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Review

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Transforming encounters: A review of the drivers and mechanisms of macrofaunal plastic fragmentation in the environment

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Abstract

Plastic has infiltrated every ecosystem on the planet, making encounters between this anthropogenic pollutant and fauna inevitable. Abiotic environmental breakdown involving light, oxygen, temperature and mechanical forces is well-characterized, while biotic degradation mechanisms are less well-understood. Reports of the role of macrofauna in the fragmentation of plastic debris are increasing. This review explores the driving factors for macrofaunal fragmentation, as well as the physiological mechanisms by which plastic items are fragmented. The presence, and access to plastic within an organism's habitat are the key determinants of macrofaunal plastic degradation. Foraging strategies, along with burrowing and nesting behaviors increase the likelihood of macrofauna interacting with plastics. Though this type of fragmentation can occur externally, it often follows ingestion, which in itself can be driven by resemblance to food. Four physical mechanisms of macrofaunal plastic fragmentation were identified, namely biting, drilling, grazing and grinding. Biting, restricted to the mouthparts of an organism, was the most common form of macrofaunal fragmentation reported in literature. Similarly, the use of specialized mouthparts for drilling or grazing can produce secondary plastic particles. Lastly, grinding, through manipulation by the gizzard or gastric mill following ingestion can significantly reduce the size of the plastic material. Prolonged and/or repeated interactions with plastics pose the risk of increased wear on the mouthparts and digestive organs involved. Through mechanisms that directly affect the plastic's structural integrity, physical fragmentation by macrofauna can amplify overall plastic degradation rates and the formation of micro- and nanoplastics in the environment, while long internal retention times can contribute to their dispersal, trophic transfer, and the organism's exposure to plastic additives. To more fully understand the extent of macrofaunal plastic fragmentation and allow predictive modeling, we suggest the reporting of evidence in a unified and systematic way. Our findings further highlight the urgency for the implementation of a global plastic waste management system to reduce the burden of micro- and nanoplastics.

Impact statement

As plastic is found in every ecosystem of the planet, encounters between organisms and this anthropogenic pollutant are inevitable. The breakdown of plastic through exposure to environmental elements and microbes is well understood, however, the role of larger organisms in this breakdown is unclear. By systematically categorizing both drivers and aspects of encounters with plastic debris, and internal and external mechanisms directly causing plastic to fragment, this work highlights the extent of the contribution of macrofauna to the environmental fate of plastic debris. Beyond expected mechanical wear on the mouthparts and digestive tract of the animals, the resulting smaller size makes the plastic particles availability to a wider range of organisms and contribute substantially to the cycling of micro- and nanoplastics through global food webs. This work establishes the presence of plastic waste in the environment as the root cause of this form of breakdown and therefore calls for the implementation of adequate plastic waste management systems. Clearly and consistently documented findings from both laboratory studies and field observations will aid deeper understanding of the implications of this form of widespread, rapid environmental breakdown of plastic debris. Understanding the global plastic cycling processes constitutes the foundation for effective legislative measures to mitigate the risks posed by this anthropogenic pollutant.

Introduction

Plastics have become a universal part of modern-day society and as a consequence, the natural world. Their lightweight, versatile and durable nature makes them suitable for a multitude of applications and leads to high demand, with worldwide production having reached 367 million tons in 2020 (Plastics Europe, 2021). Packaging materials represent the largest end-use market in the plastic industry (Plastics Europe, 2021): By acting as a lightweight yet impermeable barrier, plastic packaging protects goods from mechanical forces, moisture and microbial degradation. The inherent potential of plastic products for long product service lives is often in stark contrast to their actual usage time. In the case of packaging materials, which commonly fall into the single-use plastics category, service life is typically under 1 year (Luijsterburg and Goossens, 2014).

Plastic waste is ubiquitous, entering the environment from both "managed" sources, that is, landfills, and as "mismanaged" waste, that is, improperly discarded plastic waste (Jambeck et al., 2015). Between the start of large-scale plastic production in 1950, and 2015, an estimated 4,900 Mt plastic waste has accumulated in landfills and the environment worldwide, equivalent to 79% of plastics materials produced over that time span (Geyer et al., 2017). The quality of local waste management systems, as well as population densities are directly linked to the flux of plastic waste from land into the oceans (Jambeck et al., 2015), a fact that highlights the interconnectedness between societies' relationship with plastics and their impact potential on a global scale. The quantities in which plastic, as a novel entity, is produced and emitted into the environment are beyond the planetary boundary (Persson et al., 2022). The release of micro, and nano-sized plastic particles due to material breakdown has been argued to be an important aspect in this context, as it drives exposure, fate and hazard (Arp et al., 2021). Further, plastic particles small enough to become airborne are suggested to have radiative effects similar to aerosols in the atmosphere, hence potentially affecting the global climate (Revell et al., 2021).

