

Feces in Aquatic Ecosystems

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Think of trophic levels, and what probably comes to mind is an illustration from a biology text showing a pyramid, with solar energy trapped by photosynthesizing plants on the bottom, plants fed upon by herbivores in the middle, and herbivores eaten by carnivores on top. These models may also show arrows indicating that feces and dead plants and animal bodies provide inputs to the detritus pool, illustrating how this organic matter is recycled by microorganisms, and how at all trophic levels, aerobic respiration results in the loss of energy from the ecosystem. Such conceptual models provide a basis for energy budgets to be investigated, but the focus of early studies was on energy production and consumption by plants and animals. In many contemporary studies scientists continue to concentrate on feeding, investigating food webs, optimal foraging, predator-prey interaction, or the dynamics of functional feeding groups. Partly this is because the diet of animals, and the mode of food capture, can be used to model complex processes, and the strategies and tactics differ among populations. Much less attention has been paid to the role of feces in ecosystems, yet fecal pellets are often very abundant, represent a repackaging of available organic matter, and are readily transported.

Aquatic plants photosynthesize only where light penetrates, and the photic zone makes up only a tiny fraction of the depth of oceans, but a greater fraction of the depth in most lakes. Primary production in the surface waters supports the biotic community of the photic zone, and feces and dead matter produced there descend through the water column. Feces thus provide an important flux of carbon from surface to deeper waters in oceans, and a similar vertical flux occurs in lakes. Unlike oceans and lakes, rivers receive much organic matter from terrestrial sources, and animals capture this from suspension or after it becomes deposited. Feces are carried horizontally by the current in rivers, and the significance of this transport has only recently been recognized. In this article, we discuss the fate of fecal pellets in aquatic ecosystems, particularly with respect to vertical and horizontal flux. First we need to know more about the feces of aquatic animals.

FEEDING ANIMALS TRANSFORM ORGANIC MATTER INTO FECAL PELLETS, WHICH SINK OR ARE TRANSPORTED HORIZONTALLY BY CURRENTS; THESE FLUXES RELOCATE ORGANIC MATTER IN AQUATIC ECOSYSTEMS

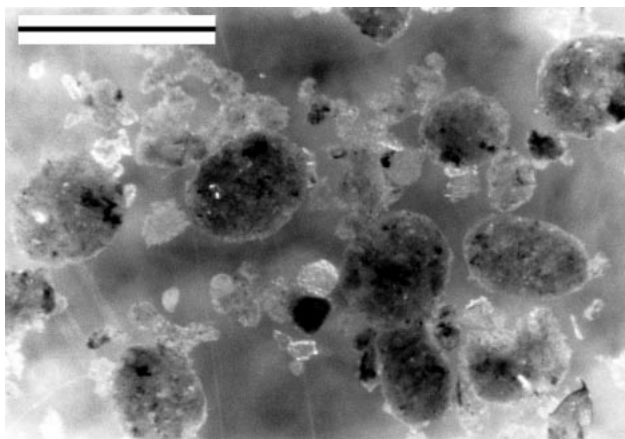
What are feces?

Almost all aquatic animals have guts into which gathered, or captured, food is ingested. Within the gut the food is subjected to abrasion, changes in pH, and the action of enzymes, all of which contribute to the breakdown of organic matter into labile compounds that are taken up across the walls of cells lining the gut. The gut lumen is thus best regarded as a space where material is concentrated and converted to molecules that can pass across the gut wall and thus be used in metabolism. Viewed in this way, ingested food is “external” to the animal, as only breakdown products enter animal tissues, and materials excreted into the gut lumen are also passed out from the animal with the egested feces. The egesta usually look very different from the materials ingested, although the extent of the difference varies with the efficiency with which digestion

