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ARTICLE

Capture, ingestion, and egestion of microplastics by suspension-feeding bivalves: a 40-year history[1]

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Abstract: In aquatic environments, suspension-feeding bivalve molluscs are exposed to a manifold of natural and anthropogenically derived particles, including micro- and nanoplastics. Plastic particles interact with feeding and digestive organs and can produce negative effects. As a result of these effects and the potential transfer of microplastics to higher trophic levels, including humans, there has been renewed interest in the ingestion of plastic particles by different species of bivalves. Many recent studies, however, have ignored the ability of bivalves to select among particles both pre- and post-ingestively. Neglecting to consider the factors that mediate particle capture, ingestion, and egestion can lead to erroneous data and conclusions. This paper outlines the current state of knowledge of particle processing by bivalves, and demonstrates how it relates to studies utilizing plastic particles. In particular, the effects of particle size, shape, and surface properties on capture, preferential ingestion, post-ingestive sorting, and egestion are summarized. The implications of particle selection for the use of bivalves as bioindicators of microplastic pollution in the environment are discussed. Only through a full understanding of the types of plastic particles ingested and egested by bivalves can internal exposure, toxic effects, and trophic transfer of microplastics be assessed adequately.

Key words: bivalve, microplastic, suspension-feeding, selection, egestion, particle, pollution.

1. Introduction

Microplastic particles have been used in laboratory feeding studies with molluscs for decades (Ward and Shumway 2004 and references therein). Polystyrene microspheres and other plastic particles have been employed as tracer and food-surrogate particles to study a range of feeding processes including particle capture, selection, and gut residence time. Williams (1978) was one of the first researchers to use synthetic latex microspheres (polystyrene) to study feeding behavior of the suspension-feeding gastropod mollusc, *Crepidula fornicata*. Since that time, polystyrene microspheres and other microplastic particles have been used to investigate feeding processes of holoplanktonic, meroplanktonic, and benthic animals (e.g., Gerritsen and Porter 1982; Holland et al. 1986; Ward and Targett 1989; Solow and Gallager 1990; Hart 1991; Mayer 1994; Ward 1996; Baer et al. 2008). As such, it is well known that many suspension feeders readily capture and ingest certain types of plastic particles.

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There are several advantages of using microspheres and other plastic particles in studies with suspension-feeding animals. First, these particles can be purchased with uniform size and shape, allowing investigators to remove these variables from feeding studies. Second, many plastic particles can be purchased with embedded fluorophores or dyes allowing for easy visualization in biodeposits and tissues. Third, microspheres and other plastic particles are relatively inert and are not bioavailable. As a result, they resist digestive processes and are good tracers for the time-course over which inorganic material passes through the gut. Finally, the surface properties of plastic particles can be manipulated by adsorbing various materials on (e.g., polysaccharides), or by covalently binding proteins to, their surfaces. These attributes have led researchers to employ microplastics to study capture efficiency, handling, ingestion, and egestion of particles in many species of suspension feeders (e.g., Gerritsen and Porter 1982; Solow and Gallager 1990; Cranford et al. 1998; Richoux and Thompson 2001; Milke and Ward 2003; Ward et al. 2003; Rosa et al. 2017). Results of these studies have been instrumental in elucidating the processes and mechanisms of feeding in these animals.

2. Summary of previous studies

Although a rich body of literature exists on particle capture, ingestion, and egestion of natural and synthetic particles, many recent publications on the topic of microplastic uptake by bivalve molluscs have neglected past work. Lack of attention to this database has led to poorly designed studies, weak and erroneous conclusions, and results that duplicate previous research. For example, several recent papers conclude that bivalves can ingest plastic microspheres ranging in size from 5 to 300 μm (e.g., Van Cauwenberghe et al. 2013; Khan and Prezant 2018). This fact, however, had been demonstrated many times previously and has been known for decades (e.g., Ward and Targett 1989; Tamburri and Zimmer-Faust 1996; Cranford et al. 1998). In this short overview, the current knowledge of how particles interact with the feeding and digestive organs of bivalves is summarized, with particular focus on interactions with micro- and nanoplastic particles including spheres and high-aspect-ratio (length : width) fibers.

