycarbonate (PC). Several cohort studies have indicated that the colonization process can vary depending on the plastic polymer used. For instance, Lagarde et al. (2016) highlighted differences in long-term colonization between high-density polyethylene (HDPE) and polypropylene (PP); Zettler et al. (2013) reported slight differences in organism richness associated with polyethylene (PE) and polypropylene (PP) on a wide range of plastic marine debris collected at multiple locations after long residence times in the environment; and Li et al. (2019) found significantly higher biomass on polystyrene (PS) than on other plastic polymers, indicating an influence of polymer composition on the biofilm formation. Despite these research efforts, a systematic examination of the colonization process occurring on different plastic polymers is still lacking. Indeed, the term 'plastics' include a wide variety of polymers with different chemical composition and properties. Even for the same type of polymer, the chemical composition may vary considerably, depending on the chemical additives (Lagarde et al., 2016). As the surface chemistry of the substrate is often not established, its influence on the colonization process generally can not be determined (Cooksey and Wigglesworth-Cooksey, 1995). Differences highlighted in plastic colonization processes may be partially explained by bearing in mind that different polymers, even if falling into the umbrella term 'plastic', are materials with distinct features. A fundamental role in the process of colonization of plastic substrate by microalgae is played by the Extracellular Polymeric Substances (EPS), which provides an attractive force maintaining cells together and attaching aggregates and cells to biotic or abiotic surfaces. It has been argued that different polymers stimulate the production of EPS in different quantities and/or with different composition, thus determining variability in the cohesiveness of biofilms and, ultimately, in the biomass of colonizing organisms (Lagarde et al., 2016).

It is worth mentioning that the studies reported above described experiments performed in both freshwater and marine environments. However, different hydrological, hydrodynamic, physico-chemical, and species compositions characterize these two systems. Therefore, biofilm attachment on the surface of microplastics in freshwater may show different features (e.g., biomass, type, and quantity of EPS), compared to those in the sea (Chen et al., 2019), such that the results obtained for marine systems should be extended to freshwater environments (and *vice-versa*) with caution.

Moreover, it should also be noted that the colonization experiments listed encompassed studies of different durations, whose variation may influence the process and the conclusions drawn.

The major part of the studies was conducted over short time scales; however, considering that synthetic polymers can persist over long periods in natural aquatic environments, incubation over longer timescales may allow for mimicking more realistic conditions (Kirstein et al., 2018). In addition, a distinction in the analysis of the different phases of biofilm development is needed, as only the initial recruits have direct contact with the polymer surface; in contrast, later recruits are more likely to interact with existing biofilm members and the abiotic components of the surrounding environment (Dudek et al., 2020; Oberbeckmann et al., 2016). Therefore, when the different phases of development are studied collectively, only generalized insights about the plastic-associated community can be obtained.

Besides, many other factors likely influence the colonization process. Among others, the age and the time that plastic material spends in the environment play an important role. Aging produces alterations of the plastic surface, and wrinkles, rough, and fractured surface textures can be observed on aged microplastics (Fu et al., 2019). This has consequences for colonization. Indeed, it has been reported that the surface "roughness" of particles is positively related to the density of attached microalgae (Carson et al., 2013). Aging processes can also vary the hydrophobicity of the different particles, which may have consequences on biofouling processes as well, as several articles have acknowledged that high-energy surfaces ("hydrophilic surfaces") tend to favor biofilm growth (Dussud et al., 2018a).

Finally, environmental factors and seasonal variations, which exert effects on primary producers in general, may influence colonizing processes (see Section 2.2).

2.2. Environmental factors and seasonal variations

As the growth and development of primary producers are dependent on several environmental factors, the colonization process on plastic substrates is influenced by their variations over time. Furthermore, biofilms are shaped to adapt to local conditions and environmental factors determine a cell's 'decision' to form or leave a biofilm (Toyofuku et al., 2016). Several studies have shown that biogeography plays an important role in the composition of MP-colonizing communities (Amaral-Zettler et al., 2015; Oberbeckmann et al., 2014), but there is still debate among researchers as to whether substrate-specific properties or environmental factors prevail in shaping microorganism assemblages on plastic materials. It is not clear whether the plastic surface 'environment' may exert a strong enough selection to drive species sorting, in order to overcome other niche-defining factors driven by seasonal and spatial patterns. Thus, it is important to study which environmental factors exert the strongest selective pressure and how their synergic relationships can shape plastic-colonizing communities.

Despite inter- and intra-site variability, there is a clear dearth of consensus among researchers that some factors with greater influence on plastic colonization can be identified. Among these, temperature plays a role in the settlement and growth of the colonizing community, as higher temperatures (within the optimum range) increase cell metabolism, resulting in the rapid development of the attached organisms. Indeed, seasonal differences, driven by temperature variations, have been observed in the plastic colonization processes. Oberbeckmann et al. (2014) highlighted the highest and the lowest overall mean diversity of PET plastisphere communities in a marine environment in summer and winter, respectively. Conceptually similar work has also been carried out in a freshwater lake by Chen et al. (2019) who, studying the biofilm development on polypropylene sheets in four seasons, pointed out that biofilm developed at a different rate in different seasons, with

the highest biofilm biomass per unit area in summer and the lowest in winter.

A pivotal role of salinity has also been recognized, which is known to shape communities in aquatic environments (Dussud et al., 2018b; Kesy et al., 2019; Oberbeckmann et al., 2018). Exposure of five types of plastic debris (polyvinyl chloride, polypropylene, polyethylene, polystyrene, and polyurethane) in the Haihe Estuary highlighted that salinity had a negative correlation with the average growth rate of the biofilm and a positive correlation with the diversity of the colonizing community (Li et al., 2019), confirming the results reported in previous studies (Kesy et al., 2019; Oberbeckmann et al., 2018).