Mechanisms of environmental degradation and fragmentation of plastics, which lead to the reduction in size and the formation of micro - and nanoplastics, can be divided into abiotic and biotic: Material deterioration caused by UV light, oxygen, temperature extremes and mechanical forces has been well-studied both in laboratory settings and field experiments. Evidence for substantial microbial degradation has been established for a number of polymers under environmentally relevant conditions (Lear et al., 2022). Often, abiotic degradation initially affects the surface integrity of the plastic material, preceding and can facilitate degradation by microorganisms (Gewert et al., 2015; Song et al., 2017; Karlsson et al., 2018). The presence of plastic in animal fecal matter has been documented for various species in different habitats, such as hyaenas, seals and sea birds (Belton et al., 2018; Donohue et al., 2019; Bourdages et al., 2021). Furthermore, as large fauna may interact with plastic materials in multiple ways beyond feeding, such as through nesting behavior, there is increased potential for facilitating physical breakdown.

Here we systematically investigate a presently under-studied aspect of the environmental fate of plastic pollution: The capacity of macrofauna (defined as multicellular organisms visible to the naked eye, inhabiting both aquatic and terrestrial systems) to fragment and transform plastics present in their habitats, and therefore highlighting their role in the fate of this ubiquitous class of anthropogenic pollutants.

Aspects of macrofaunal encounters with plastic debris

Figure 1 provides a schematic overview of the aspects, physiological mechanisms and potential negative consequences of plastic fragmentation by macrofauna.

Presence and access to plastic debris

The presence and abundance of plastic within the habitat of any organism is a key predictor of encounters and potential subsequent interactions. The accumulation of anthropogenic plastic waste initially occurs in proximity to its original source and is hence often found in and around urban centers (Barnes et al., 2009; Andrady, 2017). In a study of plastic ingestion by toads (*Rhinella diptycha*), lizards (*Tropidurus torquatus*) and geckos (*Hemidactylus mabouia*) in urban Paraguay where there is a lack of recycling facilities, 81 of 311 individuals contained microplastics, with clear fibers being the most abundant morphotype (Mackenzie and Vladimirova, 2021). Those vulture species (*Coragyps atratus, Cathartes aura*) resilient to anthropogenic presence and routinely visiting garbage dumps in Patagonia had high levels of plastic contamination in their pellets (Ballejo et al., 2021). Likewise, the visitation of garbage dumps has

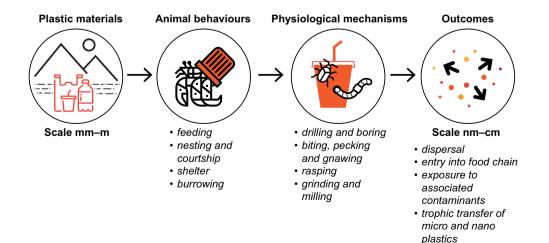


Figure 1. Schematic overview of macrofaunal fragmentation in the environment.

been suggested as the cause for the high number of plastic items found in the gizzards of juvenile and adult white storks (*Ciconia Ciconia*) in Spain (Peris, 2003).

Within the aquatic environment, a similar pattern is observed. For example, in a study of two species of sunfish (*Lepomis macrochirus; Lepomis megalotis*) from a river basin in Texas, Southern US, individuals from sampling sites categorized as "urban" had the highest microplastic stomach load (Peters and Bratton, 2016). An analysis of preserved freshwater fish from 1900 to 2017 demonstrated microplastic ingestion began in 1950, when mass production of plastic materials started, and rose with increased societal plastic use. Interestingly, all microplastics recovered were fibers, indicative of wastewater treatment plants as the probable source of microplastics to rivers and streams (Hou et al., 2021). The same trend was observed in feces of the Eurasian otter (*Lutra lutra*), which contained microplastic of mainly fibrous-shape. As otters are a top predator in freshwater ecosystems, this observation may indicate trophic transfer of the plastic fibers (O'Connor et al., 2022).