2.1. Preingestive interactions with plastic particles

2.1.1. Particle capture

Not all suspended particles are captured by the gill of suspension-feeding bivalves. In general, capture efficiency increases asymptotically with increasing particle size above ca. 1 μm (e.g., Vahl 1972; Møhlenberg and Riisgård 1978; Palmer and Williams 1980; Riisgård 1988) to a maximum efficiency of close to 100%. Capture efficiency for small particles (ca. 1–6 μm) is species-specific, and dependent upon gill architecture and structure of the laterofrontal cilia or cirri (Silverman et al. 1995; Ward and Shumway 2004; Rosa et al. 2017, 2018). If incorporated into heteroaggregations (i.e., marine aggregates, marine snow), capture efficiency of small plastic microspheres (0.5–1.0 μm) and nanospheres (100 nm) increases significantly (Kach and Ward 2008; Ward and Kach 2009). Surface characteristics of particles also can affect capture efficiency (Hernroth et al. 2000; Yahel et al. 2009). For example, larvae of the northern quahog (hard clam), *Mercenaria mercenaria*, capture negatively charged polystyrene spheres (ca. 2.2 μm) at a higher efficiency than spheres with no net charge (Solow and Gallager 1990). In adult blue mussels, *Mytilus edulis*, 2- and 3-μm polystyrene spheres are differentially captured depending upon the type of neoglycoprotein (NGP) that is covalently bound to the sphere surface. Microspheres with bound NGP containing D-mannose are captured at a significantly lower efficiency than microspheres bound with NGP containing N-acetyl-glucosamine or bovine serum albumin (BSA), and lower than microspheres that are not bound with NGP (Rosa et al. 2017).

Larger microspheres (4–10 μm) are captured at the same efficiency (>85%) regardless of coating (see also Rosa et al. 2015). Importantly, both D-mannose and BSA significantly increased the hydrophobicity of microspheres, but did not change their surface charge, compared to microspheres not bound with NGP. These results suggest that interactive effects between surface hydrophobicity (physical) and chemistry (carbohydrate) could be responsible for the observed decreases in capture efficiency of small (2–3 μm) plastic spheres bound with NGP containing D-mannose. Interestingly, the bay scallop, *Argopecten irradians*, demonstrates no change in capture efficiency with different microsphere coatings (Rosa et al. 2017).

2.1.2. Particle selection

Particle capture by the gill does not necessarily mean that the particle is ingested. Bivalves are selective particle feeders, with well-developed mechanisms for particle discrimination (Ward and Shumway 2004). Although the exact mechanisms of selection are still being resolved, it is known that particle size, shape, and surface properties (both specific and non-specific) affect preferential rejection and ingestion of material (see Ward and Shumway 2004; Rosa et al. 2018). Particles destined for rejection are bound in cohesive mucus, transported via well-developed mucociliary processes to specific sites on the mantle, and expelled as pseudofeces (Galtsoff 1964; Ward et al. 1994; Beninger and St-Jean 1997; Beninger et al. 1997; Garrido et al. 2012). The loci of selection are species-specific, and depend upon the architecture and ciliary tracts of the gill. Some species of bivalves (e.g., oysters, scallops) can select particles on both gills and labial palps (paired structures surrounding the mouth), whereas other species (e.g., mussels) only select on the palps (Ward et al. 1997, 1998; Beninger et al. 2004, 2008). Importantly, both particle quantity and quality can affect particle rejection, and at high concentrations selection of particles based upon quality diminishes in many species and indiscriminant rejection occurs (e.g., Beninger et al. 1992, 2008; Urban and Kirchman 1992; Newell and Shumway 1993). This process is likely triggered when the gills or labial palps are saturated with particles and rejection of material is used to control the amount of material ingested. Other mechanisms for controlling the amount of particles ingested exist, such as reduction in clearance rates (Widdows et al. 1979; Bricelj and Malouf 1984; Hawkins et al. 1998).