Besides temperature and salinity, nutrients are likely to influence plastic colonization, where an increase in nutrients is usually associated with greater biodiversity on the plastic-attached community (Li et al., 2019; Oberbeckmann et al., 2018). Different environmental parameters and their variation over time can shape and select the community which is able to colonize the plastic surface; for instance, photosynthetic organisms cannot be found where there is no light irradiance (Chen et al., 2019). Moreover, it should be taken into account that there is a constant interplay of different environmental parameters, the combinations of which affect biofilm development.

However, the previous research has obtained mixed results, in terms of the impact of environmental factors. For instance, no effects of geographical location or environmental factors were highlighted on the community assemblages developed on plastics sampled in the western Mediterranean basin (Dussud et al., 2018b). We postulate that these contradictory results may likely be caused by different experimental designs (e.g., polymer considered or analytical methodologies), differences in temporal and spatial scale considered, and the intrinsic diversity in the systems studied. To the best of our knowledge, factors such as hydrodynamic features, physical disturbance, or solar radiation, have not been taken into account in the studies performed to date.

2.3. Microalgae taxa colonizing plastic debris

Bacteria usually represent the most-studied organisms in the colonization process of plastic materials. Among them, organisms belonging to the photosynthetic phylum of Cyanobacteria have been widely reported as a group with the capability to colonize plastic debris (Bryant et al., 2016; Chen et al., 2019; Oberbeckmann et al., 2014). They have been shown to dominate in many plastisphere communities (Table 1) and may play an important role in the ecological processes occurring in biofilms on plastic (Oberbeckmann et al., 2014). Their occurrence and importance on plastic surfaces have also been reported in freshwater systems (Yokota et al., 2017). As colonial and filamentous Cyanobacteria are able to produce cyanotoxins and are frequently the cause of harmful algal bloom (HAB) in fresh and marine waters (Yokota et al., 2017), their interactions with microplastics can have consequences and implications at the ecosystem level (see Section 5). Among the most frequent taxa detected, Cyanobacteria of the filamentous genus *Phormidium* are commonly found as part of plastic-colonizing communities, with studies attesting to their occurrence in the North Atlantic (Debroas et al., 2017; Zettler et al., 2013), North Pacific (Bryant et al., 2016), and North Sea (Oberbeckmann et al., 2016, 2014). Other marine and freshwater Cyanobacteria that have been reported to colonize plastic surfaces belong to the following orders: Chroococcales (genus *Microcystis*), Oscillatoriales (genus *Rivularia*), Nostocales (genera *Calothrix* and *Scytonema*), Pleurocapsales (genus *Pleurocapsa*), and Synechococcales (genera *Synechococcus, Prochlorothrix* and *Leptolyngbya*) (Bryant et al., 2016; Debroas et al., 2017; Dussud et al., 2018b; Muthukrishnan et al., 2019). Due to their high ecological plastic-

ity, Cyanobacteria are capable of adapting to several conditions and changes occurring in the environment (Leoni et al., 2014b; Marti et al., 2015; Nava et al., 2017). Therefore, their ability to colonize plastic substrates in a wide range of different environments is not surprising.

Diatoms typically join Cyanobacteria among the photosynthetic representatives that are able to colonize plastic surfaces (Amaral-Zettler et al., 2020). Most studies have shown that diatoms are common and omnipresent residents of the plastisphere (Table 1) – at least on plastics that are exposed to sunlight – being able to firmly attach to plastic and resist water turbulence and wave action (Reisser et al., 2014). For instance, Carson et al. (2013), who studied small plastic items from the surface of the North Pacific Gyre, reported that pennate diatoms were among the most abundant organisms (around one thousand individuals mm^{-2}). The same result was highlighted for marine plastic debris collected from pelagic and benthic habitats across the Mediterranean coastal waters of Greece, Italy, and Spain, reporting that diatoms appeared on almost 100% of the sampled plastic debris (Masó et al., 2016). A study examining the types of organisms inhabiting the surfaces of 68 small marine plastics (median size equal to 3.2 mm) from inshore and offshore waters around the Australian continent (tropical to temperate areas) reported that diatoms were the most diverse group of plastic colonizers, growing both flat on the surface of plastic materials and erect, being attached by mucous pads or stalks (Reisser et al., 2014). All of these studies have employed SEM analysis to identify the colonizing organisms. Additional studies performing DNA metabarcoding on plastic communities highlighted the presence of diatoms on plastic surfaces (Debroas et al., 2017; Kettner et al., 2019; Oberbeckmann et al., 2016, 2014). Despite that, in some cases, diatom clades did not make up more than 1% of the eukaryotic rRNA genes due to their low biomass (as opposed to the number of individuals), compared to the other eukaryotes (Bryant et al., 2016). A high density of diatoms is typically reported on plastic surfaces and, even if their biomass contribution may be low, the presence of many different species of diatoms is often recognized; thus, they importantly contribute to the overall biodiversity of the plastic-associated community. Among the most recurring and abundant taxa of diatoms in marine and freshwater systems are species of the genera *Achnantes, Amphora, Cocconeis, Navicula*, and *Nitzschia* (Lacerda et al., 2019; Masó et al., 2016; Oberbeckmann et al., 2014; Reisser et al., 2014; Zettler et al., 2013). Many of these are known biofilm-forming taxa in aquatic environments. In general, diatoms are reported to be among the first recruits in the colonization of different substrata (Debroas et al., 2017; Eich et al., 2015; Oberbeckmann et al., 2016): after the formation of a 'conditioning layer' by bacteria, surfaces are usually colonized by diatoms; however, it has been reported that diatoms may also directly attach to virgin surfaces (Khandeparker et al., 2014). However, it still remains unclear whether an obligate succession of organisms can be determined on the plastic surface or if it is an artifact due to the method of analysis used (Cooksey and Wigglesworth-Cooksey, 1995). Regardless of the sequence, it is generally agreed that diatoms represent a fundamental step in biofouling, influencing the subsequent colonization process (Khandeparker et al., 2014; Oberbeckmann et al., 2016).