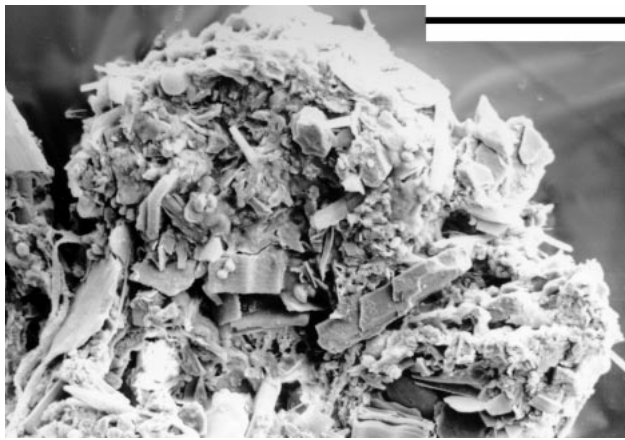
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occurs. Feces pass directly to the substratum or into the water column, and some pass from the water column to the substratum after sedimentation.

Close examination of the feces of most aquatic animals shows them to contain fragments of the undigested diet. These include the remains of plant cells, pieces of exoskeleton from invertebrates, and much unidentifiable organic matter, the extent of each varying from animal to animal. Ingested living organisms are also egested. For example, some invertebrates survive passage through the gut of bottom-feeding fish (Aarnio and Bonsdorff 1997), and the egestion of live snails by fish may facilitate their spread (Haynes et al. 1985). The feces of planktonic crustaceans, and other animals feeding on single-celled algae, often contain many living algal cells (Wotton 1994). These cells pass through the gut



(a)



(b)

Figure 1. (a) Micrograph (scale bar 500 μm) of fecal pellets produced by black fly larvae to show their characteristic shape and texture. (b) SEM micrograph (scale bar 50 μm) of part of a fecal pellet egested from a black fly larva. The original pellet was rounded and cylindrical and appeared as those in (a) but became dehydrated during preparation for scanning electron microscopy. Scanning electron micrograph: Electron Microscope Unit of the Department of Crystallography, Birkbeck College, London.

without being affected too adversely, while others are digested. Although bacteria are lysed in large numbers (Fenchel 1970, Wotton 1994), many millions of microorganisms also pass through the gut of animals, apparently little harmed by digestion (Wotton 1994). The degree of resistance of bacteria to lysis varies markedly from strain to strain, with Gram-positive bacteria always resistant (Plante 2000). Some bacteria thrive within the gut of aquatic animals (e.g., in crustaceans, mollusks, and echinoderms; Harris 1993) and thus contribute exudates, living cells, and cell fragments to the egesta.

Feces of aquatic animals are typically bound into discrete pellets (Figure 1a), although some feces are diffuse. Fecal pellets usually have a shape characteristic of each animal, and they may be spherical, cylindrical, elongated, or formed into strings (Ladle and Griffiths 1980, Ladle et al. 1987, Noji 1991, Ward et al. 1994). The size of pellets varies both among and within taxa, depending largely on animal size. Protist “pellets” are as small as 6 μm \times 9 μm (Stoecker 1984), whereas polychaete worms, tunicates, and euphausiid shrimp (krill) produce pellets several millimeters long (Taghon et al. 1984, Deibel 1990, Gonzalez 1992); fish strings can be longer still. It would be expected that the largest feces are produced by whales, but Best et al. (1995) describe the feces of humpback whales as “a stream of particulate matter” often in an oily matrix.