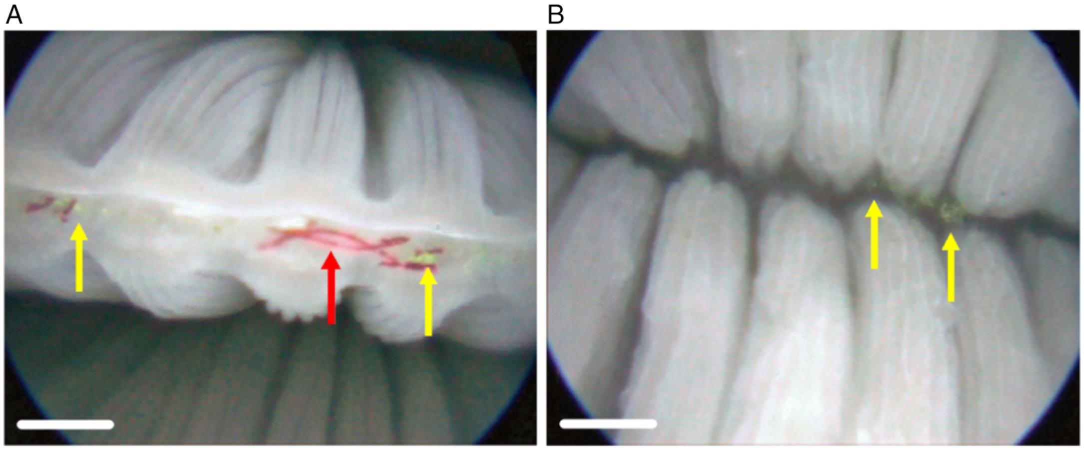
The size of particles will partially determine preferential rejection or ingestion. As particle size increases above ca. 100 μm, anatomical constraints of the gill, labial palps, and mouth begin to reduce the likelihood of ingestion. For example, in bivalves with plicate, heterorhabdic gill structures (e.g., oysters and scallops), the distance between adjacent plicae ($\lesssim$ 100 μm) precludes the entrance of large particles into the principal filaments (e.g., Cognie et al. 2003; Mafra et al. 2009). The result is that large particles usually are transported to the ventral tract of the gill where rejection as pseudofeces is more likely. Certainly, other factors will influence whether a particle will enter the principal filaments (see below), such as the shape of the particle (e.g., long thin cells and fibers) and muscular movements of the gill, which affect the distance between adjacent plicae. Similar anatomical constraints exist for the labial palps, where, in many species, some particles are transported on the crests of the ridges both proximally and anteriorly, and others become trapped in the troughs between ridges and are carried distally to the edge of the palp for rejection as pseudofeces (Galtsoff 1964; Beninger and St-Jean 1997; Beninger et al. 1997; Garrido et al. 2012). Finally, the mouth of the bivalve also constrains the upper size limit of particles that can be ingested. For example, based upon histological sections, the width of the mouth of the eastern oyster is approximated as 100–150 μm (e.g., Galtsoff 1964). As invertebrates, however, the size of the oral opening is not fixed and can stretch considerably as evidenced by the presence of particles hundreds of micrometres in size in stomach contents (Davenport et al. 2011; Peharda et al. 2012). Nonetheless, there is an upper limit to the size of particle that can be ingested, and it is likely in the range of 600–900 μm.

The ingestion of particles, including those composed of plastic, >100 μm by bivalves has received little attention. The Chilean oyster, *Ostrea chilensis*, can ingest Sephadex™ microspheres (a cross-linked synthetic gel derived from the polysaccharide dextran) ranging in diameter from 175 to 350 μm. The majority of these spheres, however, are rejected in pseudofeces indicating that ingestion efficiency is low (Chaparro et al. 1993). The cockle, *Cerastoderma edule*, can ingest polystyrene and synthetic-cellulose microspheres between 100 and 500 μm in diameter (Karlsson et al. 2003). The efficiency of ingestion of these large particles, however, was not determined. Similarly, the eastern oyster, *Crassostrea virginica*, can ingest polystyrene microspheres between 10 and 370 μm in diameter, but ingestion efficiency decreases rapidly with increasing particle size to <10% for 370 μm particles (Tamburri and Zimmer-Faust 1996). Interestingly, in the same study oysters ingested larvae of nine different invertebrate species, measuring between 100 and >500 μm in length, at efficiencies of about 80%.