Marine hotspots of high plastic debris abundance, like the South Pacific Gyre, can be the result of specific transport paths of anthropogenic plastic waste within the oceans, and provide conditions that lead to a high incidence of encounters of marine life with plastic (Markic et al., 2018). Remote locations such as Henderson Island in the South Pacific, where high amounts of plastic pieces accumulated in beach sediments, can act as a sink for plastic debris (Lavers and Bond, 2017). A study of four genera of reef-inhabiting fish (Myripristis spp., Siganus spp., Epinephelus merra, Cheilopogon simus) from around Moorea Island in French Polynesia demonstrated the ingestion of microplastic of various shapes through the presence in their digestive tracts (Garnier et al., 2019). Additionally, certain plastic products are particularly prone to improper disposal, which can then make them more likely to be encountered by wildlife, such as cigarette filters (Novotny et al., 2011) and synthetic face masks widely used as part of the response to global Covid-19 pandemic (Patrício Silva et al., 2021).

Behaviors driving interactions with plastic debris

Interactions of macrofauna with plastic debris are often motivated by behaviors such as burrowing and nesting, courtship, or as part of foraging activities for food and water. In a controlled laboratory experiment, earthworms (*Lumbricus terrestris*) were observed transporting polyethylene beads through the soil by the processes of ingestion, egestion and incorporation into their burrows (Rillig et al., 2017). This downward transport of microplastic particles through the soil profile and deposition on the walls of the earthworms' burrows was further observed in a mesocosm experiment (Lwanga et al., 2017). Additionally, microplastics can be transported through the soil profile by adhering to the body of soildwelling fauna such as collembola (*Folsomia candida, Proisotoma minuta*) (Maaß et al., 2017). Damage to buried irrigation pipes by the whitefringed weevil (*Naupactus leucoloma*) was suggested to be driven by the animals seeking moisture (Nicholas, 2010).

A range of organisms have been documented to use plastic debris as nesting materials, with an example depicted in Figure 2. This is evidenced by the elevated amounts of plastic in seabird nesting areas (Hidalgo-Ruz et al., 2021) and direct incorporation of plastic into the nests of herring gulls (Larus argentatus) and great black-backed gulls (Larus marinus) (Lato et al., 2021), as well as Northern Gannets (Morus bassanus) (O'Hanlon et al., 2019). Incorporation of plastic debris into nesting areas is not limited to vertebrates. A nest of the solitary leafcutter bee Megachile sp., constructed solely from agricultural plastic waste, was found by Allasino et al. (2019). Caddisfly larvae (Lepidostoma basale) have been observed to incorporate high-density plastic particles alongside sand into their cases, resulting the cases to be less stable and presumably providing less protection against predation (Ehlers et al., 2020). Hermit crabs (Diogenidae, unknown species) have been reported to use plastic items instead of natural materials for shelter (Barreiros and Luiz, 2009). Male satin bower birds (Ptilonorhynchus violaceus) decorate their bowers with blue plastic items to attract mates, and have been observed stealing these items from each other (Wojcieszek et al., 2006).

Certain feeding strategies and foraging behaviors make encounters of macrofauna with plastic more likely. Both aquatic and terrestrial scavengers have been reported to ingest small particles, for example, the Norway lobster (*Nephrops norvegicus*) (Cau et al., 2020) and spotted hyaena (*Crocuta crocuta*) (Belton et al., 2018). Stomach contents and regurgitated materials of 34 species of seabirds evidenced that nonselective omnivorous feeders had the highest amounts of ingested plastic particles. Foraging methods in seabird species further affect the plastic load, with those species employing surface dipping and pattering having a higher rate of plastic ingestion compared to those that plunge dive to capture their prey (Ryan, 1987). Prey selection was also identified as a key factor



Figure 2. Photos of a bird's nest containing strands of synthetic material, identified as PE and PP. Credit: Olga Pantos.

driving the higher plastic ingestion rate in the surface-feeding Eastern Hooded Plovers (*Thinornis cucullatus*) when compared to the Australian Pied Oystercatcher (*Haematopus longirostris*) (Mylius et al., 2023). A similar pattern was observed for feces of ducks in African freshwater systems, where filter-feeding Cape Shovelers (*Spatula smithii*) ingested plastics at a higher rate than species that graze on vegetation (Reynolds and Ryan, 2018).

