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Zooming in the plastisphere: the ecological interface for phytoplankton–plastic interactions in aquatic ecosystems

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ABSTRACT

Phytoplankton is an essential resource in aquatic ecosystems, situated at the base of aquatic food webs. Plastic pollution can impact these organisms, potentially affecting the functioning of aquatic ecosystems. The interaction between plastics and phytoplankton is multifaceted: while microplastics can exert toxic effects on phytoplankton, plastics can also act as a substrate for colonisation. By reviewing the existing literature, this study aims to address pivotal questions concerning the intricate interplay among plastics and phytoplankton/phytobenthos and analyse impacts on fundamental ecosystem processes (e.g. primary production, nutrient cycling). This investigation spans both marine and freshwater ecosystems, examining diverse organisational levels from subcellular processes to entire ecosystems. The diverse chemical composition of plastics, along with their variable properties and role in forming the "plastisphere", underscores the complexity of their influences on aquatic environments. Morphological changes, alterations in metabolic processes, defence and stress responses, including homoaggregation and extracellular polysaccharide biosynthesis, represent adaptive strategies employed by phytoplankton to cope with plastic-induced stress. Plastics also serve as potential habitats for harmful algae and invasive species, thereby influencing biodiversity and environmental conditions. Processes affected by phytoplankton–plastic interaction can have cascading effects throughout the aquatic food web *via* altered bottom-up and top-down processes. This review emphasises that our understanding of how these multiple interactions compare in impact on natural processes is far from complete, and uncertainty persists regarding whether they drive significant alterations in ecological variables. A lack of comprehensive investigation poses a risk of overlooking fundamental aspects in addressing the environmental challenges associated with widespread plastic pollution.

Key words: aquatic food webs, autotrophs, epiplastic organisms, harmful algae, macroplastics, microalgae biodiversity, microplastics, primary productivity, metabolic traits.

CONTENTS

I. INTRODUCTION

Plastic pollution is a pervasive global environmental issue that impacts both marine and freshwater ecosystems (Rochman & Hoellein, 2020). Although initial research primarily focused on plastic pollution in marine environments, recent analyses have unveiled comparable or even higher plastic concentrations in freshwater ecosystems (Nava *et al.*, 2023). The ubiquity of plastic waste and its far-reaching consequences extend beyond aquatic environments, and it has been proposed as a geological indicator of the Anthropocene era (Andrady, 2022). Consequently, plastic pollution may represent a threat to biodiversity and the functioning of aquatic ecosystems, especially considering the increasing pace of global plastic production and use (Hu *et al.*, 2019; Borrelle *et al.*, 2020).

Annually, an estimated 4.8–12.7 million metric tons of plastic debris enter the oceans (Jambeck *et al.*, 2015) through numerous pathways. A large portion of plastics enters the ocean from land-based sources, including mismanaged household waste, wastewater discharge, and industrial activities. The remaining fraction is believed to originate from maritime activities, such as those involving fishing vessels and cruise ships (Rochman, 2020). In addition, atmospheric deposition (i.e. wet and dry deposition of plastic particles) is a newly recognized contributor to plastic pollution, where plastic particles are transported over long distances even to remote areas (Allen *et al.*, 2019; Brahney *et al.*, 2020).

The term "microplastic" emerged in the early 2000s and has since garnered significant global attention, primarily due to the abundance and ubiquity of microplastics, and the significant threats they pose to both human health and the environment (Sun & Wang, 2023). Microplastics can be intentionally manufactured in micrometre sizes, as seen in consumer goods such as personal care products, constituting what is known as "primary microplastics" (Frias & Nash, 2019). They can also result from the degradation of larger plastic items due to weathering, ultraviolet (UV) radiation, and mechanical forces, a category referred to as "secondary microplastics" (Cole *et al.*, 2011). Microplastics are typically categorised within a size range between 1 μm and 5 mm, although various studies have adopted different ranges (e.g. Browne *et al.*, 2011; Claessens *et al.*, 2011). This lack of consistency becomes particularly problematic when comparing microplastic data, emphasising the growing importance of establishing a scientific standard (Hartmann *et al.*, 2019). Particles with a diameter in the nanometer range are termed "nanoplastics". Their minute size raises concerns about their potential interactions with biological processes at the cellular level as they have the capability to infiltrate cellular structures (Larue *et al.*, 2021).

The multifaceted nature of plastics poses threats to aquatic organisms across different organisational levels, from cells to populations (Scherer *et al.*, 2018). However, our current comprehension of the consequences of these pollutants remains limited, particularly regarding their impacts on ecosystem-level dynamics. Plastics do not represent a single compound or material type but rather encompass a diverse array of chemical compositions, each characterised by specific properties, including variations in heat and chemical resistance (Andrady, 2017). Additionally, the incorporation of numerous additives during resin processing and product fabrication further adds to the complexity of these contaminating materials (Andrady & Rajapakse, 2016). Plastics can also provide substrates for various organisms since their surface can be easily biofouled when introduced into aquatic environments. This unique ecological niche is known as the "plastisphere" (Zettler, Mincer & Amaral-Zettler, 2013). This term is widely used to describe various taxa, including bacteria, microalgae, and larger organisms like molluscs, among others, associated with plastics in numerous aquatic ecosystems (Amaral-Zettler, Zettler & Mincer, 2020). The plastisphere is sometimes referred to as a human-made "eighth continent" not only offering a stable, durable, and buoyant habitat for organisms (Barros & Seena, 2021; Gao *et al.*, 2021) but also playing a central role in several biogeochemical processes. For instance, epiplastic biofilms can harbour species resistant to metals or antibiotics, facilitate horizontal gene transfer, drive species evolution for plastic biodegradation, and serve as vectors for the transport of alien species (Dąbrowska, 2021; Du *et al.*, 2022; Rani-Borges, Moschini-Carlos & Pompêo, 2021; Leite *et al.*, 2022).

The initial observations of bacterial and diatom colonisation on plastic debris date back to the 1970s (Carpenter & Smith, 1972). Early studies of the plastisphere focused on microscopically identifying the microorganisms inhabiting such "environment" (Amaral-Zettler *et al.*, 2020). More recently, studies have investigated not only the biodiversity of this habitat through next-generation sequencing-based methods (Bakal *et al.*, 2019) but also delved into the evolution and succession of their communities, trophic interactions, metabolism, and the influence of the plastisphere taxa on their surrounding environment (Bryant *et al.*, 2016; Casabianca *et al.*, 2021; Cheng *et al.*, 2021; Hope *et al.*, 2021). Prior research has predominantly focused on bacteria, often overlooking eukaryotes, particularly microalgae, despite their being significant components of the biofilm community within the plastisphere (Barros & Seena, 2021; Nava & Leoni, 2021; Xianbiao *et al.*, 2023). Consequently, despite the increasing attention given to this subject, an in-depth comprehension of the ecological impact of plastics on marine and freshwater phytoplankton/phytobenthos is still lacking.

In this review, we explore the intricate interplay between plastics (both micro- and macroplastics) and phytoplankton/phytobenthos, addressing pivotal questions about their influence on fundamental aquatic ecosystem processes, such as productivity and nutrient cycling. We analyse and compare results from marine and freshwater ecosystems across different organisational levels, from subcellular processes to entire ecosystems. Our investigation encompasses the effects of plastics of different sizes, including both the potential direct toxic effects of smaller plastics on phytoplankton and the role of larger plastics as surfaces for colonisation (i.e. plastisphere research). We aim to provide insights into the following research questions and knowledge gaps: (*i*)

how do phytoplankton–plastics interactions occur, and what are their implications for the broader ecological community, particularly regarding biodiversity and impacted functions; (*ii*) to what extent are ecosystem processes and metabolic functions affected by the interaction between (micro)plastics and phytoplankton; and (*iii*) how do the effects mediated by phytoplankton and plastics affect the food web *via* bottom-up and top-down processes?