The shape of particles also affects their ingestion. The oyster, *C. virginica*, rejects large cells of the diatom *Pseudo-nitzschia multiseries* (ca. 82–90 μm long × 5 μm wide) relative to small cells (24–28 μm long) on the gills (Mafra et al. 2009). This effect is a result of the length of the large cells, which exceeds the width of the principal filaments (ca. 68 μm). Although some cells can enter the principal filaments if they are captured in exactly a dorsoventral orientation, the random orientation of captured cells results in more of them being directed to the ventral tract and rejected in pseudofeces. Similar results have been found for plastic fibers with a high aspect ratio (ca. 65–260 μm long × 16 μm wide). On the gill of the oyster, large fibers are transported ventrally with few being observed in the dorsal tracts. In contrast, small polystyrene microspheres (10–15 μm) are transported both dorsally and ventrally (Figs. 1A and 1B). Mussels also reject plastic fibers with a high aspect ratio (length : width), but selection occurs on the labial palps, not on the gill (C. Herrick et al., unpublished data, 2015). In this study, the great majority of polyester fibers (ca. 65–260 μm long × 16 μm wide) were rejected in pseudofeces with ingestion efficiencies of <5% after 2 h of feeding (Fig. 2A).

The influence of physicochemical surface properties on the selection of phytoplankton cells and microplastic particles has received much attention. In brief, both nonspecific (i.e., charge, wettability, hydrophobicity) and specific (carbohydrates) surface characteristics interact with mucus covering the feeding structures to affect preferential rejection or ingestion of particles (for reviews see Ward and Shumway 2004; Rosa et al. 2018). Polystyrene particles were used in many of these studies and as a result, there is a good knowledge base regarding effects of the surface properties of microplastics on selection. For example, adsorbed metabolites from microalgae affect the selection of microspheres (10 μm) by mussels (*M. edulis*), with some metabolites eliciting rejection and others ingestion of the spheres (Ward and Targett 1989; Fig. 2B). Rosa et al. (2013) examined particle selection by mussels (*M. edulis*) and oysters (*C. virginica*) when delivered polystyrene microspheres (10 μm) and the same size particles with a range of compositions, including (*i*) coated and functionalized polystyrene; (*ii*) plain, coated, and functionalized silica; and (*iii*) alumina. Results of discriminant-analysis models indicated that both species ingest particles with more hydrophobic surfaces or surfaces with a higher negative charge preferentially (zeta potential $\gtrsim -9$ mV; Fig. 2C). In addition to non-specific interactions between microplastic particles and mucus covering the feeding organs (e.g., charge–charge, hydrophobe–hydrophobe), specific interactions also have been demonstrated. Oysters (*C. virginica*) preferentially ingest polystyrene spheres (6 μm) that are covalently bound with NGP

Fig. 1. Selection between polyester fibers (ca. 65–260 μm long × 16 μm wide) and polystyrene microspheres (10–20 μm diameter) by the oyster, *Crassostrea virginica*. Fibers were collected from cloth with a lint shaver, cut into small pieces, processed in a laboratory blender, and passed through a 500-μm sieve. Fibers and microspheres were then aged in seawater for at least one week before use to promote biofilm formation. (A) Video micrograph of the ventral groove of the plicate gill of the oyster delivered red fibers (red arrows) and yellow microspheres (yellow arrows). Note that both particles have been transported to the groove. (B) Video micrograph of the dorsal tract of the same gill. In contrast to the ventral groove, only yellow microspheres (yellow arrows) have been transported to the dorsal tract, indicating selection against fibers. Scale bars ≈ 200 μm.