Planktonic crustaceans have a peritrophic membrane, which is a thin tubular sheet secreted in the midgut as a means of preventing abrasion of the gut wall. This acts as a distinct wrapper for feces (Lautenschlager et al. 1978, Lampitt et al. 1990, Gonzalez 1992). The feces of vertebrates and most invertebrates do not have such an external covering and are bound together with mucus, often remaining as discrete entities for days or weeks. Many animals have mucus-secreting cells lining the gut (derived from cells used in distant ancestry to produce mucus for protection or locomotion). Mucus is used to protect the gut wall from damage by abrasive food items, and also as a lubricant (Allen 1981). However, aquatic insect larvae often have a slow-moving peritrophic membrane surrounding the rapidly moving gut contents, so it is surprising that the fecal pellets of many larvae are bound with mucus (Shepard and Minshall 1981, Wotton 1994). This must be either acquired from the environment or secreted by captured organisms on passage through the gut. Many marine animals (e.g., comb jellies, bivalve mollusks, and salps) use mucus as a means of trapping food or as a means of lubricating food passage (e.g., gastropods), and this exudate is then ingested together with the food. Mucus secreted over the body surface and used for protection, or lubrication in locomotion, is also likely to be ingested from time to time. Stains such as alcian blue readily reveal the presence of mucus in pellets, but scanning electron micrographs often show very small amounts of this binding material, which becomes dehydrated during specimen preparation (Figure 1b).

The number and quality of fecal pellets produced by aquatic animals varies with the feeding strategy employed. Predators convert animals into smaller particles of detritus

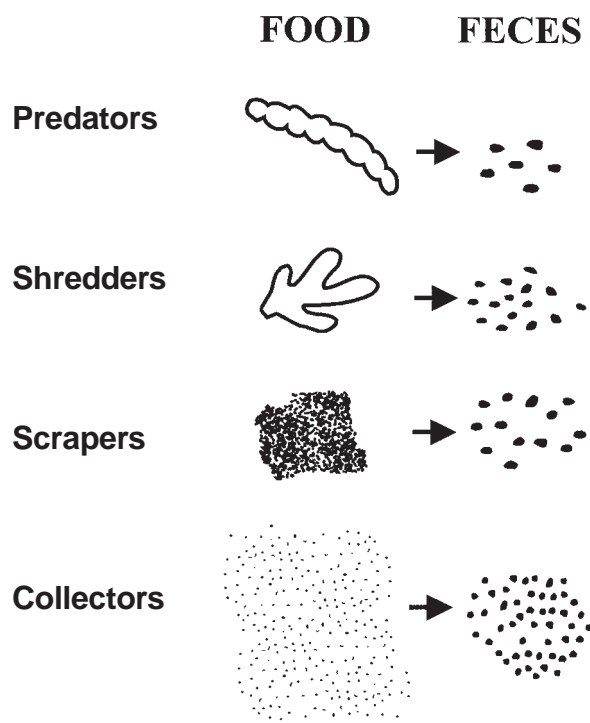


Figure 2. Diagrammatic representation of the transition of food to feces in animal functional feeding groups. *Predators transform animals into smaller fecal pellets, but in relatively low numbers, as assimilation is high. Shredders, feeding on live or dead plant material, produce larger numbers of fecal pellets than predators, but the pellets are smaller in size than the original foods. Scrapers remove the organic covering on surfaces and make fecal pellets that are larger than individual food items, but the latter are anchored within a matrix of biofilm. Collectors (suspension feeders and deposit feeders) transform very large numbers of small particles and dissolved matter into much larger fecal pellets. The number of pellets produced is often high, as many suspension feeders and deposit feeders ingest large quantities of poor-quality food.*

(Figure 2), and as they have high assimilation efficiencies, only a small number of feces are produced by members of this functional feeding group. Although predators thus have an important top-down effect on community structure, the contribution of their fecal material to organic matter dynamics is small unless they are locally abundant. *Shredders* feed largely on living or dead plants and, like predators, reduce overall particle size (Figure 2). As the assimilation efficiency of herbivores is generally lower than that of carnivores, the number of pellets produced by shredders is higher than that of predators. *Scrapers* feed on biofilms that are gathered into the gut. Often large numbers of fecal pellets are produced, and particle size is reduced if biofilm, rather than its constituents, is considered (Figure 2). Scrapers such as gastropod mollusks are found in very high densities on the surface of mud and