Several studies have reported the presence of thecate and athecate dinoflagellates (Table 1), such as *Alexandrium* sp., *Ceratium* sp., and *Prorocentrum* sp., on plastic surface, with the occurrence of harmful species (Kettner et al., 2019; Masó et al., 2016; Reisser et al., 2014; Zettler et al., 2013). The presence of organisms belonging to Chlorophyta, Cryptophyta, and Chrysophyta have also been sporadically reported (Chen et al., 2019; Debroas et al., 2017; Lacerda et al., 2019; Masó et al., 2016).

Table 1

Species of primary producers colonizing plastic debris surface in several studies performed in different environments, with specification of the methodology adopted.

| Group and genus	Environment	Methodology	References
• Bacillariophyta: *Cyclotella, Mastogloia, Pleurosigma*	Marine: Sargasso sea	Light microscope	Carpenter and Smith, 1972
• Bacillariophyta • Dinoflagellata	Marine: North Pacific Gyre	Scanning Electron Microscopy (SEM)	Carson et al., 2013
• Bacillariophyta: *Chaetoceros, Navicula, Nitzschia, Sellaphora, Stauroneis* • Cyanobacteria: *Plectonema*-like, *Phormidium, Rivularia*	Marine: North Atlantic	Scanning Electron Microscopy (SEM); DNA sequencing	Zettler et al., 2013
• Bacillariophyta: *Amphora, Asterionella, Psammodictyon, Synedra* • Cyanobacteria: *Pseudophormidium, Phormidium, Stanieria, Synechococcus*	Marine: North Sea (UK)	Scanning Electron Microscopy (SEM); Denaturing gradient gel electrophoresis (DGGE); sequencinganalysis	Oberbeckmann et al., 2014
• Bacillariophyta: *Achnanthes, Amphora, Cocconeis, Cymbella, Grammatophora, Haslea, Licmophora, Mastogloia, Microtabella, Minidiscus, Navicula, Nitzschia, Thalassionema, Thalassiosira* • Dinoflagellata: *Ceratium*	Marine: Australian-wide coastal and oceanic	Scanning Electron Microscopy (SEM)	Reisser et al., 2014
• Bacillariophyta: *Amphora, Asterionellopsis, Cylindrotheca, Diploneis, Gyrosigma, Licmophora, Navicula, Nitzschia, Pleurosigma, Striatella*	Marine: Mediterranean Sea	Light microscope	Eich et al., 2015
• Bacillariophyta • Cyanobacteria: *Leptolyngbya, Phormidium, Prochlorotrix, Rivularia* • Chlorophyta • Dinoflagellata: *Symbiodinium* • Filosa-Chlorarachnea • Ochrophyta • Stylonematophyceae • Pelagophyceae • Pinguiophyceae • Prasinophyceae	Marine: North Pacific Subtropical Gyre	Scanning Electron Microscopy (SEM); DNA sequencing	Bryant et al., 2016
• Bacillariophyta: *Achnanthes, Amphora, Ceratoneis, Cyclotella, Cocconeis, Diploneis, Entomoneis, Fragilariopsis, Licmophora, Mastogloia, Navicula, Pleurosigma, Striatella, Thalassionema, Thalassiosira, Thalassiothrix* • Cyanobacteria • Dinoflagellata: *Coolia, Dinophysis, Heterocapsa, Pentapharsodinium, Prorocentrum*	Marine: Mediterranean coastal waters of Greece, Italy and Spain (benthic and pelagic)	Scanning Electron Microscopy (SEM)	Masó et al., 2016
• Bacillariophyta • Cyanobacteria: *Phormidium, Synechococcus* • Chlorophyta	Marine: North Sea (UK)	Scanning Electron Microscopy (SEM); DNA sequencing	Oberbeckmann et al., 2016
• Bacillariophyta: *Mastogloia, Navicula* • Cyanobacteria: *Leptolyngbya, Phormidium, Rivularia* • Chlorophyta: *Eremosphaera* • Cryptophyta • Crysophyceae • Dinoflagellata: *Gymnodinium*	Marine: North Atlantic	DNA sequencing	Debroas et al., 2017
• Bacillariophyta • Cyanobacteria: *Calothrix, Leptolyngbya,* [Oscillatoriales], *Pleurocapsa, Scytonema, Synechococcus* • Dinoflagellata	Marine: Mediterranean Sea	Scanning Electron Microscopy (SEM); DNA sequencing	Dussud et al., 2018a
• Bacillariophyta • Cyanobacteria • Chlorophyta • Cryptophyta • Euglenophyta • Pyrrophyta	Freshwater: East Lake (China)	Light microscope	Chen et al., 2019
• Bacillariophyta: *Chaetoceros, Eucampia, Melosira, Navicula, Pseudogomphonema, Synedropsis, Thalassiosira* • Chrysophyta	Marine: Antarctic peninsula	Scanning Electron Microscopy (SEM)	Lacerda et al., 2019
• Bacillariophyta: *Amphora, Cocconeis, Diploneis, Fragilara, Mastogloia, Navicula, Nitzschia, Pseudo-nitzschia, Striatella* • Cyanobacteria • Chlorophyta • Dinoflagellata: *Alexandrium, Amphidinium, Prorocentrum*	Marine: Caribbean Sea	Scanning Electron Microscopy (SEM); DNA sequencing	Dudek et al., 2020
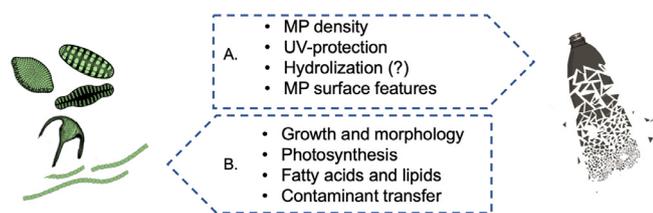
Fig. 1. Effects that (A) microalgae may have on microplastic particles; (B) microplastics may have on microalgae.