Factors driving likelihood of plastic debris ingestion

The most common and widely used size definition for microplastics is that they are <5 mm (Arthur et al., 2009), a concept based on the likelihood for ingestion by higher organisms (GESAMP, 2015). A number of factors determine the degree of attractiveness of anthropogenic plastic litter to macrofauna, and therefore the likelihood of ingestion. A field study on stranded posthatchling sea turtles suggested that ingested plastic particles in the micrometer range would resemble fish eggs in both size and diameter, and could therefore have been deliberately sought out by the animals (White et al., 2018). Color and overall appearance have also previously been linked to ingestion preference in sea turtles, indicating that soft, transparent items are mistaken for jellyfish (Schuyler et al., 2012). Distinct bite marks on washed-up marine plastic debris on Hawai'i are indicative of "attacks" by various fish species, wherein blue and yellow items were most frequently affected, pointing at a color preference (Carson, 2013). This finding is in part supported by a recent experimental study on freshwater and marine fish, where the fish had a preference for yellow, green and red color, whereas blue plastic particles ingested less frequently (Okamoto et al., 2022). Attractiveness of plastic items can further be determined by shape, as suggested in a study by Carson, who observed bite marks on stranded debris most frequently occurring on bottle-shaped plastic objects (Carson, 2013). Chemical cues are likewise demonstrated to illicit ingestion, such as airborne olfactory cues from in situ biofouled plastic, which had the same effect on the behavior of loggerhead sea turtles (C. caretta) as food, suggesting it is of equal attractiveness (Pfaller et al., 2020). The aging of microplastics and resulting biofilm also increases the likelihood of uptake of microplastic particles by marine zooplankton. Chemical cues from the biofilm were detected by copepods (spp.) and led to a preference for ingestion of biofouled over unaged plastic particles (Vroom et al., 2017). In contrast, sea urchins (Paracentrotus lividus) made no distinction between biofouled plastic and a natural food source (Porter et al., 2019).

Mechanisms of macrofaunal plastic fragmentation

Physical mechanisms by which macrofauna fragment and degrade plastic can be divided into four major groups, as outlined in Table 1. The following paragraphs explore these mechanism groups in detail.

Drilling and boring

Burrowing behavior by a range of invertebrate taxa can perforate plastic items, producing microplastics and potentially weakening the structural integrity of the item. For example, holes in a Malaysian power plant's acrylonitrile-butadiene-styrene (ABS) pipe system were caused by woodboring clams (*Martesia striata*) (Jenner et al., 2003). Small invertebrates including Isopoda, polychaetes and clam worms burrowing into expanded polystyrene (EPS) floats, commonly used in aquaculture, are potentially a significant source of secondary microplastics (Davidson, 2012; Jang et al., 2018; Zheng et al., 2023) Similarly, crabs living in EPS floats produce millions of small plastic particles by tearing the material (Zheng et al., 2023). A terrestrial example of perforation of plastic materials by macrofauna comes from a study on the prevention of damage to polyethylene (PE) irrigation systems by the Syrian woodpecker (*Dendrocopos syriacus*), who has been regularly observed perforating the plastic and thereby causing economic losses (Moran et al., 1980).

Biting, pecking and gnawing

There is an increasing evidence for macrofaunal interaction with plastic debris through biting, pecking and gnawing. Investigations into the source of "trimmed triangular fragments," washed up in South China led to the hypothesis that they were caused by marine macrofauna such as pufferfish (Tetraodontida spp.) (Po et al., 2020). Similarly, bite marks on washed-up plastic bottles in Bermuda matched with the jaws of triggerfish (Canthidermis sufflamen, Balistes capricus) and indicated that the phenomenon of fish causing physical alteration through attacking them with their teeth, is widespread (Eriksen et al., 2019). It is plausible that other species of corallivores are capable of causing a similar type of plastic fragmentation using their teeth. The gastrointestinal tract of wild caught parrotfish (Scaridae spp.) for example contained plastic particles, proving ingestion of plastic debris occurs within this family (Markic et al., 2018). Bite marks on marine plastic debris has further been linked to marine turtles (C. caretta, Chelonia mydas, Eretmochelys imbricata) (Eriksen et al., 2019). Observational studies of sea turtles, such as the loggerhead turtle (C. caretta) in the Indian Ocean have documented the ingestion and egestion of plastic items in high numbers, with more than half of the 74 individuals being affected (Hoarau et al., 2014). An ex vivo incubation of conventional, degradable and biodegradable plastic in gastrointestinal fluids of two sea turtle species (C. mydas, C. caretta) ruled out degradational processes within the animals' digestive tract as a major contributor to the breakdown to any of these tested plastic materials (Müller et al., 2012). Amphipods (Orchestia gammarellus) as an example of small semi-terrestrial crustacea created bite marks on biofouled PE sheets as they were feeding on the biofilm (Hodgson et al., 2018).