other substrata, and the presence of more than 100 pellets cm^{-2} (i.e., more than one million per square meter) is common (Ward et al. 1994). *Collectors*, and especially suspension feeders, gather many small particles, colloids, and dissolved organic matter and transform the material into much larger fecal aggregates (Figure 2). Bivalve mollusks are suspension feeders that can dominate the substratum in many types of water body, and they trap particles over the surface of their gills. Once collected, particles are coated in mucus and transferred to the labial palps, where some are selected for ingestion and others rejected. Rejected particles, and those that are drawn into the mantle cavity in excessive quantities, are bound with mucus and expelled from within the shell valves as pseudofeces (Ward and MacDonald 1996). Feces and pseudofeces thus look similar and are found mixed together in the vicinity of bivalves (Strayer et al. 1999). Pseudofeces are a true case of repackaging, as they are not affected by digestion.

Typically, suspension feeders produce large numbers of fecal pellets, for example, 3.2 pellets h^{-1} for copepods (Griffin 2000), and extrapolated means of 575 and 737 pellets d^{-1} for black fly larvae (Wotton et al. 1998, Malmqvist et al. 2001). As black fly larvae are often found in densities exceeding 100,000 m^{-2} , the total number of pellets they produce is enormous (Wotton et al. 1998). Abundant macrozooplankton also produce fecal pellets in large numbers: Alldredge et al. (1987) found more than 9×10^4 pellets m^{-3} in the surface waters off southern California. It is the abundance and feeding rate of suspension feeders that make them such significant transformers of organic matter. Although fecal pellets of many kinds abound and are utilized by communities over the substratum, the pellets of suspension feeders are not only extremely numerous but also provide the translocation of repackaged organic matter (Le Fèvre et al. 1998) from one location to another as they sink or are carried by currents. Two mechanisms are especially significant: the vertical flux of fecal pellets in oceans and lakes, and the horizontal transport of fecal pellets in rivers.

Vertical flux of fecal pellets

Feces are egested in the water column by planktonic animals or swept up from the substratum after egestion by benthic animals. Whatever their origins, the sinking rate of fecal pellets in water is often rapid (Figure 3) and depends on pellet size, shape, and surface area (Smayda 1969, Fowler and Small 1972, Ladle et al. 1987, Viitasalo et al. 1999). Sinking rate also depends on the pellets' specific gravity, varying with the food ingested, presence of mineral particles, degree of compression, and rate of decomposition (Smayda 1969, Butler and Dam 1994, Wotton 1994, Hansen et al. 1996, Yoon et al. 1996). Where the water is shallow, there is a large input of fecal pellets to the substratum, but a proportion of the pellets produced by planktonic animals is lost from the photic zone in deep waters. This is particularly true of the larger pellets of animals such as euphausiids (Keck and Wassmann 1996, Gonzalez et al. 2000). "Pellets" produced by protists are very small and are likely to sink slowly, but they are often