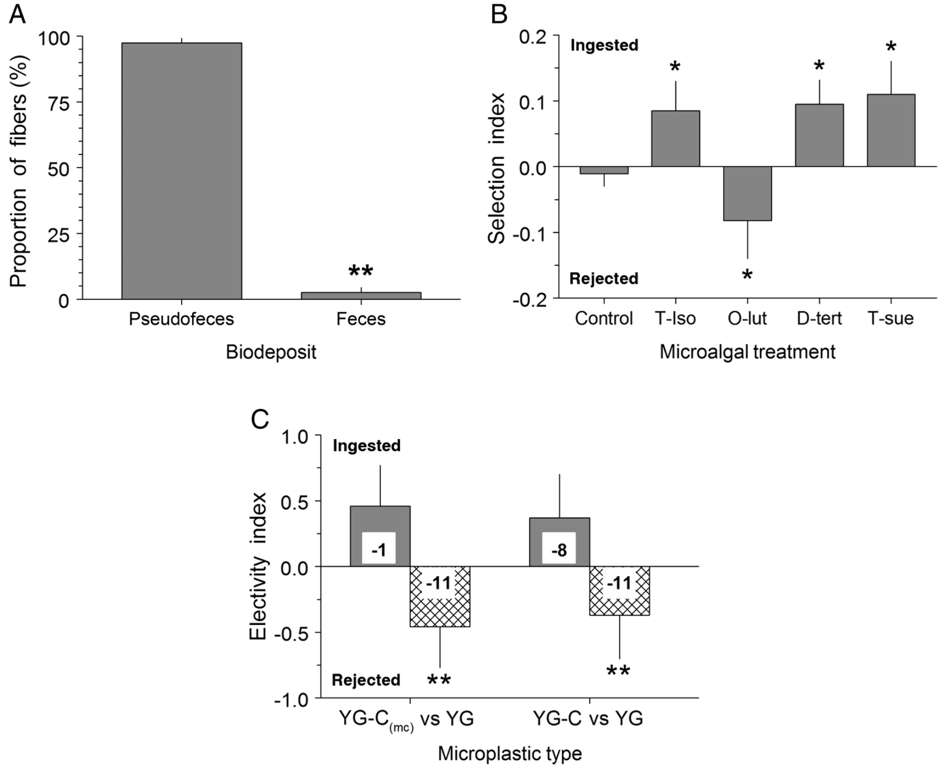


containing glucosamide compared to those bound with just BSA (Pales-Espinosa et al. 2009). Similarly, mussels (*M. edulis*) preferentially ingest the same type of microspheres bound with NGP containing glucosamide or mannopyranosylphenyl, but reject microspheres coated with BSA alone (Pales-Espinosa et al. 2010). These results demonstrate that specific interactions between surficial carbohydrates and lectins contained within mucus covering the feeding organs can mediate selection. The data also have implications for how recently-fragmented and aged plastic particles are handled by bivalves, because carbohydrate-enriched coatings could arise on microplastics during biofilm formation.

2.2. Postingestive interactions with plastic particles

Opportunities exist for differentiation of plastic particles within the gut of bivalves. As elegantly established over 60 years ago (e.g., Graham 1949; Yonge 1949; Owen 1956; Reid 1965), in the stomach the action of the rotating crystalline style and teeth of the gastric shield triturate material, breaking apart large particles and particle aggregates. Enzymes liberated from the dissolving head of the style mix with this particle slurry, and the particles are subjected to ridged sorting areas of the stomach and stomach pouches. Lighter particles and particle fragments enter the digestive diverticula (digestive gland) where more complete intracellular digestion occurs. Larger and more dense material passes into the intestinal groove and is transported to the mid-gut where it mixes with other undigested material and is incorporated into fecal pellets. More recently, numerous studies have demonstrated that some species of bivalves can discriminate among particles in the gut, including between different species of microalgae (Cucci et al. 1985; Shumway et al. 1985; Cognie et al. 2001), living and heat-killed microalgae (Brillant and MacDonald 2003), microalgae and inorganic material (Menzel 1955; Foster-Smith 1975), and sediment with and without organic coating (Gagnon and Fisher 1997). The selection mechanism seems to be based on size, density, and chemical properties of the particles and cells.