Birds interact with plastics using their beaks. Plastic items washed up on the Dutch coast, such as EPS, had identical peck marks to those present on cuttlebones originating from the Northern Fulmar's (Fulmarus glacialis) natural prey, sepia (Cadée, 2002). In insects, the ability to actively fragment polylactic acid (PLA) films has recently been observed in Caddisfly larvae (Agrypnia sp.) under laboratory conditions. Previously biofouled plastic sheets were offered with either a finite or infinite amount of leaf material, and in both cases, plastic was used alongside natural materials by the larvae to build their cases. Evidence of chewing, using their mandibles, was apparent on the plastic films, as well as the formation and release of microplastic particles >1 mm in size resulting from the larvae's building activities (Valentine et al., 2022). Indeed, insects chewing through rearing containers has been documented as early as 1976: Housefly larvae (Musca domestica) and brown apple moth larvae (Epiphyas postvittana) chew through plastic bags, likely polyethylene, without apparent ingestion of any plastic material (Singh and Jerram, 2012). Damage to plastic items by chewing is a common phenomenon, observed, for example, in termites (Isoptera spp.), that are reported to readily chew through polyvinyl chloride (PVC), cellulose and PE (Gay and Wetherly, 1969). Termites share traits of their mouthparts with other insect species such as cockroaches, grasshoppers, beetles and caterpillars,

Table 1. Recognized evidence of macrofaunal fragmentation.

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Mechanism group	Species	Polymer type	Initial size	Resulting size	Resulting shape	Location	Analysis method	References
Drilling, boring	Isopoda (Sphaeroma quoianum)	EPS	800 cm ³	242.7–491.8 μm	Particle/sphere	External	Stereomicroscope, digital analysis software	Davidson (2012)
	Polychaete (Marphysa sanguinea)	EPS	1000 cm ³	0.2 μm–3.8 mm	Particle	Internal and external	Stereomicroscope, FTIR	Jang et al. (2018)
	Bivalves (Martesia striata)	ABS	n/a	n/a	Perforation, holes 11 mm ²	n/a	Field observation	Jenner et al. (2003)*
	Woodpecker (Dendrocopos syriacus)	PE	n/a	n/a	Perforation	n/a	Field observation	Moran et al. (1980)*
	Crab (spp.)	EPS	n/a	18–948 μm	Fragments	Internal	Stereomicroscope and FTIR	Zheng et al. (2023)
	Clamworm (spp.)	EPS	n/a	19–948 μm	Fragments	Internal	Stereomicroscope and FTIR	Zheng et al. (2023)
	Isopoda (spp.)	EPS	n/a	20–948 μm	Fragments	Internal	Stereomicroscope and FTIR	Zheng et al. (2023)
Biting, pecking, gnawing	Pufferfish (spp.)	PE, PP, PS	n/a	0.22–12.97 mm ²	Mainly triangular fragments	External	FTIR	Po et al. (2020)*
	Amphipod (Orchestia gammarellus)	HDPE, "degradable," "biodegradable"	22 cm × 5 cm	86–1,351 μm	Fragments	External	SEM	Hodgson et al. (2018)
	Caddisfly larvae (Agrypnia sp.)	PLA	6 mm diameter	36–928 μm diameter	n/a	External	Stereomicroscope	Valentine et al. (2022)
	Northern Fulmar (Fulmarus glacialis)	EPS and other sponge-like polymers	n/a	n/a	n/a	External	Observation of washed- up debris	Cadée (2002)*
	Triggerfish (spp.)	n/a	n/a	n/a	Matching teeth marks	External	Observation of washed- up debris	Eriksen et al. (2019)*
	Sea turtle (spp.)	n/a	n/a	n/a	Matching teeth marks	External	Observation of washed- up debris	Eriksen et al. (2019)*
	Rodents (spp.)	n/a	n/a	n/a	n/a	External	Observation on plastic irrigation pipes	Moran (1981)*
	Canidae (spp.)	n/a	n/a	n/a	n/a	External	Observation on plastic irrigation pipes	Moran (1981)*
	Mustelidae (spp.)	n/a	n/a	n/a	n/a	External	Observation on plastic irrigation pipes	Moran (1981)*
	Viveridae (spp.)	n/a	n/a	n/a	n/a	External	Observation on plastic irrigation pipes	Moran (1981)*
	Pigs (spp.)	n/a	n/a	n/a	n/a	External	Observation on plastic irrigation pipes	Moran (1981)*