3. Effects of microalgae on microplastics

Interactions between microalgae and plastic debris can significantly alter the properties of these polymers, with consequences on their fate in aquatic environments (Yokota et al., 2017). The different processes that have been reported in literature can be summarized in two main categories: the alteration and/or biodegradation of the plastic polymer; and the alteration of the polymer density and sinking behavior (Fig. 1A).

Different studies have reported that the biofouling processes of microplastics may significantly alter their properties and, in particular, their adsorption capability seems to generally be enhanced (Kalčíková et al., 2020). For instance, Wang et al. (2020) reported that the physical and chemical surface properties of PE microplastics were changed with the development of biofilm, which resulted in different adsorption properties of microplastics for copper and tetracycline. Holmes et al. (2014) observed that metal adsorption was considerably greater in aged pellets than new polyethylene pellets. Furthermore, it has been observed that ions adsorbed from water onto biofilms were less intensively bound than to ion-exchange polymers and, thus, the ions are more easily desorbed (leached) from the biofilm (Kalčíková et al., 2020; Kurniawan et al., 2012). Therefore, the adhesion of microalgae on microplastic surfaces is of critical importance in the adsorption and desorption of pollutants from microplastics.

The capability of micro-organisms to biodegrade plastic (using plastic as a carbon source) has been reported for numerous bacterial strains, although most of the studies performed were based on the selection and testing of single strains in laboratory, which is far from environmental conditions (Jacquin et al., 2019). Among primary producers, the filamentous cyanobacteria of the genus *Phormidium* are known to degrade hydrocarbons (Oberbeckmann et al., 2016). The occurrence of species belonging to this genus on plastic surfaces has been widely documented (see section 2.3). This raises an interesting possibility that *Phormidium* in the plastisphere may be actively hydrolyzing the plastic (Yokota et al., 2017). However, as cyanobacteria are photosynthetic organisms, the advantage of higher exposure to sunlight on floating plastic pieces may be the actual explanation for their enrichment on plastic debris (Roager and Sonnenschein, 2019). Even if microalgae may not have a direct effect on the degradation of plastic, their presence can be important in determining the presence of other hydrocarbon-degrading bacteria, and it has been argued that diatoms may function as an important habitat for such micro-organisms (Dudek et al., 2020). At the same time, the biofouling of extensive surfaces may have an opposite effect, protecting the plastic from UV radiation and thus retarding photo-degradation processes (Andrady, 2011).

Another important role played by microalgae concerning plastic materials is linked to their capacity to alter the density of the colonized polymer which, consequently, affects the vertical fluxes of plastics. Chen et al. (2019) performed an experiment in a freshwater system and highlighted the changes in the buoyancy of polypropylene sheets (squares with a side length of 5

and 10 mm) following the development of microalgae biofilms. It has been reported that microplastics could potentially be incorporated into hetero-aggregates, composed of algae and small plastic materials, but this process remains little studied and, thus, is largely unpredictable. Several studies on microalgae have demonstrated significant interactions and the rapid formation of hetero-aggregates when microalgae were exposed to 400–1000 μm diameter polypropylene and high-density polyethylene microplastics at a concentration of 1 g L^{-1} (Lagarde et al., 2016); 2 mm polystyrene at 3.96 μg L^{-1} (Long et al., 2017); and microbeads from cosmetic products at around 4000 microbeads L^{-1} (Möhlenkamp et al., 2018).

Long et al. (2015) performed a lab experiment to study this interaction using three types of aggregates formed from two different algae species (the diatom *Chaetoceros neogracile*, the cryptophyte *Rhodomonas salina*, and a mix of them) and 2 μm polystyrene microbeads. The experiment highlighted that all three types of aggregates concentrated the microbeads. Once incorporated, the microbeads impacted aggregate sinking rates reaching several hundred meters per day, a high value compared to the sinking rate of free beads (less than 4 mm day^{-1}). These results support the idea that phytoplankton aggregates act as a potential MP sink. However, the extent to which different species form such aggregates is not the same, and dissimilarities were also reported for different plastic polymers in other studies (Lagarde et al., 2016). Many factors play a role in the hetero-aggregation process. For instance, major aggregate permeability increases the encounter chance between small particles and aggregates, as the small particles are not moved away from the aggregate but can go through aggregate macropores and be caught. Moreover, when an aggregate breaks, new surfaces, and macropores become available for microbeads to adhere to, where a succession of fragmentation and coagulation allows microbeads to be incorporated not only at the aggregate surface or in macropores but also into the entire aggregate (Long et al., 2015).

Resuspension processes can also occur, where several factors of the aggregates, such as size, density, porosity, shape, and stickiness play roles in determining the resuspension behavior of aggregates following settling (Möhlenkamp et al., 2018). Moreover, hetero-aggregates can also include inorganic material which both substantially enhance the settling velocity and determine lesser mobility once deposited in bottom layers (Möhlenkamp et al., 2018). The studies reported have provided interesting insight about the hetero-aggregation and the subsequent effects of microalgae on plastic debris, but they were all performed at a lab-scale and environmental conditions may widely differ from those tested. For instance, monospecific aggregates are unlikely to exist in nature and turbulence can quickly breaks up the hetero-aggregates (Lagarde et al., 2016).