II. PHYTOPLANKTON–PLASTIC–INTERACTIONS: COMPARISON OF RESULTS FROM MARINE AND FRESHWATER ECOSYSTEMS

A literature review of *Web of Science* publications from 1992 to 2022 (see online Supporting Information, Appendix S1, for search methodology, and Table S1 for list of included studies) showed that research on the interaction between plastics and phytoplankton has predominantly concentrated on marine ecosystems, representing about 60% of the identified publications (Fig. 1A).

Most studies examined the toxic effects of plastics on phytoplankton, primarily focusing on individual species (approximately 70% of all publications retrieved; Fig. 1B). In marine studies, diatoms were the most frequently investigated group (e.g. species of *Chaetoceros*, *Thalassiosira*, *Phaeodactylum tricornutum*), followed by green algae (e.g. species of *Dunaliella* or *Tetraselmis*), haptophytes (e.g. *Ochromonas* spp.), dinoflagellates (e.g. *Alexandrium* spp.), and cyanobacteria (e.g. *Prochlorococcus* spp.). In freshwater studies, the species investigated most frequently were cyanobacteria, with *Microcystis aeruginosa* being a prominent example, followed by various species of green algae (e.g. species of *Chlorella*, *Chlamydomonas*, and *Scenedesmus*).

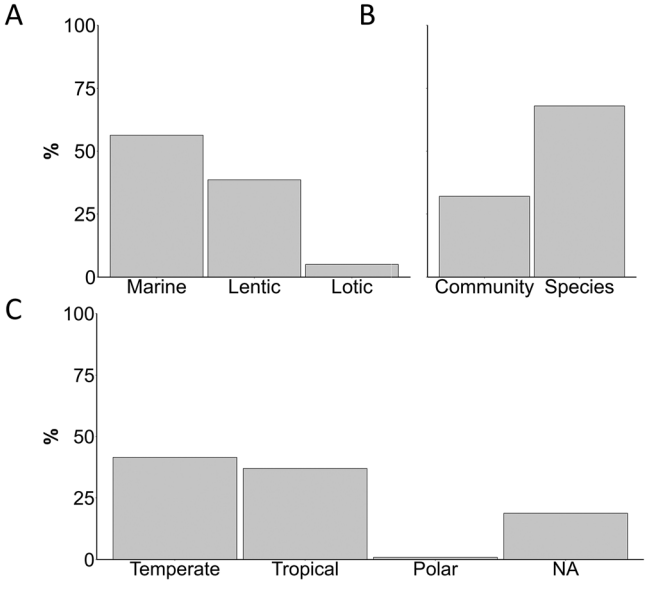

Fig. 1. Percentage of studies ($N = 244$) retrieved from *Web of Science* covering the period 1992–2022 that examine the relationship between (micro) plastics and phytoplankton (A) in freshwater (i.e. lentic and lotic) and marine ecosystems, (B) at the community or species level, and (C) in different biomes. NA denotes data not available. For the query string used, see Appendix S1. The included studies are provided in Table S1.

Of all the studies considered, approximately 80% in total focused on species or communities from temperate (42%) and tropical (39%) environments (Fig. 1C). Surprisingly, in around 20% of studies, no explicit reference was made to the environment from which the taxon was isolated or in which the research was conducted. To date, only two studies have explored the effects of plastics in polar environments or on polar organisms: Antarctic microbial biofilms (Caroppo *et al.*, 2022) and arctic cyanobacteria (Xin *et al.*, 2022).

In addition to the general patterns described above, over the last decade there has been a notable increase in the number of publications (Fig. 2). The proportion of studies focusing on freshwater ecosystems has risen from none in 2013 to 43% of the total in 2022, and the proportion on tropical ecosystems has also increased (from none in 2013 to 39% of the total in 2022). Additionally, there has been an increase in studies on individual species rather than communities (from 50% in 2013 to 72% of the total in 2022).

Different toxic effects have been reported for (micro)plastics in studies of freshwater and marine phytoplankton. For example, the presence of microplastics inhibited photosynthesis in the freshwater microalga *Chlamydomonas reinhardtii* while promoting it in the marine microalga *P. tricornutum* (Li *et al.*, 2020; Chen *et al.*, 2022). Similarly, growth of freshwater *Chlorella* sp. was reduced, whereas the marine *P. tricornutum* showed adaptive capacity, showing a positive response when exposed to the same type of microplastics (Song *et al.*, 2020). It remains challenging to determine whether these differences are associated with variations in environmental conditions or species-specific characteristics.

When examining the colonisation of phytoplankton on plastic surfaces, distinct patterns emerge between freshwater and marine environments, due to differences in nutrient availability, water temperature, dissolved oxygen, salinity

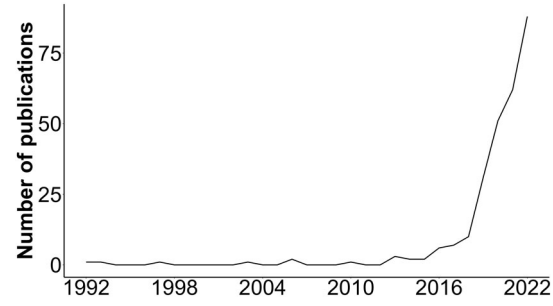

Fig. 2. Number of publications examining the effects of (micro) plastics on phytoplankton per year identified by our literature research.

levels, and microbial communities (Harrison, 2018; Barros & Seena, 2021; Miao *et al.*, 2021) influencing the establishment and development of phytobenthos communities on plastics. Consequently, distinct processes are observed, and overall patterns may differ across environments. Compared to the generally more stable temperature conditions in marine habitats, freshwater ecosystems, particularly in smaller water bodies like ponds, experience rapid temperature fluctuations (Woodward, Perkins & Brown, 2010) that can influence the development of biofilms. In water bodies with higher temperatures, biofilms can be thicker, with higher levels of chlorophyll *a*, extracellular polymeric substances (EPS), and total phosphorus content, while lower temperatures have the opposite effect (Zhao *et al.*, 2018). Salinity level also determines the types of organisms that can grow on the surface of plastic debris: in marine environments, communities tend to be dominated by species adapted to higher salinities, whilst in freshwater, less-halotolerant species are more common (Lauritano *et al.*, 2020). Furthermore, flow dynamics play a crucial role, impacting both the quantity and composition of the epiplastic community. Lentic environments, characterised by still or slowly moving water (e.g. lakes and ponds), permit nutrient accumulation in the water (Buffagni, 2021). These conditions favour the rapid proliferation of phytoplankton, often resulting in algal blooms. Conversely, lotic ecosystems (e.g. rivers and streams) are characterised by continuous water flow, which ensures variations of oxygen and temperature. This flow dynamic creates a less-favourable environment for extensive growth of phytobenthic organisms (Schneider & Petrin, 2017).

III. THE TOXICITY OF PLASTICS ON PHYTOPLANKTON AND ITS ECOLOGICAL RELEVANCE

(1) Factors affecting the toxicity and effects of microplastics

Numerous studies have documented the interactions between plastics and phytoplankton in aquatic environments, hinting at potential toxicity effects (e.g. Khoironi, Anggoro & Sudarno, 2019; Nava & Leoni, 2021). These interactions are influenced by various characteristics of the plastics, including their shape, size, polymer density, and chemical composition (Chen *et al.*, 2020b; Liu *et al.*, 2021b). Several attributes of microplastics have the capacity to affect their buoyancy, transport, and distribution, consequently modifying vertical fluxes and impacting the exposure of phytoplankton to these particles (Kooi *et al.*, 2017; Eich, Weber & Lott, 2021).