(Continued)

Table 1. (Continued)

Mechanism group	Species	Polymer type	Initial size	Resulting size	Resulting shape	Location	Analysis method	References
Rasping	Sea urchin (Paracentrotus lividus)	PE	n/a	118–15,797 μm	Fragments	Internal and external	Stereomicroscope, FTIR-ATR	Porter et al. (2019)
	Land snail (Achatina fulica)	EPS	n/a	1.343 ± 0.625 mm	Fragments	Internal and external	Optical microscope	Song et al. (2020)
	Marine Copepod (spp.)	EPS, PE, PP	1.7–21.3 mm	n/a	n/a	External	SEM	Reisser et al. (2014)*
Grinding, milling	Gammarus (Gammarus duebeni)	PE	10–45 μm	0.63–37.53 μm	Various	Internal	Fluorescent and light microscope	Mateos-Cárdenas et al. (2020)
	Norway lobster (Nephrops norvegicus)	PE, PP, PS, others	n/a	0.07–1.16 mm	Mainly fragments	Internal	Stereomicroscope, FTIR-ATR	Cau et al. (2020)*
	Krill (Euphausia superba)	PE	31.5 µm	<1 µm	Fragments	Internal and external	Fluorescent microscope	Dawson et al. (2018)
	Shore Crab (Carcinus maenas)	PP	2.5–3.0 mm	2.0–2.5 mm	Fibers, some amalgated	Internal and external	Stereomicroscope	Watts et al. (2015)
	Dragonfly larvae (Anax imperator)	Polyester	Length 8–10 mm, 1 mm diameter	Length 0.5– 3.5 mm	Fibers	Internal and external	Stereomicroscope	Immerschitt and Martens (2020)
	Petrel (Procellaria aequinoctialis)	PE	1,384.2– 1,403.7 mg	1% mass loss	Pellets–spheres	Internal	n/a	Ryan (1987)
	Japanese Quail (Coturnix coturnix japonica)	PS	3,233.11– 3,353.79 μm	8.29–1,541.33 μm	Fragments, increased circularity	Internal and external	Naked eye, Nile red staining	De Souza et al. (2022)
	Earthworm (Lumbricus terrestris)	LDPE, PLA, PBAT	20–648 μm	n/a	n/a	Internal	LDIR	Meng et al. (2023)

Note: Evidence derived from field observations is marked with *.

who can therefore be presumed to possess similar plastic-altering capabilities. Jaws of whitefringed weevils (*Naupactus leucoloma*) match puncture marks on irrigation pipes (Nicholas, 2010), which have also been reported to be chewed on by a vast array of vertebrate taxa, including mice (*Mus musculus*), rats (*Rattus rattus alexan-drines, Nesokia indica, Spalax ehrenbergi*), foxes (*Vulpes vulpes*), badgers (*Meles meles*), dogs (*Canis familiaris*) and wild boars (*Sus scrofa*) (Moran, 1981).

Rasping

Feeding structures used for the scraping of algal turf off hard benthic surfaces, such as echinoderm Aristotle's lanterns and molluscan radula, can produce miniscule plastic particles during grazing on plastics. Sea urchins (*P. lividus*) grazing on plastic-associated turf have been found to ingest plastic particles which they generate as they feed (Porter et al., 2019). They further have been observed to accumulate waterborne PS microspheres via the madreporite, followed by a translocation into organs including the gonads (Murano et al., 2020). Consequently, sea urchins could simultaneously be externally producing, and taking up plastic particles via two distinct routes.