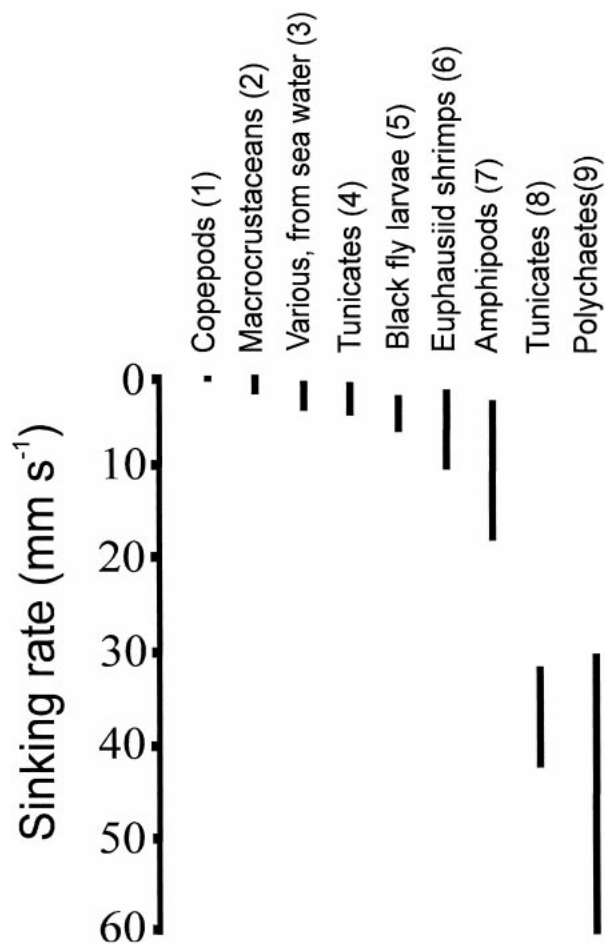


Figure 3. Sinking rates of fecal pellets (given as ranges) for the named taxa. Fecal pellets show a trend of increasing size from (1) to (9). Data are from (1) Turner 1977, (2) Alldredge et al. 1987, (3) Smayda 1969, (4) Deibel 1990, (5) Ladle et al. 1987, (6) Fowler and Small 1972, (7) Ladle et al. 1987, (8) Yoon et al. 1996, and (9) Taghon et al. 1984 (with conversion of units as appropriate).

associated with detrital aggregates that settle rapidly during blooms in spring and summer. All small pellets (like those produced by zooplankton greater than 200 μm in length) are likely to remain within stratified photic zones (Small et al. 1987, Viitasalo et al. 1999), unless they become associated with aggregates. For example, only 5% of copepod feces produced in the photic zone of the Humboldt Current were found in sediment traps at 300 m (Gonzalez et al. 2000), and Gonzalez (1992) found a more than 99% decrease in fecal strings of euphausiids from the upper 50 m to depths of 500–1000 m in polar waters. Downward flux of fecal pellets in the Gulf of St. Lawrence ranged up to 138 $\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in the first 50 m (Roy et al. 2000); fluxes are usually very much less than this, with only a tiny fraction descending to depth. Total organic carbon fluxes at depths of 2000 m are about 0.4–4 $\text{g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ in nonpolar oceans, and 0.01–6 $\text{g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ in polar oceans (Lampitt and Antia 1997). Given the area of oceans,

the global flux of organic carbon to deep water is huge and has been estimated at 0.34 Gt C y^{-1} (Lampitt and Antia 1997). How much of this material consists of fecal pellets, both free and in aggregates of various kinds, is not known. In permanently stratified oceans, the loss of larger pellets and aggregates from the photic zone means losses of organic matter, and nutrients are only restored by upwelling. However, in thermally stratified lakes, the nutrients released by microbial conditioning of pellets at depth are returned to surface waters at times of turnover.

Some mechanisms prevent sinking. Pellets are disrupted by turbulence (Viitasalo et al. 1999), and this is increasingly likely when pellets become diffuse. The microbial mineralization of pellets causes them to break up into components of smaller mass and consequently lowers sinking rate, but microbial breakdown needs to be very rapid for this to occur. Evidence suggests that zooplankton fecal pellets are broken down slowly by bacteria, although the rate of breakdown is affected by the constituents of the diet (Hansen et al. 1996). However, bacteria associated with substrata are more metabolically active than those living free in the water (Decho 1990), and this is equally applicable to those bacteria bound within fecal pellets.