Particle size has a pivotal role in determining toxic effects of microplastics, and the literature documents various size-dependent consequences. As detailed by Chen *et al.* (2020b), small plastic particles (1–2 μm) can be readily adsorbed to or internalised by cell walls, reducing phytoplankton growth through the mechanical inhibition of nutrient uptake and gas exchange (Liu *et al.*, 2020; Prata *et al.*, 2019). Nanosized plastics adsorbed to the surface of phytoplanktonic organisms may have a shading effect that reduces photosynthetic efficiency and growth (Zhang *et al.*, 2022a). Liu *et al.* (2020) found that the presence of 2 μm microplastics, in addition to causing cell membrane damage, is linked to increased cellular stress (i.e. reactive oxygen species, ROS).

Research has predominantly focused on specific polymers, such as polyethylene terephthalate (PET) and polypropylene (PP), and has revealed a negative correlation between increasing microplastic concentrations and phytoplankton growth (Khoironi *et al.*, 2019). Dose-dependent inhibition of phytoplankton growth has been also observed in the presence of nano- and micro- polystyrene (PS) beads, due to direct damage of the cell membrane and increased levels of ROS (Xiao *et al.*, 2020). In addition, PS has been found to alter the expression of genes involved in various physiological functions, including ATP synthesis, consequently influencing cell metabolic activity (Zhou *et al.*, 2021). Polyvinyl chloride (PVC) and polyethylene (PE) act by significantly reducing chlorophyll content and photochemical efficiency (F_V/F_m) of photosystem II (Wang *et al.*, 2020b; Senousy *et al.*, 2023).

The toxic impacts of plastics on phytoplankton are not solely connected to the polymers themselves but also to the leachates they produce. It has been reported that some leachates (e.g. acetophenone, fluoranthene, dioctyl phthalate, or zinc) can inhibit the growth of certain species of cyanobacteria (Capolupo *et al.*, 2020). The extent of inhibition depends on the cell size (surface/volume ratio), morphology, physiology, and the quantity of leachate (Fernández-Juárez *et al.*, 2021; Fu *et al.*, 2019; Larue *et al.*, 2021). Tetu *et al.* (2019) investigated the effect of exposure to high-density PE and PVC leachate on the marine cyanobacterial genus *Prochlorococcus* and identified effects on growth and photosynthetic capacity, resulting in genome-wide transcriptional changes. Capolupo *et al.* (2020) investigated the effects of plastic leachate on freshwater (*Raphidocelis subcapitata*) and marine (*Skeletonema costatum*) microalgae. Almost all components of the leachate (e.g. benzothiazole, acetophenone, lead) inhibited the growth of algae. Biofilm formation on plastic surfaces (see Section IV) may influence the leaching of additives, although how the dynamics of leaching are affected by biofilms is still unclear. Research has identified a "cover effect", where the biofilm forms a barrier on the surface of the plastics, potentially altering the kinetics of chemical exchange (Peng *et al.*, 2023; Binda *et al.*, 2024).

In addition, microplastics have the capacity to adsorb organic and inorganic harmful substances from the environment. By assimilating them, microplastics effectively reduce the environmental availability of such substances, thereby mitigating damage to sensitive species (Fernández-Juárez *et al.*, 2021). For instance, Fu *et al.* (2019) showed that PVC particles can adsorb copper ions, thereby limiting their toxic effects on microalgal cells. However, it is important to note that the effectiveness of this protective role is contingent upon whether or not these microplastics are subsequently absorbed

by microorganisms in the ecosystem. If microorganisms do take up these plastic particles, the absorbed harmful substances may impact the organism and/or be transferred through the food web, posing potential risks to higher trophic levels (Fu *et al.*, 2019).

Morphological changes have been extensively observed when micro- and nanoplastics adhere to cell surfaces. This is particularly evident for positively charged microplastics, which adhere to the typically negatively charged cytomembrane of microalgae. As a result, these microplastics become embedded in the cell membrane (Larue *et al.*, 2021). Researchers have observed that the presence of plastic fragments can lead to deformation of chloroplasts and thylakoid membranes, leading to a reduction in cell chlorophyll content and hence diminished photosynthetic efficiency (Mao *et al.*, 2018; Prata *et al.*, 2018; Fu *et al.*, 2019). For instance, Besseling *et al.* (2014) reported a reduction in chlorophyll content in cells of *Chlorella* and *Scenedesmus* spp. when exposed to PS nanoplastics. Sjollema *et al.* (2016) revealed a 45% decrease in photosynthetic rate of *Dunaliella tertiolecta* in the presence of microplastics, whereas Yan *et al.* (2021) demonstrated the deformation and disruption of thylakoid structures in *C. reinhardtii* when exposed to plastic-induced stress. The likely cause of these effects is the surface adsorption of plastics, resulting in decreased expression of photosynthesis-related genes and metabolic disruption. Damage to photosynthesis increases the production of ROS, culminating in oxidative damage and lipid peroxidation (Prata *et al.*, 2019; Nava & Leoni, 2021). ROS hinders the synthesis of chlorophyll *a* and *b* and disrupts electron transport between primary and secondary acceptor plastoquinones, thereby diminishing the efficiency of photosystem II (Yan *et al.*, 2021). Lipid peroxidation elevates the level of malondialdehyde (MDA) within the cells, raising the permeability of the cell membrane and facilitating the uptake of plastic particles. When exposed to micro- and nanoplastics, Yan *et al.* (2021) observed elevated levels of ROS and MDA in *C. reinhardtii* cells. This increase in oxidative stress led to greater membrane permeability, which, in turn, resulted in increased plastic uptake by the cells. To defend against oxidative stress, the production of superoxide dismutase (SOD), catalase (CAT), and carotenoids increases. However, if the ROS content surpasses the cell's self-repair capacity, it can trigger apoptosis, necrosis and cell death (Prata *et al.*, 2019; Nava & Leoni, 2021; Jiazhu *et al.*, 2022). When exposed to environmentally relevant concentrations of microplastics (range 10–1000 mg/L), Yuanyuan *et al.* (2022) noted augmented production of pigments in the microalga *Chlorella vulgaris* as a defence against oxidative stress. Jiazhu *et al.* (2022) observed increased production of SOD in *Prorocentrum donghaiense* exposed to microplastics. However, this response proved insufficient to counteract the oxidative stress, as the cell membrane sustained damage due to lipid peroxidation induced by accumulating ROS. Oxidative stress can also promote the release of harmful metabolites, such as microcystin by *M. aeruginosa* (Zheng *et al.*, 2021), as a mechanism to mitigate microplastic-induced oxidative stress (Amaneesh *et al.*, 2023).

Other defence mechanisms have been documented in microalgae in response to exposure to plastics. One common response to plastic exposure involves the homoaggregation of cells, which serves to decrease the surface area exposed to plastic particles (Yan *et al.*, 2021). Researchers have reported elevated expression of genes responsible for the biosynthesis of EPS [e.g. Yan *et al.* (2021) in *C. reinhardtii*]. EPS serve to thicken the cell wall, providing a shield against physical harm. However, microplastics can accumulate within the EPS, obstructing nutrient uptake, and limiting light availability (Prata *et al.*, 2019; Liu *et al.*, 2021b; Yan *et al.*, 2021).

Effects of microplastics can also manifest through the modification of metabolic mechanisms. Amaneesh *et al.* (2023) observed a decrease in phosphorus uptake in the cyanobacterium *Haloteche* sp. when exposed to microplastics. While this decrease was likely a result of an indirect mechanism, specifically phosphate ion adsorption to the plastic particles, it highlights the far-reaching implications of microplastic exposure. Other studies have shown that the presence of microplastics and their organic additives can change phosphate homeostasis, leading to increased alkaline phosphatase activity, while reducing the rate of PO_4^{3-} uptake (Fernández-Juárez *et al.*, 2021). In addition, reduction in the quantity of oil bodies, which function as an emergency energy source for the maintenance of normal growth, has been observed in the marine diatom *Chaetoceros neogracile* under microplastic stress-induced conditions (Seoane *et al.*, 2019). A shift in lipid composition (e.g. chloroplast galactolipids) and alterations in fatty acid profile, coupled with reductions in neutral lipid content and an increase in esterase activity, were reported in *Chlorella sorokiniana* exposed to PS (Amaneesh *et al.*, 2023). Such alterations in fatty acids can have cascading effects throughout the food web (see Section V).