Fig. 2. Selection of plastic particles by the mussel, *Mytilus edulis*. (A) When mussels were delivered polyester fibers (10 000 fibers/mL; see Fig. 1 for description) and the microalga *Tetraselmis chuii* (20 000 cells/mL), a significantly higher percentage of fibers were rejected in pseudofeces compared to those ingested and egested as feces ($p < 0.01$, $n = 3$; C. Herrick et al., unpublished data, 2015). (B) When mussels were delivered polystyrene microspheres (10 µm) treated with metabolites from four microalgal species, significantly more spheres were preferentially ingested or rejected compared to the control, with selection being dependent on the microalgal species from which metabolites were obtained ($p < 0.05$, $n = 3–6$; replotted from Ward and Targett 1989; T-Iso, *Isochrysis affinis galbana*; O-lut, *Olisthodiscus luteus*; D-tert, *Dunaliella tertiolecta*; T-sue, *Tetraselmis suecica*). (C) When mussels were delivered polystyrene microspheres (10 µm) with (YG-C) and without (YG) a carboxyl functional group, either coated (mc) or not coated with methylcellulose, significantly different selection outcomes occurred, with the higher negatively charged spheres being rejected ($p < 0.01$, $n = 13$; charges are zeta potentials; data from Rosa et al. 2013). All data are means ± standard deviation.



The discrimination of plastic microspheres in the gut of bivalves has also been demonstrated. After an exposure period of 15 min, scallops (*Placopecten magellanicus*) egested 6-µm polystyrene spheres at a slower rate than 10-µm spheres (Cranford et al. 1998). In contrast, Brillant and MacDonald (2000) found that the residence time of 20-µm spheres in the stomach of *P. magellanics* is longer than that of 5-µm spheres. They also showed that residence time of polystyrene spheres (9 µm) was significantly longer than that of similar-sized glass spheres (8 µm) with a higher density. None of the spheres, however, were observed in histological sections of the digestive gland, suggesting that the differential treatment of spheres was caused by increased retention of larger and lighter particles in the stomach. In another set of experiments, Brillant and MacDonald (2002) demonstrated that a higher proportion of microalgae (*Prorocentrum minimum*) labeled with ^{14}C is transported to the digestive gland of *P. magellanicus* compared to similar size polystyrene spheres (16–18 µm) labeled with ^{51}Cr. A higher proportion of microspheres were transported to the intestine and egested as feces. Additionally, polystyrene spheres (5.5 μm) with covalently linked protein are retained in the gut of scallops significantly longer than non-coated microspheres (5.7 μm). Taken together, these data suggest that, in the gut of scallops, selection can occur between organic material and microplastics, and between plastic microspheres of the same size, but with different surface chemistries.

Other bivalves have shown some degree of discrimination of plastic particles in the gut based upon size. For example, when delivered polystyrene nanospheres (100 nm) and microspheres (10 μm) at the same time for ca. 1 h, the proportion of microspheres egested by both mussels (*M. edulis*) and oysters (*C. virginica*) was greater than the proportion of nanospheres egested (Ward and Kach 2009). In fact, after 48 h, ca. 95% of the 10 μm spheres were egested, whereas the proportion of nanospheres being egested continued to increase. Nanospheres, however, were delivered to the bivalves incorporated in aggregates, whereas the microspheres were not. The difference in delivery may have affected gut residence time. Nonetheless, results from the studies outlined above demonstrate that within the bivalve gut, not all plastic particles are processed in the same manner. Differential processing and potential selection based upon size, shape, organic coatings, and other factors will likely affect the rate at which a specific type of microplastic will be eliminated from the animal.

3. Conclusions and perspectives

Bivalve molluscs are well adapted to a diet of relatively dilute, heterogenous particles and cells (Morton 1960). These animals rely almost entirely upon ciliary transport to conduct material along feeding organs and through the gut; thus, non-selective ingestion of large volumes of dense particles would be difficult to process. In fact, few species of bivalves simply encounter and engulf particulate matter. Rather, there is a large body of evidence demonstrating that bivalves rapidly sort particles based on physical and chemical factors, with material of higher quality being ingested and digested preferentially over that of lower quality (Ward and Shumway 2004; Rosa et al. 2018). This capability for selection is probably unsurpassed by any other particle-feeding group.