Some copepods break up pellets while ingesting little of their contents (Lampitt et al. 1990, Noji et al. 1991), and the resulting fragments thus sink at a slower rate than fresh feces. By removing the binding, copepods aid the disruption of pellets, which thus become more porous. Skin friction drag and hydrodynamic forces that resist sinking then become of greater importance. The pellets of *Gammarus* egested into fresh water are surrounded by a peritrophic membrane for up to 7 h, after which time the membrane becomes broken off, probably by swelling of the pellets (Lautenschlager et al. 1978), and they then become diffuse. Pellets of invertebrates, like those of protists, are components of marine, lake, and river “snow” (aggregates of mucus, microorganisms, protists, detritus, and algal cells). As these aggregates are flocculent, it is likely that they sink more slowly than compacted aggregates of the same mass, but flocculent masses of detritus are common features of the ocean floor, especially at some times of the year. The sinking of fecal pellets is therefore modified by the aggregate to which they have become attached.

Other mechanisms that decelerate the sinking rate of fecal pellets are the inclusion of gases that aid buoyancy, or the presence of turbulence promoting upward movement (Alldredge et al. 1987, Lampitt et al. 1990, Wassmann 1994, Yoon et al. 1996, Viitasalo et al. 1999). Some crustaceans defecate high in the water column when they migrate to surface waters at night (Alldredge et al. 1987), which, combined with the effects of turbulence, serves to prevent pellets from sinking across the thermocline when the water body is stratified. In contrast, other crustacean plankton feeding in the surface waters enhance the downward passage of fecal pellets by feeding near the surface at night and egesting fecal pellets during the day, after the animals have moved several hundred meters down in the water column (Lampitt et al. 1993). Some fish also move

to the substratum of coastal regions at night and defecate there (Krause and Bray 1994), and fish feces raining down from pens used in intensive fish farming create major problems over the substratum (Ahlgren 1998).

Horizontal flux of fecal pellets

Animals living on the ocean floor, on tidal shores, or in rivers ingest fecal pellets that are advected horizontally by currents (Rosenberg 1995). In coastal regions the pellets are carried by longshore currents and by the ebb and flow of tides, and they are eventually deposited with other components of the shoreline detritus. Water ebbing and flowing in tides contains large amounts of pelletized detritus resulting from feeding and egestion by intertidal and sublittoral suspension feeders. This is also true for the currents that sweep the bed of shallow seas (Graf and Rosenberg 1997). In shallow bays, the feeding of bivalves, found in very high numbers, results in up to 30% of the water being processed through the animals each day (Hily 1991). In addition, bivalves may control phytoplankton growth by their filtration activity (Loo and Rosenberg 1989). Strayer et al. (1999) give a range of 10% to 100% for levels of filtration of the water column per day that can be achieved by bivalves in a range of different aquatic habitats, both marine and freshwater. Only a fraction of the particles captured is ingested and egested, with the rest passed out as pseudofeces, but the consequences of both processes are similar: the formation of huge quantities of pelletized detritus bound with mucus. All fecal pellets on the surface of the substratum are likely to become resuspended from time to time and then entrained with other particles in the bedload (Rosenberg 1995, Roditi et al. 1997).

Horizontal transport of fecal pellets in rivers is an important flow of carbon. In a Swedish river approximately 100 m wide, Malmqvist et al. (2001) showed mean transport of fecal pellets to be 3.7, 1.9, and 2.7 t C d⁻¹ in each of three consecutive summers. During the summer, high densities of black fly larvae colonize the substratum of rapids, and their fecal pellets typically make up 20% to 30% of total suspended matter transport (Malmqvist et al. 2001). This compares with the 50% of particulate organic carbon (POC) made up of fecal pellets in the surface waters of oceans (Roy et al. 2000), with the range of 3% to 100% for this proportion found by UrbanRich et al. (1999) in Norwegian coastal waters, and with 3% to 35% for a Mediterranean site (Carroll et al. 1998). Many pellets in the Swedish river were deposited in dead-water zones, backwaters, river margins, and lowland reaches, with the remainder being carried to the sea.