(2) Responses of different taxonomic groups and ecological relevance

Plastics exert distinct effects on different groups of phytoplankton, with some beneficial and others detrimental (Rani-Borges *et al.*, 2021). Most studies show a negative effect of microplastics on both marine and freshwater phytoplankton (Gao *et al.*, 2021). The specific impact of microplastics often depends on group- or species-specific traits. For instance, some cyanobacteria can tolerate the presence of plastics better than other organisms (Fernández-Juárez *et al.*, 2021; Hitchcock, 2022). They can form microfilms or colonies around microplastics (Dussud *et al.*, 2018b; Hitchcock, 2022) and exhibit a greater capacity to cope with light limitation due to shading caused by microplastics (Sjollema *et al.*, 2016; Zhu *et al.*, 2021). Similarly, the capacity to form hetero-aggregates appears to enable certain marine diatoms to manage microplastic toxicity, as this may improve their photosynthetic efficiency and restore their growth (Long *et al.*, 2017; Wang *et al.*, 2020a). The formation of

hetero-aggregates depends on various factors, including the size of the particles (Wang & Chen, 2023) and the type of polymer. Lagarde *et al.* (2016) noted the formation of hetero-aggregates for PP but not for high-density polyethylene (HDPE) microplastics. Trait-specific effects of microplastics may also be influenced by the thickness of the cell wall, which acts as a barrier against microplastic penetration (Sjollema *et al.*, 2016; Nolte *et al.*, 2017; Parsai *et al.*, 2022). Furthermore, cell dimensions play a role, with smaller cells being more susceptible to the impact of microplastics due to their relatively higher cell surface area to volume ratio (Sjollema *et al.*, 2016; Chen *et al.*, 2020b; Ge *et al.*, 2022).

The majority of studies examining the effects of microplastics on microalgae focus on green algae and diatoms (Larue *et al.*, 2021). One important consideration is the environmental relevance of the microplastics used. Many investigations have assessed plastic toxicity using pristine spherical particles, such as spherical PS particles (Larue *et al.*, 2021). However, real-world environmental plastics exhibit considerable variation in terms of shape, size, polymer type, and surface characteristics. Furthermore, these characteristics can change as plastics age (Larue *et al.*, 2021), although it remains challenging to determine the associated implications. Further research will be essential to unravel ecologically relevant impacts.

IV. PLASTICS AS SUBSTRATES AND THEIR INFLUENCES ON ECOSYSTEM PROCESSES

(1) Colonisation process

In both freshwater and marine ecosystems, plastics are rapidly colonised by a variety of organisms, including bacteria, single-celled eukaryotic organisms, larvae, and spores (Amaral-Zettler *et al.*, 2020; Yu *et al.*, 2023). Upon coming into contact with plastic, free-living microorganisms can form biofilms to transition from a planktonic mode to a sessile mode. Diatoms and various bacteria, such as Gammaproteobacteria, Cyanobacteria, and Alphaproteobacteria, are well recognised as early colonisers (Amaral-Zettler *et al.*, 2020; Odobel *et al.*, 2021; Yu *et al.*, 2023).

During the initial phase of colonisation, pioneer bacteria produce EPS through the regulation of lipid/fatty acids and c-di-GMP (bis(3′−5′)-cyclic dimeric guanosine monophosphate) signals (Su *et al.*, 2022a). The secretion of EPS enhances adhesion and facilitates further colonisation by various microorganisms, for example by members of Bacteroides (Fig. 3). These organisms are highly adaptable and promote the irreversible attachment of microflora by forming pili, adhesive proteins, and additional extracellular polymeric substances (Du *et al.*, 2022). As the process continues, different organisms upregulate gene expression related to communication, adhesion, substance transport, and chemotaxis (Solano, Echeverz & Lasa, 2014). This gives rise to a tissue-like matrix (Yu *et al.*, 2023) characterised by channels that aid in distributing nutrients between cells (Amaral-Zettler *et al.*, 2020). Other groups, including fungi and archaea, also become part of the biofilm, although their precise role in the colonisation process remains poorly understood (Yu *et al.*, 2023).

Over time, the biofilm structure undergoes transformation into a more complex three-dimensional (3D) structure, accommodating both heterotrophic bacteria and prokaryotic and eukaryotic autotrophs (Yokota *et al.*, 2017). Several studies have reported that the community composition on plastic surfaces differs from that of the surrounding free-living organisms, both in freshwater and marine systems (Bryant *et al.*, 2016; Odobel *et al.*, 2021; Wang *et al.*, 2022b; Sosa & Chen, 2022). However, no group of microorganisms has been exclusively observed on plastic (Amaral-Zettler *et al.*, 2020). The diversity of the biofilm community tends to increase over time, with filamentous cyanobacteria and associated heterotrophic bacteria becoming dominant while early-colonising diatoms decrease in abundance. Nevertheless, most studies report lower species richness on plastic and greater evenness than in the community in the surrounding environment (Amaral-Zettler *et al.*, 2020).

The characteristics and properties of plastic surfaces play a crucial role in determining colonisation processes. This concept broadly applies to biofilm formation across various materials, with existing literature highlighting how substratum properties influence colonisation (Vadeboncoeur *et al.*, 2006). In plastisphere research, there is substantial debate over whether substrate properties or environmental conditions are more dominant in shaping colonising communities. Many studies suggest that environmental factors are more influential in determining community composition, particularly in mature biofilms. This is likely because only the initial layers of the biofilm come into direct contact with the substrate (Rummel *et al.*, 2017; Nava *et al.*, 2024). Additionally, recent research indicates that as biofilms mature, their community structure diverges from patterns observed after shorter incubation periods, underscoring the need for studies that investigate longer-term processes in plastisphere research. Kirstein *et al.* (2019) compared communities after short-term (6 weeks) and long-term (5 months) incubation, revealing shifts towards communities with lower richness over time for all plastic types. This suggests selection for microbes specialised to low-nutrient conditions or to specific plastic types. However, few studies have evaluated longer-term colonisation, particularly regarding the autotrophic component of the community, making it difficult to determine the time required to reach peak biomass for plastic substrates and whether this differs from naturally occurring substrates.

Ageing processes can alter the properties of plastic substrates, which in turn can affect the environmental fate of plastics, their sorption characteristics, and ultimately their impact on biological communities, including planktonic organisms (Binda *et al.*, 2024).

While the available literature has provided insights into many mechanisms related to biofilm colonisation on plastic substrates in marine and freshwater environments, many aspects remain