Although most studies on particle selection by bivalves have examined natural particles and cells, sufficient data exist on the selection of several types of microplastics to establish general concepts. Large plastic particles (i.e., ca. 500–1000 μm spheres and fibers) are captured at a high efficiency, but are more likely rejected in pseudofeces, either by the gill or labial palps, and thus are ingested in low proportions. Particles between ca. 6 and 200 μm also are captured efficiently by most species and are more likely ingested if they have hydrophobic surfaces, organic coatings, or possess surfaces with a lower negative charge (zeta potential $\lesssim -8$ mV). Capture efficiency for microplastics between ca. 1 and 6 μm is species specific, and particles $\lesssim 1$ μm are inefficiently captured by most bivalve species unless they are incorporated into aggregates or are highly agglomerated. If captured, however, the selection of small particles likely follows the same general principles as for larger particles. It should be emphasized that particle selection is never 100% efficient and inevitably some large spheres and fibers with hydrophilic, highly charged surface will be ingested by various bivalve species.

The selective capabilities of bivalves are well established, and suggest that bivalves may not be a good bioindicator of microplastics in the environment. That is, quantifying the number and types of plastic particles in the pallial cavity and gut of bivalves is not necessarily a good proxy for the number and type suspended in the aqueous environment. Recent studies of field-collected microplastics and bivalves have given a conflicting picture. For example, in a study by Qu et al. (2018), a significant quantitative correlation was found between abundance of plastic particles in two species of mussels (*M. edulis*, *Perna viridis*) and in the surrounding environment, although mussels were more likely to ingest smaller microplastics. In a related study, Su et al. (2018) found a significant positive correlation between the abundance of plastic particles in Asian clams (*Corbicula fluminea*) and in the surrounding water and sediment. Abundance and size of microplastics in clams, however, were more similar to those in the sediment. The authors concluded that *C. fluminea* is a good bioindicator of microplastic pollution in the environment. In contrast, in a recent study on field-collected marine aggregates and mussels (*M. edulis*), Zhao et al. (2018) found differences in the size of microplastic in pseudofecal, fecal, and digestive gland–gut samples suggesting that size-dependent, pre- and post-ingestive selection was occurring. Although the size, shape, and chemical type of microplastic ingested by mussels were representative of those found in aggregates, over 40% of the microplastic particles were either rejected in pseudofeces or rapidly egested in feces. Additionally, calculations of the number of plastic particles that mussels encountered per day, based on known clearance rates and the measured abundance of microplastics in aggregates, showed that at the time of collection, mussels contained only 2% of the plastic particles to which they were exposed in their pseudofeces, feces, and digestive gland–gut. Given that the transport of captured particles to the labial palps for either ingestion or rejection is on the order of minutes (Milke and Ward 2003; Ward et al. 2003), the residence time of particles directed to the hind gut is on the order of hours, and the residence time of particles passed to the digestive diverticula is on the order of days (Ward and Kach 2009), the authors concluded that the majority of plastic particles encountered by mussels in marine aggregates were either rejected in pseudofeces or rapidly egested as intestinal feces.

Finally, it is not entirely clear if bivalves bioaccumulate plastic particles. Results of the aforementioned field studies and those of recent laboratory experiments, however, suggest that they do not (Xu et al. 2017). For example, mussels (*M. edulis*) exposed for 14 days to polystyrene nanospheres (ca. 40 nm) or microspheres (ca. 5 μm) at a concentration of 0.1 $\mathrm{mgL^{-1}\,h^{-1}}$ show no bioaccumulation of these plastics in their tissues (whole animal analysis; J.E. Ward et al., unpublished data, 2019). After exposure, both types of plastic particles are rapidly eliminated from tissues, with ca. 38% of the nanospheres and 63% microspheres being egested on the first day of depuration. After 7 days of depuration, only residual amounts of plastic particles are found in the tissues. Clearly, more studies on the uptake and depuration of microplastics by bivalves need to be conducted — employing different types of microplastics, a range of species, and longer exposure times — to determine conclusively if accumulation in tissues can occur. Taken together, however, the extensive data base on particle selection and available data on rapid depuration of plastic particles by bivalves call into question the proposed use of these animals as indicators of microplastics in the environment.

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