The significance of horizontal transport and the subsequent sedimentation of fecal pellets produced by black fly larvae was seen in a study of a small stream flowing 500 m from a lake to the sea. No black fly fecal pellets entered the stream from the lake, but they were produced in such quantities in an aggregation 80–100 m from the lake outlet that the numbers in transport ranged from 400–600 pellets L⁻¹ (Wotton et al. 1998). Pellets were sedimented in lower, sandy reaches, and this contributed 87 g C m⁻² over the month when larvae were

abundant (Wotton et al. 1998). Without this mechanism of retention in streams and rivers, many very small particles and dissolved matter would be lost to the sea. The transfer of carbon from the water column to the substratum was likely to be only slightly less than the input of leaves to the stream, the energy source normally assumed to be the dominating one in low-order streams (Wotton et al. 1998). A similar impressive transfer of carbon from suspension to the substratum is likely where horizontal flows of water pass over dense beds of bivalves, whether present in rivers or the sea.

Fecal pellets and the biota

The horizontal transport of fecal pellets in rivers and the vertical transport of fecal pellets in oceans and lakes both provide translocations of repackaged organic matter. A further translocation comes in small water bodies into which terrestrial animals defecate. Feces become available for microorganisms and animals both during transport and after sedimentation to the substratum. Once sedimented, the pellets of suspension feeders join the pellets produced more locally by deposit feeders, scrapers, shredders, and predators. The relative abundance of pellets depends on the population densities of animals within each functional feeding group. Usually, the pellets of deposit feeders and suspension feeders dominate, as these animals feed for long time periods and assimilate so little of their food.

Conditioning refers to the transformation of organic matter by colonizing microorganisms. It is worth reemphasizing that feces also contain living organisms that pass through the gut little affected by digestion. Many bacteria and algal cells survive gut passage, but so do invertebrates fed upon by deposit-feeding fish (Aarnio and Bonsdorff 1997). The organisms in egested feces are thus likely to have the capacity for rapid growth as they are packed in close proximity to suitable substrates. Conditioning of fecal pellets thus occurs from within as well as from colonization of the outside of pellets.

After egestion, fecal pellets characteristically leach dissolved organic matter (DOM) into the water (Jumars et al. 1989, UrbanRich 1999). Both carbon and nitrogen are lost from pellets in the first days after egestion, and if undisturbed, the pellets of many animals remain the same size as at egestion but have reduced mass (Gonzalez and Biddanda 1990). Although a small proportion of pellets is lost from surface waters, it is important to note that all leached DOM is likely to be retained within the photic zone (UrbanRich 1999). Pellets are colonized rapidly by invading microorganisms (Yoon et al. 1996) that may be attracted by the leaching DOM, but then attach and commence conditioning, which leads to a decrease in carbon content as carbon is converted to carbon dioxide by microbial respiration. Feces undergoing conditioning by invading, or resident, microorganisms have higher microbial activity than other detritus, at least in samples taken from a stream (Ward and Cummins 1979), and this is typically a pattern that shows a peak 2–3 days after egestion (Hargrave 1976). Inorganic and organic materials from the ambient water (including metals; Fisher et al. 1991) also

become adsorbed to the binding mucus, and mucus-rich aggregates are good bacterial substrates (Hargrave 1976).

In time, the pellets are degraded (the rate depending on many factors, e.g., temperature, bacterial numbers), although labile constituents may be consumed in days (Hargrave 1976). Their value as food increases as some refractory carbon is broken down by the exoenzymes of colonizing microorganisms, nitrogen being obtained from the water to build microbial protein. The pseudofeces of bivalve mollusks seem to be broken down rapidly (Wildish and Kristmanson 1997), and this may reflect their lack of consolidation compared with bivalve feces. The amorphous feces egested by some insects also disintegrate rapidly (Shepard and Minshall 1981). During conditioning, many of the mucus bridges that bind pellets are broken, and water movements disrupt the contents.