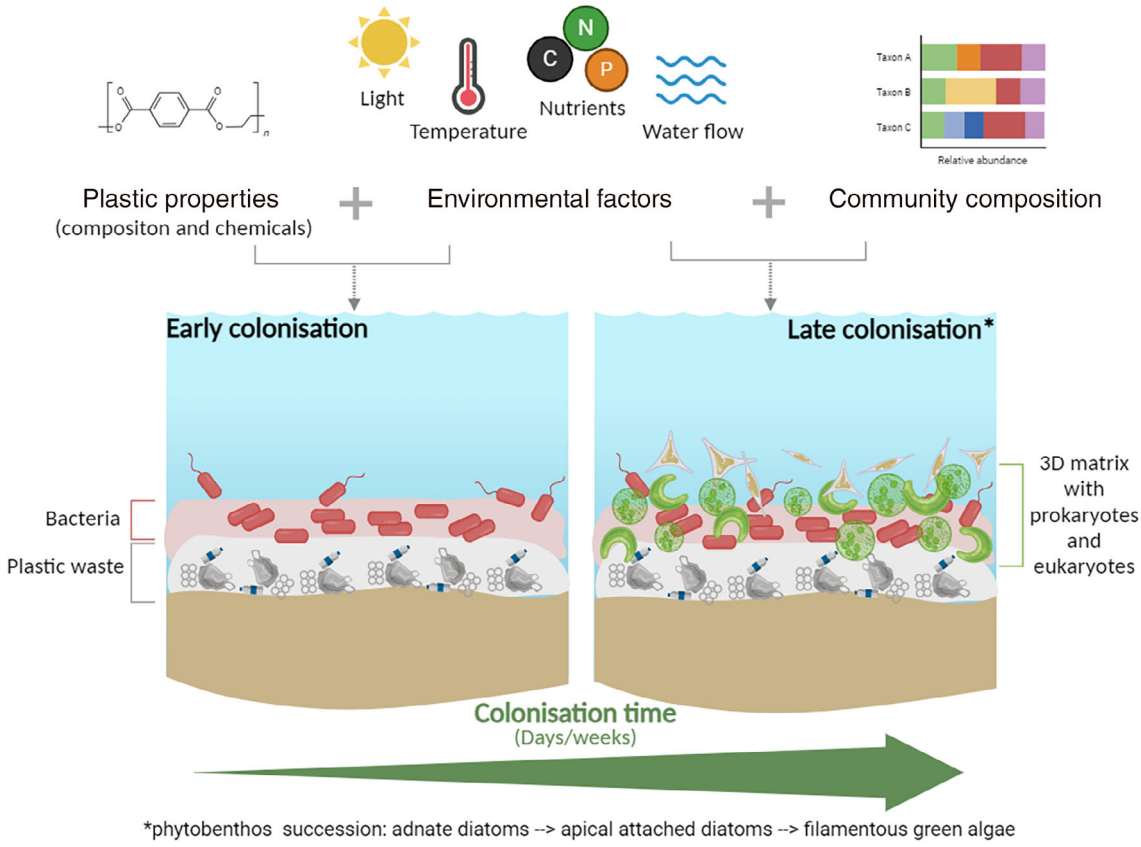

Fig. 3. Schematic representation of the colonisation process of plastic surfaces over time, from initial colonisation by pioneer species to later stages. Early colonisation involves microorganisms embedded in an exopolysaccharides (EPS) matrix. The process is influenced by various properties of the plastic substrates, such as texture, polymer composition, and colour. As the community evolves over time, the matrix becomes more complex, developing a three-dimensional (3D) structure that supports a variety of organisms. This includes the early appearance of adnate diatoms (Bacillariophyceae), followed by the growth of filamentous organisms such as cyanobacteria and Chlorophyceae.

unresolved. Further investigation is required, for example, on how light, nutrient availability or temperature modulate the colonisation by microorganisms or how the timing and rate of different stages of biofilm formation occur.

(2) Plastics as a substrate for harmful or invasive taxa

Plastics can also serve as a suitable substrate for potentially harmful microorganisms (Wang *et al.*, 2019). In a recent review, Audrézet *et al.* (2021) emphasised the association of phytobenthic organisms with plastic debris. For example, the diatom *Ceratoneis closterium* has been consistently identified on marine plastics. This organism, which is known to be associated with mucilage events (the formation of large aggregates in the water column), can pose a risk to aquatic organisms, particularly fishes, by reducing oxygen availability (Masó *et al.*, 2016). Casabianca *et al.* (2019) reported the presence of toxin-producing cyanobacteria on floating plastics in the sea, including species belonging to the toxic bloom-forming genus *Pseudo-nitzschia*. Floating plastic debris collected from various locations along the Catalan coast in the northwestern Mediterranean has been found to host potentially harmful dinoflagellates (*Ostreopsis* spp. and *Coalia* spp.), and both temporary cysts and vegetative cells of the harmful algal bloom species *Alexandrium taylori* (Masó *et al.*, 2003).

On a broader scale, plastic debris plays a recognized role in facilitating the spread of non-native invasive species (Audrézet *et al.*, 2021). This has been attributed to the ability of plastic fragments to be transported over significant distances, thereby promoting the dispersal of non-native and potentially invasive epiplastic organisms. Examples include the brown alga *Undaria pinnatifida* and the green alga *Codium fragile*, with the latter being particularly invasive in Europe (Audrézet *et al.*, 2021). This understudied phenomenon has the potential to pose a significant threat to biodiversity and ecosystem health (Casabianca *et al.*, 2019).

(3) The plastisphere and its impact on biodiversity

Plastic pollution has the potential to alter the biodiversity of the recipient environment (Du *et al.*, 2022). Plastics serve as

substrates for colonisation by microorganisms (see Section IV.1), and different taxa exhibit varying colonisation capabilities. Consequently, the plastisphere is implicated in potential changes to phytoplankton/phytobenthos community composition, influencing their biodiversity. However, current studies lack a connection between the plastisphere and descriptors of phytoplankton/phytobenthos biodiversity, such as richness, evenness, and trait- or taxonomy-based assessments. Notably, most research on the impact of plastic pollution on microorganism diversity has predominantly focused on prokaryotes (Odobel *et al.*, 2021; Du *et al.*, 2022), overlooking the broader spectrum of biodiversity, which includes eukaryotic organisms (Barros & Seena, 2021).

Several recent studies have demonstrated variations in the composition and diversity of the epiplastic community depending on different factors. For example, using 16S ribosomal RNA (rRNA) sequencing, Wen *et al.* (2020) showed that plastic colour can have impacts on the community structure and functional diversity of the plastisphere. Biofilms colonising blue plastics appeared to have a higher functional diversity than those on transparent or yellow plastics, suggesting that plastic colours/additives may drive selective pressures on microorganisms colonising plastics. Furthermore, studies have revealed differences in community composition between plastics and other non-synthetic materials, as well as differences compared with the microalgal planktonic community (Shen *et al.*, 2021). This underscores the potential of the epiplastic community to occupy a new and distinct ecological niche that favours specific organisms. For instance, Kettner *et al.* (2019) investigated the eukaryotic community composition on PE and PS, and demonstrated that the epiplastic community was significantly distinct from communities on wood and in the surrounding water, with overall lower diversity (based on richness, Shannon diversity and Simpson diversity). The authors concluded that PE and PS excluded certain organisms rather than attracting a specialised epiplastic community. In addition, no significant differences were detected between the eukaryotic communities on PE and PS, in accordance with other studies comparing microbial communities among plastic polymers (e.g. Hoellein *et al.*, 2014; Oberbeckmann, Osborn & Duhaime, 2016; Nava *et al.*, 2022). Oberbeckmann *et al.* (2014) did not find any difference in the relative diversities of communities present on different plastic types.

The effects of plastics can propagate across the planktonic community. Laboratory experiments (e.g. Hitchcock, 2022; Kettner *et al.*, 2019) have shown that phytoplankton diversity is reduced in environments with high concentrations of microplastics compared to less-polluted or control samples. This decline in diversity may be attributed to microplastics promoting the dominance of a few tolerant species, thereby reducing overall community diversity (Amaneesh *et al.*, 2023). Moreover, plastic biofilms can act as potential vectors for exogenous species that may detach from the biofilm and compete for resources within the pelagic community (Zettler *et al.*, 2013).

Alterations in phytoplankton diversity can influence secondary consumers, particularly if cyanobacteria increase in abundance while other more palatable components decrease. While there have been initial attempts to model the potential food-web implications of microplastics (e.g. Kong & Koelmans, 2019), there is a substantial need for comprehensive research to assess their impact across multiple trophic levels, in particular their effects on community structure.