4. Effects of microplastics on microalgae

Microalgae may experience toxic effects as inhabitants of pelagic areas contaminated with plastic debris. Furthermore, as primary producers essential to the functioning of aquatic ecosystems (Casado et al., 2013), small disruptions of microalgae populations may contribute to serious impacts on food webs (Fig. 1B). However, the effects and toxicity of microplastics have seldom been determined in microalgae and the current experimental results offer no consensus (Table 2).

One of the endpoints frequently measured is the effect on microalgal growth, on which microplastics seem to have a negligible impact (Lagarde et al., 2016; Long et al., 2017; Sjollema et al., 2016), even if some studies have reported effects after exposure to high concentrations of microplastics or small-sized particles (Gambardella et al., 2018;

Table 2
Toxic effects of microplastics exposure to microalgae. Only studies investigating microplastics (~1–5000 μm) were reported.

Study	Polymer	Polymer features	Size (μm)	Concentration (mg L^{-1})	Test species	Toxic endpoint	Test duration (h)	Results
Lagarde et al., 2016	HDPE		400–1000	400	*Chlamydomas reinhardtii*	Growth; Chloroplastic/stress response/apoptosisgenes	1872	• Non-significant decrease of growth • Non-significant change in expression of chloroplastic genes • No effect on stress response/apoptosis genes
	PP							• Growth decrease (18%) • Non-significant change in expression of chloroplastic genes • No effect on stress response/apoptosis genes
Sjollema et al., 2016	PS	Uncharged	0.05 0.5 6	25; 250	*Dunaliella tertiolecta*	Growth; Photosynthesis	72	• No effect on photosynthesis • Growth inhibition at 250 mg L^{-1} (57% for 0.05 μm; 13% for 0.5 μm)
		Negatively charged	0.5	25; 250	*Dunaliella tertiolecta*	Growth; Photosynthesis	72	• No effect on photosynthesis • Growth inhibition (13%) at 250 mg L^{-1}
			0.5		*Thalassiosira pseudonana*	Photosynthesis		No effect
			0.5		*Chlorella vulgaris*	Photosynthesis		No effect
Long et al., 2017	PS		2	3.96•10^{-3}	*Tisochrysis lutea; Heterocapsa triquetra; Chaetoceros neogracile*	Growth; Chlorophyll fluorescence	840	No effect
Yokota et al., 2017	Unknown (microbeads from body wash product)		20–350 (mean 60)	66.7	*Microcystis aeruginosa; Dolichospermum flos-aquae.*	Cell counts; Biomass; Growth; Cell morphology	504	• Increased algal particle counts • No effect on algal biomass and growth • Smaller algal particle size
Zhang et al., 2017	PVC		1	1; 5; 10; 50 5; 50	*Skeletonema costatum*	Growth Photosynthesis	96	Growth inhibition (40%) Decrease of chlorophyll content and photosynthetic efficiency
			1000	50; 500; 1000; 2000		Growth		No effect
Mao et al., 2018	PS		1	10; 50; 100	*Chlorella pyrenoidosa*	Growth; Photosynthesis; Cell morphology	720	• Growth inhibition until 528 h • Photosynthesis inhibition until day 144–192 h • Unclear pyrenoid, damaged membrane, distorted and unclear thylakoid, cell wall thickening until 312h

Table 2 (continued)

Study	Polymer	Polymer features	Size (μm)	Concentration (mg L^{-1})	Test species	Toxic endpoint	Test duration (h)	Results
Prata et al., 2018	PE		1–5	0.75; 1.5; 3; 6; 12; 24; 48	*Tetraselmis chuii*	Growth Chlorophyll concentration	96	No effect Significant reduction of chlorophyll at 0.9 (46%) and 2.1 (37%) mg L^{-1}
Chae et al., 2019	PE		180–212 (mean 204)	50; 100; 150; 200; 250; 300; 350	*Dunaliella salina*	Growth; Photosynthesis; Cell morphology	144	• Significant increase in growth (125–140%) and photosynthetic activity • Few effects on cell morphology
Davarpanah and Guilher-mino, 2019	Unknown		1–5	0.3; 0.9; 4	*Tetraselmischuii*	Growth	96	Non-significant decrease of growth
Fu et al., 2019	PVC	Virgin	~97–197	10; 100; 1000	*Chlorella vulgaris*	Growth; Biomass productivity	240	Growth and biomass inhibition, esp. at 10 mg L^{-1}
		Aged				Growth; Biomass productivity; Antioxidative enzymes (SOD)		• Growth and biomass inhibition, esp. at 10 mg L^{-1} • Stronger effect on biomass of aged than virgin MPs • No effect on SOD
Garrido et al., 2019	PE		1.4–42 (mean: 2–6)	0.5; 1; 10; 25	*Isochrysis galbana*	Growth	72	No effect
Seoane et al., 2019	PS	Amino-modified	2	2.5	*Chaetoceros neogracile*	Growth; Photosynthesis; Cell morphology; Esterase activity; Reactive Oxygen Species (ROS); Cytoplasmic membrane potential; Neutral lipid content	72	• Slight but significant decrease in growth rate • No effect on cell morphology or photosynthesis • Decrease in esterase activity at 24–48 h • No significant effects on ROS • No significant alterations in cytoplasmic membrane potential; • Significant decrease in the cellular neutral lipid content
Zhao et al., 2019	PVC		1	5; 25; 50; 100	*Karenia mikimotoi*	Growth; Photosynthesis	96	• Significant effect on growth: inhibition increased firstly and then decreased with the exposure time, and had a significant negative response with the increasing dose • Significant inhibition of photosynthetic activity