Many aquatic animals feed on fecal pellets (Frankenberg and Smith 1967). We fed several types of benthic animals from the lake-outlet stream we studied with fresh, labeled fecal pellets (Wotton et al. 1998). Labeled pellets were produced by black fly larvae feeding on paint particles in water, and these became mixed within the egesta. We found traces of the label in many of the animals: the guts of midge larvae, oligochaetes, and black fly larvae contained the label in abundance, and the guts of baetid mayfly larvae and water hog louse (*Asellus*) also contained many paint particles (Wotton et al. 1998). Black fly larvae have been shown to capture and ingest fecal pellets produced by larvae upstream, and this has been regarded as a means of increasing the economy of feeding (Wotton 1980). In some streams, the production of animals depends on recycling of fecal pellets. For example, coprophagy is likely to be a significant event in desert streams, as it provides the best explanation for the levels of secondary production that have been observed (Fisher and Gray 1983).

The rain-down of fecal pellets and other detritus to the ocean floor supports the biota that live there, with the only other inputs of organic matter being generated by chemosynthesis around vents (Wotton 1994). Coprophagy is also a common feature of shallow waters and reefs, and many animals consume fish and invertebrate fecal pellets that are sedimented or produced in situ. Rothans and Miller (1991) believe that coprophagy by animals is a more important process than microbial breakdown in transforming pellet organic matter over reefs. We need to more thoroughly investigate coprophagy as a significant factor in aquatic systems, although perhaps this requires us to overcome a natural dislike for the topic. There are remarkably few studies on coprophagy, despite its being a significant aspect of feeding biology.

Fecal material and seasonal supplies of organic matter

In most aquatic systems there is a seasonal pattern of biological activity. In polar and temperate oceans and lakes, activity increases during spring through summer when planktonic algae grow most efficiently. Photosynthesis thus drives biolog-

ical production and directly, or indirectly, the numbers of animals and the amount of fecal material that they produce (Turlley et al. 1995). There is thus an increase in the particle flux reflecting a marked seasonal sedimentation of fecal pellets and other organic matter at times of high primary production in the photic zone (Le Fèvre et al. 1998).

Benthic algae and marginal plants also contribute seasonal inputs, but emergent plants often die back in fall, providing a rich source of organic matter that is subsequently broken down to provide energy through the winter and for the next growing season. Streams and rivers also receive large inputs from outside the water body that may be from the valley or from leaves in fall. Again this is a pulsed resource in temperate regions and is broken down over time as leaves and leaf fragments settle to the substratum. Fecal pellets from suspension feeders sediment whenever feeding is taking place, and the production of suspension feeders is often highest following the period of high primary production in spring and summer. Shepard and Minshall (1984) conclude that the benthic community uses feces of many stream invertebrates as food once leaf litter and seasonal inputs of terrestrial matter have been consumed. They suggest that feces therefore maintain a "homeostasis of function" in streams and probably provide a vital, and continuous, supply of usable particulate organic matter in all water bodies.

Other roles of feces in aquatic ecosystems

In addition to their importance as a means of recycling nutrients and as food for animals, feces also have other functions. Any animals that utilize sediments in constructing tubes and similar structures are likely to incorporate fecal pellets; for example, pellets produced by midge larvae are built into the tubes in which larvae live (Hirabayashi and Wotton 1998). Another unusual function for feces is as an antipredator device. It has been found that the feces of pike contain alarm pheromones from one species of fish they attack and eat (Brown et al. 1996). Fish of the same species can detect the pheromones diffusing from pike feces and are warned of the presence of the predators (Brown et al. 1996). Such cues do not occur with all fish, but this is a role of feces that may be operating in a wide range of predator-prey systems and should be investigated.

Conclusions

Studies of feeding by animals have dominated our thinking on the functioning of aquatic ecosystems. Although the importance of fecal pellets in vertical transport of organic matter in oceans is widely recognized, the role of feces has been little considered in other aquatic habitats. Pellets are usually very different in particle size compared with ingested material and are readily transported within the water column. They are also sites of microbial activity and play a part in aggregation processes. In many habitats, fecal pellets are very abundant, and we are only beginning to discover their significance.

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