(4) Role of the plastisphere in nutrient provisioning and cycling

While carbon is typically abundant in aquatic ecosystems, nitrogen, phosphorus, and/or iron are limiting in most ecosystems on Earth. Plastic debris provides a surface that enhances the accessibility of these limiting nutrients compared to the more diluted surrounding water system (Amaral-Zettler *et al.*, 2020; Wright *et al.*, 2020). In general, autotrophic biofilms play a pivotal role in nutrient cycling. Although experimental studies have demonstrated lower nutrient uptake rates from the water column of biofilms compared to free-living phytoplankton, biofilms appear to be more effective at nutrient retention (Vadeboncoeur & Steinman, 2002). Microorganisms within the biofilm have the capacity to derive nutrients not only from the water column but also through internal cycling and from the substrate to which they are attached (Vadeboncoeur & Steinman, 2002). Therefore, the plastisphere can provide a competitive advantage in terms of nutrient acquisition. Barros & Seena (2021) demonstrated that, in environments with high nutrient levels, microplastics efficiently adsorb these nutrients, transforming plastics into nutrient-rich surfaces for early-colonising microorganisms. This nutrient adsorption fosters microbial growth and enzymatic activities, resulting in more cohesive microbial communities. Moreover, nutrient limitation can be less severe in the plastisphere due to various mechanisms. For example, cyanobacteria with more efficient light-harvesting systems (phycobilisome antenna protein-encoding genes as opposed to Chl *a*/*b*-binding light-harvesting protein-encoding genes) have been observed on the surface of plastics (Bryant *et al.*, 2016). These more efficient systems require lower protein (i.e. nitrogen) investment per tetrapyrrole (e.g. in chlorophyll and phycobilin), thus providing an advantage in low-nutrient conditions (Bryant *et al.*, 2016). Another example is the increased presence of nitrogenase genes (i.e. *nifH*, *nifD*, and *nifK*) in metagenomes associated with plastic particles, indicating that nitrogen fixation might represent a strategy to overcome nitrogen limitation (Bryant *et al.*, 2016; Du *et al.*, 2022).

Autotrophic organisms can release nutrients into the surrounding environment, and these can potentially affect the local planktonic community (Priya *et al.*, 2022). Moreover, leaching of additives by microplastics can even promote microbial growth by serving as an auxiliary nutrient source (Rummel *et al.*, 2017). Plastic leachate has been reported to influence microbial communities, increasing bacterial

biomass at lake surfaces. Bacterial growth was found to be 1.72 times more efficient in the presence of plastic leachate compared to natural organic matter, primarily due to the greater accessibility of carbon (Sheridan *et al.*, 2022).

(5) The impact of the plastisphere on ecosystem processes

Primary productivity is a crucial ecosystem process and supports the overall functioning of ecosystems (Larue *et al.*, 2021). Several studies have investigated the potential effects of the plastisphere on primary productivity in different ecosystems (Larue *et al.*, 2021; Miao *et al.*, 2021; Conan *et al.*, 2022). The impact can vary depending on the ecosystem, specific organisms involved, and factors such as water velocity, nutrient and light availability, and the chemistry of the substrate surface (Fig. 4) (Battin *et al.*, 2016; Bridier *et al.*, 2017; Castro-Castellon *et al.*, 2022; Chaudhary *et al.*, 2022; Vincent *et al.*, 2022). While some studies suggest that the plastisphere may enhance primary productivity and microbial diversity, others indicate potential negative effects through changes in species diversity and altered community composition (Zettler *et al.*, 2013; Oberbeckmann, Kreikemeyer & Labrenz, 2018; Amaral-Zettler *et al.*, 2020). Plastics can provide a substrate for the attachment and growth of photosynthetic organisms, potentially enhancing local primary productivity. However, the overall effect on ecosystem-wide productivity is often negative (Amaneesh *et al.*, 2023). Plastics can also harbour species that outcompete photosynthetic organisms, leading to rapid decreases in primary productivity (Zettler *et al.*, 2013). Moreover, impacts on primary productivity are not due solely to the plastics themselves but also to the leaching of additives/plasticizers. Compounds such as phthalates and bisphenol A, for example, can reduce photosynthetic capacity (Wright *et al.*, 2020; Chaudhary *et al.*, 2022).

Microbial communities are sensitive to environmental changes (Fig. 4) and these can influence the structure and functioning of biofilms, thereby affecting primary productivity (Cross, Wallace & Rosemond, 2007; Battin *et al.*, 2016).

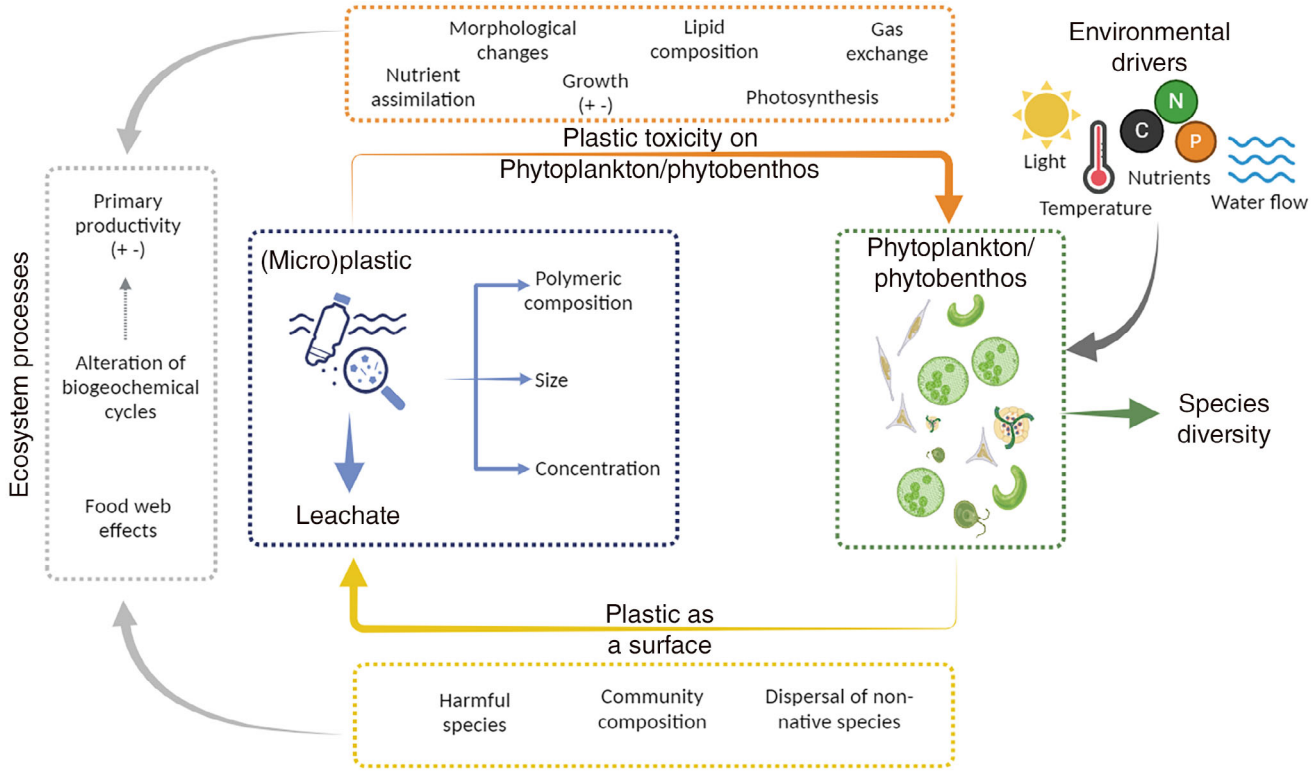

Fig. 4. Representation of the interaction between phytoplankton/phytobenthos, (micro)plastics and environmental factors (e.g. light, nutrients, temperature), and their subsequent effects on wider ecosystem processes. The effects of microplastics depend on their size, concentration, and polymeric composition, and by their leachates. These interactions may have toxic effects on phytoplankton/phytobenthos, that is morphological changes, alterations in nutrient assimilation, shifts in gas exchange, increased production of fatty acids, and impacts on growth and photosynthetic activity. The phytoplankton/phytobenthos–plastic interaction also involves effects linked to plastics serving as a surface for algal colonisation. (Micro) plastics can potentially influence community composition, provide a habitat for harmful species, and act as a vector for non-native species. Together, both toxicity and provision of a substrate for growth by (micro) plastics can impact crucial ecological processes, including primary productivity and nutrient cycling, with possible repercussions throughout the entire aquatic food web. ± denotes instances where the effects may be positiv or negative.