Similarly, radula scraping can mechanically alter the surface structure of plastic substrates. Indentations of up to 4 mm depth have been observed on expanded polystyrene following the grazing activities of terrestrial snails (*Achatina fulica*) (Song et al., 2020). While it may not be surprising that soft plastic materials like polystyrene (PS) foam can be physically damaged by mechanical scraping, similar grazing marks have also been seen formed by marine gastropods on hard, nonfoamed plastics such as PE and polypropylene (PP)(Weinstein et al., 2016). Grazing copepod crustacea have specially adapted mandibular gnathobase which have been found to leave characteristic indentation on the surface of plastic substrate, a process presumed to lead to the formation of small plastic particles (Reisser et al., 2014).

Grinding and milling

Upon ingestion of plastic debris, the presence of a gizzard, or gastric mill, is often associated with reported physical alteration of the material. This specialized organ, found across different phyla, is capable of grinding or "milling" hard and indigestible food items.

In aquatic crustaceans, the gastric mill contains chitinous teeth, and can lead to the fragmentation of ingested plastic particles. Initially observed in a feeding trial involving shore crabs (Carcinus *maenas*), passage through the digestive tract of these animals results in a size reduction and amalgamation of PP fibers (Watts et al., 2015). In Antarctic krill (Euphausia superba), the ingestion of polyethylene (PE) microspheres under controlled conditions led to their fragmentation (Dawson et al., 2018). This occurrence has been confirmed by field observations in the Norway lobster (N. norvegicus). Within the animals, particle numbers significantly increased, while particles size decreased with progression through the gastrointestinal tract. Polymer type did not influence their fragmentation (Cau et al., 2020). In freshwater amphipods (Gammarus duebeni) the same mechanism is suggested to be, at least in part, behind their observed ability to fragment PE microspheres into nano-sized particles of various shapes (Mateos-Cárdenas et al., 2020), and the gizzard in dragonfly larvae (Anax imperator) has a similar effect on ingested polyester fibers, as demonstrated in a feeding experiment (Immerschitt and Martens, 2020). Through presenting earthworms with three types of polymers mixed into soil, sand naturally occurring in soil was identified to facilitate the fragmentation of PE, whereas polyester appeared to be degraded solely by the mechanical action of the gizzard (Meng et al., 2023). In a similar experiment, surface changes such as cracks and pitting on tire rubber particles were observed after ingestion by earthworms (Sheng et al., 2021).

Gizzards in birds are similarly capable of physically altering ingested plastic debris: In an early study investigating the residence time of PE fed to Petrels fledgelings (Procellaria aequinoctialis), Ryan (1987) measured a plastic mass loss of 1% during 12 days, although no surface changes were detected in this feeding trial. Upon ingestion by Japanese quails (Coturnix coturnix japonica), the size of aged PS fragments reduced in diameter as they transitioned from the gizzard to the intestines and feces. Furthermore, some fragments translocated into the liver of the animals had become more spheroidal, indicating both size reduction and shape alteration by an avian gizzard (de Souza et al., 2022). In fact, one study on the digestive tract of birds has likened their gizzards to mammalian molars, as turkey gizzards enable them to crush or "pulverize" walnut shells and surgical scalpels (Feduccia, 2011). Herring gulls drop larger prey items from a certain height, whereas smaller bivalve shells are swallowed whole and crushed internally (Cadée, 1995).

Implications of macrofaunal plastic fragmentation

At the scale of an individual organism, consequences resulting from the interactions between macrofauna and plastic items described above depend on the nature of the interaction, its frequency, the polymer type and physiological structures involved. As plastic material has mechanical properties distinctly different from natural materials biota encounter within its habitats, physiological consequences resulting from interactions are of importance when considering the overall risk profile of plastic in the environment. Irrespective of whether ingestion occurs, wear on the mouthparts involved in the fragmentation as outlined in this review is to be expected, particularly in cases where interaction with plastic material is frequent. The functionality of organs of the digestive tract has evolved in the absence of present-day levels of environmental plastic pollution. This not only gives raise to speculations on whether and how this anthropogenic pressure influences future evolution (Davis and Turpin, 2015), it also points toward the necessity of including physiological effects of interactions with plastics in future toxicological assays. When of sufficiently small size, plastic particles can translocate into tissue and organs of exposed organisms, with evidence of their adverse effects on health and fitness (Dong et al., 2023). Beyond a mechanical irritant, small plastic particles can act vectors for hazardous chemical additives, such as polybrominated diphenyl ethers (PBDEs), phthalates, nonylphenol, bisphenol A (BPA) and antioxidants. Upon ingestion, exposure to these additives can disrupt physiological process, and negatively affecting an organism's fitness (Browne et al., 2013; Hermabessiere et al., 2017).