Sjollema et al., 2016; Venâncio et al., 2019; Zhang et al., 2017; Zhao et al., 2019). These findings point out two important aspects that should be taken into account: the relevance of the concentration and the features of the plastic particles tested. The characteristics of the microplastic used can play a fundamental role in determining the toxicity exerted. Besides the wide variety of polymers and additives that can be tested, other features such as the size and the charge of the plastic particles may be of paramount importance in their effect on organisms. The relationship among particle dimension and toxicity has been widely observed and it is generally agreed that smaller dimensions lead to higher toxicity in microalgae (Chae et al., 2019; Garrido et al., 2019). Very small particles may be more likely to inhibit the growth of microalgae through adsorption on the surface of the algal cell; for instance, inducing shading, blocking algal pores or gas exchanges, and embedding in microalgae cells (Fu et al., 2019; Zhang et al., 2017). Additionally, the surface ionic charge of microplastics seems to affect their toxicity. Weathering and degradation processes such as photo-oxidation, which can lead to carbonyl group formation (Bellingeri et al., 2019), can change the ionic charge of the microplastic surface. Furthermore, it has been shown that detrimental effects on microalgae growth were found only when exposing micro-organisms to positively charged particles, while, to the contrary, no impacts were reported in the same experimental conditions for uncharged particles (e.g., Feng et al., 2019). The effects may differ not only due to the types of polymers but also from the various responses of different microalgal species. It is likely that interactions between microplastics and microalgae may vary with cell characteristics, such as size and shape, as algal cell walls act as barriers to particle penetration and different cell wall characteristics may consequently influence particle sorption (Chae et al., 2019; Fu et al., 2019).

Toxic effects on microalgae may not only be physical but also related to interactions with the chemicals associated with plastics. Indeed, MPs can potentially transfer contaminants adsorbed onto their surface, residual (unpolymerized) monomers deriving from incomplete polymerization reactions, or additives, which may represent a high percentage of the final plastic materials (see, e.g., Hermabessiere et al., 2017; Maity and Pramanick, 2020). Most additives are not covalently bound to the plastic polymer and, thus, they can migrate to the material surface, potentially being released into the environment. Capolupo et al. (2020) investigated the effects of plastic leachates on the microalgae *Raphidocelis subcapitata* (freshwater) and *Skeletonema costatum* (marine), reporting that quite all of the leachates (i.e., benzothiazole, phthalide, acetophenone, cobalt, zinc, lead) inhibited algal growth. However, it has been hypothesized that the leaching of some additives, which are usually released at low concentration, may also stimulate the growth of microalgae due to a "hormesis" phenomenon (Chae et al., 2019; Song et al., 2020).

Besides the effects on microalgae growth, studies have found that microplastics seem to affect algal photosynthesis, as both chlorophyll content (Fu et al., 2019; Prata et al., 2018; Zhang et al., 2017) and photosynthetic efficiency (Mao et al., 2018; Zhang et al., 2017) decreased under microplastic exposure. Moreover, microplastics may induce morphological changes in microalgae (Mao et al., 2018), modulate the energy metabolism by decreasing the oil bodies that could serve as energy sources (Seoane et al., 2019), and may be ingested and internalized by mixotrophic algal species through phagocytosis processes (Long et al., 2017). However, many of the effects experienced by microalgae appear to be temporary, with an initial period of vulnerability followed by adaptive responses leading to recovery (Prata et al., 2019 and references therein). Different mechanisms of detoxification have been hypothesized to influence the recovery reported in microalgae activities, such as membrane thickening, reduction of surface exposure

through homo-aggregation, and hetero-aggregation (Mao et al., 2018; Prata et al., 2019). With respect to the latter point, it has been reported that the bioavailability of plastic particles changed during the different experiments, due to adsorption to experimental containers, or embedding in organic aggregates. This underlines the need to quantify the bioavailability and distribution of MPs in the experimental systems, in order to obtain accurate values of the actual MP concentration to which the microalgae are truly exposed (Long et al., 2017).

A recent laboratory study has suggested that microplastics may also affect microalgae lipid and fatty acid composition,which are important dietary components for primary consumers as a source of energy and essential nutrients (Guschina et al., 2020). Indeed, the exposure of *Chlorella sorokiniana* to polystyrene microplastics (<70 μm, 60 mg/L) resulted in the alteration of essential fatty acids – major structural compounds in algal cell membranes – and chloroplast galactolipids –which have important functions in photosynthesis. These findings raise questions about the impact of microplastics on algal productivity and the transfer of important lipid compounds through food webs, thus requiring further investigation.

It is important to stress that the ecological relevance of laboratory observations is likely to be low, as they are far from reflecting the complexity of the aquatic environment, in which we must consider non-equilibrium conditions, large volumes, lower algal cell concentrations, the co-existence of different microalgal species, different polymers, sizes, doses, and so on (Long et al., 2017; Sjollema et al., 2016). Moreover, in nature, mixtures of microplastic with different contaminants can also occur (see, e.g., Davarpanah and Guilhermino, 2019; Johansen et al., 2019; Zhu et al., 2019); however, studies regarding this topic are still scarce.