The consequences of plastic pollution, therefore, are not simply due to the physical modification of habitats but may also impact the biogeochemical processes of aquatic ecosystems. Biofilms that develop on plastic substrates support robust microbial growth that affects similar ecosystem processes as natural substrates, thus affecting the base of aquatic food webs (Hoellein *et al.*, 2019; Amaral-Zettler *et al.*, 2020; Wright *et al.*, 2020).

The plastisphere can exert an influence on the metabolic traits of primary producers. Enzymes involved in nitrogen and phosphorus acquisition may be upregulated in plastisphere-associated communities in response to the altered nutrient environment around plastic debris. Consequently, this can alter the stoichiometry of nutrient cycling, potentially affecting the growth dynamics and community composition of phytoplankton populations (Fig. 4; Hutchins & Fu, 2017; Jacquin *et al.*, 2019).

The plastisphere may also affect carbon sequestration, perturbing carbon cycling, and potentially triggering cascading effects on ecosystem functioning (Arias-Andres, Rojas-Jimenez & Grossart, 2019; Amaneesh *et al.*, 2023). For example, the presence of microplastics in aquatic environments can affect the cycling of organic matter. The activity of enzymes crucial for the decomposition of organic substances can be altered by microbial consortia that colonise plastic debris by increasing the intensity of denitrification and N_2O production, thereby influencing the overall rate of organic matter turnover (Su *et al.*, 2022a). For instance, biofilms on plastic can exhibit a high abundance of saprotrophic Chytridiomycota, which are known to play a key role in the decomposition of organic matter within biofilms (Oberbeckmann *et al.*, 2016; Kettner *et al.*, 2017).

To summarise, (micro)plastics result in changes to the community composition of the epiplastic community and are likely to shape the development and evolution of phytoplankton/phytobenthos. Consequently, these alterations have far-reaching implications for the dynamics of the entire ecosystem (Amaral-Zettler *et al.*, 2020).

V. EFFECTS ON THE AQUATIC FOOD WEB

Due to their small size, microplastics are readily accessible to organisms throughout the food web, as highlighted by their presence in a variety of species (Li *et al.*, 2020). Microplastics can affect food webs (Fig. 5) by alteration of (*i*) trophic relationships between producers and consumers; (*ii*) the flux of energy across different trophic levels; and (*iii*) the behaviour and physiology of consumers (Foley *et al.*, 2018; Gerdes *et al.*, 2019; Malinowski *et al.*, 2023).

The interaction of phytoplankton with plastics plays a crucial role in shaping food web processes. Plastic particles adsorbed by phytoplankton at the base of the trophic chain can thus reach subsequent trophic levels. Chae *et al.* (2018) observed the uptake of microplastics by fish species including *Orizias sinensis* and *Zacco temminckii*. The plastic particles entered the fish through the consumption of the crustacean *Daphnia magna*, which fed on the green alga, *C. reinhardtii*. Ingestion of microplastics by this route led to histopathological changes in the liver of the affected fish. Of concern, microplastic ingestion extended into the next generation through penetration of embryo walls, establishing a direct link between plastic ingestion and inter-generational physiological consequences (Chae *et al.*, 2018). Similarly, Mattsson *et al.* (2017) attributed behavioural abnormalities in goldfish *Carassius carassius* to the accumulation of plastic particles in the brain. In their study, positively charged PS nanoparticles ingested by the zooplankton *D. magna* through its diet of *Scenedesmus* spp. algae were subsequently consumed by the goldfish. In a similar experiment, Cedervall *et al.* (2012) documented altered fish feeding behaviour and reduced fat reserve metabolism as a result of food chain exposure to microplastics. Biofouling of plastics (see Section IV.1) can increase ingestion rates at higher trophic levels, as plastics become more appealing to organisms like zooplankton due to the accumulation of biofilms with microalgae on their surfaces (Polhill *et al.*, 2022).

The processes underlying transfer of microplastics through the food web are complex and involve various organisms at different trophic levels. Microplastics can impact the functioning of aquatic ecosystems by affecting both bottom-up and top-down regulatory mechanisms. For instance, the consumption of hetero-aggregates formed by phytoplanktonic organisms and microplastic particles has potential negative impacts on zooplankton, including a reduction in the neutral lipid content and quality of the diet, in addition to dilution of food (i.e. replacement part of the diet with non-nutritive particles) (Bucci *et al.*, 2024). The resulting reduced assimilation rate of nutrients ultimately can lead to a decline in zooplankton population density (Casabianca *et al.*, 2020; Nava & Leoni, 2021). Microplastics also can block the digestive tracts of zooplankton (Rosenkranz *et al.*, 2009; Nasser & Lynch, 2016), reduce their feeding rate (Nasser & Lynch, 2016), or directly interfere with their feeding processes (Au *et al.*, 2015; Blarer & Burkhardt-Holm, 2016). The consequences include energy deficiency, decreased growth, reduced activity, impaired reproductive capacity, and even mortality [Besseling *et al.*, 2014; Wang *et al.* (2019) and references therein]. Thus, increased microplastic concentrations can directly lead to a decline in zooplankton populations, and consequently impact food web dynamics. Malinowski *et al.* (2023) investigated the impact of increasing microplastic concentrations on filter-feeding crustaceans (*Daphnia dentifera* and *Arctodiaptomus dorsalis*) concurrent with phytoplankton exposure. The study found that higher microplastic levels reduced zooplankton grazing pressure on phytoplankton, leading to increased algal populations. Similar results were observed in a trophic cascade experiment conducted by Pan *et al.* (2022) which found that increased microplastic load reduced the grazing activity of *D. magna* as well as its population density. The diminished density of zooplankton can subsequently restrict the density or abundance of planktivorous fishes and, ultimately, of piscivorous fishes that