In a wider ecosystem context, several aspects of macrofaunal plastic fragmentation are of importance. As with all forms of physical breakdown of plastics in the environment, the resulting increase of the surface to volume ratio influences ensuing degradation rates as well as bioavailability of the material. Macrofaunal fragmentation appears to be more rapid than abiotic degradation (Mateos-Cárdenas et al., 2020), therefore constituting a central factor in the environmental fate of plastic. Studies of rasping organs like the radula have broadened the view of the scientific community that these types of plastic breakdown do not necessarily require plastic particles to be smaller than the organism's mouthparts (Reisser et al., 2014). In fact, evidence explored in this work highlights the complexity of biologically mediated (Cau et al., 2020) plastic fragmentation, akin to the general concept of bioerosion as outlined by Davidson et al. (2018). Species acting as ecosystem engineers could play a large part in macrofaunal plastic fragmentation due to their physical capability of actively modifying their habitats (Zheng et al., 2023). Further, predator-prey interactions and resulting trophic transfer of plastics materials are well documented. In a laboratory experiment, fish ingested a higher amount of microbeads through their preexposed prey, mysids (Neomysis spp.) than from the water column alone. The study authors suggest the capability of mysids to fragment plastics can facilitate the observed trophic transfer (Hasegawa and Nakaoka, 2021). Field observations on the ingested prey items of tuna (Thunnus albacares) as a large predatory fish species likewise indicated a connection between the microplastic load of predator and prey (Justino et al., 2023). Trophic transfer has been further confirmed experimentally from blue mussel (Mytilus edulis) to shore crab (C. maenas) and from mussel (Brachidontes variabilis), to rock snail (Reishia clavigera) (Farrell and Nelson, 2013; Xu et al., 2022).

In a global context, the uptake, retention and depuration of plastic debris items by macrofauna can greatly increase its mobility, as shown for a variety of bird species. Plastic islands generated through the accumulation of plastic debris over vulture roosts highlight the immense dispersal potential, as the plastic found in this study is suggested to have originated from waste sites >50 km away (Ballejo et al., 2021). Seabirds are known to act as vectors for plastic material from sea to land (Bourdages et al., 2021). The individual retention time within the bird species plays an important role, and is affected by the polymer type, regurgitation, and the occurrence of aforementioned internal fragmentation, leading to size reduction and finally, excretion (Ryan, 2015; van Franeker and Law, 2015). Macrofauna-aided plastic dispersal has been further documented in the Asian elephant, who appears to spread ingested plastic debris into areas free from anthropogenic influence after foraging at waste sites (Katlam et al., 2022).

Conclusion and outlook

As outlined in this review, the mere presence of plastic debris in the environment can initiate a cascade of biologically mediated fragmentation processes, with far-reaching implications for global ecosystems. This work explored the drivers behind this presently under-studied and potentially underreported aspect of environmental material breakdown, the mechanisms by which macrofaunal fragmentation occurs, and the nature of anticipated negative effects for the individuum involved. As the rate of this form of biological fragmentation is predicted to be higher than through other degradational pathways, it can substantially contribute to the bioavailability of micro- and nanosized plastic particles to lower trophic levels, and hence facilitate their trophic transfer. Finally, macrofauna can act as spreaders of the plastic material, enhancing its dispersal and ultimately affecting the cycling of plastic debris in the environment. Encounters of macrofauna with plastic debris have therefore the potential to alter the risk profile of this class of anthropogenic pollutants significantly.

Based on these findings, our recommendations are twofold: Firstly, to better understand global patterns and allow the use of predictive models estimating size and mass reductions in plastics, we recommend that work reporting on macrofaunal fragmentation should state the resulting particle size. Documenting the physical state of plastic particles found within field-collected biota aids the understanding of the preceding interactions. To facilitate discoverability of literature, we additionally propose a unified use of the term macrofaunal fragmentation when reporting observations of plastic fragmentation through macrofauna. Finally, there is urgency in implementing adequate plastic waste management practices globally as an effective measure to prevent or at least limit macrofaunal plastic fragmentation.

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Data availability statement. Data are available within the article.

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