5. Ecosystem implications

Many of the effects obtained through lab-scale experiments, as discussed in the previous sections, may potentially have consequences on the ecosystem functioning. However, it is difficult to predict how specific results obtained through laboratory experiments can manifest in real aquatic systems. As microalgae are keystone organisms, impacts and alterations of such communities can have substantial consequences for the whole aquatic ecosystem (Wright et al., 2013). Increasing levels of plastic pollution may not only exert pressure at the individual or population level but, additionally, may cause cascading secondary effects on the functioning and services of other communities and, ultimately, on the ecosystem as a whole (Kong and Koelmans, 2019; Leoni et al., 2018).

One of the key mechanisms that has been claimed to be crucial is the perturbation effect that the interaction between plastics and microalgae may have on the aquatic food web. There are substantial issues regarding whether microplastics affect the quality and quantity of algal production and whether this may propagate through food webs. Microalgae mixed with plastics may exhibit morphological changes that affect their detectability, palatability, and ease of handling by grazers (Lacerda et al., 2019; Yokota et al., 2017). Due to biofouling, microplastics may become more available for interaction with animals within the water body. Although many species are able to discriminate between inert and edible particles, the developed biofilm "camouflages" plastic particles, thus allowing them to potentially become attractive food items to grazers, such as zooplanktonic organisms (Vroom et al., 2017). Consequently, biofilms may alter the interactions between microplastics and primary consumers, increasing ingestion rates of 'flavored' microplastics. Ingestion of microplastics aggregated with microalgae leads to the dilution of food due to the co-ingestion of inert plastic together with regular food or prey

(Kong and Koelmans, 2019). Ecological implications are expected to be triggered especially by the responses of zooplanktonic species, which represent the natural predators of algae (Kong and Koelmans, 2019). Kong and Koelmans (2019) applied a theoretical model to investigate the negative impacts of microplastics on food webs. The research reported that reduced assimilation rates due to the ingestion of MPs resulted in a lower population density of the corresponding organisms. Considering zooplankton, decreased population density lessens the grazing pressure on phytoplankton, which leads to increased population sizes of diatoms and green algae. In response to the loss of zooplankton, planktivorous fish feeding on zooplankton become largely limited, thereby restricting the piscivorous fish population. Consequently, benthivores fish start to dominate the fish community, reducing the abundance of zoobenthos through predation. This results in stronger perturbation on the sediment and increased water turbidity due to resuspension (Kong and Koelmans, 2019). Despite the model being applied to shallow lakes and using high concentrations of MPs (40 and 4000 particles L^{-1}), the results provided valuable insights about how the impact of MPs, whose concentration is expected to increase in the near future, can propagate through whole aquatic systems.

The decreased quality of algae ingested by zooplanktonic organisms is not the result of the dilution of food with inert particles, but also by the direct effects of microplastics on algal quality. Recent evidence has suggested that microplastics may also affect the lipid and fatty acid composition of microalgae (see Section 4), which are critical regulators of the survival, reproduction, and population growth in invertebrates and fish. As polyunsaturated fatty acids are highly retained during transfer through aquatic food webs, any factors affecting their quantity and quality in phytoplankton may affect the growth, reproductive capacity, and fitness of aquatic invertebrates and fish (Guschina et al., 2020; Leoni et al., 2014).

Furthermore, microplastics may exert potential effects on the quantity of algal production. As plastic debris provides an abundant growth matrix and better floating conditions for microalgae, while exerting adverse effects (i.e., toxicity or "food dilution") on phytoplankton consumers (i.e., zooplankton), it has been argued that plastic pollution can promote the multiplication of microalgae in large quantities, with consequent detrimental effects for aquatic ecosystems already disturbed by eutrophication processes (Zhang et al., 2020); for instance, it has been reported that plastic surface represents a net autotrophic "hot spot" in the oligotrophic ocean, with high density of chlorophyll a and high oxygen production (Bryant et al., 2016). Thus, plastic pollution might affect ecosystem productivity, with substantial consequences for those ecosystems that are characterized by oligotrophic conditions. To date, studies that have attempted to calculate the increase of primary productivity due to the presence of plastic debris are still missing and, so, quantitative data are not available to determine whether the occurrence of plastic is relevant to the perturbation of primary productivity. However, an opposite mechanism may be observed: microplastics may exert toxic effects on microalgae (see Section 4), causing a decrease in phytoplankton species, and eventually leading to losses in ecosystem productivity. This can induce cascading impacts on biodiversity, ecosystem services (e.g., fish provisioning), which are also influenced by the productivity at lower levels of the trophic chain, and cultural services (e.g., tourism and recreation). Evidences supporting one mechanism over the other are still missing, and, to the best of our knowledge, field and experimental approaches regarding this topic are lacking. There is no consensus even about the primary effects that microplastics may have on organisms and, so, scaling up results to the ecosystem level is complex and it is only possible to postulate some hypotheses about the plausible mechanisms.

Moreover, indirect effects can also occur. Microplastic-associated bacteria have the ability to alter the nutrient cycling processes (e.g., increasing the denitrification capability, or transforming phosphorus through microbe-mediated processes). Nutrients can be assimilated by plastic materials and then released into the surrounding water, altering the nutrient concentration and thus affecting primary producers (Chen et al., 2020). Therefore, microplastics seem to be able to interact with several biotic and abiotic factors, creating new "micro-ecosystems" in which both nutrients and primary producers can be concentrated and not dispersed into the pelagic environment.