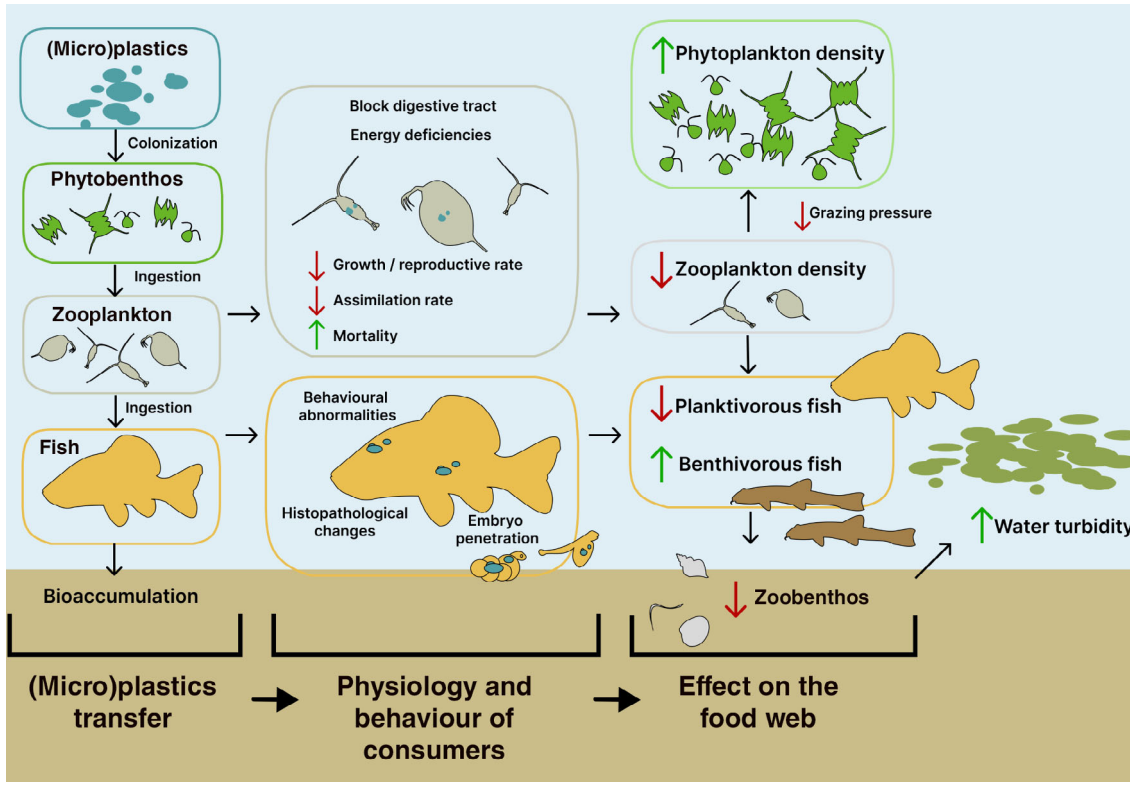

Fig. 5. How microplastics may shape aquatic food webs. Microplastics, due to their small size, are available to organisms throughout the aquatic food web, influencing energy flow, physiology and consumer behaviour. Microplastics can form hetero-aggregates with phytoplankton, affecting zooplankton and limiting nutrient uptake. Increased microplastic concentrations can lead to increased mortality of zooplankton, reducing predation pressure on phytoplankton, and thereby leading to an increase in phytoplankton populations. Declines in the abundance of planktivorous fish can change the composition of fish communities, positively affecting benthivorous fish which might result in increased sediment disturbance. Additionally, the egestion of microplastics by zooplankton may negatively impact the zoobenthos. ↑/↓ indicate positive or negative effects of microplastics on the functioning of a population in the aquatic ecosystem.

depend on them, as modelled by Kong & Koelmans (2019). Consequently, benthivorous fishes can become more prevalent, reducing the abundance of zoobenthos and increasing sediment disturbance and water turbidity (Casabianca *et al.*, 2020; Nava & Leoni, 2021). Zooplankton can egest microplastics in the form of faecal particles and plastic residuals therein can adversely affect benthic fauna communities feeding in the sediment by causing physical damage or exerting toxic effects (Green, 2016).

In addition to direct adverse effects, both micro- and macroplastics, when ingested, can introduce a variety of substances into the food web. These substances include additives, pollutants, and potentially harmful microorganisms [Wang *et al.* (2019) and references therein]. For instance, plastic debris can act as a vector in the transport of toxic benthic algae, and therefore of the toxins they produce, into the marine food web (Leite *et al.*, 2022). Recent studies have shown that toxic chemicals, heavy metals, pathogenic organisms, and degraded plastic particles can accumulate in biofilms associated with plastics, ultimately entering higher trophic levels (Okeke *et al.*, 2022). By contrast, evidence from some studies does not support the suggestion that plastics contribute significantly to the biomagnification of contaminants. Koelmans *et al.* (2016) found that the flux of hydrophobic organic compounds (HOCs) accumulated from natural prey typically exceeds the flux from ingested microplastics in most environments. This suggests that microplastic ingestion is unlikely to elevate significantly exposure to HOCs in aquatic ecosystems. Although microplastics could potentially accumulate and biomagnify through the food web at higher trophic levels, there is a lack of empirical multitrophic studies (Bhatt & Chauhan, 2023). A few modelling approaches have found weak evidence of biomagnification at higher trophic levels, for example in cetaceans (Alava, 2020) and otters (O'Connor *et al.*, 2022).

VI. CONCLUSIONS

(1) Deepening our understanding of the ecological implications linked to plastic pollution is essential to comprehend its impacts fully. This begins with understanding how plastics interact with the organisms at the base of aquatic food webs, such as phytoplankton/phytobenthos. (Micro)plastics exhibit

both toxicity for phytoplanktonic organisms and act as a substrate for the growth of phytobenthos, thereby expanding the potential impacts of these contaminants. However, determining the direction of these impacts, whether positive or negative, remains challenging, and further research is needed.

(2) While existing studies on microplastics have predominantly focused on their toxicity to phytoplankton, often considering single species, a more comprehensive understanding of the functioning of the plastisphere and of microplastic–phytoplankton interactions requires research focused on complex natural communities. Expanding our comprehension of toxic effects beyond well-known polymers (e.g. PE, PET, PP) to other types of plastics and their additives with different chemical compositions is crucial. This research should extend beyond marine ecosystems to encompass freshwater environments, especially lotic ecosystems, and consider underrepresented biomes, particularly boreal and polar ecosystems, as well as other areas vulnerable to the impacts of plastic pollution.

(3) While we are beginning to understand the process of biofilm colonisation on different plastic surfaces, the precise role of environmental factors such as light, nutrients, hydrodynamic conditions and temperature in biofilm development remains less understood. It is unclear whether these environmental parameters modulate biofilm development on plastic as they do for biofilms on natural substrates (i.e. benthic sediment). Many studies have reported differences between biofilm communities on plastic and those in the surrounding environments, suggesting that responses observed in biofilms growing on natural substrates may not be applicable to biofilms growing on plastics.

(4) Plastic is known to be colonised by diverse phytobenthic communities that become more complex over time. Within these communities, harmful and invasive microorganisms can thrive on plastic, posing a threat to biodiversity. Plastic substrates induce changes in the structure and functioning of photoautotrophic communities, potentially leading to local alterations in biogeochemical fluxes, particularly in the nutrient cycles. This, in turn, could impact ecosystem functioning and productivity and the carbon cycle. Given the fundamental role of biofilms in various ecosystem processes and the widespread nature of plastic pollution, we stress that more information is needed on the role of biofilms growing on plastic substrates in these processes.

(5) Microplastics, due to their small size, can enter the food web, affecting organisms through the introduction of toxins and from structural features of the plastic itself, leading to impaired body functions or behaviours. These effects have been observed across ecosystems and regions, however, there is still limited information on trophic transfer dynamics and its consequences. Only a few studies have attempted to address the bioaccumulation and biomagnification of microplastics at higher trophic levels, particularly at an empirical level. Furthermore, recorded responses to microplastic exposure at the assemblage level in natural aquatic populations at different trophic levels are still insufficient for a comprehensive understanding of the ecological impacts of microplastics resulting from trophic interactions.

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VIII. AUTHOR CONTRIBUTIONS

Conceptualization: V.N., J.Y.D., V.D.S., L.F., J.P., O.A.A., B.B., M.J.C., T.CH., M.C., F.D., A.M.D., A.F., G.G., D.H., D.R.H., V.M-V., B.M., L.M-B., V.M., F.R., B.S-P., C.M.T., J.G.; Writing – original draft preparation: V.N., J.Y.D., V.D.S., L.F., J.P., O.A.A., B.B., M.J.C., T.CH., M.C., F.D., A.M.D., A.F., G.G., D.H., D.R.H., V.M-V., B.M., L.M-B., V.M., F.R., B.S-P., C.M.T., J.G.; Writing – review and editing: V.N., J.Y.D., V.D.S., L.F., J.P., O.A.A., B.B., M.J.C., T.CH., M.C., F.D., A.M.D., A.F., G.G., D.H., D.R.H., V.M-V., B.M., L.M-B., V.M., F.R., B.S-P., C.M.T., J.G.; Supervision: V.N., J.Y.D., V.D.S., L.F., J.P., J.G.; Visualization: V.N., J.P., G.G.; Project administration: V.N., J.G.; Funding acquisition: V.V., J.G.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Methodology for the literature search.
Table S1. List of references included in the review of plastic–phytoplankton interactions.

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