As previously discussed, the colonization of microplastics by microalgae adds additional weight to the plastic particles facilitating the sedimentation and burial of these pollutants. Thus, microplastics can influence energy fluxes not only in the pelagic compartments but also in benthonic environments, where they may negatively affect the general fitness of benthonic organisms (Bellasi et al., 2020)

Another aspect that should be considered is the threat that microplastics may pose to aquatic biodiversity. Plastic debris offers a new colonization substrate for organisms and a durable dispersal medium for several organisms, raising their dispersion capacity. As plastics can be transported by winds and currents over long distances, the dispersion of debris containing epiplastic organisms may cause the transport of alien species and changes in aquatic biogeographical patterns (Dudek et al., 2020; Kettner et al., 2019). Barnes (2002) has estimated that human litter, the majority being plastic, more than doubles the rafting opportunities for biota, which could endanger aquatic biodiversity. Considering microalgae, concerns have been stated regarding harmful bloom-forming organisms, such as some species of dinoflagellates or cyanobacteria (Amaral-Zettler et al., 2020; Masó et al., 2016). The increasing colonization opportunities provided by the presence of microplastics in aquatic ecosystems can allow the colonization of microalgae able to produce toxins (synthesized for defense from predation), which can lead to harmful algal blooms (HABs), with consequent negative impacts on aquatic ecosystem services and, thus, representing a pressing environmental and human health problem. For instance, the presence of the cyanobacterium of the genus *Phormidium* has been widely reported on microplastic surfaces, which is a cosmopolitan genus found in diverse substrates and habitats in both oligotrophic and eutrophic conditions. Under favorable hydrological and environmental conditions, *Phormidium* forms cohesive mats that can cover large areas and species belonging to this genus can produce a range of cyanotoxins, such as the neuromuscular-blocking anatoxin-a (ATX) and homoanatoxin-a (HTX) and their structural derivatives, causing HABs (McAllister et al., 2016).

6. Conclusion and future research recommendations

Different studies have reported that plastics can and do interact with microalgae, which represent the base of the aquatic food web and, thus, play a key role in marine and freshwater ecosystems. However, studies investigating the relationships between plastic debris and microalgae are still scarce, especially in freshwater systems. Therefore, many aspects (as described in previous sections) require further research and fundamental gaps exist in the current state of knowledge regarding this subject.

The available literature has suggested that the "epiplastic" community of microalgae consistently differs from the surrounding aquatic communities; however, it is still not clear whether such differences in colonization are linked to the compositions of the surfaces or more to the availability of a "hard" substrate on which organisms can attach and grow; thus, further studies are required to address this question. Furthermore, we need to better understand to what extent the properties of different plastic materials

and different environmental factors – which can also act synergistically – may affect the growth of microalgae on plastic debris. In particular, field-studies on microplastic colonization by microalgae are especially missing for freshwater environments. Therefore, future studies, taking as an indication the information gathered from previous studies performed in marine systems, should address this topic. The colonization and hetero-aggregation between microplastics and microalgae lead to changes in particle buoyance, thus resulting in settling and influencing the fate and bioavailability of plastics in surface waters. At the same time, microplastics can harm microalgae, by inhibiting their growth, reducing chlorophyll and photosynthesis, and causing changes in morphology. As reported, previous research regarding the toxic effects that plastic can exert on microalgae is controversial and, thus, it is not clear whether these effects are of concern for microalgae. The difficulty in obtaining a clear answer is linked to the several confounding factors (e.g., microplastic dose, features, and size) in laboratory experiments, resulting in conflicting results on plastic toxicity. Thus, future studies need to clarify the differences in effects of microplastics on primary producers due to microalgae species and the properties of plastic materials (e.g., polymer type, chemical composition, weathering condition, surface charge, and size). Most of these studies have tested high concentrations of plastic particles, thus not accurately reproducing the current environmental concentrations reported in studies investigating the occurrence of plastic in marine and freshwater systems. However, the concentrations of these pollutants are expected to increase in the near future and, so, testing higher concentrations can provide important insight into the future situation. Furthermore, the transport via the rafting of the microalgae themselves is also of concern, as this community is distinct from that of the surrounding water, with potential impacts such as the introduction of harmful or non-native algae into new environments, potentially impairing local aquatic biodiversity. The effects that microplastics can have on the biodiversity of microalgae, with subsequent cascading effects on entire aquatic ecosystems, have not yet been fully considered; therefore, future studies should attempt to include and evaluate this theme.

As highlighted in this review, the largest gap in the current knowledge is our understanding of the ecosystem implications of the microplastic-microalgae relationships. Although some attempts have been made to address this issue, the effects that plastic debris can have on aquatic ecosystems – which are already affected by other anthropogenic impacts such as climate change, eutrophication, and food web alteration – remain unclear. When experimental results indicate reciprocal impacts between plastics and microalgae, it is difficult to predict how these impacts manifest themselves at the ecosystem level. For instance, the effects that microplastics have on algal photosynthesis, the hormesis phenomenon linked to the leachates of additives, or the alteration of microalgae lipid and fatty acid composition could trigger subsequent effects throughout the whole aquatic ecosystem. Further investigations are urgently needed, as this theme is of pivotal importance for aquatic environments and their ecosystem services. Future studies should take into account the results reported from the different laboratory studies, in order to prioritize research questions and test the same hypotheses in real systems. The effect that microplastic-microalgae interactions can have on the primary productivity of aquatic ecosystems, which may be negatively or positively affected, should be studied; in particular, quantitative estimations are needed. Modeling approaches can be useful to test the broad-scale consequences of different scenarios of plastic pollution. However, it is important to validate these models and, so, realistic in-field observations are needed to improve their performance. However, the results of in-field studies may be difficult to interpret, due to the many possible confounding factors. Thus, a useful tool that can be used for testing the consequences of microplastic-

microalgae interactions for aquatic ecosystems can be represented by mesocosms, including artificial ponds or enclosures in natural environments. These are physical models of natural systems which allow for the controlling of experimental conditions for research purposes, while also providing some level of realism.

Author contribution

V.N. researched data for the article and wrote the article; B.L. contributed to discussion of the content and reviewed and edited the manuscript before submission.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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